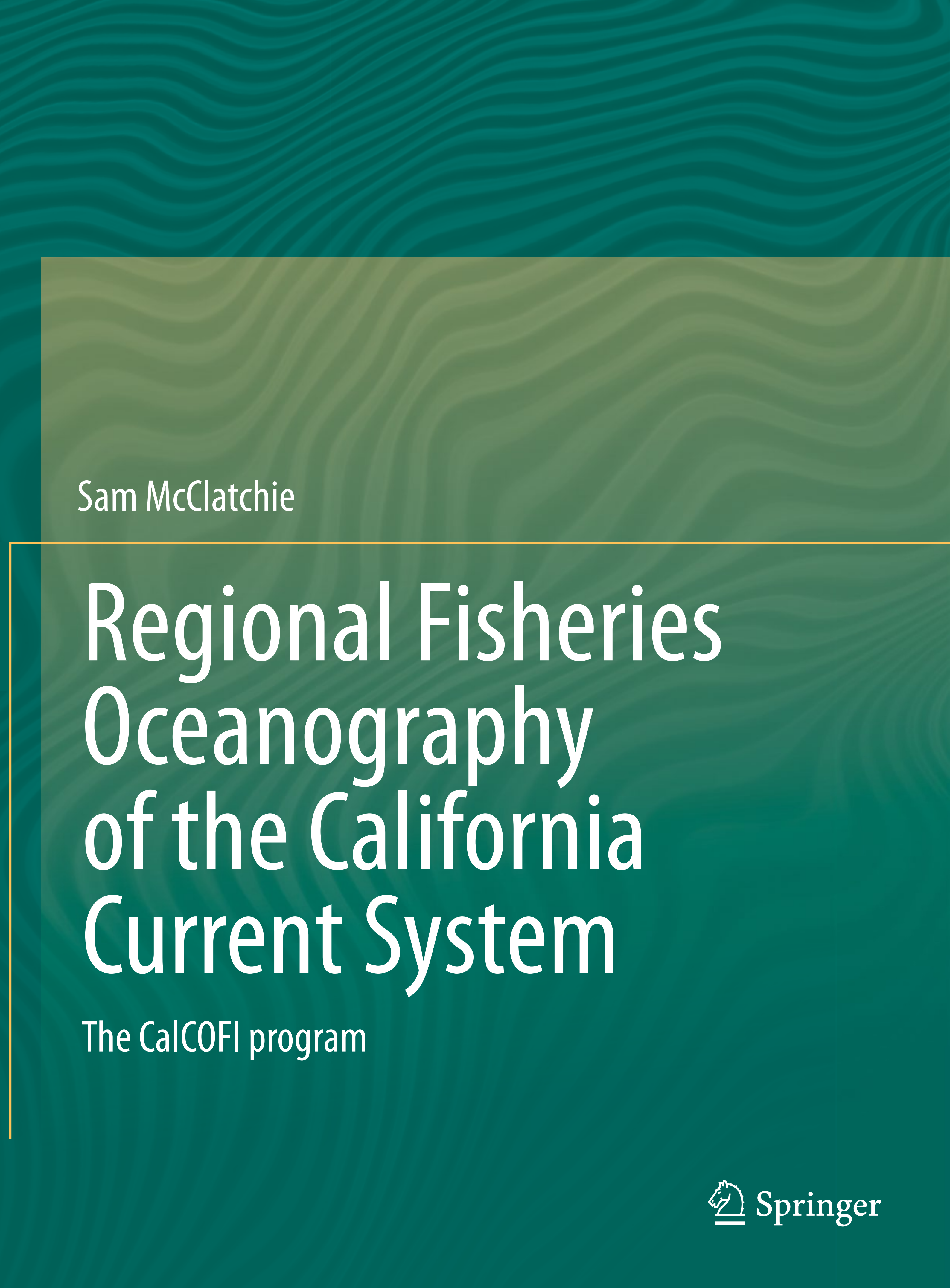

Sam McClatchie

Regional Fisheries Oceanography of the California Current System

The CalCOFI program

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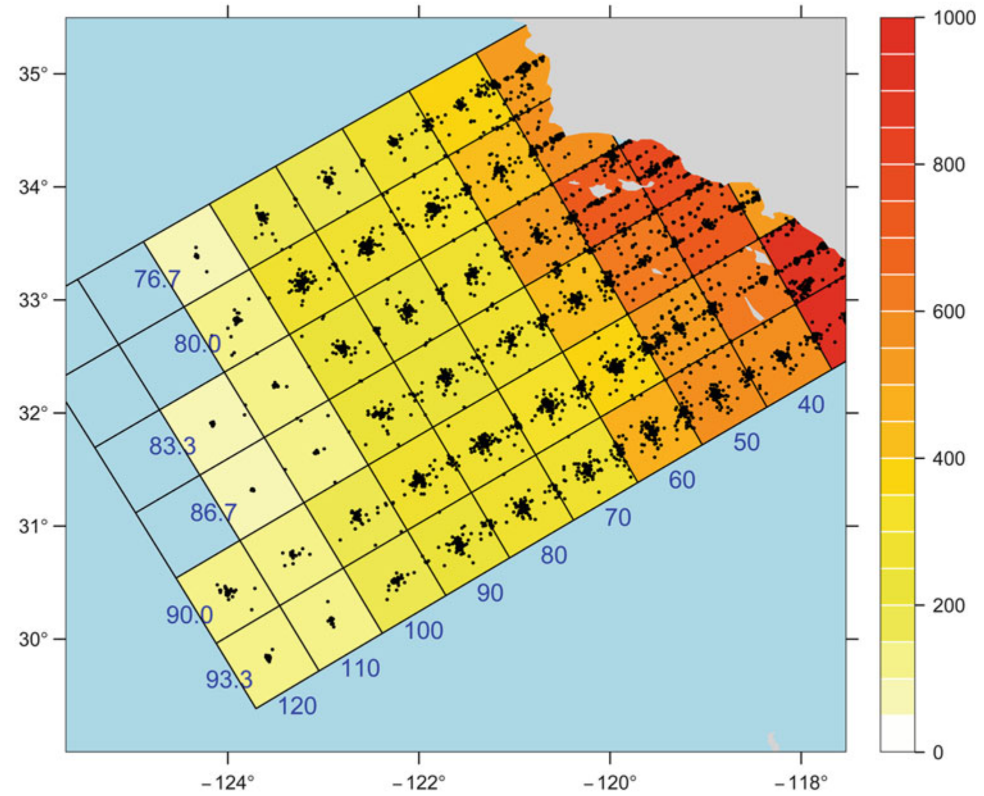

Grid pattern of 3.3-line by 10 station cells in the core CalCOFI sampling area (CalCOFI lines 76.7–93.3). *Color key* indicates the actual number of sorted oblique tow samples collected within each cell for the period 1951–2010. *Black dots* indicate the actual sample locations (Courtesy of Ed Weber, NOAA Fisheries SWFSC)

Sam McClatchie

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The CalCOFI program

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Sam McClatchie
NOAA Fisheries Service
La Jolla, CA, USA

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This book is dedicated to my wife, Elena Turin, who is "my best friend in the whole world".

Preface

My purpose in this book is to bring together in one place a summary of the voluminous information relevant to fisheries oceanography that has been published during the more than 60 year span of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). Though providing a large bibliography, my intent was to extract themes relevant to current research rather than to prepare a compendious review of the literature. The scope of this book is regional to the California Current System stretching from British Columbia, Canada, to Baja California Sur, Mexico, and the time frame extends from the late 1940s to the present.

This book is aimed at graduate students and researchers in oceanography with a special interest in the California Current System. As such I have not made any effort to provide background for a more general audience, which is not to say that the material is inaccessible to non-specialists. The book can potentially provide a reference text for a graduate-level university course on the regional fisheries oceanography of the California Current System. It is not a general fisheries oceanography textbook, and so does not outline the underlying paradigms for this field that one would expect in a broader textbook. The book should provide a useful review and reference point for scientists with an interest in fisheries oceanography of the California Current System. Surprisingly the current literature provides no comprehensive, integrated review of the regional fisheries oceanography of the California Current System. The closest references to such a review are already dated by at least 20 years, although still very useful as reviews from their time [152, 208, 284, 410]. This book updates some of the material in the earlier contributions, but also has a different focus. While most of the earlier works [152, 208, 284] compiled a series of papers by authors who were experts in their field, I attempted to produce a book with a more consistent flavor and style, hopefully without losing too much of the depth that experts bring to their contributions.

The broader aim of this book is to provide an up-to-date reference on the fisheries oceanography in the California Current System. While "up-to-date" pertains to the publication date, this book should continue to provide a solid foundation of knowledge that can be updated with more recent material over time. The California Current System is one of the best studied ocean regions of the world, and the level of oceanographic information available is perhaps only surpassed by the northeast and northwest Atlantic. The volume of studies in these regions is partly a result of the number, concentration, and historical legacy of oceanographic, fisheries and marine biology institutes, university departments and consulting firms. It is also the result of the long-running oceanographic and fisheries survey programs conducted under the banners of International Council for the Exploration of the Sea (ICES), Sir Allistair Hardy Foundation for Ocean Science (SAHFOS), and CalCOFI. CalCOFI, now in its 63rd year since regular surveys began in 1950, is the second longest running fisheries oceanography survey program in the world, after SAHFOS, started in 1931. Understanding of the California Current System is well-established, and so even as new studies are undertaken at an ever increasing pace, the foundation for this book is unlikely to change radically.

To understand the California Current System and the drivers for environmental variability affecting its pelagic fisheries, one must understand the physical oceanography, at very least on the descriptive level. For this reason, in Chap. 2 I spend a considerable amount of time on the descriptive physical oceanography of the region, with additional focus in Chap. 4 on processes that impact the production and productivity of the system and variability of its fisheries. A review of this nature is inadequate to cover all the relevant detail, so I provide a substantial body of literature in the bibliography that the reader can delve into. Many of these papers originated from work with little connection to the CalCOFI program, but they provide essential background to understanding the results of the CalCOFI program as well as the structure and functioning of the California Current System.

In a region as well studied as the California Current System, it is also important to understand the historical context, and researchers should have a firm grounding in the historical literature. CalCOFI has a wealth of now retired or emeritus researchers (e.g., Joe Reid, John McGowan, Paul Smith, John Hunter, Ron Lynn, Bob Owens, Geoff Moser, Dave Ambrose, Gail Theilacker, Arnold Mantyla, Elizabeth Venrick, Richard Eppley, Richard Schwartzlose, Nancy Lo) who are still with us, and others who have passed on: Reuben Lasker, Ahlie Ahlstrom, Mike Mullin, Ed Brinton, Warren Wooster and John Isaacs among them. Their work and collaborations often provided the foundation for more recent studies. I review many early studies because I believe one should understand what has already been done, and its relationship to the questions that are currently being addressed. This work, and that which followed, forms the core of the legacy of CalCOFI. Reference to the work of these researchers is scattered throughout the book. In Chap. 3, I write about the classic CalCOFI sampling methods that provided the basis for the historical work, and summarize the contribution of the CalCOFI Atlases that were an important contribution of the CalCOFI program.

One chapter reviews what I term "themes" in the regional fisheries oceanography. These are ideas or concepts that have received considerable attention by researchers and have guided trends in the interpretation of research results. In Chap. 4, I organize these themes on the basis of temporal scales and discuss the decadal, inter-annual, seasonal and weather scales. I discuss regime shifts, the basin hypothesis of range contraction and expansion, cycles in fish assemblages, and geographical shifts of assemblages with secular trends in climate. I then focus on effects of El Niño/La Niña, recruitment dynamics and environment, the flow hypothesis, and studies relevant to essential fish habitat. When focusing on seasonal scales, I discuss upwelling and production and the related topics of the timing of the spring transition and the optimal environmental window concept. I then discuss mesoscale features, connectivity and larval dispersal. Last, I discuss weather scale variability encompassing daily to weekly time frames, and ideas about mixing, stability and recruitment, mortality and patchiness.

In Chap. 5, I turn from the surveys to the experimental work that was an important part of CalCOFI at the Southwest Fisheries Science Center in the 1970s and 1980s, but has since taken a less prominent role. These experimental studies were focused on the two principal factors affecting the survival of the early life history stages of small pelagic fish, notably starvation and predation. I review the work on bioenergetics, growth, cannibalism and predation relevant to CalCOFI, but make no attempt to cover the wider topics, like fish reproduction, which have been addressed elsewhere.

For this book, I have drawn extensively on figures and data from the literature on the oceanography of the California Current System, including some of my own work. This includes a variety of sources, including published papers in peer-reviewed journals, reports, as well as "gray literature," particularly in the fisheries and stock assessment fields. Relevant literature on this topic is so vast that I will undoubtedly have missed some key publications. I have imposed on colleagues to read sections of the book and alert me to glaring omissions, but some important material will inevitably be overlooked, for which I apologize. In many cases I have drawn extensively on the careful literature reviews included in published papers. When doing so, I cited both the authors of the original papers and those of the review. I have paraphrased and synthesized the material in these reviews and tried to be mindful of the dangers of plagiarism. I have also gone over the majority of the original papers to check that I am not compounding any potential errors by citing literature that I have not read myself. Where I did not check the original reference, I cited the original as attributed to. The nature of the material is also both multidisciplinary and technical so there are dangers of misinterpretation or misrepresentation of the original material in my syntheses. I have tried to minimize these errors by drawing on colleagues who are experts in the sub-fields of oceanography or fisheries to read sections of the book and to offer criticism and comments. It would have been impossible to write this book without drawing on the reviews in previously published work and I extend my thanks to those authors for their careful syntheses of the literature which I have been able to use.

Readers familiar with the literature of the California Current System will note some biases and omissions in my material, as this book is slanted toward fisheries-related studies of southern and central Californian waters. This is the natural outcome of the evolution of the CalCOFI program from a program ranging from the Oregon border to southern Baja California, Mexico, to the current focus on southern and central Californian waters. I have also focused on the peer-reviewed literature and there is a wealth of other material in the gray literature (i.e. not peer-reviewed, not commonly cited, that may not be readily available), most of which were omitted from the bibliography in the book. Another notable gap is that I have neglected salmon. This is partly because the regional focus is on the southwest rather than the northwest US, but it is also partly due to the fact that there is already an abundance of literature on salmon. Attempting to cover even part of it would dilute the focus on CalCOFI. Some readers will notice that I have not covered alternation of small pelagic fish species. This topic is really a subset of the broader topic of low frequency variability that I address in the section on small pelagic fish and the PDO. While alternations of sardine and anchovy occurred in the California Current System, the paleoclimate record shows that sardine-anchovy alternations are not detectable over long time scales. I have not reviewed the literature on climate and pelagic fish in different eastern boundary currents because this is covered well in the book by Checkley et al. (2009) [103]. I have not covered the seabird and marine mammal work that are an important component of CalCOFI. I have also neglected some of the phytoplankton (e.g., many studies by Elizabeth Venrick) and zooplankton work related to CalCOFI (e.g., many of the copepod studies by Michael Mullin), instead choosing to include those studies that are relevant to production processes underpinning fisheries. The justification for these omissions is that these studies are not really fisheries oceanography. The bird and mammal studies are fundamental to ecosystem studies, and to the development of indices for the "state" or "health" of the California Current ecosystem. Their omission in this book is a matter of limiting the scope of this edition rather than any comment on their importance in the suite of CalCOFI measurements and time series. I have not covered much of the literature from the Mexican IMECOCAL program, some of which is in Spanish, nor have I covered the results from the NSF LTER program. The LTER program is focused more on biological than fisheries oceanography. I also had to draw a fine line between summarizing scientific results and material best categorized as history of the CalCOFI program. In reviewing the literature I have been inevitably drawn into the historical aspects of how the data came to be collected, the scientific lineages of some of the scientists and technicians involved, and the formation and dissolution of various groups. There is a tremendous amount of material in the Scripps Institution of Oceanography archives on these historical aspects of the CalCOFI program, but these topics are beyond the scope of this book, and await the attention of a historian. In recognition of the importance of history, Chap. 8 presents personal perspectives by people who have been deeply involved with CalCOFI over the years. These contributions to this book are idiosyncratic, and add color to the more technical material.

Southwest Fisheries Science Center, La Jolla, CA *Sam McClatchie*
March 2013

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List of Participating Authors

George Hemingway
John McGowan
Carl Boyd
Roger Hewitt
Dave Griffith
Ron Dotson
James Wilkinson
John Butler
Geoff Moser
Bill Watson
Andrew Thompson
Paul Smith
Tony Koslow
Gail Theilacker
John Hunter
Nancy Lo
Steve Bograd
Ralf Goericke
Bertha Lavaniegos
Dan Rudnick
Amanda Netburn
Noelle Bowlin
Rebecca Asch

Acronyms

ABC	Allowable Biological Catch
ADCP	Acoustic Doppler Current Profiler
AHC	Agglomerative Hierarchical Clustering
BEST	Bivariate ENSO Time series
CalCOFI	California Cooperative Oceanic Fisheries Investigations
CalVET	CalCOFI Vertical Egg Tow
CCE	California Current Ecosystem
CCMP	Cross-Calibrated Multi-Platform
CCS	California Current System
CMSP	Coastal Marine Spatial Planning
COADS	Comprehensive Ocean-Atmosphere Data Set
CPSMT	Coastal Pelagic Species Management Team
CPUE	Catch Per Unit Effort
CPS	Coastal Pelagic Species
CTD	Conductivity Temperture Depth [sensor]
CUFES	Continuous Underway Fish Egg Sampler
DEPM	Daily Egg Production Method
EBM	Ecosystem Based Management
ENSO	El Niño – Southern Oscillation
EOF	Empirical Orthogonal Function
FAO	Food and Agriculture Organization of the United Nations
FMP	Fishery Management Plan
ICES	International Council for the Exploration of the Sea
IEA	Integrated Ecosystem Assessment
LTER	Long-Term Ecological Research
MEI	Multivariate ENSO Index
MIK	Modified Isaacs-Kidd midwater trawl
MOHT	Matsuda-Oozeki-Hu Trawl
MSY	Maximum Sustainable Yield
NAO	North Atlantic Oscillation
NCAR	National Center for Atmospheric Research
NCEP	National Centers for Environmental Prediction
NDBC	National Data Buoy Center
NMFS	National Marine Fisheries Service
NOAA	National Oceanic and Atmospheric Administration
NOI	Northern Oscillation Index
OFL	Over-Fishing Level
ONI	Oceanic Niño Index
PairoVET	Paired Vertical Egg Tow
PAR	Photosynthetically Active Radiation
PDO	Pacific Decadal Oscillation

PDO^+	Positive or warm phase of the Pacific Decadal Oscillation
PDO^-	Negative or cool phase of the Pacific Decadal Oscillation
PFMC	Pacific Fishery Management Council
PNA	Pacific North American pattern
PRPOOS	Plankton Rate Processes in Oligotrophic Ocean Systems net
SAHFOS	Sir Alister Hardy Foundation for Ocean Science
SBB	Santa Barbara Basin
SCB	Southern California Bight
SCE	Southern California Eddy
SCCOOS	Southern California Coastal Ocean Observing System
SeaWiFS	Sea-viewing Wide Field-of-view Sensor
SIO	Scripps Institution of Oceanography
SHAT	Soutar-Hemingway Animal Trap
SLP	Sea Level Pressure
SOI	Southern Oscillation Index
SPAR	Surface Photosynthetically Active Radiation
SR	Stock Recruit
SSB	Spawning Stock Biomass
SST	Sea Surface Temperature
SSH	Sea Surface Height
SWFSC	Southwest Fisheries Science Center
TAO	Tropical Atmosphere Ocean
TNI	Trans-Niño Index
TOGA	Tropical Ocean–Global Atmosphere
VPA	Virtual Population Analysis
XBT	Expendable bathythermograph

Introduction to the Fisheries and the Surveys

1

Abstract

Fisheries oceanography of the California Current System is intimately linked to the California Cooperative Oceanic Fisheries Investigations (CalCOFI). The current 75-station CalCOFI surveys cover the waters off southern California quarterly, and the full suite of CalCOFI measurements are made in this core area. NOAA Fisheries Service extends the sampling in the 113-station pattern to San Francisco in spring with more emphasis on trawl sampling. Since 2006, contingent on funding, NOAA fisheries conducts west coast-wide surveys from the Mexican to the Canadian borders with much more limited CalCOFI-type sampling and an evolving focus on acoustic-trawl survey. The rationale for CalCOFI has changed in its more than 60 year existence from a focus on understanding reasons for the collapse of the Pacific sardine fishery. The goal of the modern CalCOFI program can be broadly expressed as the understanding of long-term changes in the California Current System. The 66-station CalCOFI provides a consistent, accurate, multi-decadal oceanographic survey that now operates in an extraordinarily data rich environment. It has become a more broadly focused effort enhanced by relationships with ancillary programs. These include the NSF-funded Long-Term Ecological Research (LTER) program, NOAA Fisheries stock assessment surveys for Pacific sardine, Pacific hake, rockfish, and salmon, the west coast-wide triennial NOAA protected resources survey, the Mexican IMECOCAL program covering Baja California, the Columbia River plume Pacific sardine survey, the Northeast Pacific line P transect, and individual transects sampled off Newport, Oregon, Trinidad Head and Monterey, California. Additional relevant data come from the Ocean Observing network, including glider transects, instrumented moorings, drifters, HF-radar, pier sampling, tide gauges and satellite remote sensing. The length of time series collected by these diverse sampling efforts ranges from 60+ years (since 1950) for the core 66-station CalCOFI pattern, to as few as 6 years (since 2008) for the new Trinidad Head line. The net result is an almost unparalleled wealth of data, perhaps surpassed only by efforts in the northeast and northwest Atlantic. CalCOFI data have been used in many hundreds of peer-reviewed publications, not including voluminous numbers of reports, in physical, biological, and fisheries oceanography, as well as in climatology, modeling, fisheries biology, and stock assessment. It is difficult to accurately quantify the value of CalCOFI simply because the program touches so many aspects of the understanding of the California Current System and how the system is changing with climatic and anthropogenic pressures.

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Keywords
California Cooperative Oceanic Fisheries Investigations • Fisheries of California • Decline of Pacific sardine • Historical context for California Cooperative Oceanic Fisheries Investigations

> The California Current has been referred to as the most intensively studied piece of ocean in the world. This reputation is enjoyed for two reasons: one, because the large number of marine institutions located along the coast of North America have each conducted many and varied field research programs; and two, because of the CalCOFI program.
>
> (Roger Hewitt, 1988 [204])

> Despite a long and proud tradition of American high-seas research in Pacific waters, the 1930's decade was one of stagnation in ocean research on the west coast... As early as 1950, there had been a fundamental change in this situation. New projects underway for high-seas and coastal fisheries research, using newly commissioned oceangoing research vessels, had placed American science in the forefront of oceanographic studies; the reunification of marine biology with chemical and physical oceanography had begun in earnest; and a major effort was underway to recruit top-rated young scientists from the individual disciplines for a host of available positions in ocean science projects. In sum, the New Oceanography of the modern era had taken form.
>
> (Harry N. Scheiber, 1986 [488])

> Defending science for its own sake disproportionately benefits the fundamental-science agencies, which can claim to be doing the most prestigious and therefore the most apparently worthwhile science. In the face of the new budgetary reality, advocacy for science must take a new, strategic approach — one that insists on balance between the fundamental-science agencies and the mission agencies that link science to the public good. Otherwise, the value of the public investment in science will decline right along with the budget.
>
> (Commentary in Nature, 2012 [485])

1.1 The Decline of the Pacific Sardine Fishery and Origins of the CalCOFI Program

The fishery for the Pacific sardine (*Sardinops sagax*) used to be the largest volume fishery on the North American Pacific coast. The sardine fishery developed in the 1920s, was at its heyday in the 1930s, collapsed in the 1940s, disappeared in the 1950s, 1960s and 1970s, and only began to recover in the 1980s. Conflicting views concerning the cause of the collapse of the sardine fishery in the 1940s, and whether it was predominantly due to fishing or due to changes in the environment, lay at the heart of the developing CalCOFI program [454]. Statements in the literature concerning these conflicting views appear disingenuous today. For example, Radovich (1982) wrote:

> For many years, federal personnel from the National Marine Fisheries Service debated vigorously with personnel from the California Department of Fish and Game on what was happening to the Pacific sardine. The Federal scientists, working for an agency whose fundamental charter was to assist the development and maintenance of U.S. commercial fisheries, looked for reasons other than fishing, for the sardine's declining condition, while the scientists employed by the State (whose basic role was protector of the State's resources) supported the premise that overfishing was having a detrimental effect on the standing stock. These were capable, competent scientists using the same data and coming up with different conclusions in part because they were employed by agencies whose fundamental goals were different. [454]

Early warning of the potential collapse of the sardine fishery, and recommendations that the annual catch limit be set at 200,000 tons, were given by Scofield in 1931 [501] and 1934 [502], and a catch limit of 250,000 tons per year was recommended by Frances Clark in 1939 [118, 119]. Sardine landings peaked in 1936–37 at 791,334 tons, of which 726,124 tons were landed in California, and 65,210 tons were landed in the Pacific northwest [454]. Landings in the Pacific northwest peaked seven years later in 1943–44 at 101,000 tons when the total sardine landed on the Pacific coast (including Canada) had declined to 579,129 tons [454]. In the subsequent decade from 1943 to 1953, sardine catches on the Pacific coast declined by an order of magnitude to about 80,000 tons in 1954–56 [454]. To put this in perspective, total United States landings of sardines in 2010 was a little over 66,000 tons [563]. In the decade following the mid-1950s, the sardine catches declined even further to about 20,000 tons in 1965–67 [454].

From 1937 to 1949 Oscar Elton Sette, formerly at the Bureau of Fisheries, led investigations into fluctuations of the sardine fishery, and from his post at Stanford University, served as the scientific adviser for the California Cooperative Sardine Research Program that later became CalCOFI [262]. The original Marine Research Committee was composed of nine members, five of which were actively involved in the canning or fish meal reduction industries. The other four members were from the California Fish and Game Commission, the Division of Fish and Game, and the California Academy of Sciences. In 1955, the committee was changed to include a member of organized labor, a representative of organized sportsmen and two public members. It was not until 1957 that the California Cooperative Oceanic Fisheries Investigations (CalCOFI) Committee was constituted by a representative from each of Scripps Institution of Oceanography (SIO), the California Department of Fish and Game (CDFG), and the U.S. Bureau of Commercial Fisheries (USBCF, later named the National Marine Fisheries Service, NMFS, now called the NOAA Fisheries Service). A fourth member was hired as chairman by the still extant Marine Research Committee [454]. The Marine Research Committee was dissolved in 1978 [454] and the modern CalCOFI committee retains only the three institutional representatives (from NOAA, Scripps, and California Department of Fish and Game, now called the California Department of Fish and Wildlife).

The origins of CalCOFI were viewed sceptically by some. Radovich (1982) went so far as to suggest that the early origins of CalCOFI in 1937–38 under Oscar Sette lay in a diversionary tactic initiating a special study of sardine abundance in order to delay legislation restricting the take of sardines for fishmeal [454]. After the sardine fishery reached a low point in 1947, the Marine Research Committee was created, funded by a tax on fishery landings "to seek out the underlying principles that govern the sardine's behavior, availability and total abundance" [359], but Radovich [454] asserted that this step was yet another delaying tactic to prevent regulation of the fishery.

The entry of the United States into the Second World War led to an expansion of naval and military research spending at U.S. west coast research institutions, and particularly at Scripps Institution of Oceanography which undertook new programs in sonar, naval electronics, wave and current studies and microbiology [488]. The effect of the war on fisheries research was less positive, with emphasis on maximizing fisheries output, and little focus on conservation or sustainable management [488]. By 1950, as the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program began, the situation changed and there was renewed interest in fisheries and oceanographic research. The years from the end of World War II until the 1970s saw a rapid expansion of oceanographic knowledge, sampling capacity, and integration of the marine sciences into truly interdisciplinary oceanography [488].

The CalCOFI program was an outgrowth of field studies in the 1920s, 1930s and 1940s conducted as collaborations between California Department of Fish and Game, Scripps Institution of Oceanography, the California Academy of Sciences (CAS), and the U.S. Bureau of Commercial Fisheries [204]. The initial rationale for the CalCOFI survey program was to determine why the Pacific sardine fishery drastically declined in the 1930s and 1940s, by studying the pelagic environment and the fishery. Specifically, the program was charged with "investigating the sardine in relation to its physical and chemical environment, its food supply, its predators and its competitors, in attempting to evaluate the findings in terms of the survival of the young, and in terms of the distribution and availability of the sardines when they reach commercial size." [204][1]. It was hoped that an oceanographic approach would underpin better management of the fishery in the future [204, 427, 489].

CalCOFI developed in the context of competing hypotheses to explain the observed fluctuations in fish stocks. The two main hypotheses were that fluctuations, and in particular collapses, in small pelagic fish stocks were primarily driven by the environment or, alternatively, were mainly controlled by fishing pressure. Initially the causes of the sardine decline were thought to be related to environmental variability, but there was increasing realization, largely based on observations of the effects of bottom trawling on demersal fisheries elsewhere, that fishing pressure might also impact the sardine stock.

In his time as advisor for the California Cooperative Sardine Research Program, Oscar Sette maintained that human impacts on fisheries could only be understood in the context of environmentally driven variability and he developed an extensive program to understand the sources of mortality of the early life history stages. Sette was a student of Henry Bryant Bigelow, who himself was influenced by the seminal work of Johan Hjort. Hjort was the proponent of two key hypotheses regarding environmental influences on the year class strength of fishes, namely the critical period hypothesis and the hypothesis that advection from areas favorable for survival could influence mortality. Sette's academic lineage defined the focus of CalCOFI: essentially the effect of environment on the mortality and survival of early life history stages. This focus has largely been maintained throughout the program. By 1955 the proponents of overfishing (Frances Clark from CDFG) and advocates of adverse environment (John Marr from USBCF) as the cause of the 1930s sardine collapse were clearly opposed in their views [204]. However, by the early 1960s it was apparent that sardine stocks were overfished. At the same time the effects of the environment on the spawning success of sardine were also widely recognized. In particular, Reid et al. (1958) [466] suggested that increased winds, enhanced upwelling and cooler temperatures led to sardine spawning failures.

If environmental influences drove the inter-annual variability of small pelagic fish, then the mechanisms driving mortality and survival were thought to be starvation or growth of the early larvae through a critical period, or their loss by advection to unfavorable areas for recruitment. Emphasis on environmentally driven variability contrasted with the other, not mutually exclusive hypothesis, that the decline of the sardine fishery was driven primarily by overfishing.

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[1] Quoted by Hewitt (1988) [204] from the first California Cooperative Sardine Research Program Progress Report (1950). This series is now informally called the CalCOFI Reports, indexed as the California Cooperative Oceanic Fisheries Investigations Reports.

A third more recent hypothesis affecting research direction in the CalCOFI program was that predation on ichthyoplankton and juvenile fish was an important determinant of recruitment success. This predation thread has been less followed than the ideas that starvation in the critical period, or advection to unfavorable areas, determine recruitment success. Nevertheless, experimental work on predation was a key area of research at the SWFSC in the 1970s and 1980s. Perhaps not surprisingly, the modern view partly integrates these opposing hypotheses, such that linear and non-linear interactions of components of all three of these hypothesized mechanisms can contribute to fluctuating biomass of small pelagic fish. The balance of these influences changes on more than one time scale. For further discussion on the role of CalCOFI in the development of ecosystem science, see Sect. 7.1.1).

The context and rationale for the CalCOFI program has changed since the first 3-ship west coast-wide cruises in 1949[2] initiated under the California Cooperative Research Program [204]. After the first decade, the rationale of the CalCOFI program was already changing focus and broadening away from just sardine to try and understand fluctuations in other commercially important species, including northern anchovy (*Engraulis mordax*)[3] [204]. The increasing abundance of anchovy in the 1960s became a focus for research as the anchovy replaced the sardine [204]. The goal of the modern CalCOFI program can be broadly expressed as the understanding of long-term changes in the California Current Ecosystem, or CCE [427]. This goal is recognized as being intimately linked with basin-scale processes, and CalCOFI has been embedded in larger scale studies of the Pacific since its early days [79, 108, 156, 378, 464]. The current focus of the CalCOFI program is now enabled by numerous other programs that piggy-back on and supplement the core survey program (see Sect. 1.4).

1.2 The Commercial Fisheries of California

In terms of tonnages landed, California commercial fisheries are now, and have been in the past 90 years, dominated by pelagic species (pelagic fishes and/ or squid) rather than by demersal or semi-demersal species. In terms of value, the modern commercial fisheries are dominated by crustaceans (crabs) and molluscs (squid) rather than by pelagic fishes. Of these, the most valuable commercial fisheries in California are Dungeness crab (*Metacarcinus magister*) and market squid (*Doryteuthis opalescens*).

In years when market squid are very abundant, the squid fishery can be more valuable than Dungeness crab. Total U.S. landings of Dungeness crab were 30,000–31,000 metric tons (t),[4] or tonnes, worth \$131–140 million[5] in 2010–2011 [564]. California constituted 29 % of the total Dungeness crab landings (10,000 t), which were caught off Washington, California, Oregon, and Alaska, in order of the size of landings [564]. The catch of Dungeness crab in Oregon was slightly smaller than in California in 2010–2011, whereas Washington provided 40 % of the total, and Alaska had by far the smallest catches [564]. By comparison, in the same two years, total U.S. landings of market squid were 150,000–153,000 t worth \$110 million [564]. About 81 % of the squid were caught in Californian waters [564]. Compared to market squid, the Dungeness crab are a "high value - low volume" fishery.

The California market squid fishery is an example of a fishery that has attracted relatively little research effort. The market squid fishery began in the late 1970s, and since the mid-1980s showed a steady upward trend over the next 15 years (Fig. 1.1), except during El Niño years when the fishery collapsed (see Sect. 4.2.1.5). Historically, the market squid fishery has origins in Monterey but the Southern California Bight dominates the fishery in terms of landings by a factor of 2–10 times [30]. Squid are taken with purse seines, light boats and brail or dip nets [30]. Market squid catches declined from 2000 to 2009 and a seasonal catch limit of 107,048 t was imposed by the State of California in 2005 [26] (excluding the low-volume, high-value live bait fishery for market squid). Following this decade of declining catches, seasonal catch limits were exceeded in 2010–2011 [30] when catches almost tripled in one year, and were exceeded again in the 2011–2012 fishing season. In both years the fishery was closed early by management action.

The sardine no longer holds pride of place among Californian fisheries, as it did in the 1930s. It is now a relatively small commercial fishery with total U.S. landings of 46,000–66,000 t valued at \$12 million in 2010–2011 [564]. Commercial fisheries for other small pelagic fish species are even less significant. Total U.S. landings for northern anchovy were 1,000–3,000 t worth \$0.5–0.6 million. Chub mackerel (*Scomber japonicus*) landings were 1,000–2,000 t worth \$0.3–0.4 million, and jack mackerel (*Trachurus symmetricus*) were almost insignificant, with landings of 110–310 t in 2010–2011 [564].

Current catches are a far cry from 1936, the year of the highest catch in California history, when 798,000 t [564] were landed during the height of the sardine fishery and

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[2] The fixed CalCOFI sampling grid was established in 1951 and earlier surveys in 1929 – 1932 and 1937 – 41 [514] were more exploratory [204].

[3] Henceforth referred to as anchovy

[4] All landings are rounded to the nearest 1,000 t.

[5] All commercial values are rounded to the nearest million dollars.

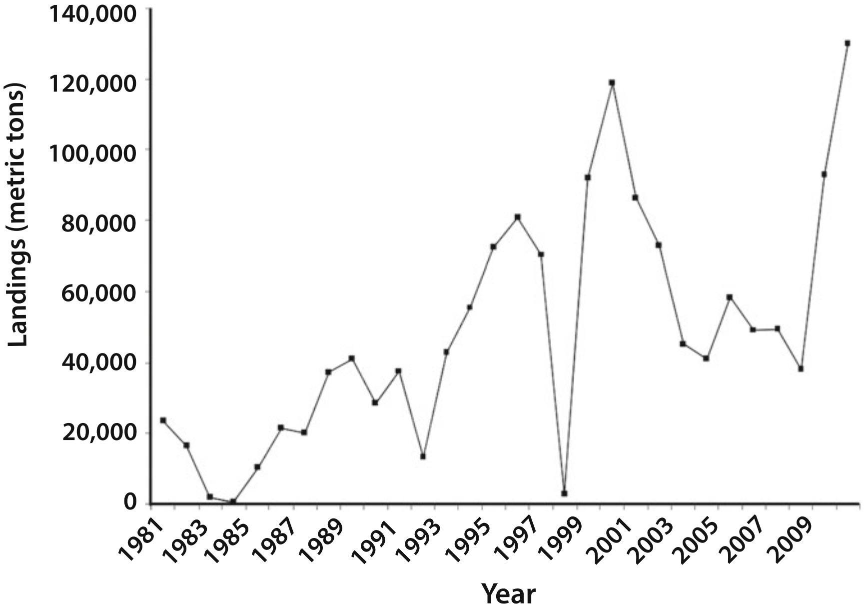

Fig. 1.1 Market squid (*Doryteuthis opalescens*) landings in California (From [30])

sardine landings dominated the catch. To put the historically large Californian sardine catch in perspective, the Peruvian anchovy catch reached 13,000,000 t in both 1970 and 1994. The current Peruvian fisheries, which are still dominated by anchovy, landed 6,914,000 t in 2009 and 4,261,000 t in 2010 [564]. Even during years when California's catches of small pelagic fish were highest (798,000 t), they still only comprised approximately 12 % of the 2009 anchovy catch (6,914,000 t) off the coast of Peru. Total U.S. landings of all species were 3,733,000 t in 2010 and 4,472,000 t in 2011 [564]. Alaskan pollack (883,000–1,275,000 t in 2010–2011) and Atlantic menhaden (667,000–850,000 t) constituted the largest U.S. catches [564]. When compared to the huge Peruvian anchovy fishery, or to the landings of other large, modern fisheries in the United States, the historical total Californian fisheries landings have never been extraordinarily large, nor especially valuable (Fig. 1.2). Nevertheless, the sardine collapse had significant economic ramifications for coastal communities that lasted for decades.

The present day U.S. sardine fishery is a shadow of its former self, with catches on the order of 50,000 t in the decade following 2000 (Fig. 1.3). This is less than one-tenth of the Californian catches at the peak of the historical fishery in 1936–37, on the order of 725,000 t (see Sect. 1.1). Only since 1985 have Californian catches begun to recover from the collapse of the 1940s. The sardine fishery off Oregon was slower to recover and did not equal the Californian catches until 2004 (Fig. 1.3). The fishery off Washington is still considerably smaller than either the California or Oregon sardine fisheries [30].

Sardine are the largest fishery in the coastal pelagic finfish complex. Coastal Pelagic Species (often referred to as CPS) is a term often used to define a group of four fish species; Pacific sardine (*Sardinops sagax*), northern anchovy (*Engraulis mordax*), Pacific mackerel (*Scomber japonicus*), and jack mackerel (*Trachurus symmetricus*), but has also come to encompass market squid (*Doryteuthis opalescens*), and more recently, krill (see below). In 2010 sardine comprised 91 % of the combined CPS finfish complex landed and 82 % of their combined value. The largest annual landing of sardines in California since the recovery began in the late 1980s was almost 81,000 t in 2007 [30].

The most detailed and up to date information on Californian fisheries is found on the Pacific Fisheries Information Network (PacFIN) web pages. This joint federal and state project aims to provide "timely and accurate data to aid effective management of fisheries and fishery resources". Data from the Washington, Oregon, California, Alaska and British Columbia marine fisheries are provided to the database. Catch and effort data by species and by year have been published as reports for Washington, Oregon and California over the last 30 years.

California landings by major groups based on the PacFIN reports clearly show the dominance of Coastal Pelagic Species[6] (Table 1.1). As mentioned previously, Coastal Pelagic Species encompass both market squid and sardine, the two taxa constituting the largest tonnages. The catches

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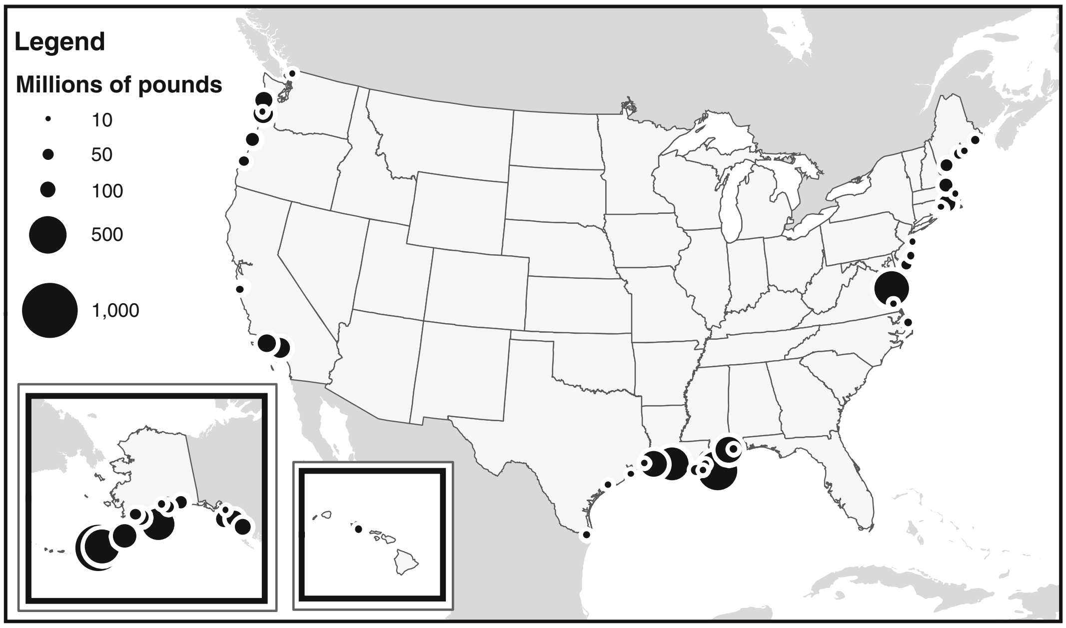
[6] I use the term Coastal Pelagic Species (CPS) here since it is widely used in fisheries management and research documents, but it should be noted that some of the species included under the CPS category are definitely not coastal species. sardine and jack mackerel, for example spawn a long way offshore, well beyond the coastal zone. Anchovy have also been found far offshore at times. A better name for this group would be Small Pelagic Fishes or Small Pelagic Species.



Commercial Fishery Value at Major U.S. Ports 2011

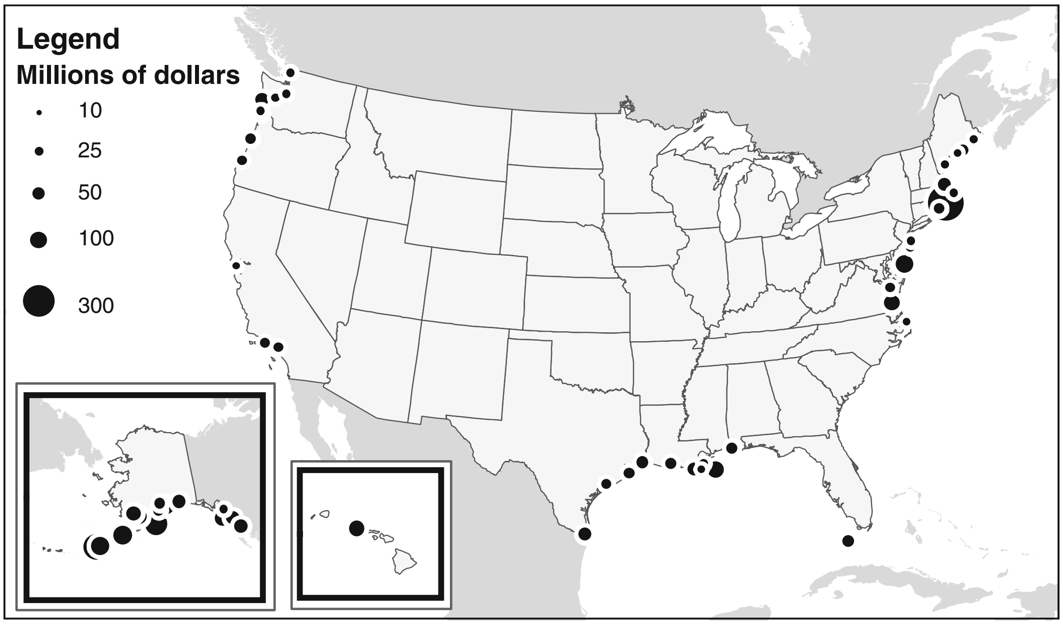


Fig. 1.2 The relative size and commercial value of California fisheries landings in 2011 relative to other fishery landings in the United States (From [564])

of the coastal pelagics are generally an order of magnitude larger than the next two largest landings categories, which are crabs and groundfish (Table 1.1). In the crab category, Dungeness crab landings are generally an order of magnitude larger than rock crab, which is the next most frequently landed crab. Landings of Dungeness crabs are comparable to landings of groundfish, and also to the "other" species category (Table 1.1). Among groundfish, Dover sole, rockfish, sablefish, and Pacific whiting (or Pacific hake, *Merluccius productus*[7]) are important, often individually exceeding 10 % of the groundfish landings. Sea urchins are the most important component of the group listed as "other". The remaining landings categories made up of highly migratory species, shrimps, and salmon are small, and contribute little to California fisheries landings (Table 1.1).

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[7] Henceforth referred to as hake.

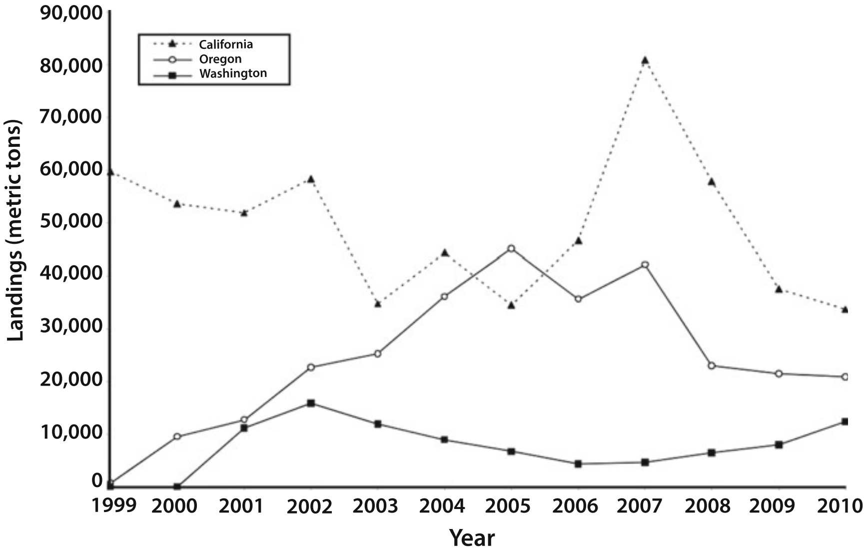

Fig. 1.3 Recent commercial landings of sardine (*Sardinops sagax*) in California, Oregon and Washington (From [30])

Table 1.1 California fisheries landings (metric tonnes) by year and species categories over the last decade from Pacific Fisheries Information Network (PacFIN) reports published by California Department of Fish and Game

Species category	2003	2004	2005	2006	2007	2008	2009	2010	2011
Coastal pelagics	87,536	97,794	105,377	118,818	147,312	115,556	141,217	167,923	153,418
Crab	10,761	12,064	5,467	12,471	5,629	4,472	7,563	10,598	10,082
Groundfish	10,625	12,280	11,174	12,086	10,549	13,204	10,348	10,091	7,363
Other	6,932	7,342	6,766	6,592	7,288	7,235	7,911	6,990	7,174
Shrimp	1,588	1,597	477	482	627	424	1,633	282	3,729
Highly Migratory species	5,127	3,551	2,016	1,094	1,819	1,193	1,412	1,235	1,526
Salmon	3,338	3,235	2,258	539	793	<1	<1	118	514
Total	126,010	138,078	134,411	152,183	174,328	143,036	170,100	199,122	185,384

Note that coastal pelagics landings include market squid

In 2006 the Coastal Pelagic Species Fishery Management Plan (CPS FMP) was amended to include all species of euphausiids, or krill (see Sect. 3.2.1), within the CPS "management unit species" and to denote krill as a "prohibited harvest species". In addition, it is not possible to fish krill under the "exempted permit process", thereby affording them further protection from exploitation [27]. Prior to Amendment 12 of the CPS FMP, there were only two categories of species in the management plan; managed and monitored species. "Managed stocks" must have an annual harvest guideline that is tied to the size of the spawning stock biomass. These include sardine and Pacific mackerel. "Monitored stocks" are small fisheries that are not subject to harvest guidelines, and that are fished at levels that are no threat either to the fished stock itself, or to other species that depend on the stock. These include jack mackerel and anchovy, and rather oddly, market squid.[8] Amendment 12 of the CPS FMP added a third category, which is the "prohibited harvest species", and placed all krill species into that category [27]. Krill are a key forage resource for commercially exploited species such as hake, rockfish and salmon ([165] cited in [27]). Protection of krill from exploitation was intended to conserve the krill themselves, but also to protect the fish, mammal and seabird predators that depend upon the krill resource. The measure was further designed to protect the fisheries for species that are sensitive to variability in the krill resource, and the industries such as whale watching, that depend on cetaceans feeding on the krill. This management development to protect krill as an important forage group can be seen as one step along the way to Ecosystem Based Management (Sect. 7.1).

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[8] Squid are an oddball in that they support a large and valuable fishery, but they are not a managed species, although there is a squid Fishery Management Plan [26]. Most California fisheries occur within the 3 mile State waters limit (some hake and rockfish being exceptions), but the stocks extend far offshore into Federal jurisdiction waters. Squid differs in the sense that both the stock and the fishery are in State waters and consequently this fishery is managed by the State of California. However, squid was the last FMP to be developed under the CPS group, and political considerations also play a part in why the squid fishery is managed by the State of California, rather than by the Federal government (personal communication: Ray Conser, SWFSC, NOAA Fisheries).

1.3 The CalCOFI Sampling Domain

The sampling design and numbering system for CalCOFI stations appears curious when first encountered. The station pattern was based on a centric-systematic-area design ([281] attributed to [393]). The background to this sort of sampling design can be found in statistical reviews [88, 240]. The CalCOFI transect lines were designed to be normal to the central California coast, centered on line 80 at Point Conception, and so were set to run 30° southwest of lines of latitude. The original pattern extended from line 10 at the U.S.–Canadian border to line 120 off Point Eugenia, Baja California, Mexico with a spacing between lines of 120 miles. The spacing was set so that additional lines could be added with convenient decile line numbering, but it was subsequently decided that 40-mile spacing was sufficient, and so lines had to be numbered in fractions of 3s and 7s [281]. Lines were later added as far south as line 157 at Cabo San Lucas in Baja California. Stations were centered on station 60 on line 80 and laid out perpendicular to all lines parallel to line 80 [281]. Stations were initially set 40 miles apart to permit stations to be spaced as close as 4 miles without resorting to fractional station numbers. Stations inshore of station 60 were later added at 20 mile spacing, and additional nearshore stations have been added in recent years (referred to as SCCOOS[9] stations, Fig. 1.4).

The CalCOFI surveys can be grouped into sampling domains that were the most commonly used over the duration of the time series. The time series is usually considered to begin in 1951 because this is when more regular surveys were initiated. The largest sampling domain is the original, or near original, area spanning the US west coast from the California-Oregon border to the tip of Baja California Sur, Mexico (surveyed in 1951, 1952, 1954, 1956, 1958–1960, 1969 and 1972) (Fig. 1.5). The next largest sampling domain ran from San Francisco to southern Baja California (surveyed in 1953, 1955, 1957, 1961–1966, 1968, 1974, 1975, 1978, 1980 and 1981). The smallest of the common sampling domains is the 66 station survey from San Diego to Avila Beach, often referred to as the "core CalCOFI lines" (sampled over the entire time series, with the exception of the late 1970s–mid-1980s when sampling was done every third year). A series of inshore Southern California Coastal Ocean

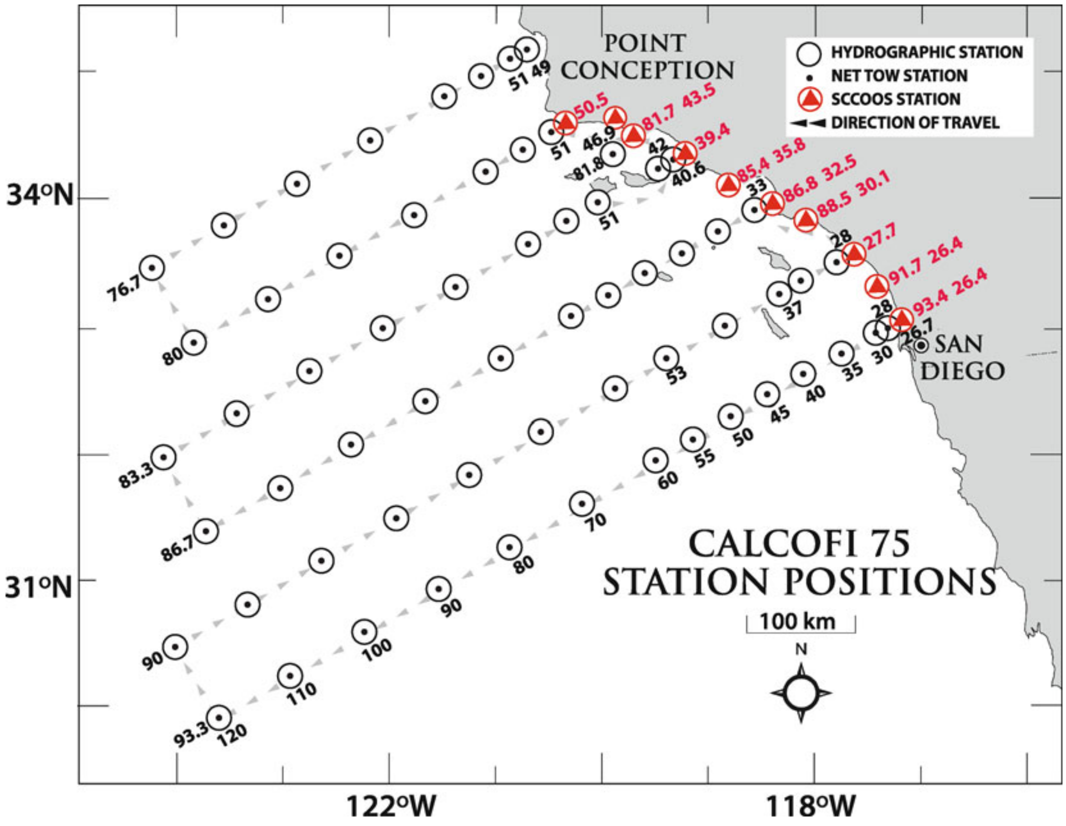

Fig. 1.4 Map showing the "core" CalCOFI sampling domain comprising 6 lines or transects from San Diego to Avila Bay, now sampled quarterly. This is also referred to as the 75 station pattern. These stations have been sampled consistently since the beginning of the CalCOFI program except for the inshore stations (*marked in red*) that were added later as part of the Southern California Coastal Ocean Observing system (SCCOOS). Note that the 66-station pattern, or the "core" CalCOFI pattern prior to SCCOOS is simply the 75 station pattern without the SCCOOS stations

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[9] Southern California Coastal Ocean Observing System.

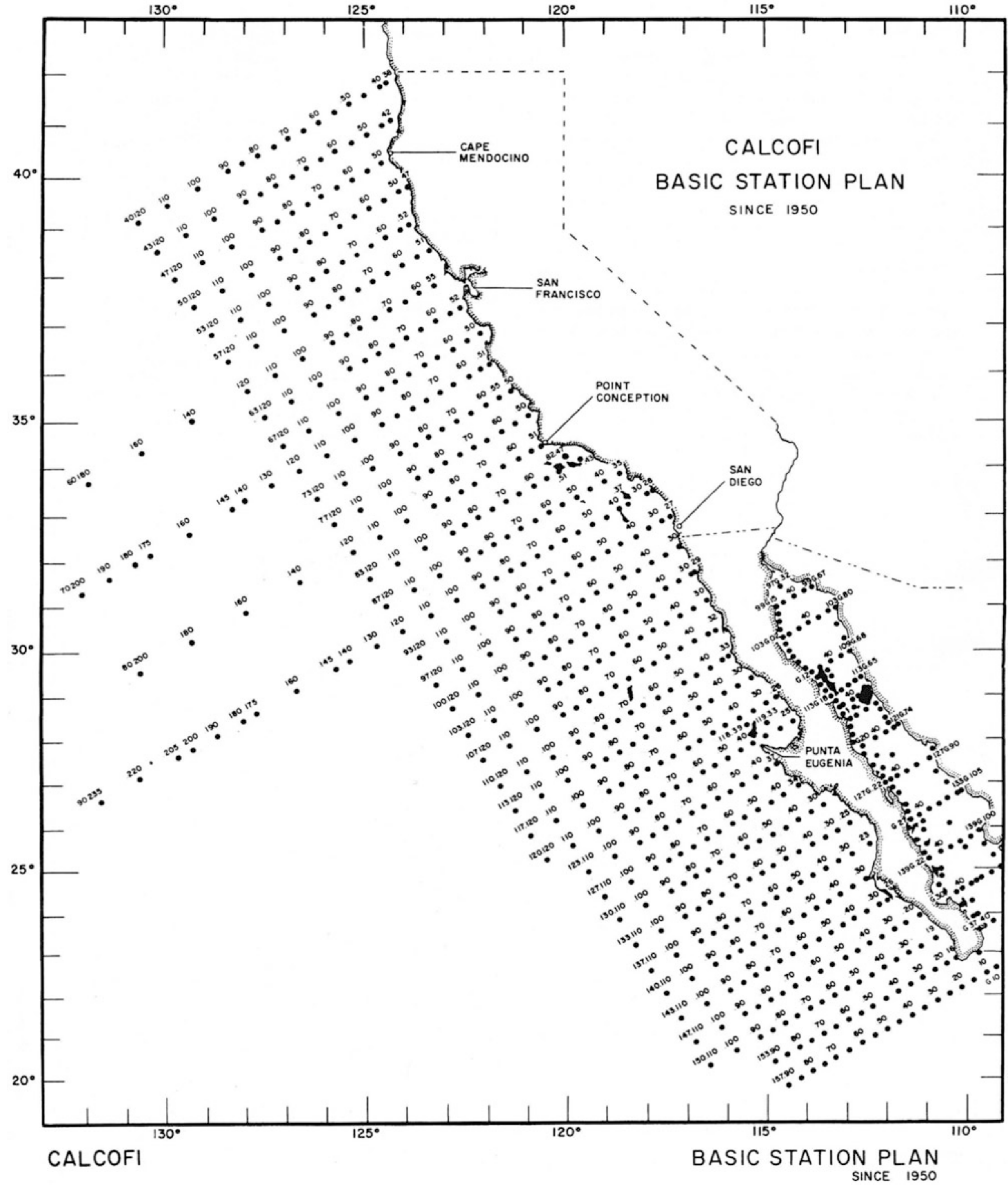

Fig. 1.5 Map showing the original (1950) station plan for CalCOFI which was intended to be sampled approximately each month. The area from the California-Oregon border to the tip of Baja California was surveyed in 1951, 1952, 1954, 1956, 1958Ű-1960, 1969 and 1972. Note that stations sampled were often approximated by dead-reckoning in the early days when weather precluded accurate position fixes

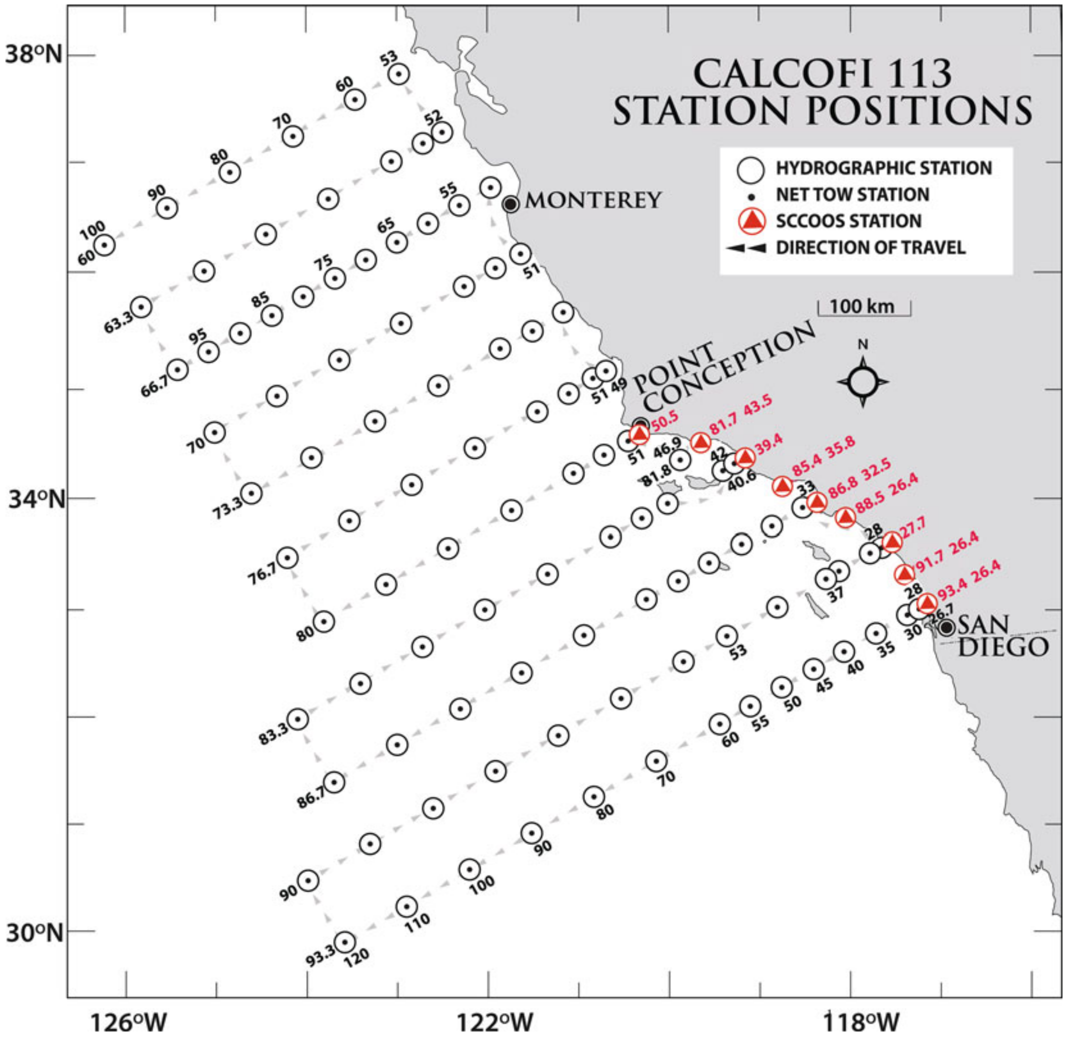

Fig. 1.6 Map showing the extended 113 CalCOFI station pattern sampled in springtime. Transects were extended along the southern part of the central California coast as far north as San Francisco to capture most of the spatial domain of sardine spawning. Northern lines from Avila beach to San Francisco are commonly referred to as the DEPM (Daily Egg Production Method) survey pattern by SWFSC scientists. Samples collected differ in some important respects from sampling on the core CalCOFI pattern shown in Fig. 1.4

Observing System (SCCOOS) stations were added to the core CalCOFI lines creating a 75 station pattern (Fig. 1.4).

Among the CalCOFI surveys there are also some less common sampling domains. These are San Francisco to mid-Baja California (1979, 1984), San Francisco to San Diego (1982, 1983), Point Conception to mid-Baja California (1977), and Point Conception to southern Baja California (1967, 1970). The less common sampling domains all were sampled in the interval 1967 to 1984 during the period of the sardine fishery collapse, when sardine eggs were rare. However, the San Francisco to San Diego 113 station survey is now the standard spring survey used for sardine stock assessment (Fig. 1.6). This pattern was adopted to cover the expanded domain of sardine spawning off the southern central California coast when sardine populations began to increase after the late 1980s. Recently there have been intermittent coast-wide surveys covering the entire U.S. west coast in April–May 2006, 2008 and 2010, and also July–August 2008 and 2012. Two intense survey efforts in the southern California Bight were mounted by SWFSC Fisheries Resources Division in response to El Niño events. The first was focused on physical oceanography of the California Undercurrent and involved 25 cruises mounted over 45 months from February 1996 through October 1999 [337]. The second was during the winters of 2002–2005 and involved intensive biological sampling of the Cowcod Conservation area [557]. In addition, CalCOFI line 90 was sampled monthly from March 1983 to January 1984 [382].

Within these broad sampling domains, some lines and stations have been more regularly sampled than others. Line 90 across the mid-Southern California Bight (Fig. 1.4) is the best sampled line in the time series. The sampling differs not only in terms of the temporal and spatial frequency (see Fig. 7.3 as an example), but also in terms of the properties that were sampled. Further, there were changes in gear used during the time series for some properties. Additionally, there are different levels of taxonomic identification for ichthyoplankton and zooplankton samples that have been sorted. All of these differences need to be taken into consideration in any analysis (see Sect. 3.1).

1.4 The Spatial Domain and Time-Scales of Other Surveys Related to CalCOFI

CalCOFI now operates in an extraordinarily data rich environment focused on the California Current System and its value is both extended and enhanced by a wealth of other ship-based surveys. These include the NSF-funded Long-Term Ecological Research (LTER) program [428], three separate NOAA Fisheries Service stock assessment surveys for sardine ([366]), rockfish ([45, 456, 484]) and hake [201], a combined coast-wide survey for sardine and hake (SaKe) focused on the shelf, the west coast-wide nominally triennial NOAA cetacean ecosystem assessment survey [48], the Investigaciones Mexicanas de la Corriente de California (IMECOCAL) program covering Baja California [53] (Fig. 1.7), the Columbia River plume sardine survey [149], the Northeast Pacific line P transect [348, 351], individual transects sampled off Newport, Oregon and Humboldt, California (see State of the California Current papers, e.g. [66, 184, 371, 372]), and the Marine Ecological Reserves Research Program (MERRP, 1995–1999). The length of time series collected by these diverse sampling efforts ranges from 60+ years for CalCOFI, to as few as 5 years for the MERRP program. With few exceptions, I cannot cover the results of these surveys in this book, despite their relevance to CalCOFI.

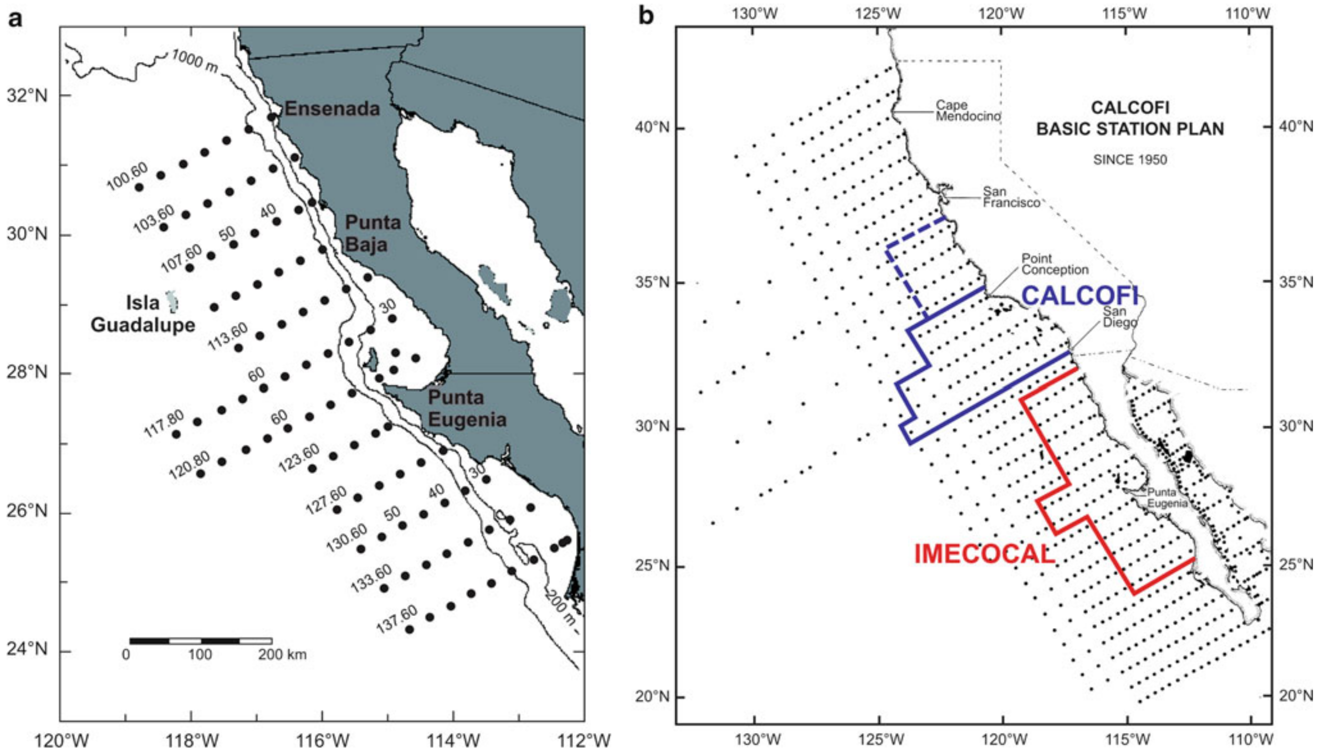

Fig. 1.7 (**a**) Station plan for the quarterly surveys of Investigaciones Mexicanas de la Corriente de California (IMECOCAL), conducted since October 1997. Numbers for lines and stations deliberately follow the CalCOFI system. (**b**) IMECOCAL survey in the context of the original CalCOFI station plan (Fig. 1.5), the 113 station plan (Fig. 1.6) and the 75 station plan (Fig. 1.4) (From [53])

Oceanography of the Southern California Current System Relevant to Fisheries

2

Abstract

The descriptive physical oceanography of the California Current System has been well reviewed in the literature. In this chapter I provide an up to date summary of the features that are most relevant to fisheries oceanography. I start with the various regional physical classifications of the California Current System, followed by the main bathymetric features of the core CalCOFI area. I describe the water sources and properties, and then the geostrophically mapped currents. The relative importance of advection and upwelling to production in the California Current System is a key theme of this chapter. I describe the seasonal cycle based on remote sensing, and the spring transition from winter to upwelling conditions. I address processes affecting biological production off central California, and both in and offshore of the Southern California Bight (SCB). These processes include advection, geostrophic adjustment, wind stress curl, seasonal overturn, Sverdrup transport, wind-driven upwelling and wind relaxation events. I discuss important processes and structures in their regional context. Wind-driven coastal upwelling, wind-relaxation events, and eddy-like flows are more important off central California. Geostrophic adjustment, seasonal convective overturn, wind stress curl, Sverdrup transport in the nearshore, the deep chlorophyll maximum and fronts are described in the context of southern California.

Keywords

California Current System • Hydrography of the California Current System • Production of the California Current System • Seasonality of the California Current System • Regional structures of the California Current System

> At Scripps Institution and the Tuna Commission, there have been studies of coastal upwelling, oceanic fronts, and of processes such as those Cromwell labeled "doming" or "ridging". Dr. Sette and his colleagues have been examining past weather and the marine climate, looking for long-term changes related to those in the fisheries. All of these investigations have been facilitated by the presence of certain conspicuous features or discontinuities. As Henry Stommel has suggested, studying the oceans resembles dissecting a lobster – it is easier to do at the joints.
>
> (Warren Wooster, 1961 [588])

> We seemed to find eddy-like surface flow wherever we followed drogues.
>
> (Joe Reid, 1988 [465])

> The nearshore positive wind stress curl makes the dynamics of the California Current System very interesting . . . If the hypothesis that wind stress curl-induced offshore upwelling [between San Francisco and northern Baja California] is responsible for the offshore peak in zooplankton volume is true, then not only is coastal upwelling unimportant to the dominant large-scale variability of zooplankton abundance as demonstrated in earlier studies by Bernal, Chelton, and McGowan, but it is also not of secondary importance (at least over the large spatial scales considered here). This would indicate that coastal upwelling effects on biological variability must be only of very localized importance (both spatially and temporally).
>
> (Dudley Chelton, 1982 [107])

S. McClatchie, *Regional Fisheries Oceanography of the California Current System: The CalCOFI program*,
DOI 10.1007/978-94-007-7223-6_2,

The California Current System is characterized by the offshore, southward-flowing California Current, a deep northward-flowing California Undercurrent, seasonal wind-driven upwelling developing after a spring transition, and the coastal winter-time northward-flowing Davidson Current. Regional differences in the California Current System are apparent in the riverine influence off the Washington and Oregon coasts, wind-driven upwelling that is most intense off central California and Baja California Sur, mesoscale features which are most active off central California, and a region with a large summer-intensified cyclonic circulation off southern California.

2.1 Regional Classification of the California Current System

Regional divisions of the California Current System have been defined in different ways depending on the focus of investigators. As pointed out by Longhurst (2007) [332], biogeographers initially took a different approach to oceanographers, but the two approaches later converged. However, the convergence was subsequently undermined by necessary caveats concerning the relationships between biogeographic boundaries with physical features in the ocean. Phytoplankton researchers found fewer divisions of communities than did the zooplankton researchers, and pelagic biota showed less fixed patterns than benthic assemblages. Cultural differences also often entered the mix, such as Russian scientists' tendency to define more regional divisions than non-Russians. Underlying the whole discussion is the issue of how classical taxonomy and the new genetics-based phylogeny are changing the concept of biodiversity. More recently, the advent of remote sensing once again changed the perspective and led to what might be called "taxonomy-free" classifications that combined phytoplankton dynamics with physical forcing to create a new regional perspective.

In Sect. 3.2, I briefly review some of the classic biogeographic works that relied at least in part on the CalCOFI survey data to describe the biogeography of the California Current System. Early biogeography of pelagic organisms focused on the zonal patterns associated with temperature, and later evolved to focus more on the influences of ocean circulation on temperature and the distributions of assemblages [332]. Researchers at Scripps Institution of Oceanography produced seminal works on biogeography of the California Current System and the wider Pacific and the effects of ocean circulation on the distribution of plankton. These works came to define the understanding of the regional biogeography.

Thomas and Strub (2001) [556] delineated six regions in the California Current System based on remotely-sensed satellite imagery: Pacific Northwest (48.4–42.8°N), Cape Blanco to Cape Mendocino (42.8–40.4°N), northern California (40.4–37.8°N), central California (37.8–34.5°N), southern California (34.5–32.5°N), northern Baja California (32.5–29.4°N) and southern Baja California (27.9–22.9°N) (Fig. 2.1a). Curiously, their scheme does not include a separate region for the Southern California Bight. The original survey design of the CalCOFI program covered five of these regions, but only went as far north as the Californian border with Oregon (between Cape Mendocino and Cape Blanco), and excluded the Pacific northwest part of the ecosystem (Figs. 1.5 and 2.1a).

An alternative scheme presented by Bernal (1979) [58] was based on hydrographic and faunistic patterns (Fig. 2.1b). In this scheme the south-central California coast (38–34°N) is dominated by sub-arctic and transitional zooplankton, the SCB and its offshore area (34–31.5°N) has a mixture of water masses and faunas, northern Baja California (31.5–29.5°N) and southern Baja California (28–25°N) are dominated by equatorial forms, and the area far offshore from the SCB and northern Baja California is dominated by the assemblage of the subtropical Central Pacific water mass [58] (Fig. 2.1b). It is notable that zones defined by hydrography and zooplankton fauna [58] match quite well with the zones defined by remotely sensed ocean color [556] (compare Fig. 2.1a and b).

The most quantitative regional classification of the California Current was presented by Mendelssohn and Schwing (2002) [388], based on state-space modeling of wind stress and sea surface temperature time series. From their analysis of interannual trends in wind stress, they were able to separate three regions in the California Current System: a southern region (22–32°N) covering Baja California, Mexico, a central region (32–40°N, Ensenada, Mexico to Cape Mendocino), spanning California, and a northern region (40–48°N, Cape Mendocino to Canada), comprised mainly of Oregon and Washington. The northern region differs from California and Baja California by having mean poleward wind stress to the north of 43°N (i.e. positive in Fig. 2.2a). Wind stress off California and off Baja California is predominantly equatorward (i.e. negative in Fig. 2.2a). Wind stress in the central region is stronger than in the northern or southern regions (Fig. 2.2a). Winds in the Southern California Bight are uncoupled from the rest of the central region. However, winds immediately offshore of the Bight are similar to wind stress trends in the central region [388].

Trends in sea surface temperature (SST) separate into the same three regions as the wind stress trends [388]. Trends in the northern region are relatively weakly correlated with trends in the southern region, implying a different pattern of inter-annual variability [388]. However on 1–5 year time scales, SST is better correlated in space than is wind stress (Fig. 2.2b). SST decreased consistently to the north from 22–40°N, but was relatively constant with latitude north of 40°N (Fig. 2.2b). SST was more responsive to the regime shift of

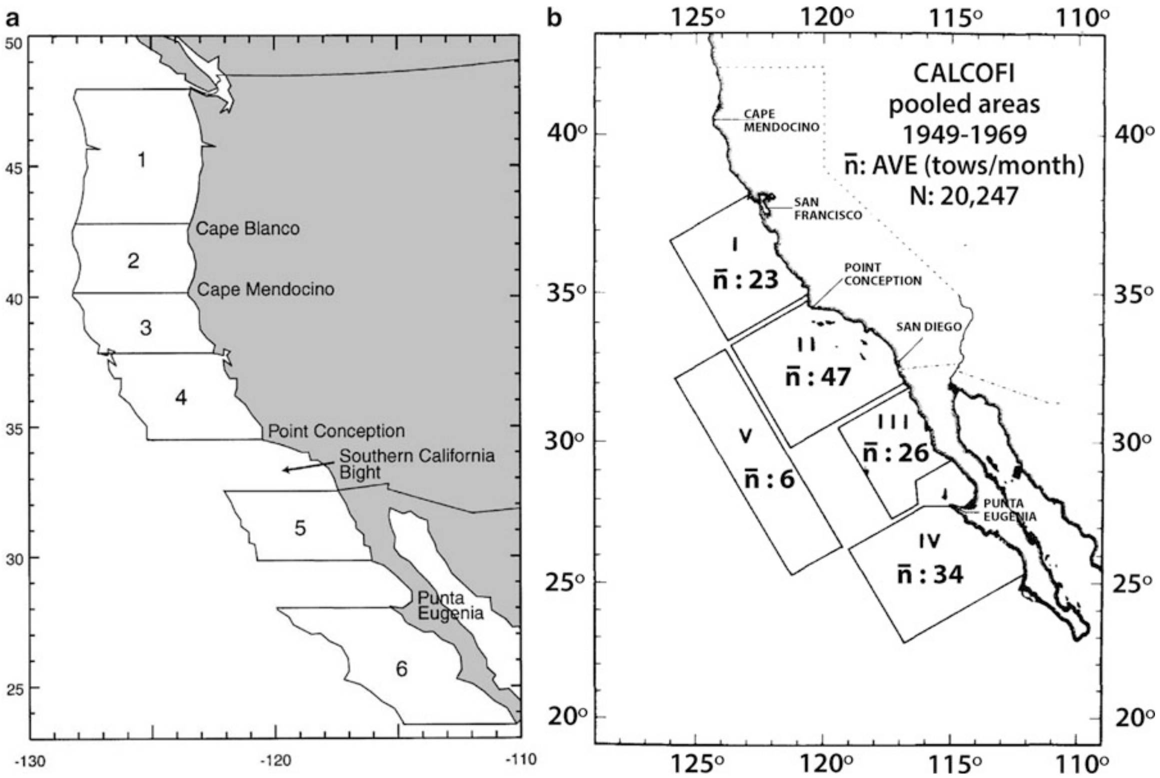

Fig. 2.1 (**a**) Regions of the California Current System derived from climatologies of ocean color (From [556]). (**b**) Regions of the California Current System derived from considerations of hydrography and zooplankton fauna (From [58])

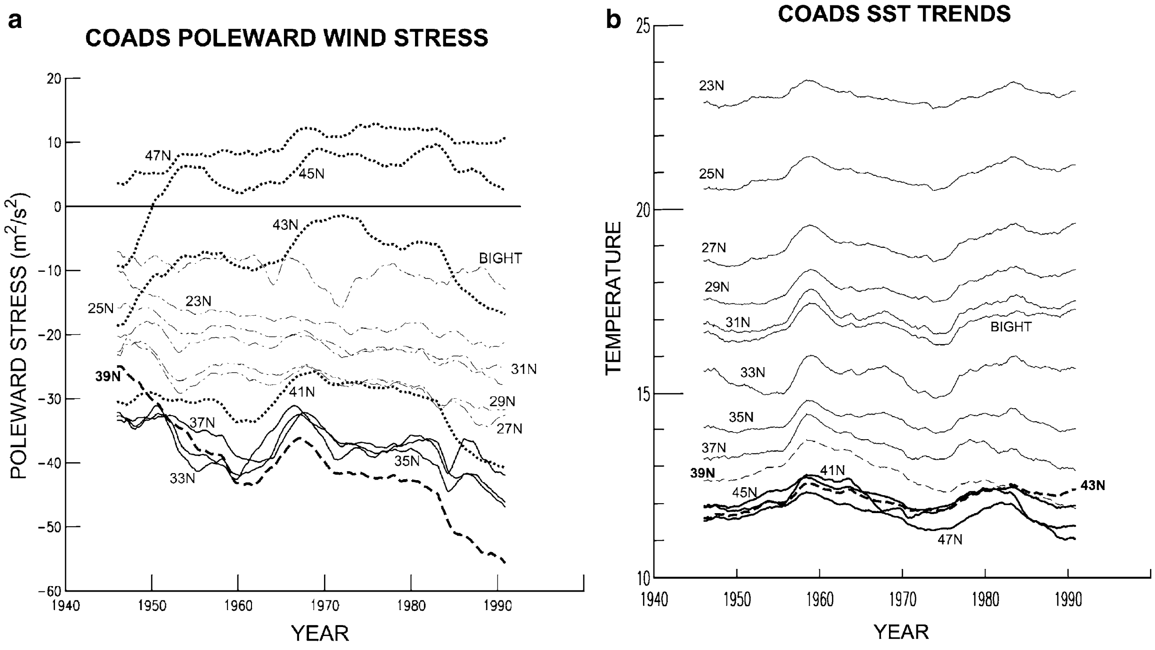

Fig. 2.2 (**a**) Trends of poleward pseudo-wind stress derived by squaring the northward wind component from the monthly mean Comprehensive Ocean-Atmosphere Data Set (COADS) for 2° latitude by 2° longitude boxes along the North American West Coast. *Dashed-dotted lines* are from the Southern region (22–32°N). *Solid lines* are time series from the Central region (32–40°N). *Bold dotted lines* denote the Northern region (40–48°N). *Bold dashed line* is the 39°N time series. (**b**) Sea surface temperature (SST) time series from the same dataset and locations as in (a). *Bold lines* mark time series north of 40°N and *fine lines* represent time series south of 40°N (From [388])

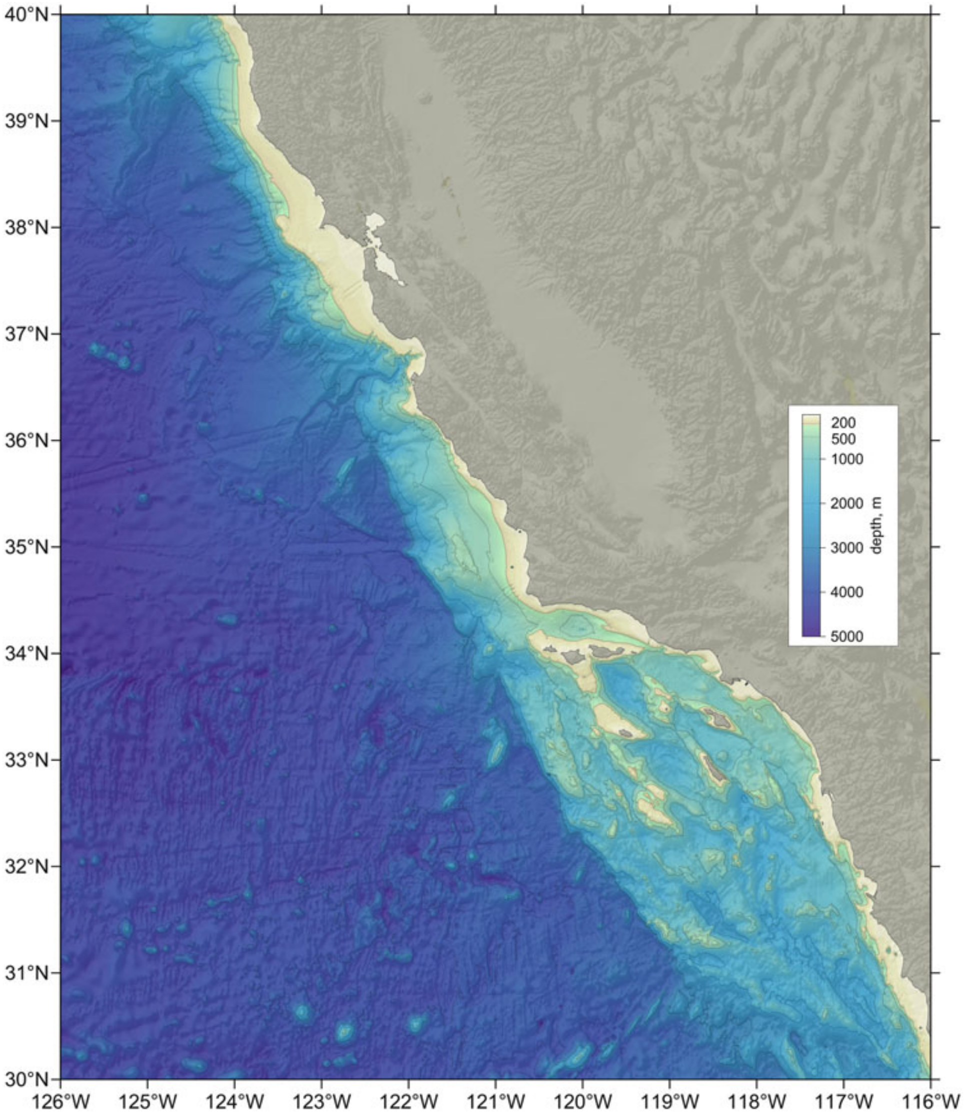

Fig. 2.3 Bathymetry of southern and central California coast. Land is *shaded gray* (Data: SIO, NOAA, U.S. Navy, NGA, GEBCO. Map prepared by Paul Fiedler, NOAA SWFSC, from SRTM30_PLUS V8.0 Global bathymetry [56, 524])

1976/77 and El Niño events than is wind stress. Figure 2.2b shows the distinct warming of the 1958 El Niño, which was especially notable in the central region off California. The SST time series also show the warming trend beginning in 1976. Neither of these phenomena were evident in the local wind time series, suggesting that decadal scale SST variability in the California Current System is controlled by large scale pressure and wind fields rather than by local wind forcing [388].

2.2 Bathymetric Features of the Core CalCOFI Region

Bathymetry off southern California and the region to the west of the Southern California Bight (SCB) is complex, with a narrow shelf inside the 200 m depth contour and a complicated "rough borderland" [148] of deep basins and banks. The western limit of the SCB is the Santa Rosa Ridge[1] running southward from between Santa Cruz and Santa Rosa Islands, then to the east of San Nicolas Island (Figs. 2.3 and 2.4).

The ridge continues from the west of San Nicolas Island towards the southeast, bordering the western side of a deep basin on the western side of San Clemente Island (Fig. 2.3). A second Y-shaped ridge extends from Santa Cruz Island and splits into two ridges extending to Santa Catalina and San Clemente Islands, respectively. The three deep basins of the SCB south of Santa Cruz Island, west of Santa Catalina Island and west of San Clemente Island are all deeper than the Santa Barbara Basin to the north of Santa Cruz, Santa

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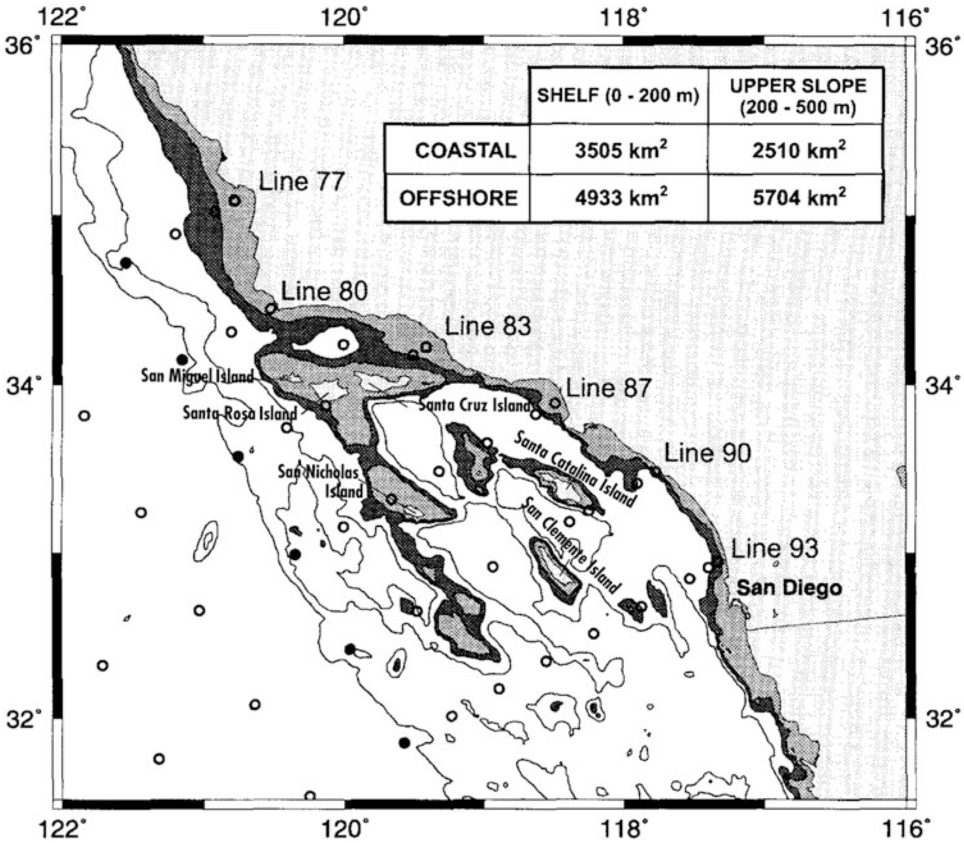
[1] Another definition places the western boundary of the Southern California Bight at the base of the Patton Escarpment offshore of the Santa Rosa Ridge (about at the 2000 m isobath in Fig. 2.4), which is quite a lot further offshore.



	SHELF (0 - 200 m)	UPPER SLOPE (200 - 500 m)
COASTAL	3505 km^2	2510 km^2
OFFSHORE	4933 km^2	5704 km^2

Fig. 2.4 Bathymetry off southern California illustrating how the islands and Santa Rosa Ridge greatly extends the area of shelf habitat in the offshore areas. *Gray area* are 0–200 m, *black areas* are 200–500 m, deeper contours are 1,000 and 2,000 m (From [403])

Rosa and San Miguel Islands. In the Southern California Bight, water at temperatures between 9–5 °C is generally deeper than 100 m and, based on physical characteristics, shows stronger southern affinities [245]. The dominance of Equatorial Pacific water at depths of 200–300 m is likely due to the opening of the deep basins at their southern margins [245] (Figs. 2.3 and 2.4).

The islands of the Southern California Bight and Santa Rosa Ridge greatly extend the area of shelf depths into the offshore (Fig. 2.4). The area in shelf depths (0–200 m) offshore (4,933 km^2) is actually considerably greater than it is along the coast (3,505 km^2) [403]. There is also more upper slope depth (200–500 m) habitat offshore (5,704 km^2) than along the coast (2,510 km^2) [403]. This has considerable implications for the distribution and abundance of near shore rocky habitat fishes, and also for invertebrates.

2.3 Water Sources and Properties

The California Current originates from the southward flowing branch of the North Pacific Current. The North Pacific Current is a broad, surface-intensified flow arising from the Kuroshio Extension [125], an offshore component of the Kuroshio Current that is the dominant flow of the western Pacific. As the North Pacific Current approaches the west coast of North America, it bifurcates into northward and southward flows that are associated with the sub-polar and sub-tropical gyres respectively [125] (Fig. 2.5). Variability in the California Current System is strongly linked to basin-scale variability of the North Pacific Current and its bifurcation at the coast. Chelton and Davis (1982) [110] discovered an oscillation of sea-level height that is in phase along the North American coast from Baja California to the Aleutian Islands, and suggested that it represents an anti-correlated mode reflecting the relative strengths of the sub-polar and sub-tropical branches of the North Pacific Current ([110] cited in [125]). Cummins and Freeland (2007) [125] discussed this "bifurcation mode" in terms of constant flow of the North Pacific Current and compensatory flows in the relative strengths of its sub-polar and sub-tropical components. In addition to the bifurcation mode, earlier work by Freeland (2006) found in-phase variability between the sub-polar and sub-tropical modes, which they termed a "breathing mode" ([174] cited in [125]). Most of the variance (67 %) in the modeled stream function at two reference points (x_{SP} = 210°E,[2] 55°N and x_{ST} = 210°E, 35°N, Fig. 2.5) is explained by this breathing mode [125]. The remainder (33 %) is explained by the bifurcation mode with invariant North Pacific Current [125]. Time series from numerical

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[2] 210°E is the same as 150°W.

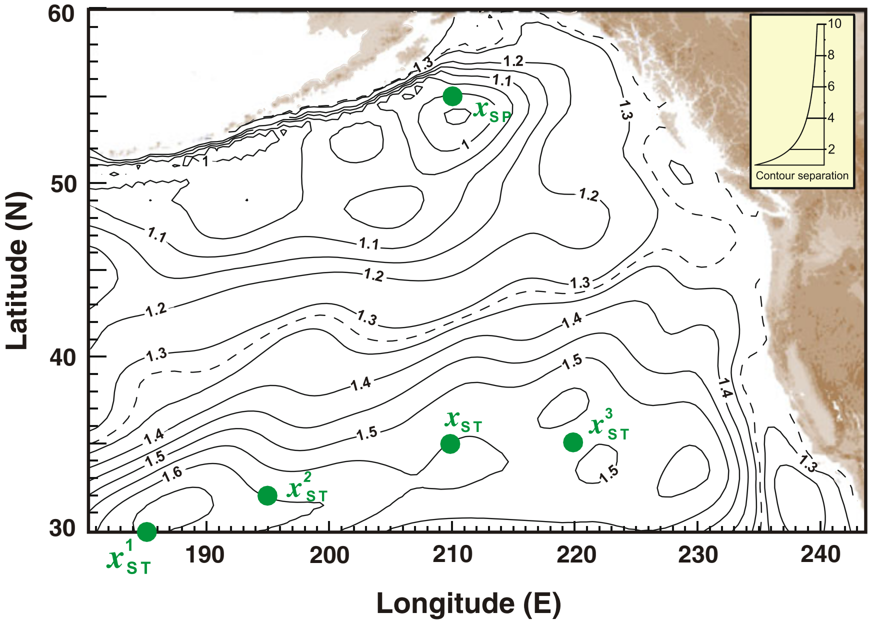

Fig. 2.5 Time-averaged dynamic height (m) contoured from the Argo array of floats (October 2002 – September 2006). *Dashed line* indicates a streamline separating the time-averaged sub-polar and sub-tropical gyres (From [125])

simulations of wind-forced variability over 50 years were consistent with shorter time series derived from the Argo array (see Glossary), both in terms of anti-correlated and correlated periods, and in the proportion of variance that could be attributed to bifurcation and breathing modes of the North Pacific Current. In addition there was a strong correlation between the transport stream function derived from numerical simulations and the measured variation in sea surface height across the North Pacific Current. Cummins and Freeland (2007) [125] concluded that there is compelling evidence that the variability in the strength of the North Pacific Current is wind-forced and that a climate model driven by Ekman pumping can describe variability in sea surface height at large scales in the northeastern Pacific.

The sub-tropical gyre contains the southward flowing California Current in the eastern Pacific. The California Current leaves the coast at 40°N, approximately at Cape Mendocino (Fig. 2.5). Further south, the California Current is far offshore (160–530 km, see Fig. 2.9) and the Davidson Current forms a seasonally recirculating northward flow near the coast. There appears to be no clear boundary between the western side of the California Current and the sub-tropical gyre [125].

There are four basic sources of water in the California Current System that can be distinguished on the basis of temperature, salinity, oxygen concentration and nutrient levels [245, 465, 466, 543] (Table 2.1). Pacific Subarctic Water, originating in the North Pacific Current, brings relatively cool, low salinity, high oxygen, high phosphate water southward. The North Pacific Current, also known as the Subarctic Current or the West Wind Drift separates the Subarctic and Subtropical gyres of the North Pacific [546]. The North Pacific Current is both the northern edge of the anticyclonic subtropical circulation and the southern edge of the cyclonic subarctic circulation. Subarctic Water in the North Pacific Current enters the California Current at around 42–48°N [449, 546] and leaves the California Current near 25°N [466] (120 miles north of the tip of Baja California), to flow into the Subtropical Frontal Zone [546]. The properties of Pacific Subarctic Water contrast with the Eastern North Pacific Central Water [449, 544] from the west, which are relatively warm, salty, and low in dissolved oxygen and nutrients. The Pacific Subarctic and Eastern North Pacific Central Water mix in the upper 200 m surface layers as the California Current flows southward [245]. The third water source, Equatorial Pacific Water [449, 544] entering the southern California region from the south, is also relatively warm and salty, but is distinguished by lower oxygen concentrations and higher nutrients, and moves below the thermocline in the deeper California Undercurrent (200–500 m). The Pacific Subarctic and Equatorial Pacific waters mix at depth to create the cold deep water [245] that comprises the fourth water source, Coastal Upwelled Water. Sverdrup (1937) reported that the upwelled waters just north of Point Conception originated from no deeper than 200 m [541]. Seasonal wind-driven coastal upwelling brings this relatively cold, salty, nutrient rich, low oxygen but more acidic Coastal Upwelled Water to the surface within 50 km of the coast [339]. Water mass property extremes can be used to identify source waters and infer flow paths by the degree of mixing of water masses ([114, 543]).

Water masses off southern California are quite complex with combinations of properties that indicate both mixing and advection occurring along isopycnals (surfaces of constant density) [245]. Sigma-t (σ_t) surfaces indicate certain features in the California Current System. The California Undercurrent is associated with a subsurface maximum in

Table 2.1 Characteristics of the four principal water masses in the California Current System

	Temperature	Salinity	Oxygen	Nutrients
Surface water masses (0–200 m)				
Pacific Subarctic	L	L	H	H
North Pacific Central	H	H	L	L
Coastal upwelled	L	H	L	H
Subsurface water masses (200–500)				
Equatorial Pacific	H	H	L	H

L low, *H* high
From [339] and [506]

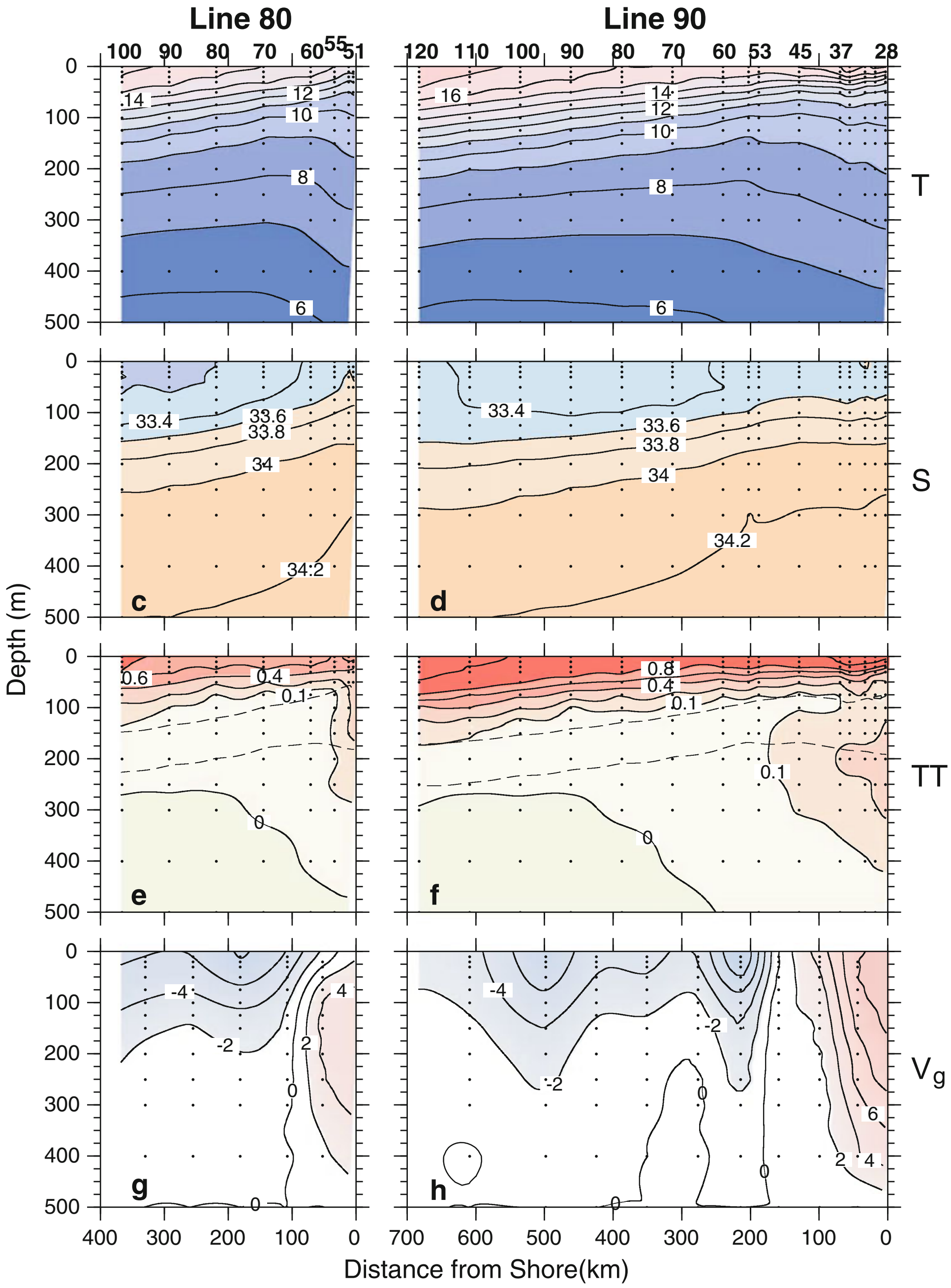

Fig. 2.6 Mean properties for CalCOFI lines 80 (*left*) and 90 (*right*) during 1950–1999. (**a** and **b**) Temperature (°C); (**c** and **d**) salinity; (**e** and **f**) spiciness (kg m^{-3}); and (**g** and **h**) geostrophic velocity (cm s^{-1}). The mean depth of the $\sigma_t = 25.8$ and 26.4 kg m^{-3} isopycnal surfaces on lines 80 and 90 are shown by *dotted lines* on the spiciness section (From [69])

spiciness (π) that contains the 26.4 σ_t surface [69] (Fig. 2.6). The effect of the California Undercurrent is seen in the doming of the 26.4 isopycnal at 50–200 km offshore [69] (Fig. 2.7). Temperature maps on isopycnals (e.g. $\sigma_t = 26.6$ between 200–300 m depths) suggest that water in the Bight is coming from the west while oxygen concentrations sug-

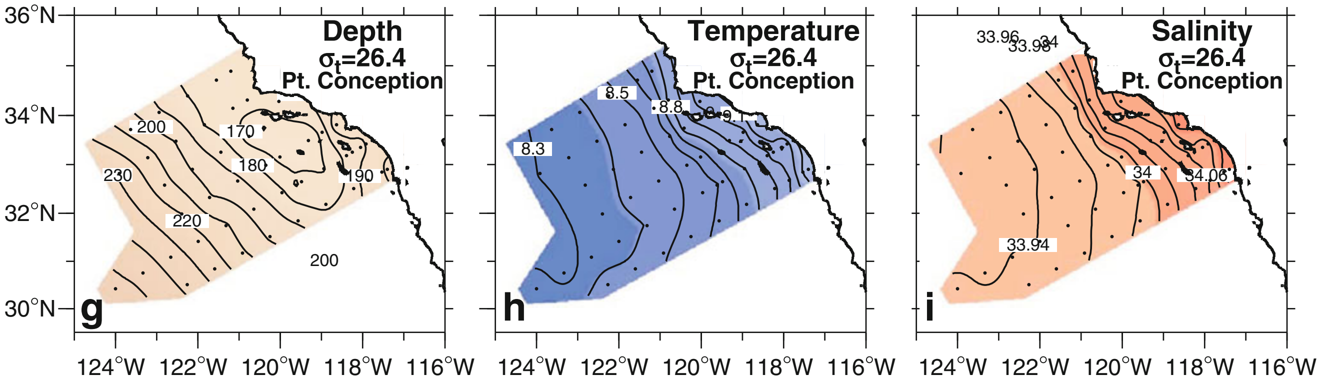

Fig. 2.7 Mean property maps of isopycnal depth (m), temperature (°C) and salinity for 1950–1999 on the $\sigma_t = 26.4$ isopycnal surface (From [69])

gest a southern origin. Jackson (1986) [245] interpreted geostrophic flow maps to indicate that water in the Southern California Bight originates from the California Current but that it reaches the Bight after reversing direction south of the Mexican border. This could produce the observed properties by a combination of advection and mixing along density surfaces. Lynn and Simpson (1987) [339] label the poleward surface flow the Inshore Countercurrent and the equatorward surface flow the California Current (but see the next section).

2.4 Currents

The flows in the California Current System can be grouped into geostrophically resolved currents, flows modified by bathymetry [245], wind-driven Ekman flows, and the ubiquitous eddy-like motions that are not resolved by geostrophic calculations based on the CalCOFI stations [465, 494, 495]. Both the strength of geostrophic flows and the number of eddies vary with the seasons. The magnitudes of the geostrophic flows are on the order of 5 cm s^{-1} but coastal currents resolved by finer station spacing can be 10 cm s^{-1}. In nearshore areas, currents cannot be measured geostrophically, and there are both cross-shore and along-shore flows. The intensity of along-shore flows is greatest at about 60 m depths in the Southern California Bight. Very nearshore flows may be modified by kelp beds, slowing currents by as much as a third [245, 248].

2.4.1 Geostrophically Mapped Currents

Large scale advective flow, derived from geostrophic calculations, is important to production in the California Current System (Sect. 2.4.2), is used in spawning habitat models (Sect. 4.2.2.3), and is fundamental to our understanding of ichthyoplankton advection and recruitment. The California Current originates from the eastward-flowing North Pacific Current. The eastward flow bifurcates approximately at Cape Mendocino (40.4°N) (but this varies inter-annually), flowing southward toward southern California, and northward along the Oregon and Washington coasts [125] (Sect. 2.3). Off southern California, an intersected bathymetric ridge, called the Santa Rosa Ridge, extends south-east along the angle of the central California coast from Santa Rosa Island in the Channel Islands (Fig. 2.3). The California Current is found to the west of the Santa Rosa Ridge, which includes San Nicolas Island and Cortez Bank (Sect. 2.3).

The width of the California Current ranges between 500 to 900 km, depending on location, between San Francisco and mid Baja, California ([97, 358, 539, 590] cited by [33]). The California Current is located in the region of negative wind stress curl and downwelling, approximately 100 km offshore, whereas the upwelling region is nearshore and associated with positive wind stress curl. In the surface layer (i.e. shallower than the Ekman depth), "offshore Ekman velocity is comparable in magnitude and perpendicular to the alongshore geostrophic flow" [33]. The combination of substantial geostrophic flow, Ekman transport, and mesoscale eddy activity all interact to rapidly spread near-surface coastal waters offshore and alongshore. The relatively large offshore component of the flow interacts strongly with the energetic eddy field and coastal upwelling, ensuring exchanges between the inshore upwelling zone and the California Current [33]. This has considerable implications for the primary and secondary production, assemblage structure of the pelagic biota, and fish recruitment (see Sects. 2.4.2, 3.3, and 6.1.1.8).

The California Current can be identified based on its property distributions, its flow speed relative to the ocean interior circulation, or by certain dynamical properties. Auad et al. (2011) [33] used the salinity field, the relative flow velocities, and an analysis of stability to identify the California Current, observing that any of the definitions might be considered appropriate, depending upon the application (Fig. 2.8). Their analyses were based on the multi-year (2004–2010) Argo array dataset, supplemented by high resolution XBT tran-

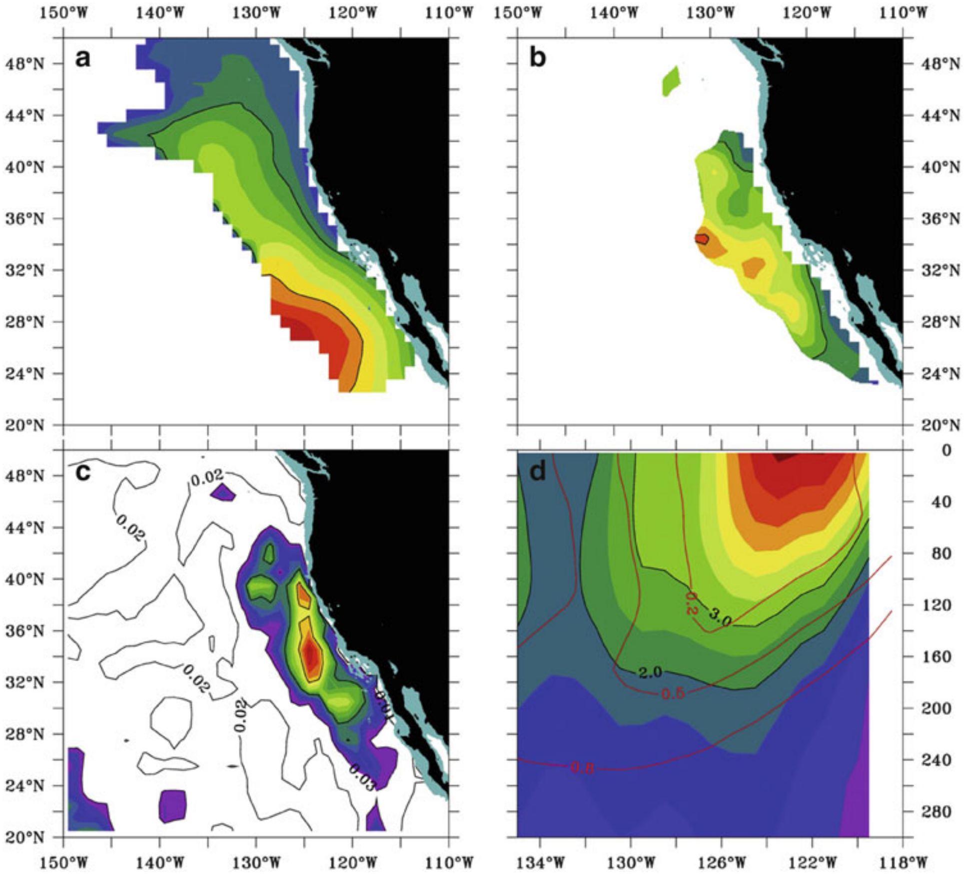

Fig. 2.8 (**a**) Estimation of the California Current annual mean boundaries from the salinity field. Color interval = 20 dbar and dark contours are 100, 200 dbar. (**b**) Same as (a) except for California Current boundaries from geostrophic current speed. (**c**) Same as (a) except California Current boundaries from comparison of local growth rates of baroclinic waves. Growth rates larger than 0.03/day are shown by color shading, with contour lines every 0.01/day. (**d**) Vertical section along 32.5°N, versus longitude and pressure. *Color shading* indicates the geostrophic current speed $(u^2 + v^2)^{0.5}$ at intervals of 0.5 cm/s, with *black contour lines* showing the 2 and 3 cm/s levels. *Red contour lines* show the salinity difference with respect to the salinity minimum at this latitude (From [33])

sects from Honolulu to San Francisco (1999–2010) and Los Angeles, and CTD profiles from CalCOFI line 90. They wrote that "The California Current by any definition is broad compared to . . . a western boundary current. It is a shallow, eddy-enhanced southward flow, with consistent descriptions provided by its property distributions, its velocity relative to the ocean interior, and its tendency to grow baroclinic waves[3]" [33].

The low salinity core of the California Current is derived from the excess precipitation over evaporation in the northern regions where the current originates (Sect. 2.3). Although the low salinity anomaly is reduced as the current flows southward, it remains a distinguishing feature [33]. Auad et al. (2011) [33] defined the California Current boundary in terms of the salinity minimum as $S(x,y,z) - S_{min}(y) = 0.5$ psu when sea surface salinity is within 0.5 of S_{min} (Fig. 2.8a). The second definition of the California Current was based on the relative mean velocity of the current compared to velocities in the interior of the subtropical gyre. Large-scale southward surface velocity in the gyre interior derived from the Argo data is 1–2 cm s^{-1}. Auad et al. (2011) [33] used a criterion of 3 cm s^{-1} mean southward surface velocity to define the California Current. The velocity criterion defines a smaller area for the California Current compared to the salinity criterion, and shows narrower current width both to the north and south (compare Fig. 2.8a and b). The comparison shows that the California Current carries a distinctive water property signature, but that its flow is not much faster than flows in the gyre interior [33]. The third definition was based on a stability analysis of the mean flow of the California Current. The rationale for this analysis is based on fact that regions with the largest vertical displacement of isopycnals will tend to have larger geostrophic speeds and be more unstable in the baroclinic sense. A growth rate of baroclinic waves > 0.03 day^{-1} can be used as a criterion to define the spatial extent of the California Current (Fig. 2.8 c). Finally, the California Current is relatively shallow, compared for example to the Kuroshio. There is little in either the salinity distribution or the geostrophic shear below 200–300 db to distinguish the California Current from the ocean interior (Fig. 2.8d).

The core of the mean flow is located near CalCOFI station 80 on line 83.3 (Fig. 2.9) which when the flow is averaged appears to be a broad, slow flow [69]. The original view of the California Current as a broad, weak, equatorward flow [207, 589] has been modified by more recent work. It is now recognized that the California Current can manifest as narrow meandering jets with core velocities of 50–80 cm s^{-1}

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[3] Estimated from the analysis of stability.

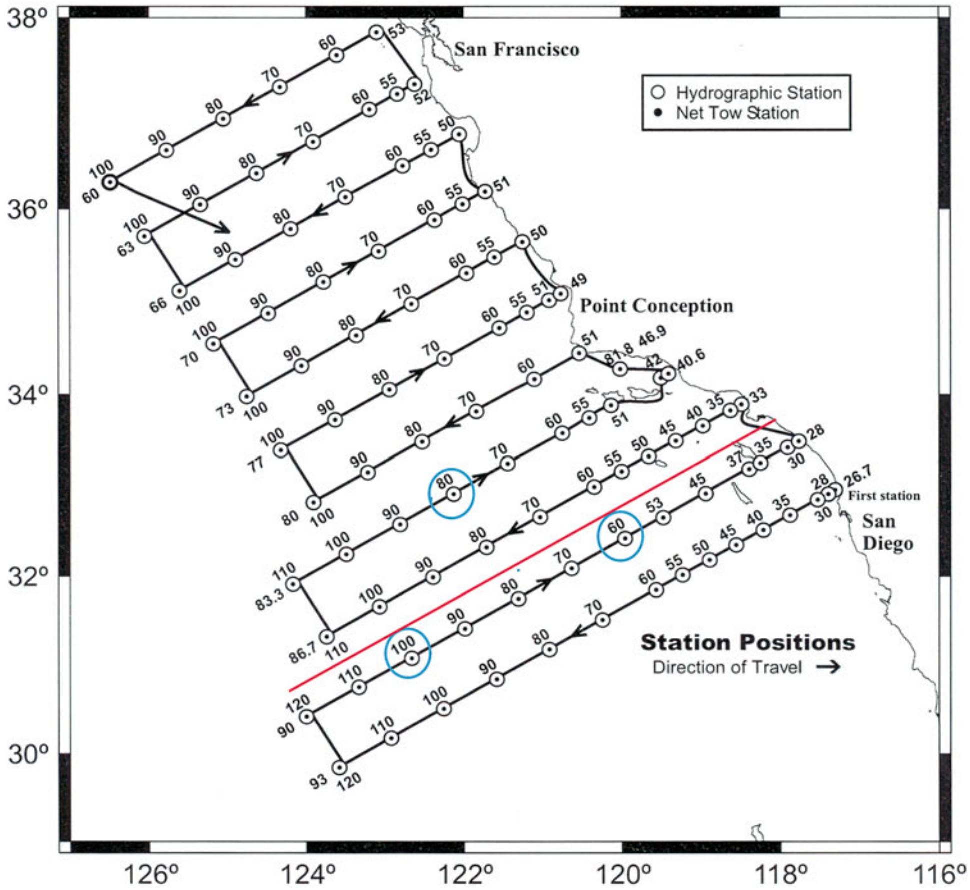

Fig. 2.9 Core of the California current is marked with *blue circles* [69], but the current has also been described as consisting of "multiple meandering equatorward jets" [337] based on work by [207, 590] and [115]. From long-term mean patterns the highest velocity core is centered between stations 53 and 90 on line 90 [336]. Distance from shore along line 90 to station 120 (*red line*) is 683 km and the distance to station 100 from shore is 535 km (From [337])

[50,109,277,278,540] embedded in a rich eddy field [78,261, 538]. These core velocities are much higher than the mean geostrophic velocities (5–10 cm s^{-1}) [33, 465, 494, 495]. On line 90 two cores are apparent; nearer shore at station 60, and offshore at station 100 [69]. The double velocity core may be a manifestation of offshore propagation of energy from a springtime equatorward coastal jet. It is common to think that the California Current is closer to shore than it actually is off southern California. From long-term mean patterns the highest velocity core is centered between CalCOFI stations 53 and 90 on line 90 [336] (Fig. 2.9). Distance from shore along line 90 to station 90 is 465 km (251 nautical miles), and the mid-point between station 90 and station 53 (station 70) is 325 km (or 175 nautical miles) offshore.

The flow of the California Current varies seasonally in intensity with strongest flow in the summer. The core of the California Current lies ~250 km offshore from San Francisco compared to ~325 km offshore on line 90 off southern California. The distance from shore to its core varies from year to year, as well as seasonally. The mean position of the core is closest to shore in spring and summer [69].

The Southern California Bight is a relatively quiescent part of the California Current System where the change in the angle of the coastline causes reduction in wind stress in comparison to the central California coast. Although the flow in the SCB is generally poleward, equatorward flow is observed at the coast during the summer (June–August). The California Current sweeps towards the east at ~32°N (the latitude of Enseñada, Mexico) forming the southern edge of a permanent cyclonic gyre called the Southern California Eddy [114]. Tanner Bank, rising up to 20 m on the Santa Rosa Ridge, separates the offshore and inshore flows of the eddy [339]. The eastward, onshore-directed flow is associated with mesoscale eddies and a strong east-west frontal zone referred to as the Ensenada Front [114] (see Sect. 2.6.2.2). As the flow approaches the coast, it splits into two branches; one flowing northward along the coast in the Southern California Bight and the other flowing southward along the coast of northern Baja California [114]. In late fall (October–November), the nearshore (out to ~150 km) undergoes a seasonal transition to conditions where surface (upper 300 m) flow becomes poleward. This narrow, coastal poleward flow which persists through the winter is called the Inshore Countercurrent in the SCB or the Davidson Current north of Point Conception [339]. The Inshore Countercurrent is the surface manifestation of the California Undercurrent, and Todd et al. (2011) [560] considered that there was little justification for two names because there is no vertical separation in the velocity section.

The poleward flow at depth known as the California Undercurrent has been known for decades from studies based on the CalCOFI survey data ([77, 339] cited in [560]). The classic pattern derived from CalCOFI CTD profiles, which mostly extend to 500 m depth, shows a nearshore California Undercurrent, with highest velocities at 100–300 m, and seasonally reversing surface flows near the coast. To the south of Point Conception the California Undercurrent flows inshore of the Santa Rosa Ridge, but gaps in the ridge provide exit points for the Undercurrent [340]. Glider [130] and ADCP measurements [179] show mean subsurface poleward flow within 100 km of the coast and a second core at 200–250 km offshore. The second core is evident at 500 m depths offshore from the Santa Rosa Ridge along CalCOFI lines 90, 86.7 and and 83.3, but there is no second core on line 80 off Point Conception (Fig. 2.10) [560]. The speed, transport, and sometimes even the direction of this current cannot be determined by geostrophic calculations referenced to 500 m [179]. The flow of the deep offshore current is strongest in the fall [179].

Vertical profiles of temperature and salinity are collected on CalCOFI and fisheries surveys with a CTD (Sect. 3.1.1). Additional profiles and the sections derived from them can now be obtained from gliders operating on CalCOFI lines [480]. Field comparisons between Spray gliders and the towed undulating SeaSoar vehicle showed that the Spray gliders provide accurate vertical profiles. However, the slow movement of gliders along transects results in the projection of high frequency temporal variability onto the spatial structure mapped with hydrographic sections (compare Fig. 2.11a and b). The projection is caused by both Doppler smearing due to finite speed, and to aliasing due to discrete sampling [480]. These artifacts are evident in properties measured on depth surfaces or in sections showing isopycnal depths (Fig. 2.11). The high frequency variability is likely caused by internal waves [480]. The projection of high frequency variability is not visible for properties measured on isopycnal (constant density) surfaces because internal wave variability is filtered out [480].

Geostrophic shear is calculated from density gradients on constant depth. It is valid to calculate geostrophic shear from glider data only at scales larger than 30 km [480, 560]. This is not a problem because the dynamics of geostrophic balance are also valid only at larger spatial scales. The same problem occurs in traditional ship surveys where the distances between stations are large (40–70 km in the case of CalCOFI) relative to the buoyancy period, but the high frequency variability is not visible in ship-based sections because the vertical profiles are much further apart [480]. On the other hand, temperature and salinity (or spiciness) can be examined on isopycnal (constant density) surfaces without any problem from projected high frequency variability. Thus, for gliders isobaric properties, like geostrophic shears, can only be calculated over scales larger than 30 km, but isopycnal properties, like spice, can be calculated at scales as small as the gliders can measure.

Current profile data are routinely collected on CalCOFI surveys using the ADCP. These data have been used in many physical oceanographic studies of the California Current System including geostrophic flow in the California Current [115], inter-annual variability of mass, heat, salt and nutrients [68], the spring transition [338], seasonal variability of the California Undercurrent [179], and circulation in the Ensenada Front [114], among others. ADCP data have also been used to examine the retention and advection of rockfish larvae [547]. It is nevertheless true, that today the ADCP data collected on CalCOFI cruises are archived, but generally unprocessed.

It is interesting to compare geostrophic flows based on gliders and a numerical simulation published in 2011 (Fig. 2.10) with geostrophic flows estimated from shipboard CTD profiles published in 1982 (Fig. 2.35). The improvement in resolution is remarkable. Todd et al. (2011) [560] combined measurements from gliders on three CalCOFI lines with numerical simulations from a global circulation model. By combining long-term, high resolution measurements from a fleet of gliders with the modeling they were able to characterize the northward flows of a deep offshore branch of the California Undercurrent. They were also able to demonstrate that this current propagates westward in a manner consistent with Rossby wave dynamics rather than mesoscale eddies. Todd et al. (2011) [560] found that the mean glider-based geostrophic flows (which are referenced to the mean velocity profile rather than a depth of no motion) agree well with the mean flows from a decade of shipboard ADCP measurements [179], "which suggests that the glider surveys now provide sufficient data to calculate stable mean fields" [560]. The conclusion to be drawn from these studies is that gliders operating on CalCOFI lines provide highly spatially resolved and much more frequent measurements of temperature, salinity and geostrophic flow, and these data are an extremely valuable complement to the CalCOFI survey data.

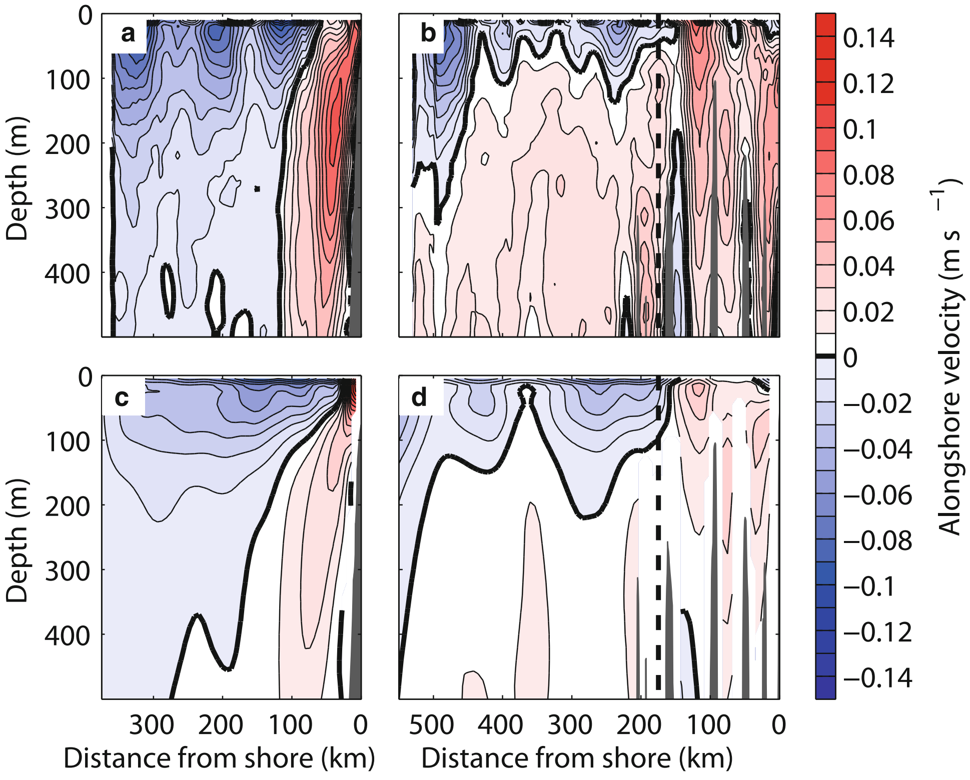

Fig. 2.10 (**a** and **b**) Mean alongshore currents from all glider observations and (**c** and **d**) the numerical simulation along CalCOFI Line 80.0 (**a** and **c**) and CalCOFI Line 90.0 (**b** and **d**). Positive velocities are poleward. The *dashed line* at 175 km along Line 90.0 (**b** and **d**) denotes the location of the Santa Rosa Ridge. *Dark gray shading* represents the bathymetry along the survey lines. The mean in (**a**) and (**b**) is over the period October 2006 to November 2009 while the mean in (**c**) and (**d**) is over the period January 2007 to July 2009 (From [560])

2.4.2 Importance of Advection Versus Upwelling to Zooplankton Production

It was well known that cooler temperatures in the California Current System were generally associated with higher zooplankton biomass [466], but cool temperatures are associated both with advection of Pacific subarctic water in the California Current and coastal upwelling (Table 2.1), and the driving mechanisms had not been distinguished. The importance of advection to zooplankton variability in the California Current was first suggested by Wickett (1967) ([583] cited by Chelton (1981) [106]). Wickett (1967) found a positive correlation between wind forcing in the Alaska Gyre and zooplankton volume off California one year later. He suggested that nutrients from the Alaska Gyre are advected southward by the California Current, affecting the response of zooplankton off southern California. Later, Colebrook (1977) [122] studied the inter-annual fluctuations of 17 functional groups of zooplankton from 1955–1959 and found considerable coherence both between different taxonomic groups and between different regions across the California Current System, as one might predict for an advective regime. However, Roessler and Chelton (1987) [477]commented that seasonal trends might have biased Colebrook's (1977) results.

Bernal (1981) [60] reviewed a 21-year time series of zooplankton displacement volume from CalCOFI surveys and compared the zooplankton volume anomalies to indices of southward advection and wind-driven coastal upwelling. He concluded that large-scale anomalies of zooplankton volume were correlated with transport from the north, but were uncorrelated with upwelling [59, 60]. On seasonal scales, reduction of zooplankton displacement volume was correlated both with lower southward advection (minimum in December), and with relaxation in upwelling (lowest upwelling in January) [60]. Bernal (1981) [60] argued that the spatial pattern of zooplankton displacement volume, although patchy, resembles the spatial pattern of nitrate and chlorophyll-a. Higher primary production (indexed by chlorophyll) and higher nitrate are associated with the low salinity signal of the California Current, suggesting that the spatial pattern of zooplankton is affected by the large scale advective flow.

Time series of zooplankton displacement volume showed that the California Current System exhibits low frequency variability at much longer time scales than those controlling the production processes of phytoplankton (hours to days) or zooplankton (a few months) (Fig. 2.12) [59, 60]. When the seasonal signal is removed, zooplankton volume shows inter-annual variability that persists for 1–3 years [106]. Chelton [106, 110] independently verified Bernal's findings regarding the low frequency variability in advection by using tide gauge and steric height data. Chelton also showed that advection was correlated with zooplankton volume anomalies.

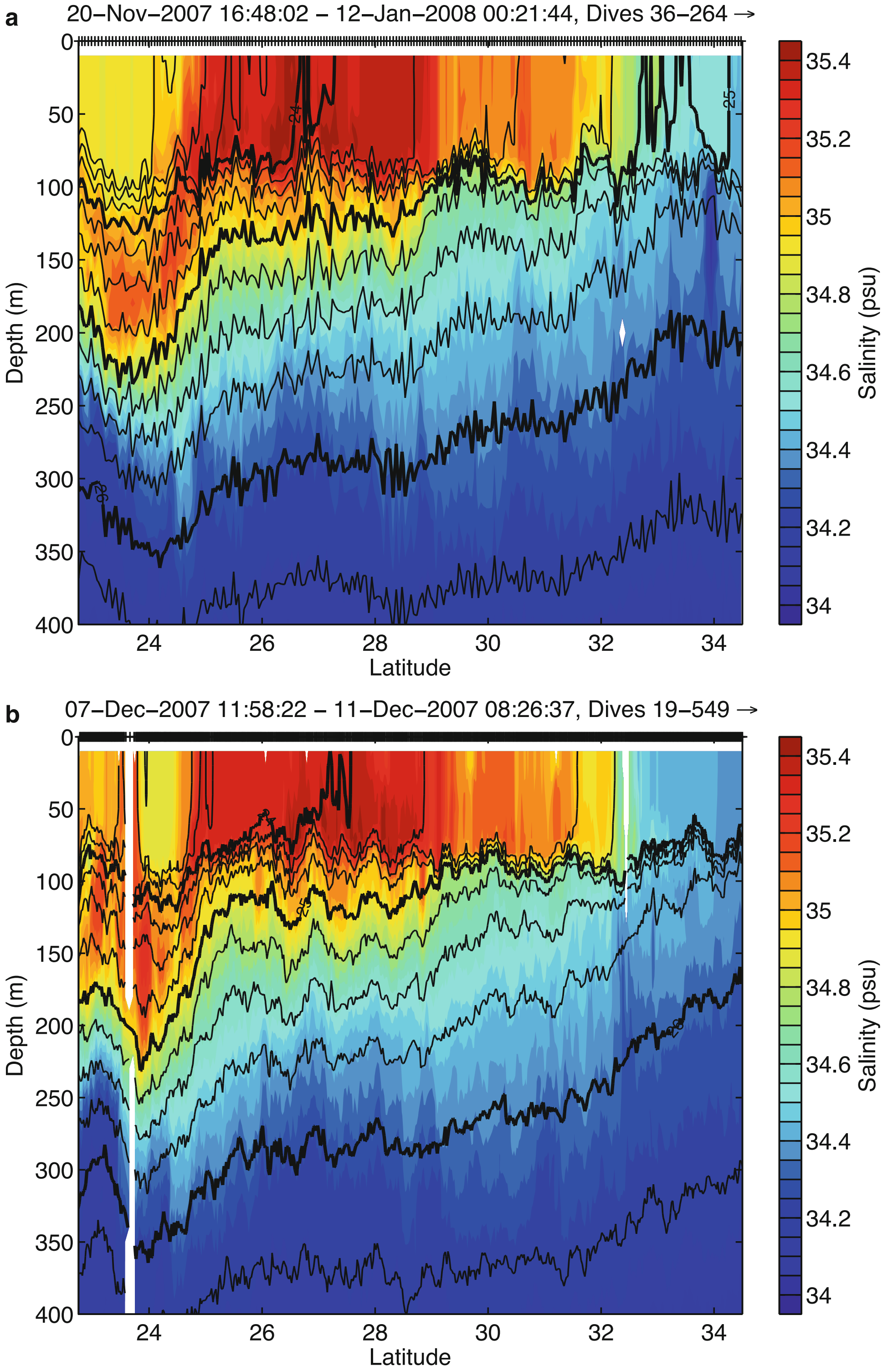

Fig. 2.11 Sections of salinity and potential density plotted as a function of depth and latitude for (**a**) Spray and (**b**) tow of SeaSoar. Salinity is shown by *filled color contours*. Isopycnals (*black*) have a contour interval of 0.25 kg m^{-3} with heavy 24, 25, and 26 kg m^{-3} contours. *Tick marks* along the upper border of each section mark the locations of profiles. Time intervals, profile numbers, and direction of travel are indicated above each section. Note the similarity of large-scale structure and the enhanced small-scale variability in isopycnal depth in the Spray section (**a**) (From [480])

The California Current System is about an order of magnitude wider (up to 500–800 km) than the zone of wind-driven coastal upwelling (which is approximately one baroclinic Rossby radius of deformation, R_ϕ, or about 50 km wide). However, the zone of higher zooplankton displacement volume is several hundred kilometers wide, and well offshore of R_ϕ and the upwelling zone [60]. On CalCOFI lines 90 and 60 (see Fig. 1.6), zooplankton displacement volume peaks at about 180 km offshore, declining to low oceanic levels around 500 km offshore. Offshore from San Diego, the low salinity California Current is clearly evident in the upper 200 m at 126 °W (about 500 km offshore on

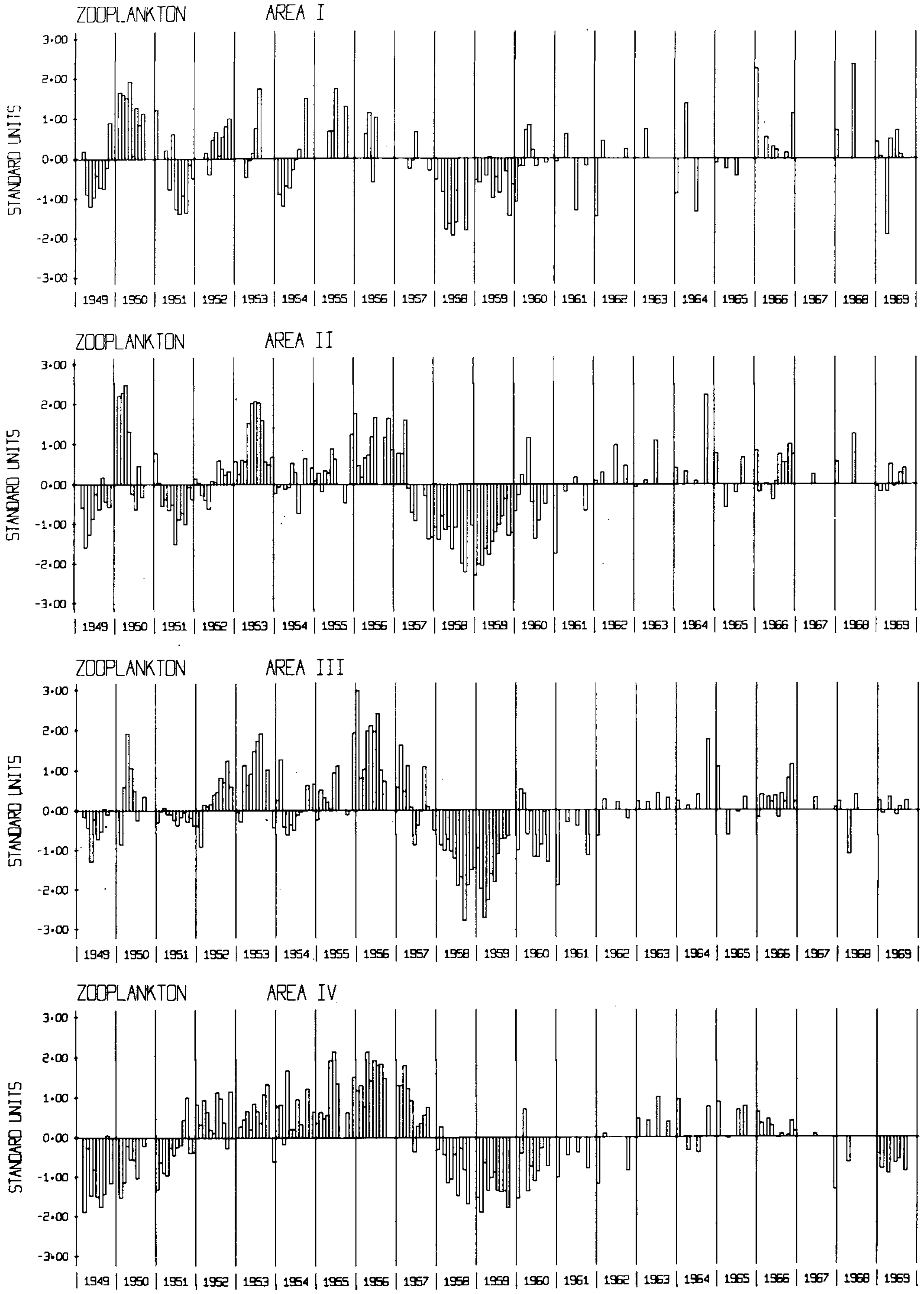

Fig. 2.12 Time series of log-transformed mean zooplankton displacement volume data for regions of the California Current System defined on the basis of zooplankton assemblages. See Sect. 2.1 and Fig. 2.1b (From [60])

line 80), associated with higher nitrate (Fig. 2.13), cooler temperatures and higher oxygen. Further west at 128 °W and 1,270 km offshore, the environment is totally different, with a well developed halocline and high salinity, oligotrophic waters indicating the North Pacific Central Water mass (Table 2.1) [59, 60]. In keeping with the physical structure, the eastern Pacific at sub-tropical latitudes contains at least two oceanic plankton communities, one associated with the California Current System, and the other associated with the North Pacific Central Water mass [59, 60] (see Sect. 2.1).

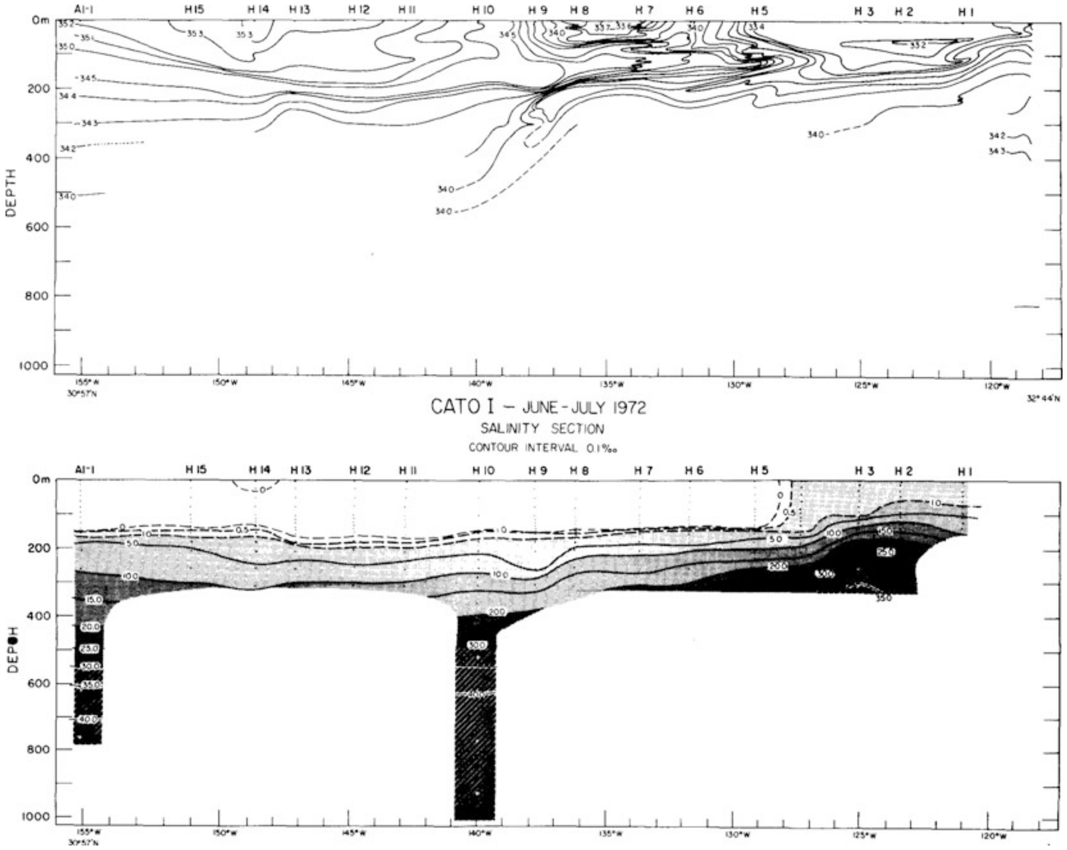

Fig. 2.13 Section of salinity contoured at 0.1 ppt (upper panel) and nitrate contoured at 5 μg-atoms L^{-1} (*lower panel*) from 74 km off San Diego (32°44'N 120°W, *right-hand side*) to a point in the Central Pacific Gyre (30°57'N 155°W, *left-hand side*). Station H5 (labeled on the *top axis*) is the boundary between the California Current and the oligotrophic central gyre waters, and is 800 km offshore (From [59])

Bernal used lagged cross-correlations between zooplankton volume anomalies and either Bakun's upwelling index [38] or transport from the north across CalCOFI line 80 (off Point Conception) to infer the forcing driving fluctuations in zooplankton [59, 60]. Cross-correlations between upwelling and zooplankton anomalies were not significant (Fig. 2.14). This lack of correlation was surprising, and could have been due to failure of the upwelling index to describe upwelling intensity. However, Bernal asserts that a more likely explanation is that "upwelling intensity has little to do with large-scale variations in secondary productivity[4] in the main body of the California Current" [59, 60]. Bernal also made the case that inshore stations do not show any local peak in zooplankton volume, and that the broader regional pattern of zooplankton volume reflected the large-scale pattern for California Current System.

There is considerable inter-annual variability in the advective transport from the north by the California Current [60]. Bernal (1981) calculated the average transport across line 80 between 0–200 m depths for January and July, between 1950 and 1978 and found significant cross-correlations between advective transport and zooplankton volume anomalies. In areas downstream of line 80, cross-correlations were significant and highest at lags of 0–7 months in and offshore of the Southern California Bight (Area II) or 0–4 months off northern Baja California (Area III) [60] (Figs. 2.15 and 2.1b). Bernal concluded that large-scale advective transport drives the variability in zooplankton "biomass" in the California Current System off central and southern California, and that upwelling is relatively unimportant.

Chelton [106] revisited the issues raised by Bernal, using a longer time series (30 years instead of 21 years) and different methods. He compared the climatological seasonal cycle of mean log-transformed zooplankton volumes from the areas defined by Bernal (1979) (see Fig. 2.1b) [58], with mean equatorward along-shore wind stress representative of the same areas. Stronger equatorward along-shore wind stress was used as an index of stronger upwelling. Chelton pointed out a correlation between upwelling favorable winds and

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[4] See the units for productivity as opposed to production in the Glossary. Units for zooplankton displacement volume in CalCOFI data are mL 1000 m^{-3} which is a not a rate. What Bernal was referring to was a proxy for zooplankton production, not zooplankton productivity (which is a rate).

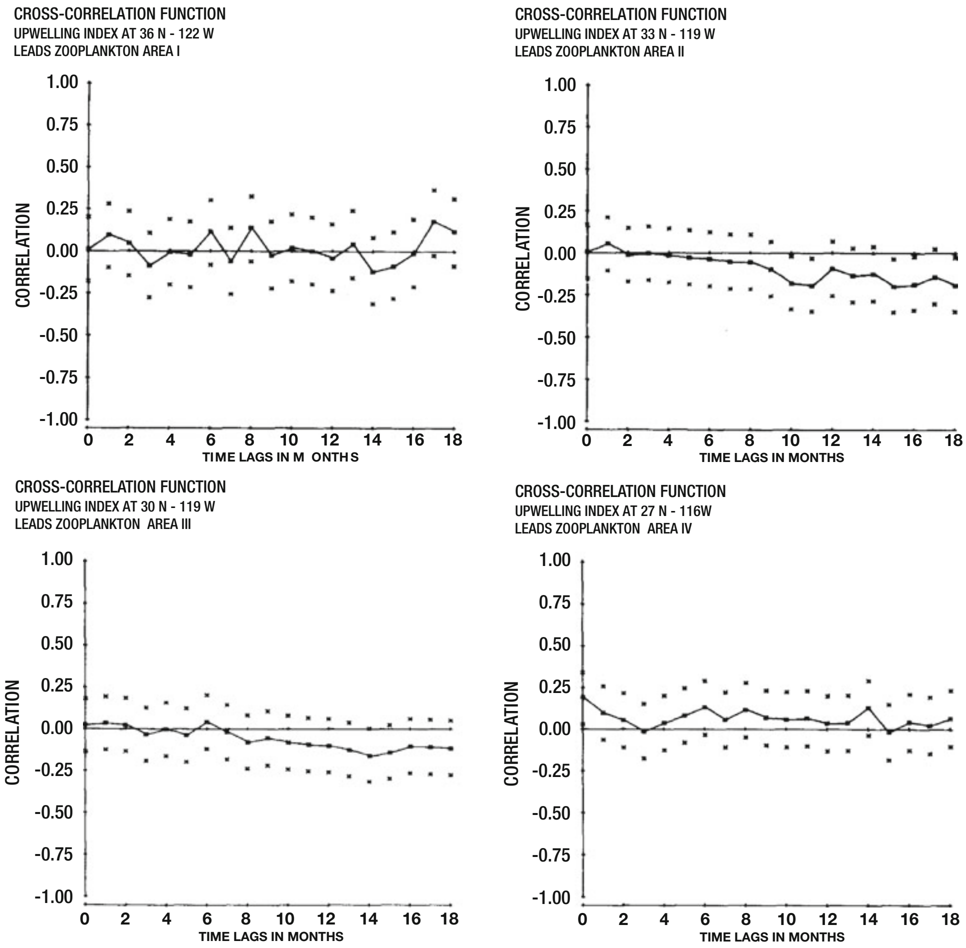

Fig. 2.14 Cross-correlation between zooplankton displacement volume and the index of wind-driven upwelling at four latitudes (27–36°N) along the California coast. *Crosses* represent the 95 % confidence limits (From [60])

zooplankton volumes a month later in the area off northern Baja California (Area III, Fig. 2.16), but went on to show that there was no correlation between the upwelling favorable winds and zooplankton volume in any of the other areas (in Fig. 2.1b). From this he inferred that "some other process is at least partially responsible for controlling the zooplankton variability" [106]. He then performed a cross correlation analysis between the de-seasonalized mean zooplankton volume in each of the four areas and an index of upwelling. Chelton et al. (1981) [106] correlated zooplankton volume with the along-shore equatorward wind stress (to index upwelling), obtained by removing the seasonal trend from the geostrophically computed winds produced by the Fleet Numerical Oceanography Center [106] (Fig. 2.17), whereas Bernal (1979) [58] correlated zooplankton with the Bakun's upwelling index [38] (Fig. 2.14). Like Bernal, Chelton [106] concluded that the large-scale relationship between zooplankton volume and upwelling was, at best, very weak.

Chelton (1981) [106] used eigenanalysis to separate the spatial and temporal scales of variability and infer the forcing mechanisms for the temporal variability of zooplankton volume at large scales in the California Current System. The dominant spatial EOF of water temperatures at 50 m explained about half of the variability at the CalCOFI stations that he analyzed, between San Francisco and southern Baja California.[5] The spatial pattern of this principal EOF showed that temperature tends to vary synchronously over much of the California Current (but see [388] and Sect. 6.1.1.8). The 30-year temperature trend from all four regions in Fig. 2.1b is shown in Fig. 2.18b. In cool years, zooplankton production is higher, and in warm years, production is lower (Fig. 2.18a and b). Low temperatures are also generally coincident with low salinities (Fig. 2.18b and c). Water in the California Current System can cool by two processes; either by upwelling of deep cold water or by advection of cold water from the north. Increased flow of the California Current (i.e. advection) is associated with geostrophic adjustment of the density field, tilting the isotherms so that waters in the nearshore are cooled [106]. Spatiotemporal analysis of salinity helps to separate the effects of upwelling and advective processes.

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[5] Chelton (1981) [106] analyzed 150 of the CalCOFI stations available between San Francisco and southern Baja California for the years 1950–1978. Monthly values for this period were interpolated to 16 standard depths down to a maximum of 1,000 m. Data were sorted by grid location, and grid points with less than 40 observations over the 30 year period were excluded.

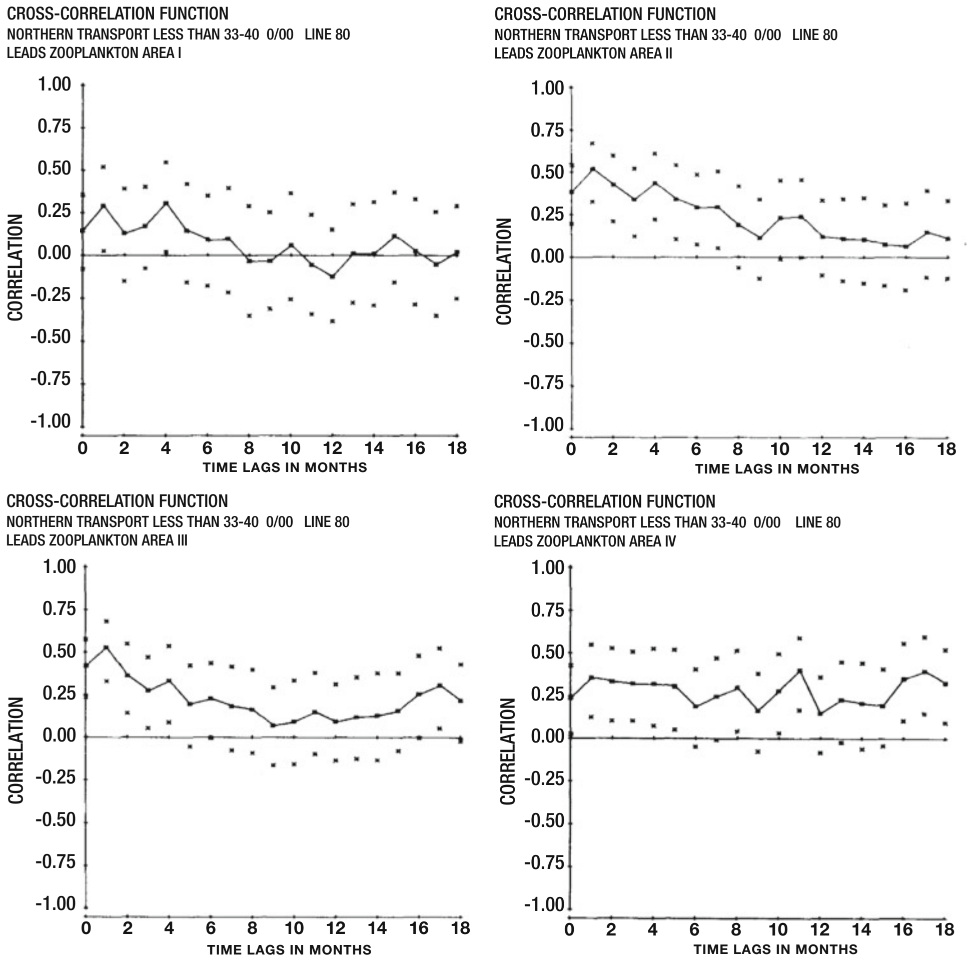

Fig. 2.15 Cross-correlation between zooplankton displacement volume and an index of transport from the north. *Crosses* represent the 95 % confidence limits (From [60])

Salinity increases with depth and decreases offshore, out to about CalCOFI station 100. Consequently if zooplankton production were solely associated with upwelling, then zooplankton volume and salinity would be positively correlated [106]. In fact, they are negatively correlated (Fig. 2.18a and c). While salinity does increase with depth, a clear signal of the California Current is the low salinity tongue, clearly defined at 50 m depth and extending southward in offshore waters [477]. Stronger advection is associated with lower salinities (Fig. 2.18c and d), and higher zooplankton volume is correlated with lower salinities (i.e. the negative correlation) (Fig. 2.18a and c). Chelton (1981) concluded that the evidence favored advection as the source of nutrients supporting zooplankton production, but stated that advection could not be the only source of nutrients, since there were some years when temperature and salinity were not in phase, and there are years like 1978 when low zooplankton volume was unexpectedly associated with low salinities [106] (i.e. zooplankton was positively correlated with salinity rather than the reverse, which is more usually the case).

The results of the studies described above explain the importance of advection to zooplankton production in the California Current System, but they do not distinguish between production due to advection of zooplankton from the north, or alternatively, *in situ* production following the injection of nutrients from the north by the California Current. Roessler and Chelton (1987) addressed this problem with a more spatially resolved analysis [477]. They divided the regions from San Francisco to southern Baja California into the 23 spatial blocks used by Colebrook (1977) [122]. These blocks were considered to be sufficiently large to provide monthly averages smoothing the potential biases from patchiness and vertical migration. From these twenty-three, Roessler and Chelton (1987) retained 14 spatial blocks with sufficient samples for an analysis of zooplankton displacement volume and large-scale advection over the 32-year period from 1951–1983, which more than tripled the spatial resolution of previous studies (Fig. 2.19). To examine non-seasonal variability they further aggregated the data into four regions (similar to [107]) with sufficient samples to permit them to remove the seasonality by fitting harmonic regressions (Fig. 2.19). The analysis was performed on anomalies calculated by removing the seasonal trend. These authors also performed their analysis on both untransformed and $\log_e$ transformed anomalies because they considered that removing the outliers by transformation removes valuable information that could

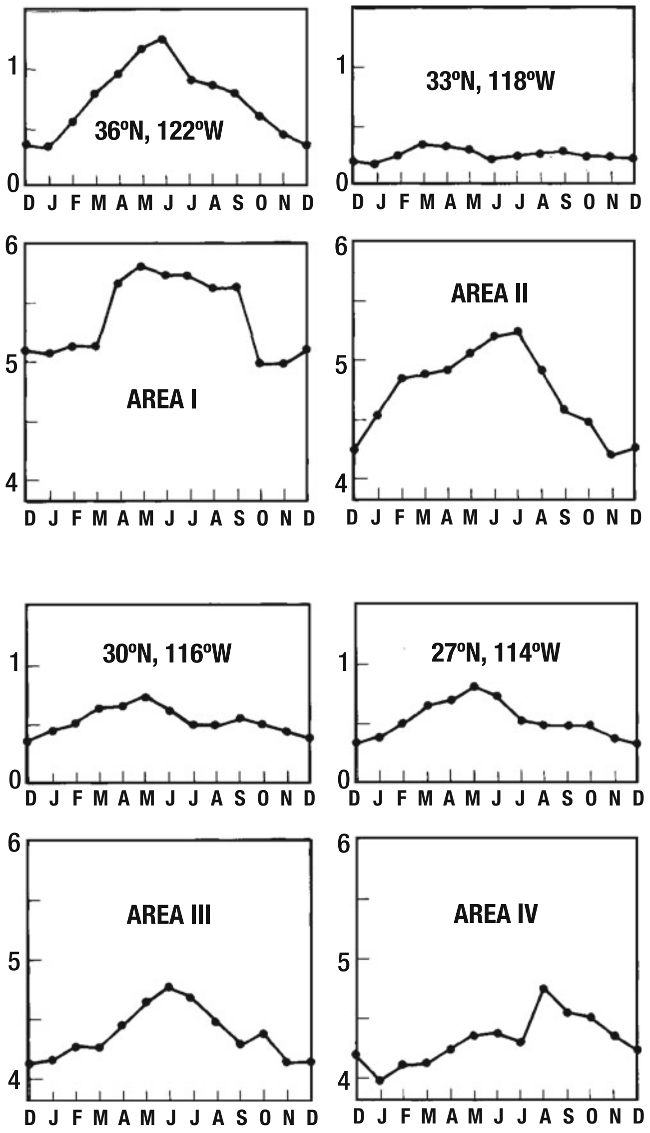

Fig. 2.16 Annual cycle of the 30-year (1950–1979) mean monthly zooplankton volume, $\log_e$mL 1,000 m^{-3} (From CalCOFI stations in the blocks in Fig. 2.1b) shown in *lower panels*, and along-shore equatorward component of wind stress, dynes cm^{-2}, shown in *upper panels*. Monthly values are the means for each month over the time series, i.e. a climatological mean (From [106])

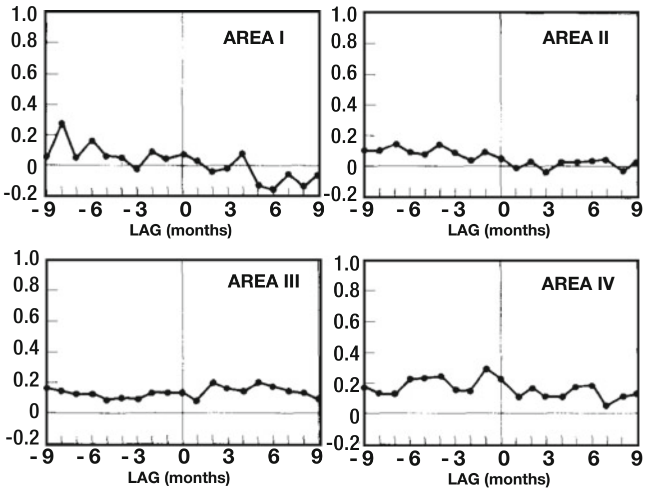

Fig. 2.17 Cross-correlation between seasonally detrended mean zooplankton displacement volume from four areas defined by Bernal (1979) [58] (Fig. 2.1b) and the seasonally detrended upwelling favorable wind stress (From [106])

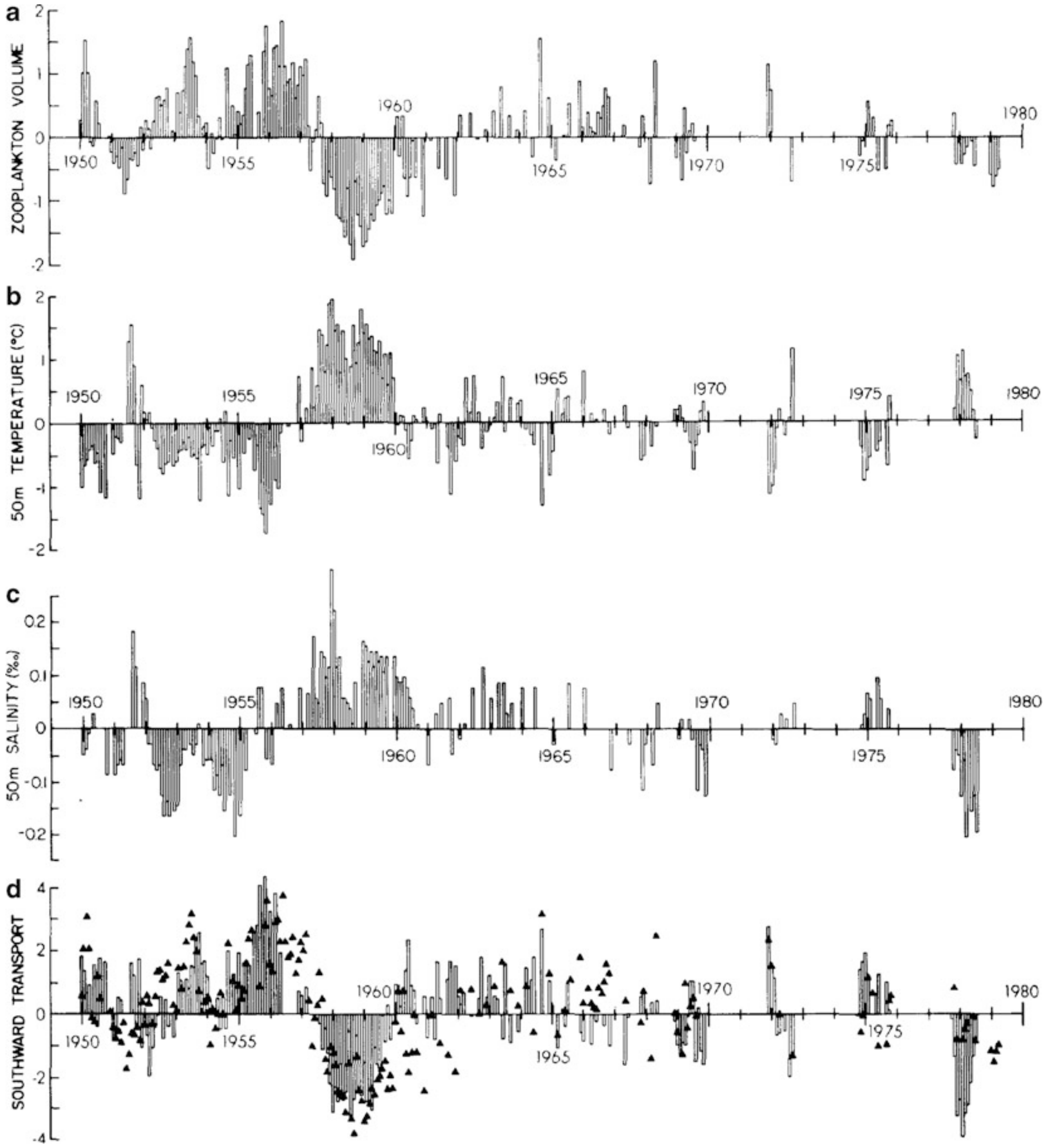

Fig. 2.18 (**a**) Average of the zooplankton time series from all four regions in Fig. 2.1b. (**b**) Amplitude time series of the principal EOF of temperature at 50 m for the CalCOFI stations analyzed between San Francisco and southern Baja California. (**c**) Amplitude time series of the principal EOF of salinity at 50 m. (**d**) Amplitude time series of the principal EOF of 0/500 db steric height. The zooplankton time series in (a) is replotted as points in (d) (From [106])

provide insight concerning the forcing mechanisms. It is interesting to note that careful vetting for sample size and representativeness, the adequate removal seasonal trends, and attention to the potential biases that transformation may introduce have often been neglected in analyses of CalCOFI data. Chelton's papers provide an inspiring example for how these data should be handled.

The highest non-seasonal variance in log-transformed zooplankton volume distributions occurs in a 500 km wide alongshore band centered at about 29°N (Fig. 2.20) [477]. This band straddles a transition zone between high and low zooplankton biomass ([58, 379] cited in [477]). Poleward shifts in the boundary of northern transition and subarctic zooplankton species (see Sect. 2.1) occur in warm years with weak advection, and equatorward shifts occur in cool years with strong advection [477]. The spatial distribution of the non-seasonal variance of log-transformed zooplankton volume (the zooplankton anomalies) and the dominant EOF[6] of the zooplankton anomalies were very similar over 32 years (Fig. 2.20). The similarity indicates that the variability is coherent over the entire spatial domain, which as Fig. 2.20 shows, was from Monterey to south of Punta Eugenia. The

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[6] The first EOF explained 46 % of the variance.

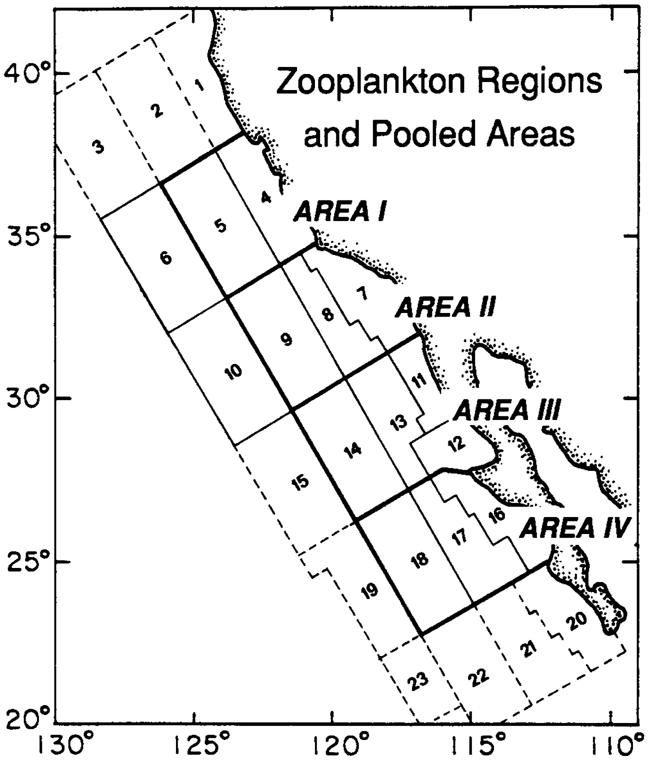

Fig. 2.19 Location of the 23 geographical regions for which spatially averaged CalCOFl zooplankton time series were available over the 32-year period from 1951–1983 (provided by Paul E. Smith). The 14 regions outlined by the *solid borders* form the basis for the analysis. The four large-scale areas outlined by *heavy borders* and labeled as areas I, 11, Ill, and IV were used in the temporal analyses of nonseasonal zooplankton and large-scale advection (From [477])

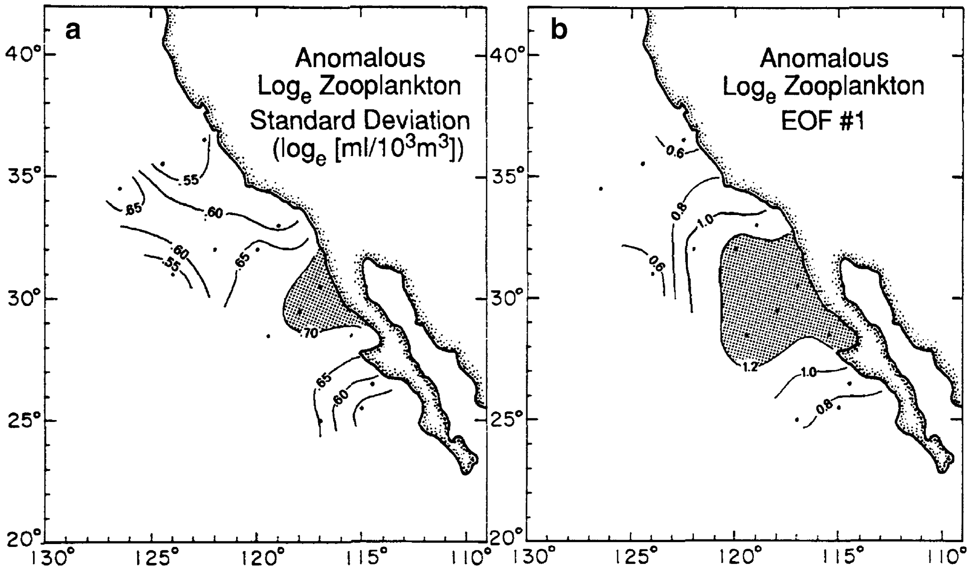

Fig. 2.20 (**a**) Standard deviation of log transformed, seasonally corrected zooplankton displacement volumes in the 14 regions shown in Fig. 2.19 denoted by *dots*. (**b**) The dominant EOF of log transformed zooplankton volumes computed over the same 14 regions from seasonally corrected time series (From [477])

time series of the dominant EOF of zooplankton anomalies defines the temporal variability of the zooplankton anomalies. When the time series is positive (Fig. 2.21c and d) there are anomalously high zooplankton values throughout the region in Fig. 2.20, and when the series is negative there is anomalously low zooplankton throughout the region [477], with the highest variability occurring in the region shown in Fig. 2.20. As demonstrated by earlier work [107] the zooplankton anomalies are significantly correlated with both the index of current flow (Fig. 2.21b) and with average corrected sea level height (Fig. 2.21a) [477]. The correlations are highest when advection lags sea level by three months, the zooplankton anomaly lags advection by two months (and consequently zooplankton anomaly lags sea level by five months) [477]. The time lags between the zooplankton anomaly and advection are shorter further north. The lag is only 1 month in Zones 1 and 2 of Fig. 2.19, but two months further south, reflecting the likely dominance of advection further north, and *in situ* production further south.

The EOF analyses were not sufficient to distinguish between the effects of advection of zooplankton and advection-driven stimulation of *in situ* zooplankton production, so

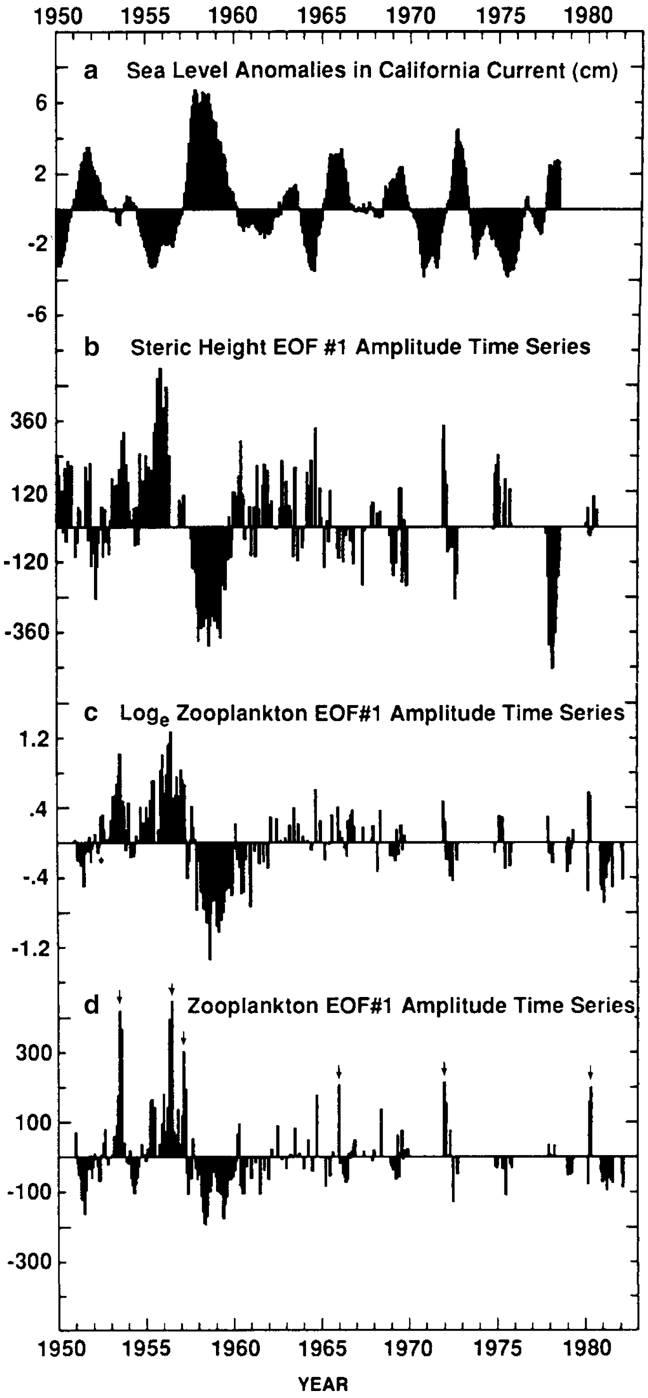

Fig. 2.21 (**a**) Time series of sea level anomalies in the California Current (averaged over San Francisco, Los Angeles, and San Diego and corrected for inverse barometric effects of atmospheric pressure) in centimeters. (**b**) The amplitude time series of the first EOF of steric height shown in Chelton et al. (1982). This time series represents the time dependence of the dominant mode of variability in equatorward advection in the California Current. (**c**) The amplitude time series of the dominant EOF of log transformed zooplankton displacement volumes shown in Fig. 2.20. When the time series is positive (negative) zooplankton biomass is anomalously high (low) over the full CalCOFl region (with the largest amplitude variability in the stippled region in Fig. 2.20). (**d**) The amplitude time series for the dominant EOF of untransformed zooplankton displacement volumes (From [477])

Roessler and Chelton (1987) [477] looked at the biology in more detail to try and distinguish the two processes. If stronger equatorward flow is acting to enhance *in situ* zooplankton production by injection of nutrients into the food web, the process should be associated with greater densities of zooplankton larval stages, because the population would be young and growing rapidly. In contrast, if stronger equatorward flow is bringing zooplankton populations into the northern CalCOFI area, one would expect to find greater concentrations of adult zooplankton [477]. Roessler and Chelton (1987) found this to be the case when they compared April 1955 with April 1958 using Brinton's (1967) [80] maps of krill distributions for 1955–1958. In 1955, an anomalously cool year with strong equatorward flow, the distribution of the krill, *Euphausia pacifica*, was dominated by adult stages, consistent with zooplankton having been advected into the region. Roessler and Chelton (1987) viewed the result as consistent with "advection of zooplankton [being] the

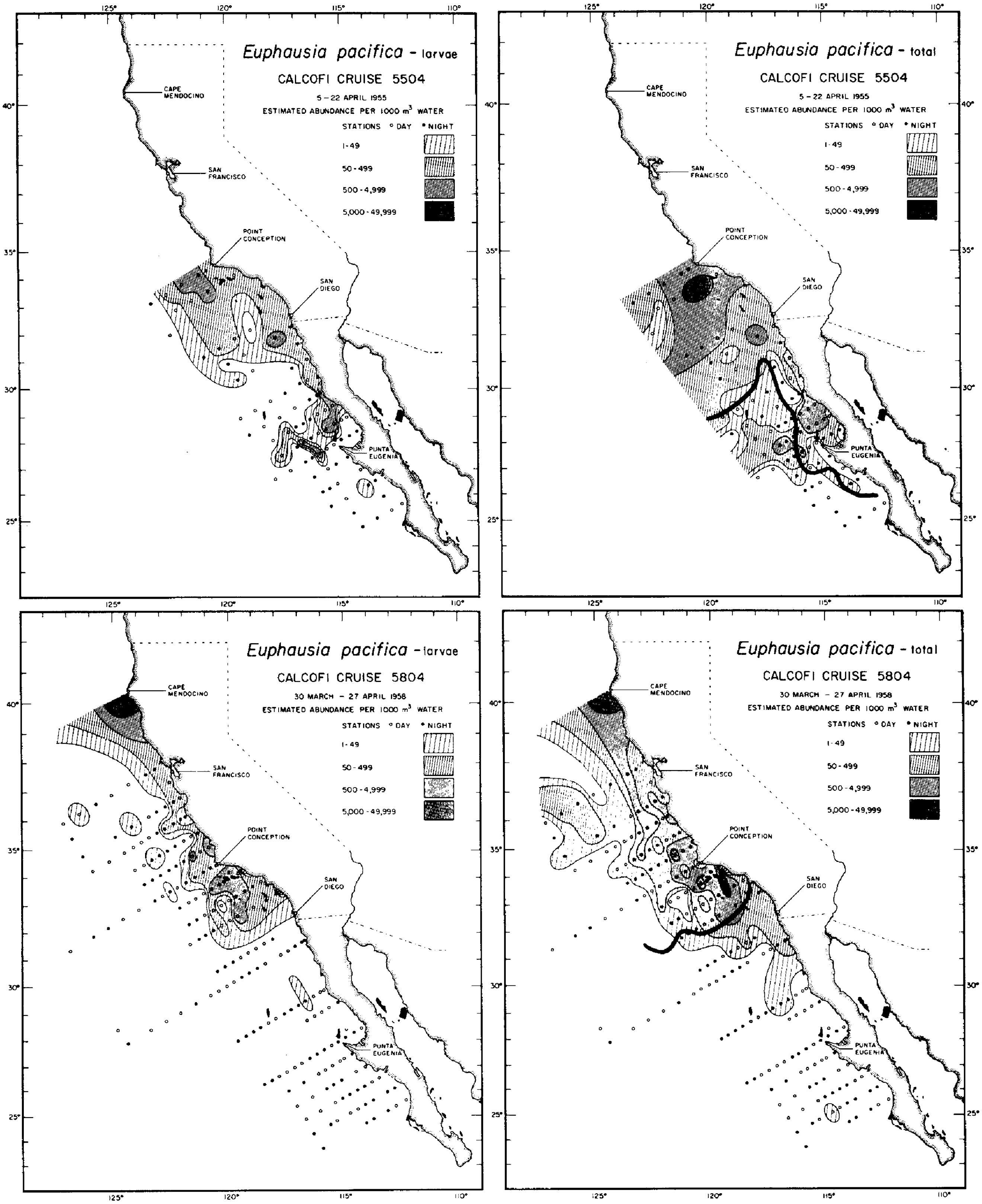

Fig. 2.22 Larval versus total zooplankton distribution of *Euphausia pacifica* for April 1955, an anomalously cold year with strong equatorward flow, and April 1958, an anomalously warm year with weak equatorward flow. The *black line* on the total distributions indicates the approximate location of the 15.5 °C isotherm for each date. Anomalously warm or cold refers to whether temperatures were much warmer or much cooler after removing the seasonal trend (From [477])

dominant mechanism controlling zooplankton abundance in the northern CalCOFI region". 1958 on the other hand, was an anomalously warm year of weak equatorward advection, and the population of *E. pacifica* was dominated by larval stages ([80] cited by [477]), suggesting that *in situ* production was occurring. This is an intriguing idea that should be further tested, as the maps that Roessler and Chelton (1987) [477] presented in support of dominance of larvae or adults in these respective years are not very convincing (Fig. 2.22).

More recent studies have shown that the offshore region of the California Current and the nearshore upwelling region are more connected than was previously known (see [33] and references therein). The combination of offshore flows and an energetic mesoscale eddy field propagating westward ensures that the areas experiencing upwelling interact with the offshore areas dominated by the California Current (Sect. 2.4.1). The mechanisms underlying zooplankton production are consequently unlikely to be dominated by north-south advection alone, since the offshore advection is now known to be of comparable magnitude [33].

2.5 Seasonality

2.5.1 Spring Transition

The spring or coastal transition refers to a seasonal change along the North American west coast between ~23–49°N that is forced by changes in the wind. It can be viewed as a change from winter to summer conditions but is probably better viewed as a transition from winter to upwelling conditions. The spring transition is a key seasonal event in the California Current System. There have been more studies of the spring transition in the northern part [239, 278, 537] than in the southern region of the California Current System [338], likely because the phenomena is more marked in the north. Despite its long time series, the current 75-station pattern is too small, and temporal resolution of CalCOFI is too coarse, to capture the spring transition event [338]. This is partly because the limits on the duration of the transition are about 1 month [338] and the process often occurs over a considerably shorter time period, sometimes as short as a week (Fig. 2.23). The March and April 1995 surveys between San Diego and San Francisco [338] captured a snapshot of the spring transition in the southern California Current (Fig. 2.24) which is not generally available from the CalCOFI surveys, as they tend to show either the winter or summer regimes, but not the transition.

The coastal transition is driven by southward winds that create southward along-shore flows and offshore-directed Ekman transport [537]. Coastal upwelling induced by the Ekman transport brings denser (cooler and more saline) water onto the shelf which creates a cross-shore density gradient associated with vertical shear in the along-shore current [537]. Sea level and currents change first (Fig. 2.25), followed by the development of baroclinic shear and the density gradient [239]. The transition event described by Strub et al. (1987) took place over 5–10 days [537]. The changes include intensified southward wind stress, a change from downwelling-favorable to upwelling-favorable conditions, changes in the strength of wind mixing and patterns of wind stress curl, leading to reduction in coastal sea level and changes the distribution and abundance of phytoplankton pigments [556].

The spring transition between 33–48°N can be seen in the fall of sea level height in March and April based on tide gauge data, after removal of means and long-term trends, and correcting for surface atmospheric pressure [537] (Fig. 2.25). The transition can also be seen in the change from northward to southward wind stress [537] (Fig. 2.25). Low sea levels are more persistent and less variable in the summer than are high sea levels in winter. Low sea levels are more persistent in the north than in the south, and the spring transition occurs more quickly off northern central California and southern Oregon (38–45°N) [537] (Fig. 2.25). The southward summer wind regime lasts longer in the south than the north, which is the opposite to the pattern for sea level. Wind reversal is greatest in the north where the transition changes most rapidly [537].

Shifts of timing in the seasonal cycle of physical events that affect ecosystem structure and productivity are important when assessing the impacts of climate change on marine systems [145]. Inter-annual differences in the spring transition occur in its north-south timing and abruptness of development, the along-shore extent of the wind and sea level effects, and the duration of the summer regime [537]. The timing of the spring transition, whether the onset of upwelling occurs earlier or later, has profound effects in the California Current ecosystem. For example, 2005 was an unusual year that exhibited anomalies as strong as those observed in an El Niño year, but the effects were caused by delayed spring transition and onset of coastal upwelling in the northern California Current System [497], not by an ENSO event.

2.5.2 Wind-Driven Coastal Upwelling North of the SCB

Spring upwelling commonly occurs along the central Californian coast [236, 278] and extends to the south off Point Conception, but diminishes in the SCB. Winds are upwelling favorable (i.e. blowing along-shore from the north) to the south of about 33°N (i.e. just north of San Diego) throughout the year, but the upwelling season is progressively shorter towards the northern latitudes [70]. Maximum summer upwelling-favorable wind stress occurs off northern California [556], where the season is only 151 days on

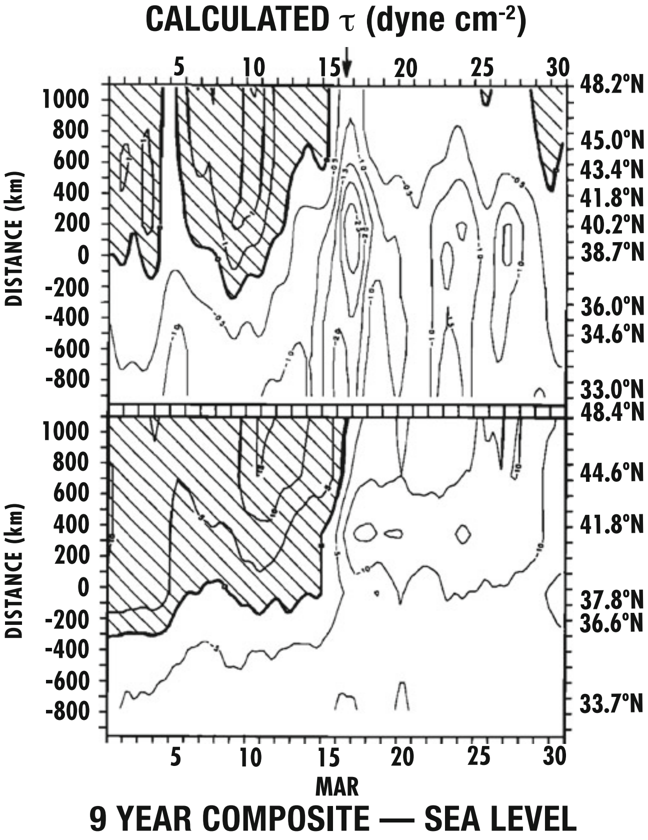

Fig. 2.23 Composite 9-year (1971–1975 and 1980–1983) time series of along-shore wind stress and sea level, centered on a date chosen for each year's transition event at 41.8°N, plotted for reference as "March 16". Positive values are *shaded* (From [537])

average at 48°N compared to 357 days at 33°N [70]. With increasing latitude, winter downwelling winds intensify for longer periods, transitioning to upwelling-favorable winds over the summer. Based on 5 years of satellite data (1979–1983) Thomas and Strub (2001) [556] showed that the timing of the start of upwelling-favorable wind stress, as well as its duration and intensity, varies considerably between years.

Bograd et al. (2009) developed metrics to quantify the inter-annual variability of upwelling timing, duration and intensity from the summation of the daily mean upwelling indices [38, 500] at each of a series of locations in the California Current System over a 41 year period [70] (Fig. 2.26). Their analysis confirmed, based on a much longer time series, that there is substantial latitudinal and inter-annual variability in upwelling along the west coast, as reported by Thomas and Strub (2001) [556]. Bograd et al.'s analysis was restricted to the United States coast (33–48°N) [70], whereas Thomas and Strub (2001) [556] covered the coast from southern Baja California to the Canadian border.

The relationship between the timing of the seasonal maxima in coastal chlorophyll-a and cross-shore extension of chlorophyll-a with wind forcing is much stronger between Point Conception and San Francisco (central California), between Cape Mendocino and San Francisco (northern California) and from Cape Blanco to Cape Mendocino (straddling the Oregon–California border) than in other areas of the California Current System [556]. Even in these areas, the correlation between wind stress, offshore expansion of chlorophyll-a, and the timing of maximum chlorophyll-a concentrations is not always consistent [556] (bear in mind that this conclusion was based on 5 years of data). A non-parametric correlation analysis [556] showed that between Cape Blanco and Cape Mendocino most metrics of chlorophyll-a distribution were correlated with along-shore wind stress and wind mixing. Strongest correlations between chlorophyll-a and wind stress were found at a lag of 10 days, but the highest correlation between chlorophyll-a and wind mixing occurred at a lag of 20 days [556] (see Glossary for definitions of wind stress and wind mixing). North of Cape Blanco, inter-annual variability of wind forcing and chlorophyll-a structure is stronger, but wind forcing and chlorophyll-a are still correlated.

2.5.3 Seasonality of Currents

In addition to the wind-driven seasonality of the spring transition, the currents of the southern California Current System also show seasonality. The California Undercurrent is strongest in summer, showing some intensification in the upper 70 m, but almost continuous down to 400 m (Fig. 2.27) [179]. While the California Undercurrent peaks

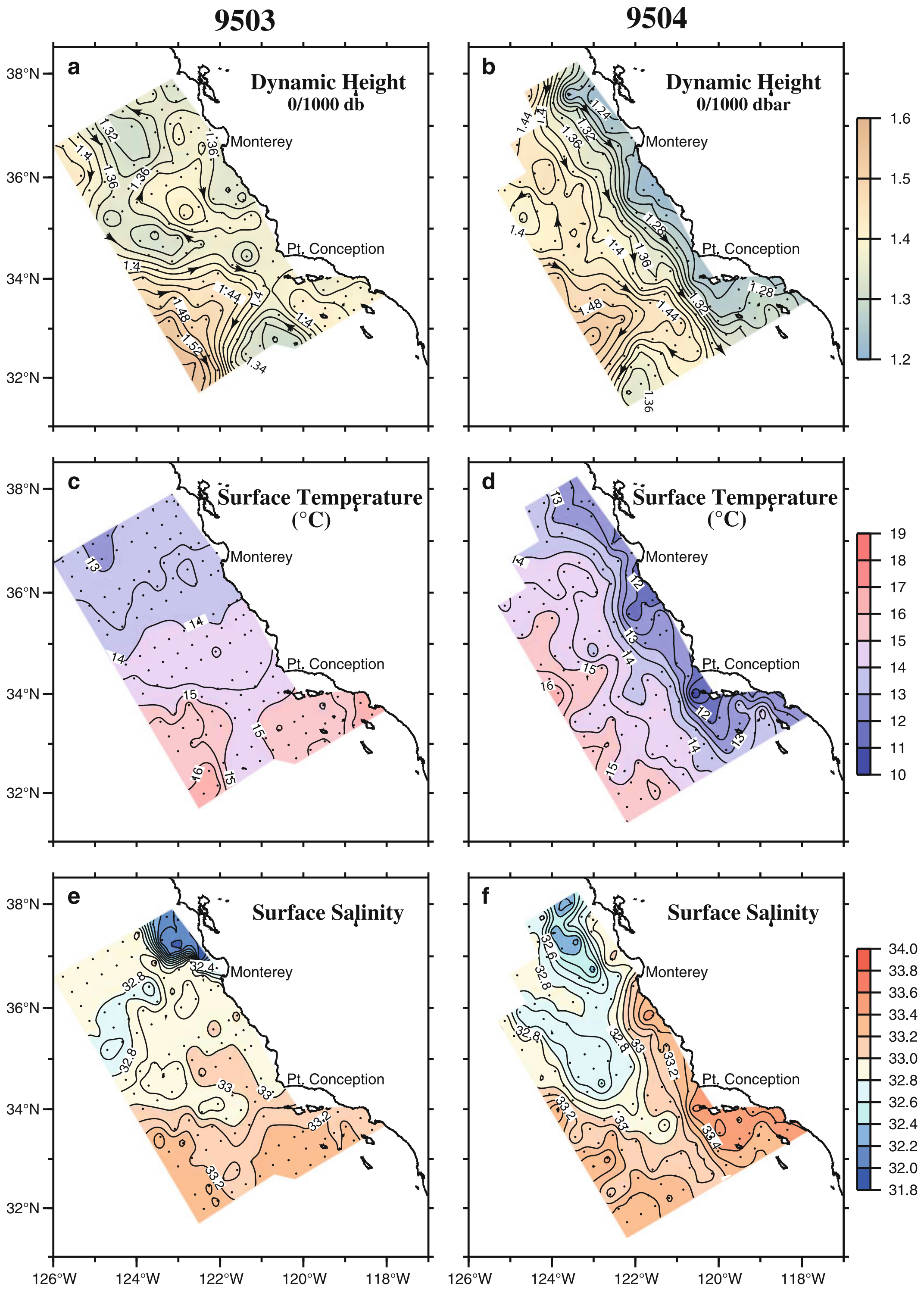

Fig. 2.24 (**a** and **b**) Dynamic height (m^2s^2), (**c** and **d**) surface temperature (°C), and (**e** and **f**) surface salinity from two surveys in March (*left*) and April (*right*) 1995 (From [338])

in the summer in the Southern California Bight and off Point Conception, the peak flow on the Santa Rosa Ridge is in the fall (Fig. 2.27 and 2.28) [179]. In the fall the flow of the California Undercurrent off the Santa Rosa Ridge is straighter and comes more directly from the south [179]. Weakest flows of the Undercurrent are seen in the spring and winter, and poleward current flow weakens more in the Southern California Bight than off Point Conception (Fig. 2.27). The

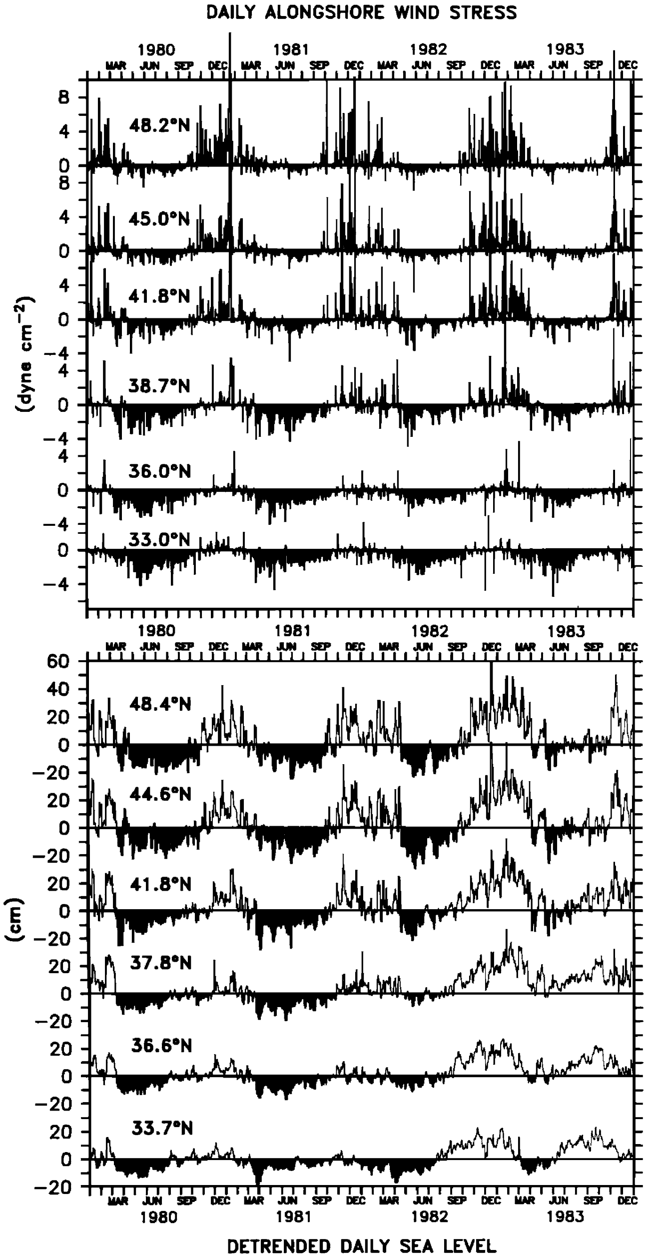

Fig. 2.25 Seasonal time series of along-shore wind stress (*upper panel*) and sea level height (*lower panel*) for 1980 through 1983, showing how sea level falls with the onset of southward directed winds in the spring initiating the spring or coastal transition (From [537])

Undercurrent appears to have a rather complex spiciness signal that is stronger in the Southern California Bight in summer, and strongest over the Santa Rosa Ridge in autumn (Fig. 2.29) [179]. There is a strong recirculation of anomalously spicy water in the Southern California Bight in spring which is released to flow northward past Point Conception in the summer and fall (Fig. 2.29) [179]. A counter-clockwise eddy off San Clemente and a clockwise eddy off Los Angeles also appear more frequently in the fall [179]. These small eddies are distinct from the larger offshore eddies seen in Fig. 2.29.

2.5.4 Seasonal Cycles of Remotely-Sensed Variables

Remote sensing of sea surface temperature (SST), ocean color and sea surface height provides the most spatially and temporally comprehensive coverage for determination of seasonal and inter-annual variability in the California Current System. The variability of the seasonal cycle (or seasonality) as measured by the magnitude of seasonal extremes and the timing of maxima and minima of temperature and chlorophyll differs regionally between waters off Oregon, northern

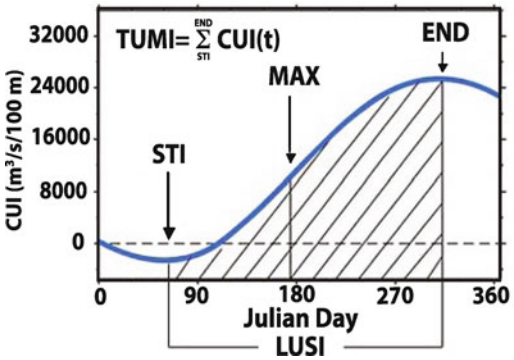

Fig. 2.26 Annual cycle of the cumulative upwelling index at 39°N showing the indices used to characterize inter-annual variability in upwelling. STI (spring transition index), LUSI (length of upwelling season index), and TUMI (total upwelling magnitude index). MAX (maximum slope of CUI curve) and END (annual maximum of CUI) give the dates of peak upwelling and end of upwelling season, respectively (Modified from [70])

or central California, southern California, and northern or southern Baja California, Mexico [301] (see Sect. 2.1). Seasonality also differs between inshore and offshore waters, and the nature of this difference varies by region. The timing of seasonal maxima and minima of both temperature and chlorophyll varies between years at any given location [301].

The mean seasonal cycle of chlorophyll across the California Current System interpreted from ocean color imagery shows development of a widespread phytoplankton bloom at the onset of seasonal upwelling, followed by retreat of the bloom closer to shore where a strong frontal gradient develops in association with an upwelling jet [301] (Figs. 2.30, 2.31, and 2.32). A second widespread and diffuse bloom develops in the early fall season (Fig. 2.30). Subsequently phytoplankton chlorophyll-a concentrations in offshore waters drop to a winter low, and a narrow band of higher concentrations remains inshore [301].

Based on seasonal amplitudes of SST, the seasonal cycle is weakest in nearshore waters off the Pacific northwest and Cape Blanco–Cape Mendocino, offshore of the Southern California Bight and off northern Baja California [301, 554, 556] (Fig. 2.33). The reduced seasonality between Cape Blanco (42.7°N) and Point Conception (34.5°N) (i.e. Cape Blanco–Cape Mendocino, northern California and central California) is caused by coastal upwelling, which depresses the seasonal heating cycle and creates lower annual temperature amplitudes than are found offshore [301]. Minimum seasonal temperature amplitudes occur near the coast off Cape Blanco–Cape Mendocino and northern California (~37.8°–42.8°N) (Fig. 2.33) [301]. Reduced seasonal temperature amplitudes are confined to the coast in the Pacific

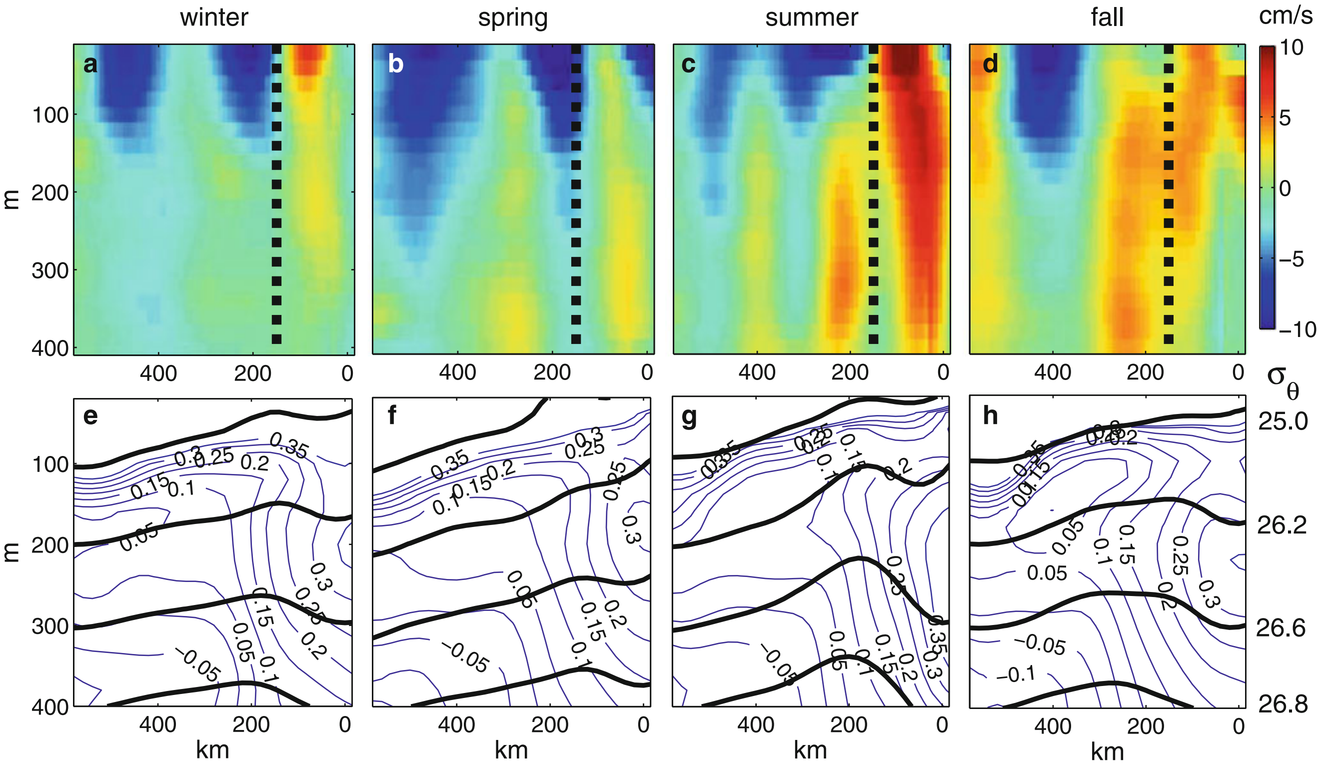

Fig. 2.27 (**a–d**) Seasonal mean cross-track velocity and (**e–h**) mean spiciness in the Southern California Bight and offshore of the Santa Rosa Ridge (averaged over lines 87, 90, and 93) with depth and distance offshore. Also shown are the 25.0, 26.2, 26.6, and 26.8 isopycnals. The *vertical dashed lines* in (**a–d**) indicate the location of the Santa Rosa Ridge (From [179])

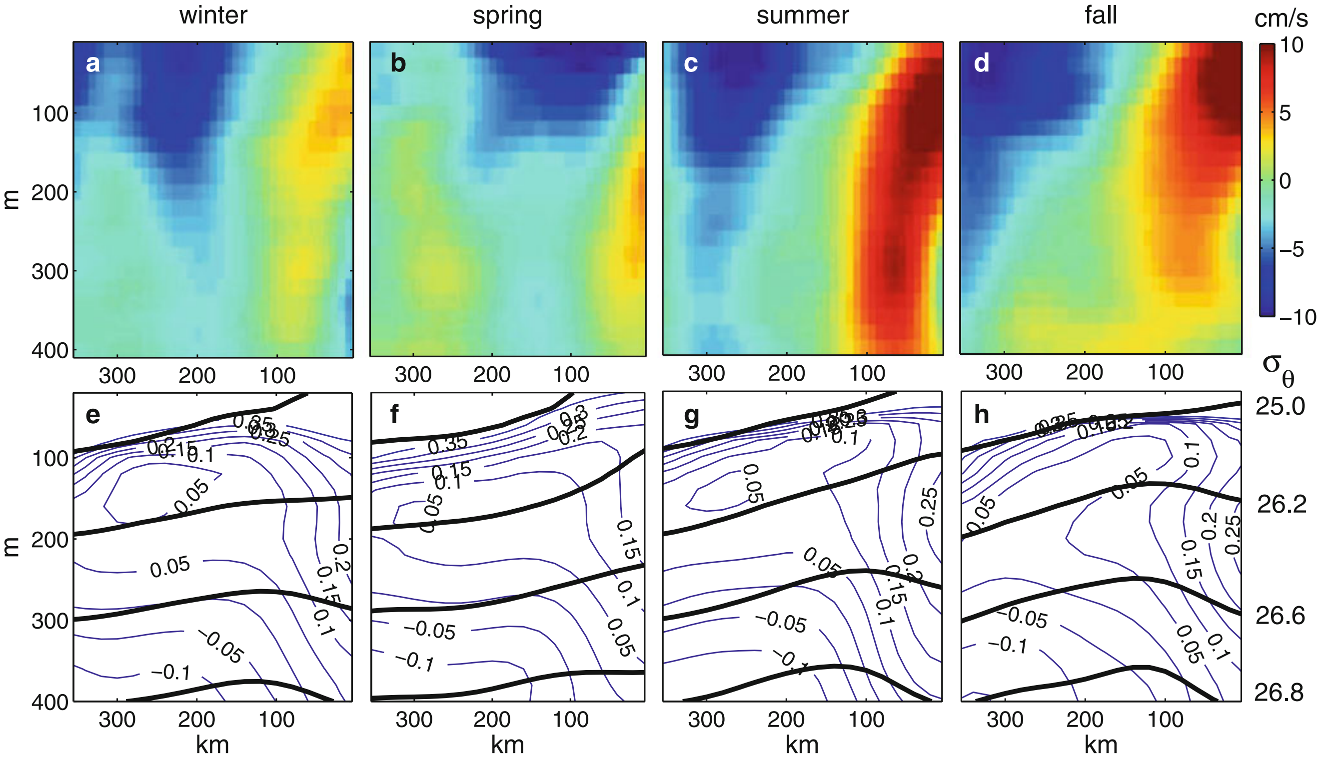

Fig. 2.28 (**a–d**) Seasonal cross-track velocity and (**e–h**) spiciness off Point Conception (averaged over lines 77, 80, and 83) with depth and distance offshore. Also shown are the 25.0, 26.2, 26.6, and 26.8 isopycnals (From [179])

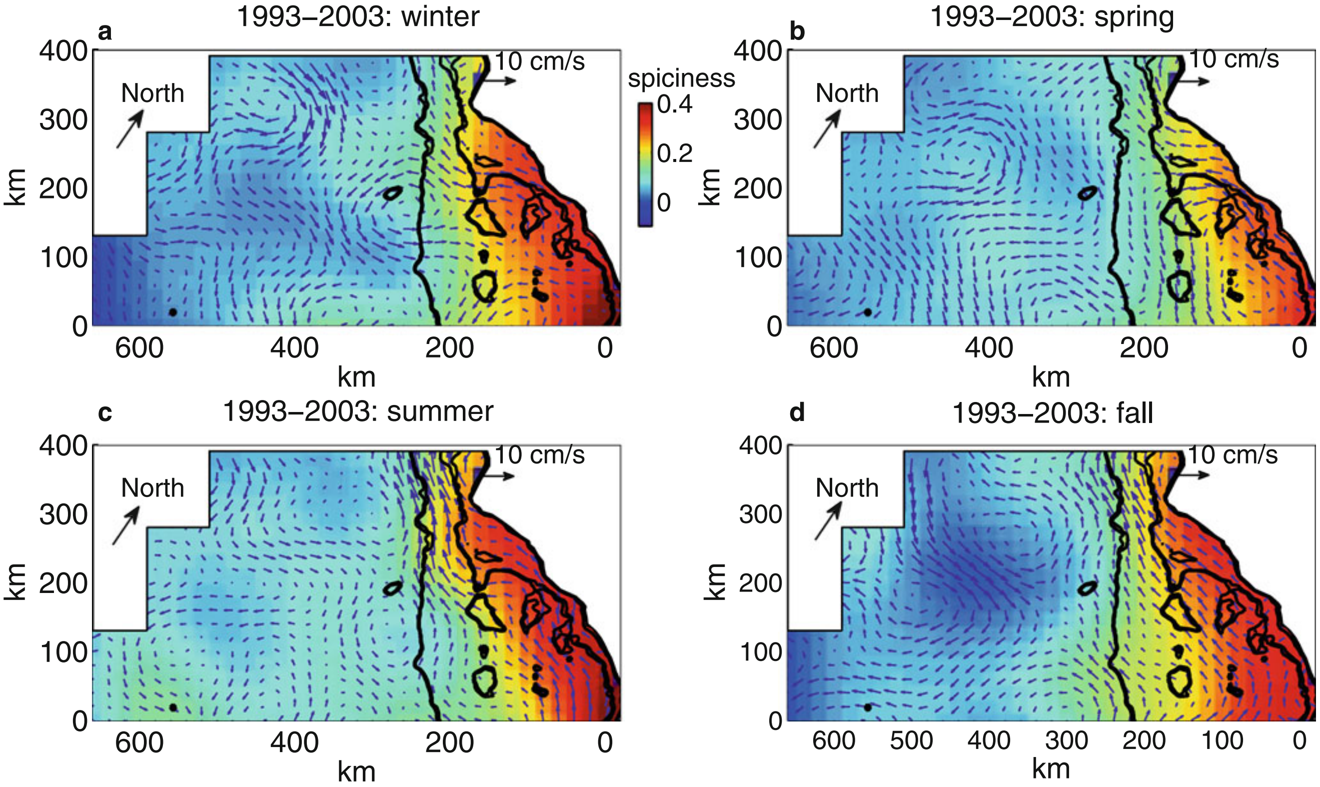

Fig. 2.29 Seasonal mean velocity field at 200 m depth, mapped from the ADCP observations where color represents spiciness. The scale for velocity is shown by the *arrow* at the *upper right* (From [179])

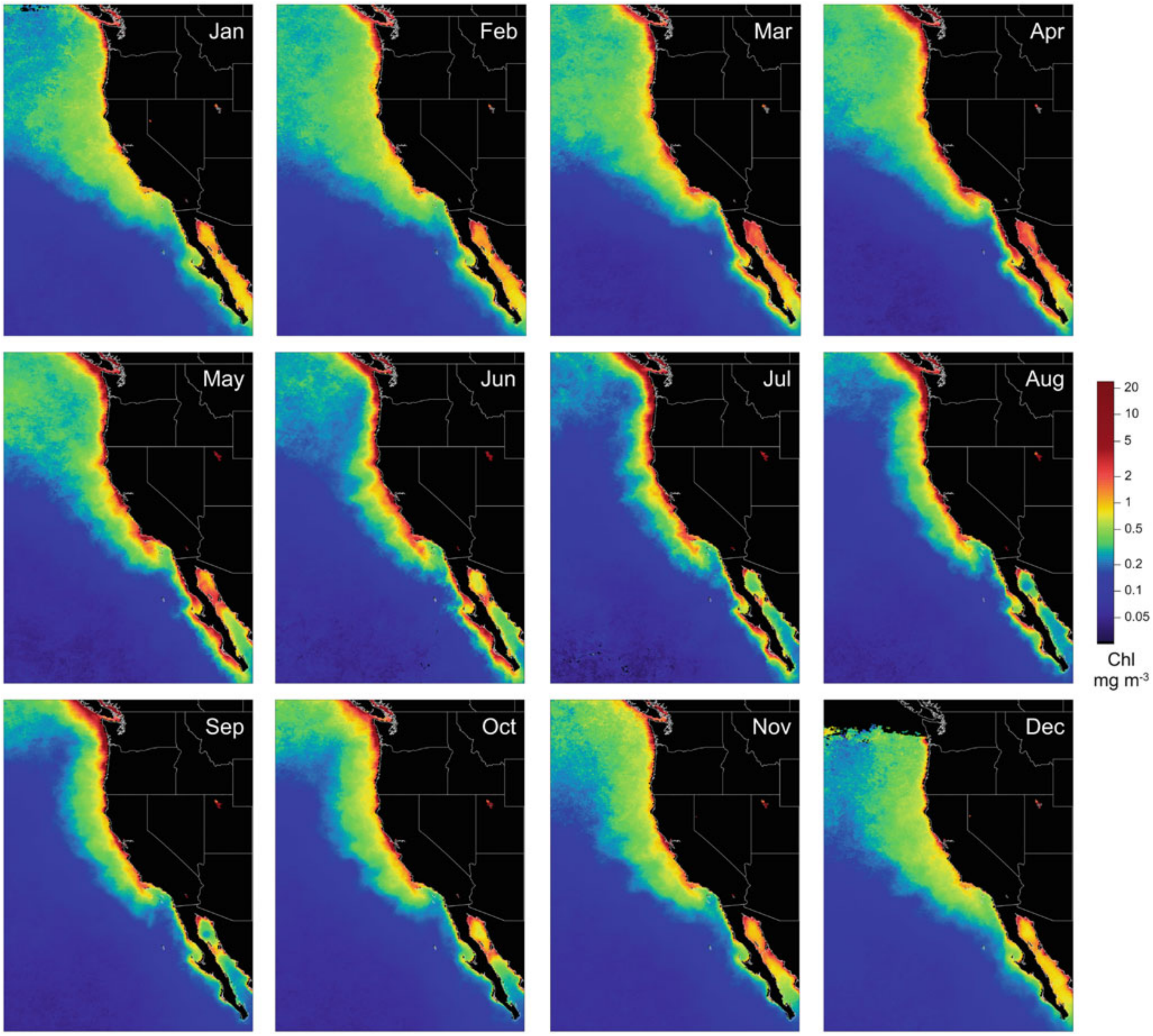

Fig. 2.30 Climatology of ocean color based on 1998–2012 SeaWiFS data (Courtesy of Paul Fiedler, SWFSC)

northwest to the north of ~45°N, but extend offshore to the south of this latitude consistent with the seaward expansion of upwelled water associated with mesoscale filaments (i.e. cross-shore directed fronts) and eddies [301]. Coastal upwelling also delays the timing of the seasonal maximum and minimum temperatures, with greatest delay occurring at Point Arena (39.2°N) off central California [301].

The seasonal cycle is stronger in the offshore waters (37.2°N, 126.1°W) of Central and northern California (40.0°N, 130.1°W) but inshore off southern Baja California (26.0°N, 112.5°W) (Fig. 2.33). Seasonal amplitude is also higher in the eastern Southern California Bight compared to offshore. High seasonal amplitudes of SST over the shelf and slope south of Punta Eugenia, Baja California, are likely associated with surface heat exchange driven by advection of air from the Mexican mainland [301]. Strong seasonality also extends to much of the Gulf of California [153]. In the eastern Southern California Bight, the change in the angle of the coast protects the nearshore waters from northwest winds and upwelling is localized to headlands. Annual maxima and minima of SST in the eastern Bight lead the seasonal maxima and minima to the north and south as well as those offshore by a month [301]. Summer surface heating plays a stronger role and inshore SST varies more than the offshore SST (Fig. 2.33).

Time series of SST imagery from central California and Baja California show seasonally recurrent structure of filaments and eddies associated with coastal topography

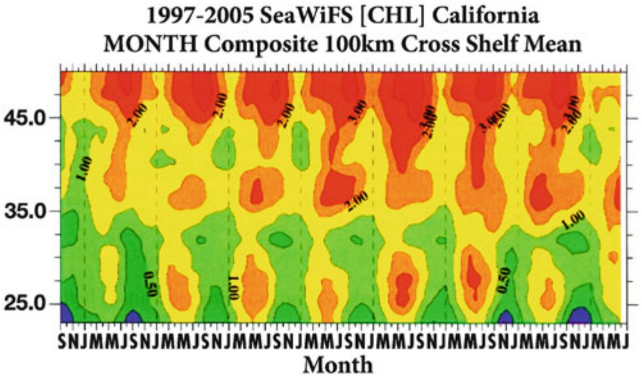

Fig. 2.31 Hovmöller diagram showing the latitudinal gradient and seasonal variability in mean remotely-sensed chlorophyll, averaged from the coast to 100 km offshore. Contours are 0.25 (*dark blue*), 0.5, 1.0, 2.0, 3.0, and 5.0 mg chlorophyll-a m^{-3} (*red*). Months are plotted as September (S) to June (J). 23°N corresponds to the southern tip of Baja California, Mexico and 49°N is the Canadian–US border (see also [301]) (Modified from [209])

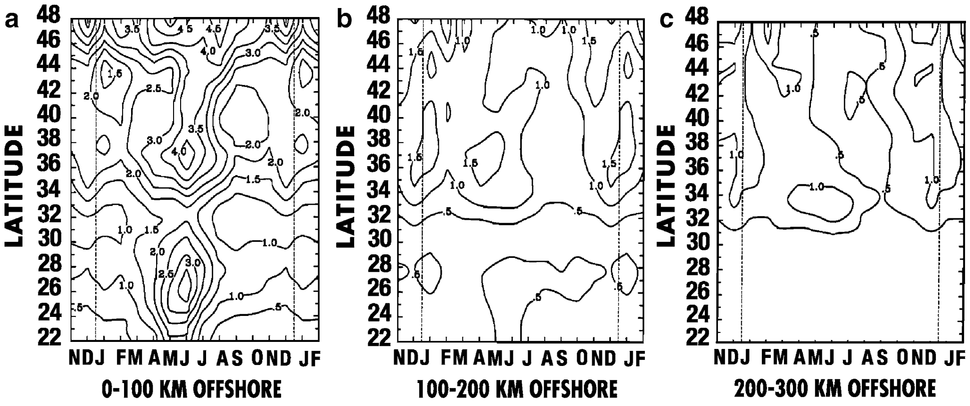

Fig. 2.32 Mean seasonal cycle of remotely sensed chlorophyll (mg m^{-3}) in three 100 km-wide bands parallel to the coast. Data are averaged from 100 × 100 km bins along the coast (From [554])

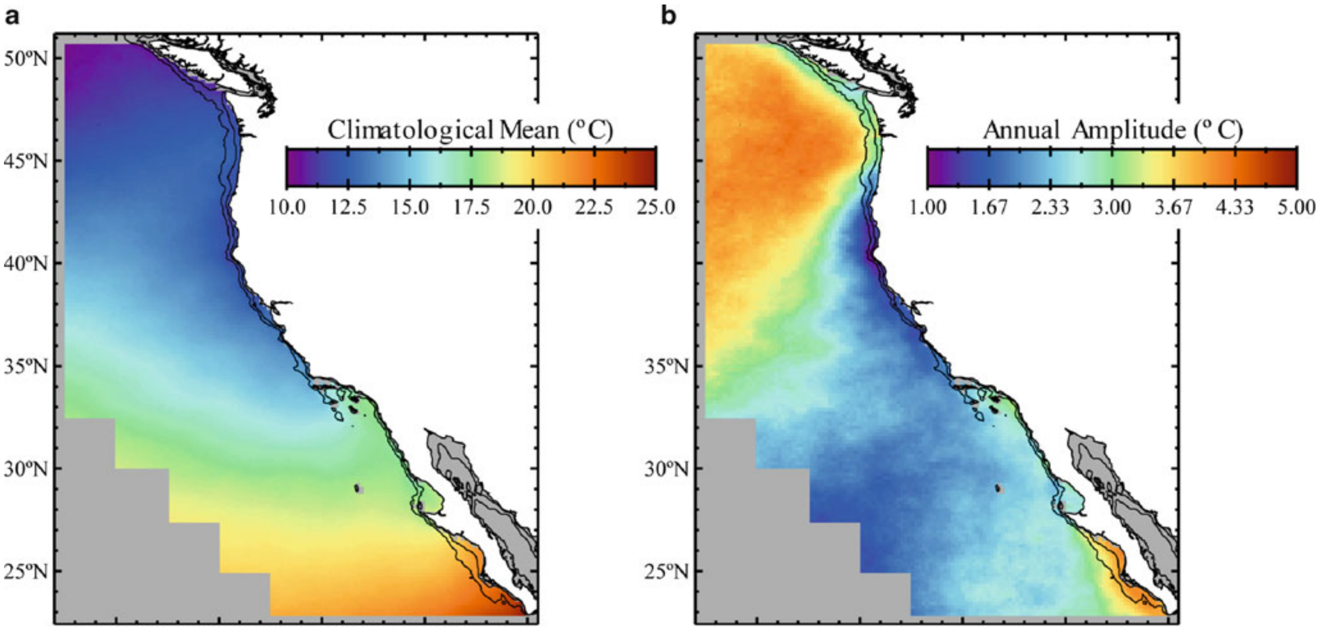

Fig. 2.33 (**a**) Climatological mean remotely sensed sea surface temperature (SST) after removing the harmonic regression fit to seasonal variations. (**b**) Annual amplitude of the harmonic fit to seasonal variations in SST (From [301])

and/or variations in wind forcing ([282, 301][31, 176] cited in [301]). Superimposed on this structure, large-scale phytoplankton chlorophyll-a patterns can change rapidly in phase and correlated with wind forcing, although the correlations vary with latitude and with season [301, 556]. Earlier work indicated that seasonal patterns are dominated by current structure and/ or wind forcing, and that seasonality is reduced in the Southern California Bight [1]. Over time scales of days to weeks, phytoplankton distributions can be interpreted as passive tracers of mesoscale circulation because the processes of growth, mortality and sinking have a much smaller effect than advection [132].

2.6 Regional Structures and Processes Affecting Production

Many of the different physical characteristics of the regions of the California Current System can be seen in the cross-shore sections of averaged seasonal oceanographic properties (temperature, salinity, sigma-t, dissolved oxygen and dynamic height) at standard depths along CalCOFI lines as published by Lynn et al. (1982) [336] in CalCOFI Atlas 30.

The CalCOFI atlases were used to publish surfaces and sections of physical properties that still provide helpful summaries of the California Current System at different seasons and locations. Temperature and salinity at 10 m, measured during the monthly CalCOFI cruises between 1950 and 1959, as well as mean monthly temperatures, were mapped in the first CalCOFI atlas [25]. The authors mapped temperature and salinity at 10 m, rather than at the surface, to avoid the effects of surface transients. Wyllie and Lynn (1971) [591] published the second decade (1960–1969) of near-surface temperature and salinity values, and the mean temperature, salinity and oxygen values at 150 m for both decades (1950–1968), spanning the time period of the earlier atlas. They chose the 150 m depth to match the maximum depth (at that time) of the CalCOFI oblique plankton tows [591]. These data are now available on the CalCOFI program web site.

One problem with these atlases is that the compendious nature of the work and the separation of the plots by variable and by month makes them a little difficult to use. I have abstracted the maps from Lynn et al. (1982) [336] into new composite figures that make the information more accessible. Figures 2.34, 2.35 and 2.36 show panels of averaged sections for of temperature, density, oxygen concentration, salinity, hydrostatic stability, and geostrophic velocity referenced to 500 db for CalCOFI lines 120, 90, and 60 centered on April from Lynn et al. (1982) [336]. This provides a more usable summary of these valuable data than the format in the atlases. A worthwhile update would be to create a series of panel plots showing orthogonal sections of averaged properties at standard depths based on the 66-station pattern for each of the spring, summer, fall and winter seasonal cruises using more recent data.

2.6.1 Central California

2.6.1.1 Wind Relaxation Events

Along the coast of California, wind relaxation events can generate warm coastal currents by poleward advection of water from further south [573]. Warm water retained in the shelter of headlands and in embayments during active upwelling is advected poleward when the wind relaxes ([573] citing [237,276,504]). When wind relaxations occur in the northern part of the California Current upwelling system in summer, poleward currents are generated and warming occurs over the continental shelf ([573] citing [285, 504]) (Fig. 2.37). Wind reversals and relaxations also cause poleward currents and warming over the continental shelf near Point Conception in the northern Southern California Bight and along the southern part of the central California coast ([573] citing [194,387,585,586]). As an example, at Point Arguello about 8 km north of Point Conception in late October to early November, on the 15 m isobath, wind relaxations drove warming from 12 °C to 16 °C in only 5 days, sustaining the warmer temperatures for 4 days, followed by a return to 12–13 °C temperatures over the next 3 days [573] (Fig. 2.38). Washburn et al. (2011) [573] identified 186 wind relaxation events near Point Conception during 2000–2006.[7] Their analysis shows that current reversals transporting warm water from the Southern California Bight past Point Conception, and the associated relatively large episodic temperature fluctuations that the reversals cause, are a common phenomenon in the area. The pattern observed at Point Arguello (Fig. 2.38) was consistent with the patterns on the 15 m isobath at Point Purisima and Point Sal, approximately 32–40 km north from Point Conception. Temperatures increased nearly simultaneously at all depths at these moorings [573]. The along-shore flows were also associated with cross-shore flows toward shore at the surface and offshore at the bottom [573].

These sorts of frequent short-term temperature fluctuations are sufficiently large to be physiologically significant for fish that experience the fluctuations. Among these fishes might be the recruits of coastal pelagic species (CPS), but the Marine Ecological Reserves Research Program (MERRP) study found little evidence for significant spawning in the nearshore Point Conception area. Apart from the temperature fluctuations, both the along-shore currents rounding the

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[7] Washburn et al. (2011) [573] identified wind relaxation events using the first zero-crossing of the first EOF of the major principal axis wind time series from four NDBC buoys located near the 300 m or 400 m isobaths between Point Sal and Santa Barbara to the north and south of Point Conception.

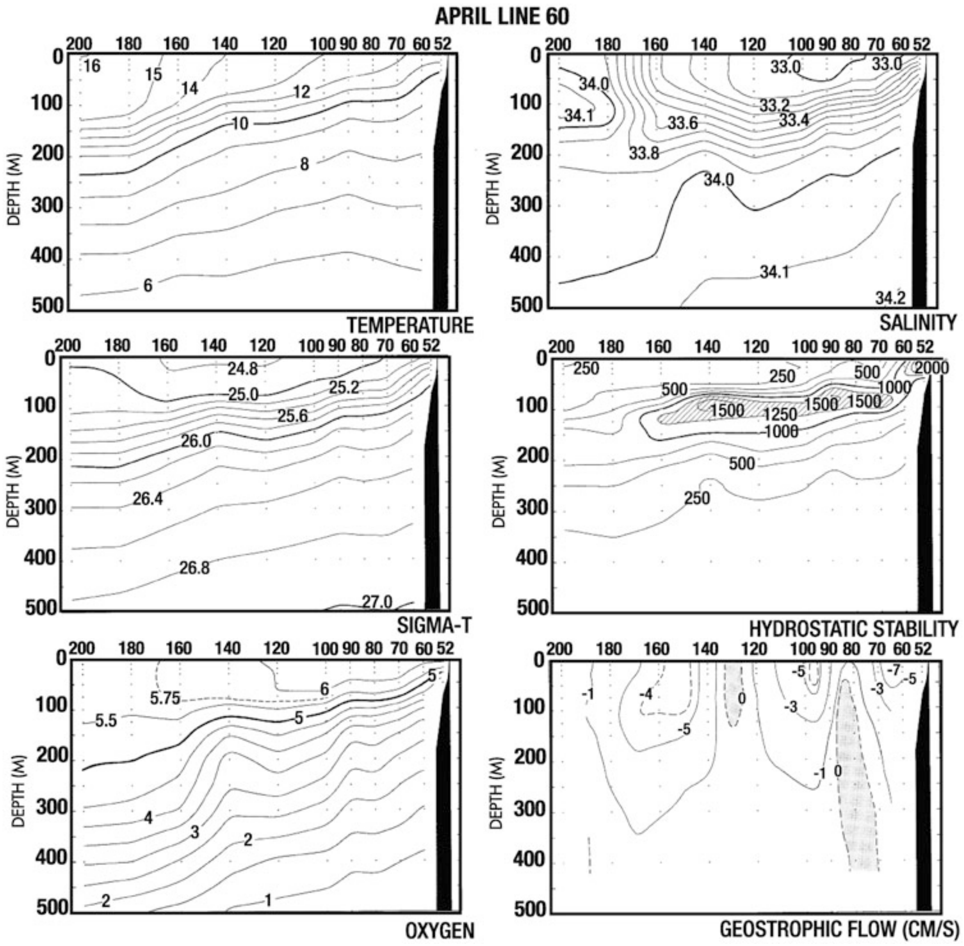

Fig. 2.34 Orthogonal sections of averaged properties at standard depths along CalCOFI line 60 off San Francisco centered on April (with an average width of 55 days) during the 1950–1978 period. *Left upper panel*: Temperature (°C). *Left middle panel*: Density plotted as sigma-t. *Left lower panel*: Oxygen concentration (mL/L). *Right upper panel*: Salinity (ppt). *Right middle panel*: Hydrostatic stability calculated as $d\sigma_t/dZ \times 10^5$. *Right lower panel*: Geostrophic velocity referenced to 500 db (meters) (cm s^{-1}). Negative velocities indicate southward flow (Redrawn from [336])

headland, and the associated cross-shore currents moving shoreward at the surface should have significant implications for transport of larvae of both invertebrates and any fishes that are spawning in the area.

The mechanisms underlying wind-related current reversals can be understood using numerical models. Poleward currents that develop following wind relaxation events are driven by pressure gradients set up by equatorward wind-driven flow on the continental shelf, interacting with variations in bathymetry and coastline shape ([573] citing [177]). Poleward pressure gradients develop south of coastal headlands during equatorward wind forcing, and equatorward pressure gradients develop north of headlands. Equatorward winds drive offshore surface Ekman transport, creating equatorward Coriolis forces produced by a compensatory deep onshore flow.[8] The equatorward Coriolis forces are balanced by the poleward pressure gradient south of the headlands. When the equatorward wind relaxes, the pressure gradient south of the headlands becomes unbalanced as the surface offshore Ekman flow weakens, the deeper onshore compensatory flow weakens, and the associated Coriolis forces weaken. Unbalanced pressure gradients force nearshore currents poleward around the headlands. The model shows that southward pressure gradients north of the headlands remain balanced by non-linear advection of equatorward momentum as the coastal currents accelerate around the headland ([573] citing [177]) (Fig. 2.37). Larger scale poleward pressure gradients develop in the model, consistent with more extensive poleward currents over the continental shelf during wind relaxation events ([573] citing [177]). In this way, warmer waters of the Southern California Bight, moving north along the shelf during wind relaxation events, displace colder, previously upwelled waters further offshore [573].

2.6.1.2 Eddy-Like Flows

From the inception of the CalCOFI program it was apparent that eddy activity was ubiquitous in the California Current System. Early studies of the seasonal and inter-annual variability of the circulation showed very irregular dynamic topography, which was originally ascribed to internal waves of semi-diurnal period [465]. Removal of the tides considerably smoothed the along-shore flow, but did not remove all of the smaller features [131, 465]. The application of a new

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[8] Both directed to the right of the downstream flow in the northern hemisphere.

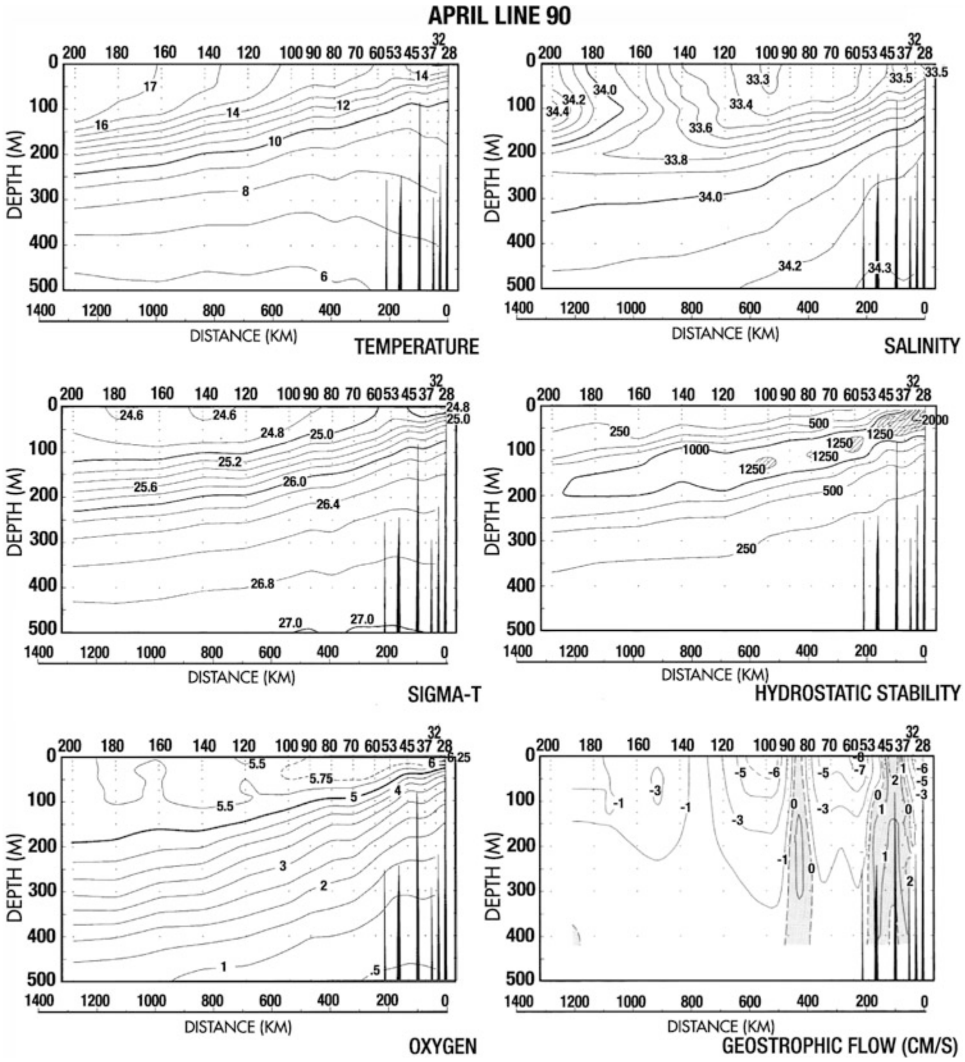


Fig. 2.35 Orthogonal sections of averaged properties at standard depths along CalCOFI line 90 crossing the southern California region centered on April (with an average width of 55 days) during the 1950–1978 period. *Left upper panel*: Temperature (°C). *Left middle panel*: Density plotted as sigma-t. *Left lower panel*: Oxygen concentration (mL/L). *Right upper panel*: Salinity (ppt). *Right middle panel*: Hydrostatic stability calculated as $d\sigma_t/dZ$ X 10^5. *Right lower panel*: Geostrophic velocity referenced to 500 db (meters) (cm s^{-1}). Negative velocities indicate southward flow. Spikes reflect the complex bathymetry of the SCB (Redrawn from [336])

instrument, the Geomagnetic Electro-Kinetograph showed that underway hourly measurements of surface currents were far more variable and were not representative of the 24 h-averaged surface currents at one position which represented the mean large-scale flow (Fig. 2.39) [465]. Studies with drogues and time series measurements of the flow indicated that there was considerable eddy activity at both diurnal and semi-diurnal periods with differences between inshore and offshore [465]. Reid (1988) reported that "we seemed to find eddy-like surface flow wherever we followed drogues" [465]. These eddies had no surface manifestation, did not affect the mixed layer depth, and had no outcropping of cooler, denser water. Horizontal shear associated with the eddies that they studied occurred below the mixed layer and there would have been no SST signal detectable from satellites [465] (even if the technology had been available at the time).

Methods used to detect eddies have improved during the long CalCOFI time series and are now largely based on remote sensing imagery (SST, ocean color, altimetry and synthetic aperture radar) or high-frequency radar closer to shore. Since the advent of satellite oceanography, images of SST and ocean color are often used to illustrate the surface manifestation of eddies [574]. Sea surface height anomalies derived from melded altimetry data sets now play a key role in delineating mesoscale eddies, since they reflect the pressure balance over the water column, whereas SST only shows surface features in the upper few centimeters and ocean color sensors detect chlorophyll-a to one optical depth. Altimetry is also not affected by cloud cover, unlike SST and ocean color sensors. Cloudiness is a serious problem for remote sensing in the California Current System, especially in the spring and summer when upwelling of cool water causes the formation of a dense marine layer of clouds that SST and ocean color sensors cannot penetrate (see mid-May to end of June in Fig. 2.40). Techniques for detecting mesoscale eddies from altimetry include detection of closed contours of sea surface height anomalies, and calculation of the Okubo-Weiss parameter, an index of vorticity [111, 112].

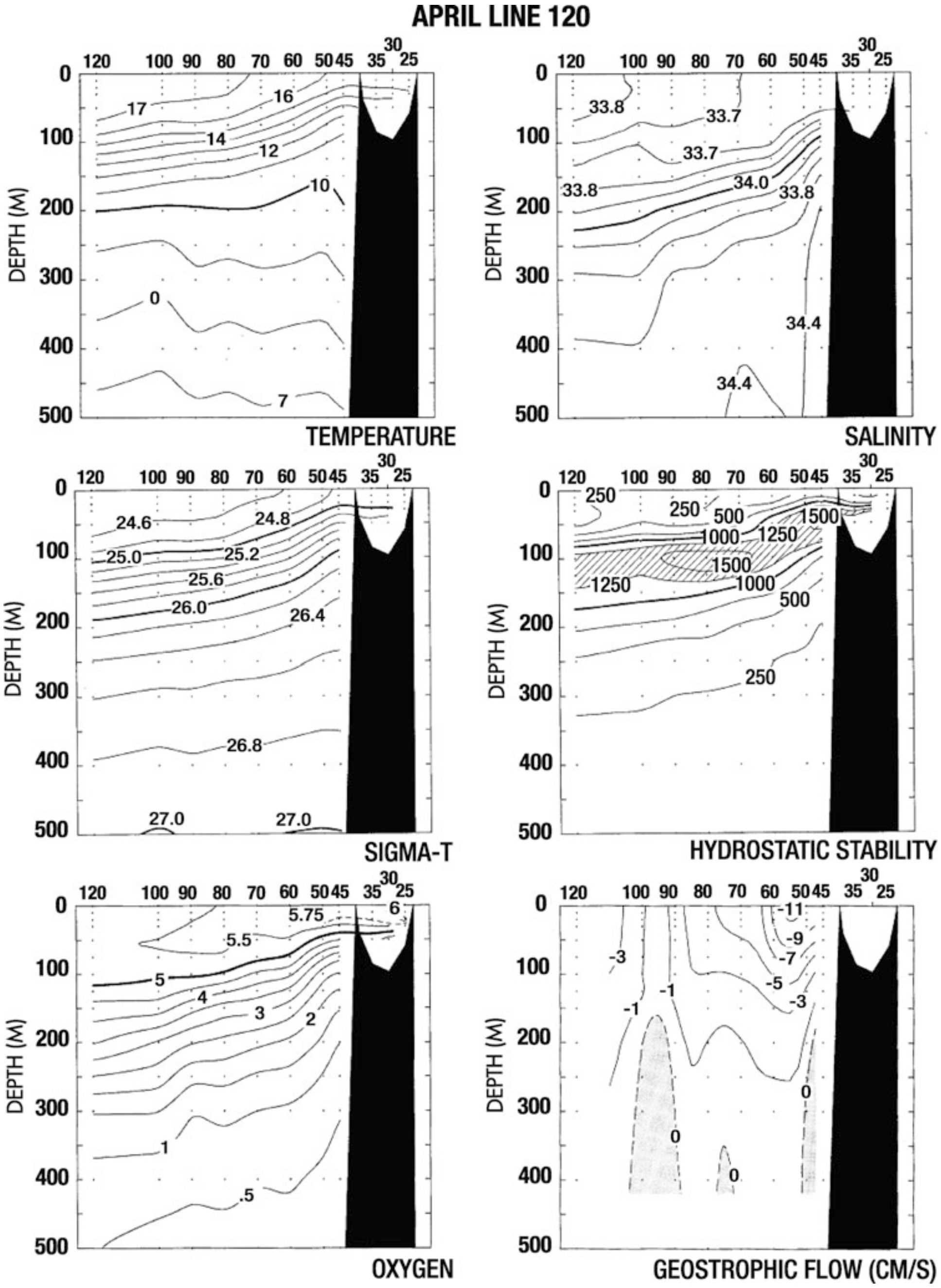


Fig. 2.36 Orthogonal sections of averaged properties at standard depths along CalCOFI line 120 off Punta Eugenia, Baja California centered on April (with an average width of 55 days) during the 1950–1978 period. *Left upper panel*: Temperature (°C). *Left middle panel*: Density plotted as sigma-t. *Left lower panel*: Oxygen concentration (mL/L). *Right upper panel*: Salinity (ppt). *Right middle panel*: Hydrostatic stability calculated as $d\sigma_t/dZ$ X 10^5. *Right lower panel*: Geostrophic velocity referenced to 500 db (meters) (cm s^{-1}). Negative velocities indicate southward flow (Redrawn from [336])

Sub-mesoscale eddies (diameters < 50 km, 70 % with diameters of 10 km or less) in the Santa Barbara Channel and Santa Monica-San Pedro Basin have also been well-resolved by synthetic aperture radar imagery from satellites [140] and high-frequency radar from shore stations [51].

Stegmann and Schwing (2007) [532] characterized eddies lasting more than 35 days as robust eddies, and those lasting longer than 70 days as long-lived eddies. Long-lived eddies are surprisingly persistent. Cyclones last 137 ± 53 days on average and anticylones persist for 152 ± 69 days [532]. In the case of long-lived eddies, mean longevity, propagation speed and size did not differ significantly as a function of direction of rotation. About twice as many long-lived cyclonic eddies form each year between 30–45°N. Both Stegmann and Schwing (2007) [532] and DiGiacomo and Holt (2001) [140] found that almost all of the eddies in the SCB were cyclonic. Earlier work reported that the average lifetime of eddies in the California Current System was about 100 days but Stegmann and Schwing (2007) [532] found that some eddies persisted for two or three times as long, and that 15 % of eddies lasted more than 200 days. In Sect. 4.2.2.1 discuss studies concerning the effects of eddies on small pelagic fish survival.

Although the California Current is sometimes depicted as a straight flow it is actually composed of meandering jets with an area of characteristically higher variability on

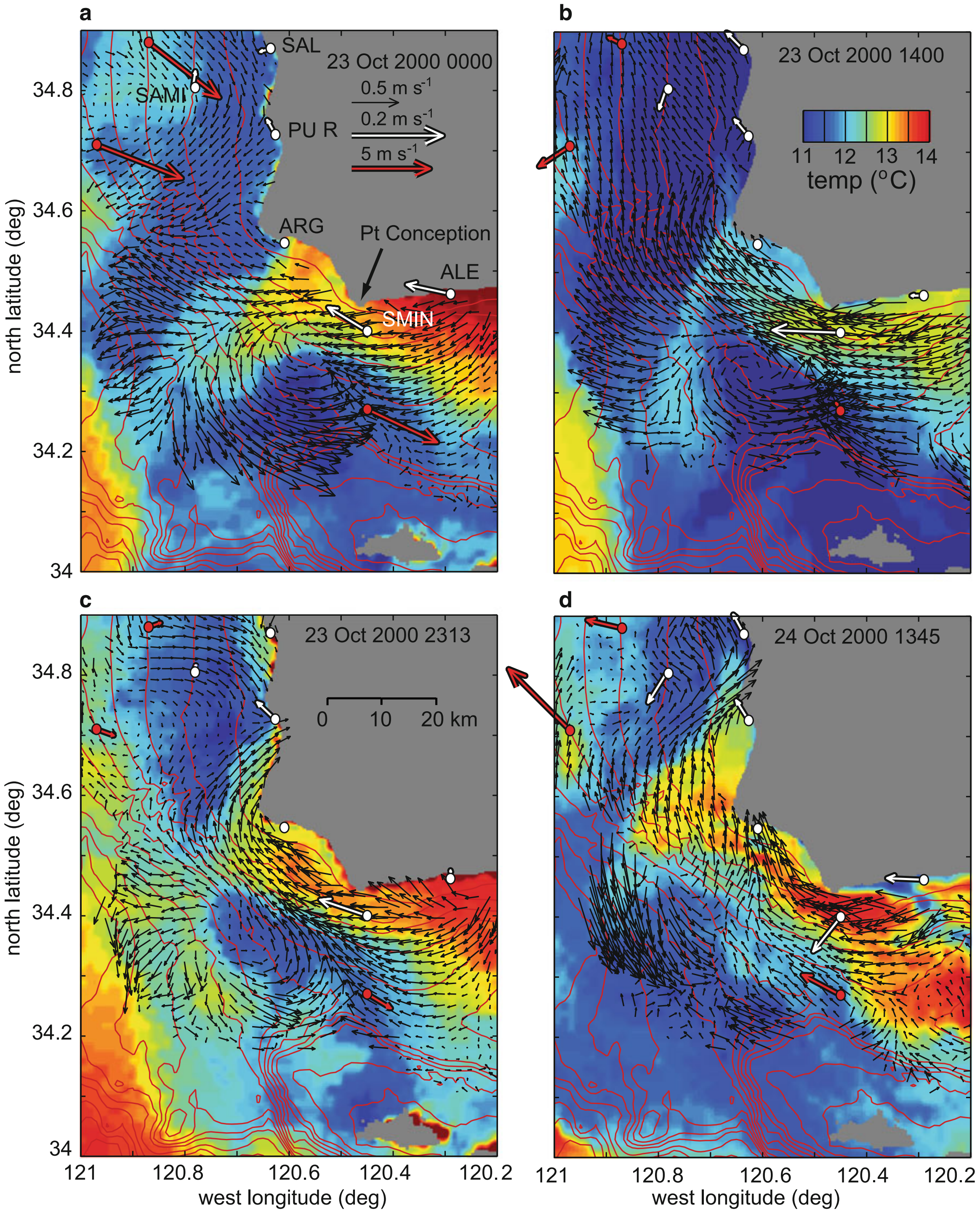


Fig. 2.37 Satellite sea surface temperature (SST) images and surface currents overlaid on bathymetry around Point Conception following a wind relaxation event on October 22, 2000. Isobaths at 50, 100 and subsequent 100 m depths are the red lines. Colored background is SST. *Small black arrows* show surface current vectors from HF radars centered on the times in the *top right* of each image (From [573])

its western edge that has been referred to as "eddy alley" [339]. The processes generating the higher variability and mesoscale anticyclonic (clockwise, warm-core, downwelling center) eddies on the western margin of the current are not well understood. It appears that variability increases with increasing advection [136]. In other words, there are more anticyclonic eddies in years when the flow of the California Current is stronger.

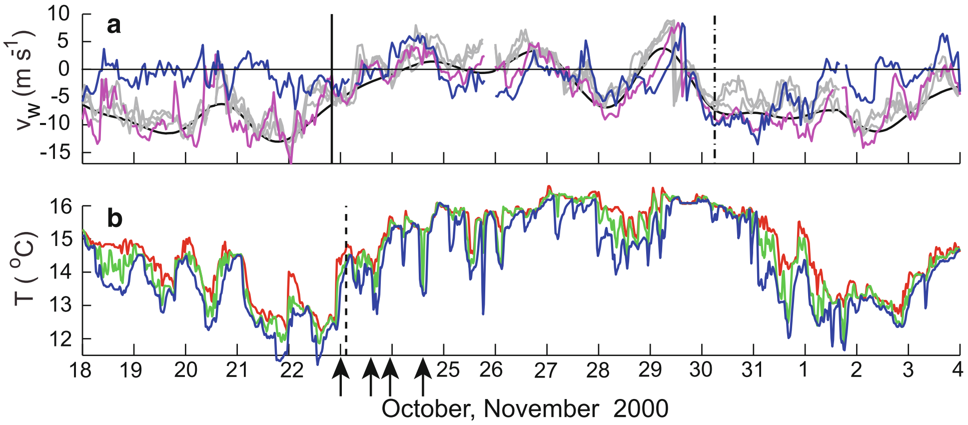


Fig. 2.38 Along-shore wind velocities and water temperatures at a mooring on the 15 m isobath at Point Arguello, just north of Point Conception, October 18–November 4, 2000. Along-shore winds are from 2 NDBC buoys near the 400 m isobath to the south of Point Conception (*magenta and blue lines*), and 3 buoys to the north of Point Conception on the same isobath (*gray lines*). The *smooth black line* is calculated from the first EOF of wind velocity at one of the buoys south of Point Conception. Beginning time and ending time of wind relaxation are indicated by *vertical lines* in (**a**). Poleward winds are positive. *Vertical line* in (**b**) indicates the arrival time of warm water (From [573])

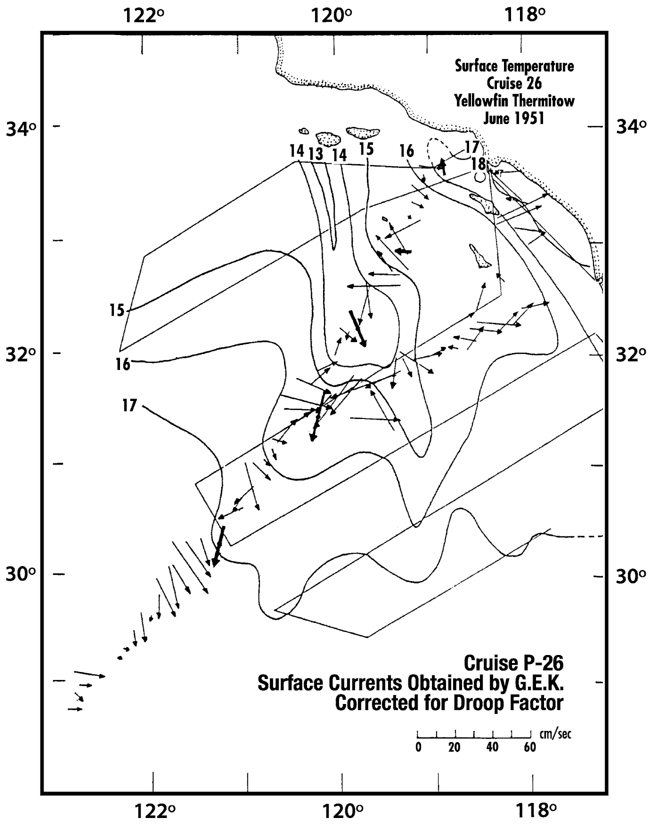
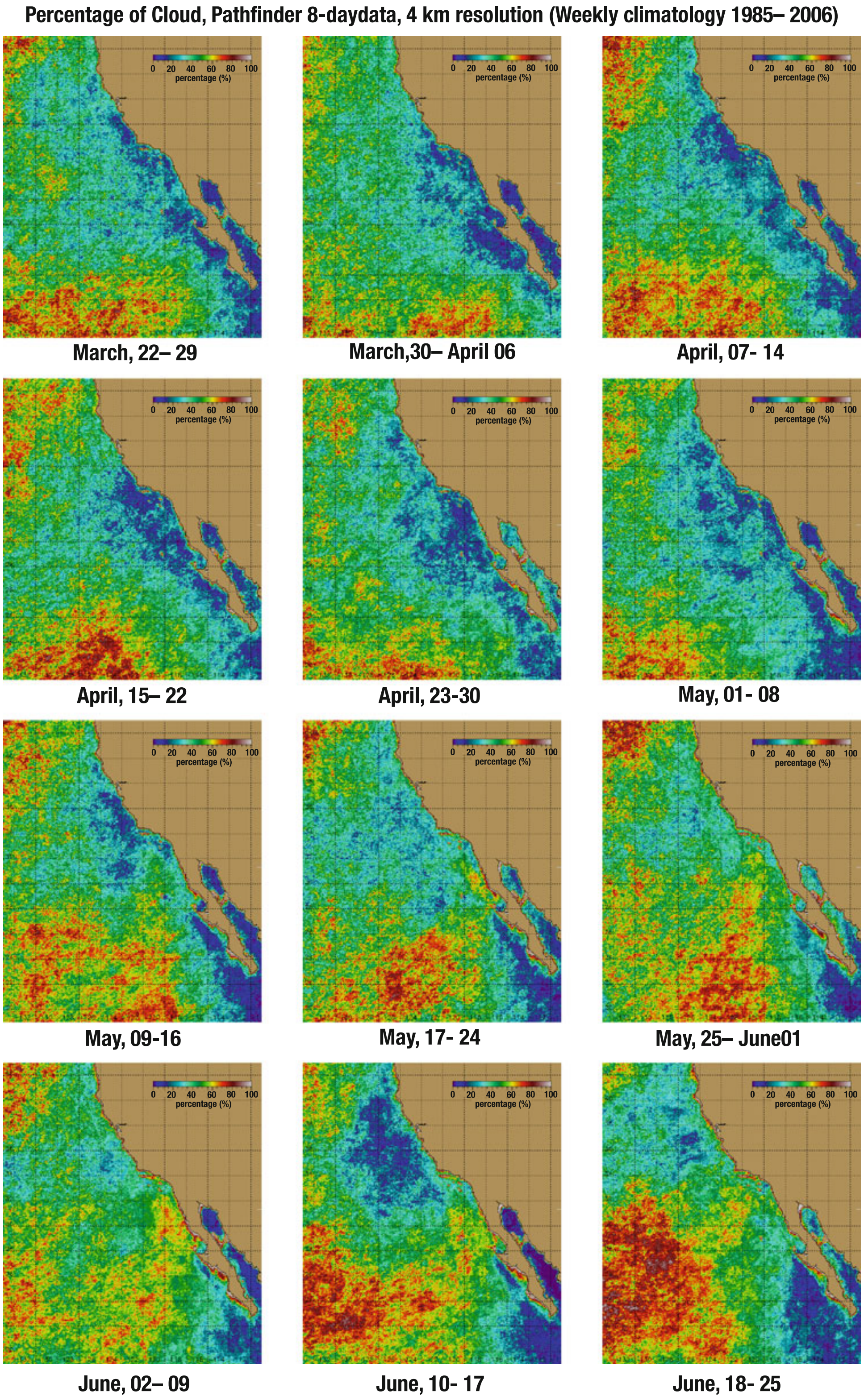


Fig. 2.39 Surface temperature and surface currents in June 1951. *Heavy arrows* are the 24 h-averaged surface current (From [465])

2.6.2 Southern California

The ocean off southern California is a nutrient-limited region where the depth and concentration of primary production is driven by five mechanisms: large-scale advection, geostrophic enhancement of current flow, convectively-driven seasonal overturn limited, seasonal wind-driven coastal upwelling, and wind stress curl [58–60,107,108,357]. Geostrophic enhancement and wind stress curl show many of the same effects, but the forcing may differ, as in the case of rotational currents creating eddies. Since coastal upwelling is less important off southern California than along the central California coast, winter convection and geostrophy appear to be more significant than upwelling in



March, 22– 29

March,30– April 06

April, 07- 14

April, 15– 22

April, 23-30

May, 01- 08

May, 09-16

May, 17- 24

May, 25– June01

June, 02– 09

June, 10- 17

June, 18- 25

Fig. 2.40 Average cloudiness in the California Current System from mid-March to mid-June including the period of the spring spawning of sardine (Image produced by K. Nieto, 2010–2011 NRC postdoc, SWFSC)

regulating the spatial and temporal pattern of chlorophyll. Winter input of nutrients into the euphotic zone driven by physical forcing on an annual cycle may set the conditions for phytoplankton growth in the following year [357]. This suggests than an important lag in the system may be the 3 to 6 month lag between winter convective mixing and spawning when considering the recruitment of spring-spawning fishes.

Fig. 2.41 Summer (July 23–24, 1998) along CalCOFI line 77 just north of Point Conception (**a**) Temperature (°C, *black lines*) section with geostrophic current speeds (cm s^{-1}, *gray lines*) superimposed. *Solid contours* indicate poleward flow, *dashed contours* indicate equatorward flow. (**b**) Matching salinity section (From [357])

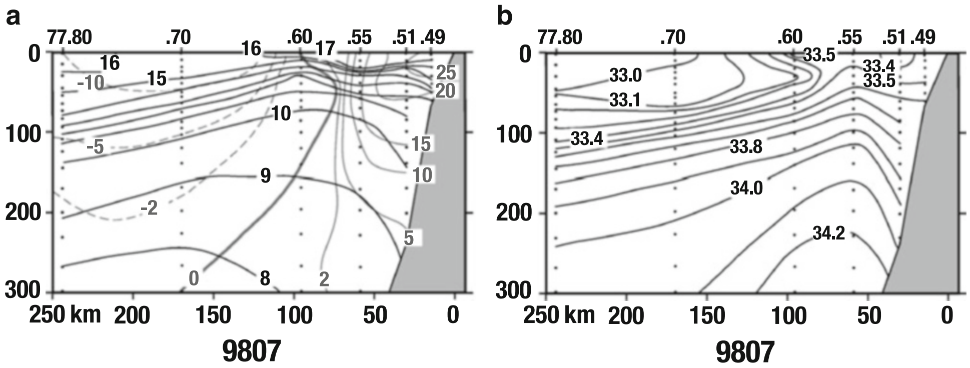
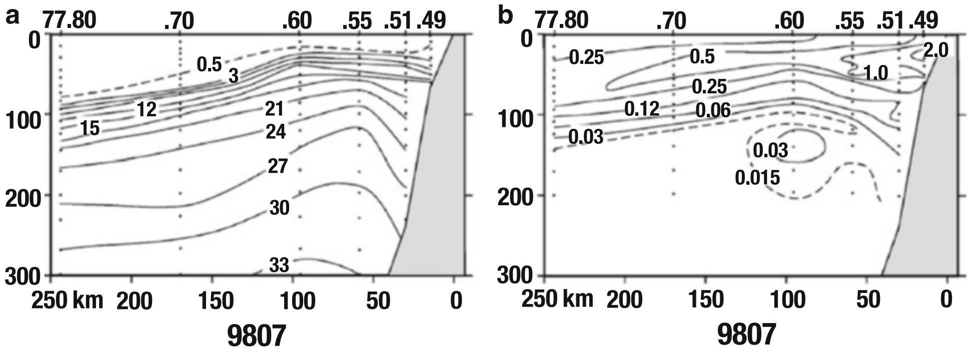


Fig. 2.42 Summer (July 23–24, 1998) along CalCOFI line 77 just north of Point Conception (**a**) Nitrate (μM L^{-1}) section. (**b**) Matching chlorophyll-a (μg L^{-1}) section (Modified from [357])



2.6.2.1 Nutrient Enrichment

Geostrophic Adjustment

Geostrophic adjustment to current flow can be seen in the doming of isotherms and isopycnals in the summer (July 23–24, 1998) along CalCOFI line 77, just north of Point Conception. The slope of the isotherms and isopycnals reverses at the point offshore where currents reverse from poleward to equatorward (Fig. 2.41, [357]). The effect of geostrophic adjustment on nitrate concentration is visible in the uplift of the isopleths and shoaling of the nitracline (Fig. 2.42). Enhanced primary production at the nitracline is evidenced by the sub-surface chlorophyll maximum (Fig. 2.42, [357]).

The effect of geostrophic adjustment on nutrient enrichment is also clear in surfaces of dynamic height and nitracline depth in a summer CalCOFI cruise (July 2–17, 2002) (Fig. 2.43, [357]). Geostrophic flows are stronger where dynamic height anomaly streamlines are closer together. The meandering flow of the California Current can be seen in Fig. 2.43c, associated with shoaling of the nitracline from 50–60 m to 10–20 m (Figs. 2.43b and 2.42a) on the eastern margin of the current. The depth of the chlorophyll maximum shoals from 60 to 30 m (Fig. 2.43a), with an associated increase in the concentration of chlorophyll (see Fig. 2.54b). A cyclonic eddy (counter-clockwise rotating) in the southwest of the survey is evident in the circular-shaped depression of dynamic height anomalies (Fig. 2.43c). The eddy caused doming of the nitracline from 90 to 70 m (Fig. 2.43b) and shoaling of the chlorophyll maximum layer from 80 to 70 m (Fig. 2.43a). An anticyclonic eddy (clockwise rotation) in the northwest of the survey grid can be seen from the circular-shaped elevation of dynamic height anomaly, which caused deepening of both the nitracline and the chlorophyll maximum from 40 to 70 m (Fig. 2.43a and b) [357]. The cyclonic Southern California Eddy centered in the SCB can also be seen as a depression in the dynamic height anomaly (Fig. 2.43c) associated with a smaller elevation of the nitracline from 20 to 10 m (Fig. 2.43b) and shoaling of the chlorophyll maximum from 30–40 m to 10 m (Fig. 2.43a).

Seasonal Convective Overturn

Convective overturn is driven by instability in the water column created by changes in the vertical density distribution. The seasonal cycle of water column instability can be indexed by the timing of maximum surface density (minimum SST), which differs from inshore to offshore off southern California (Fig. 2.44, [339, 357]). The date when maximum surface density occurs in the SCB varies from early February in the California Current to mid-May in the upwelling plume off Point Conception (Fig. 2.44). Both winter convection and seasonal upwelling around Point Conception play a role in creating instability by lifting the density surfaces [357]. Although the amplitude of the seasonal cycle is reduced off southern California relative to other areas of the California Current System, seasonal convective overturn is an important process for nutrient enrichment because of the lesser importance of other, stronger enrichment processes, such as

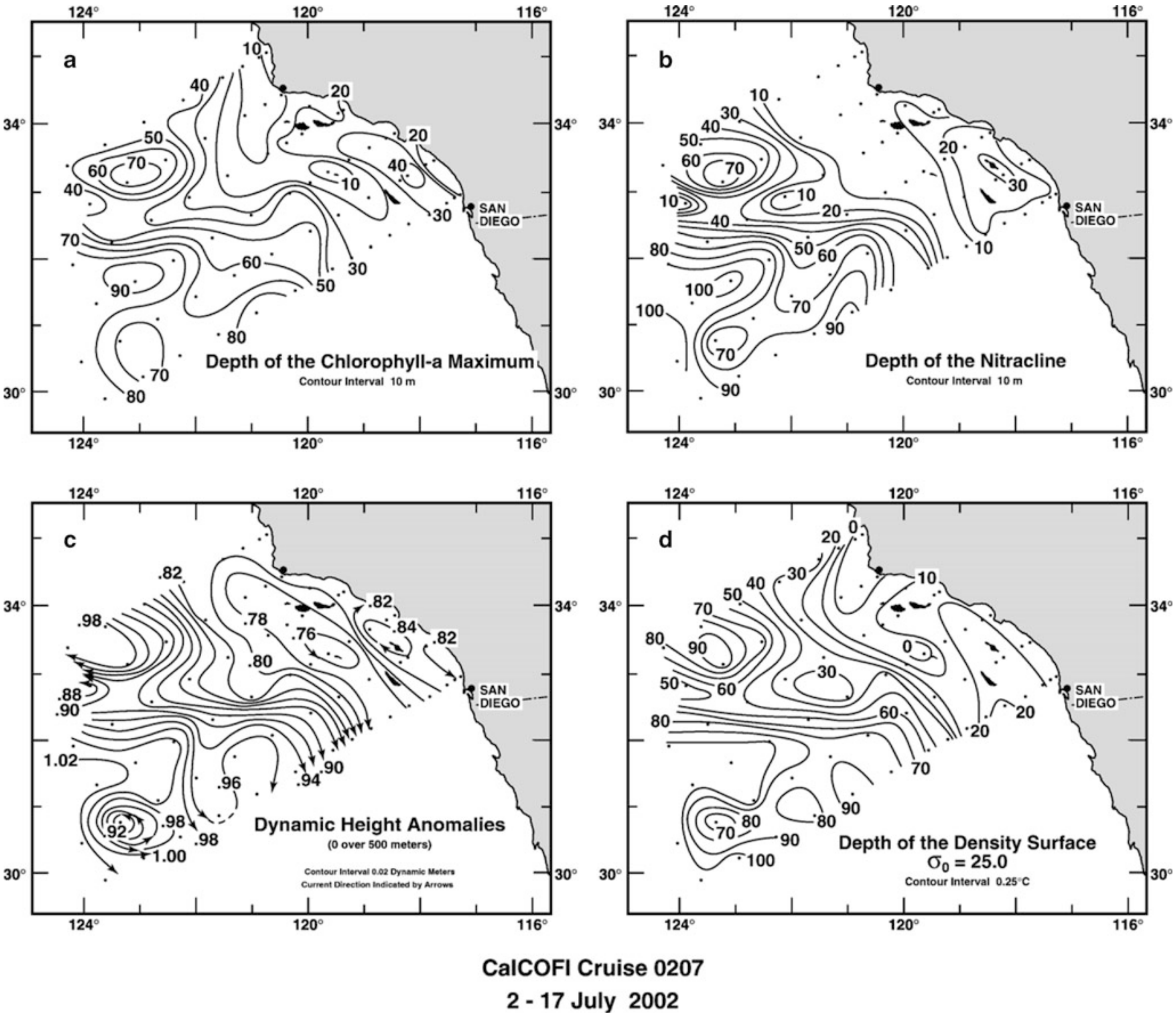


Fig. 2.43 Surfaces from the July 2002 CalCOFI survey. (**a**) depth of the chlorophyll maximum; (**b**) depth of the nitracline (nitrate = 1.0 μM L^{-1}); (**c**) geostrophic currents based on dynamic height relative to 500 m; (**d**) depth of σ_t = 25.0 surface (Modified from [357])

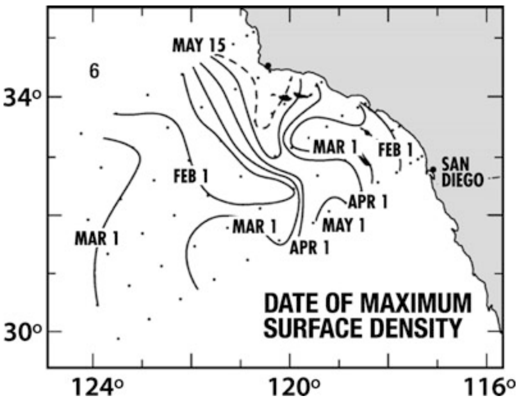


Fig. 2.44 Mean date of maximum surface density over the core CalCOFI sampling area from 1984–2004 (Modified from [357])

upwelling [357]. Following winter convective overturn, the nitracline reaches its shallowest depth (mixed layer shallower than 10 m), and primary production is set for the following year, until the next seasonal replenishment of nitrate. The depth of winter mixing affects the phytoplankton production, so Mantyla et al. (2008) [357] suggested that winters with shallower convective overturn are followed by less production, while winters with deeper mixing prime the system for greater production in the months to follow. They showed a negative relationship between a 4-season mean integrated chlorophyll (mg Chl$a$ m^{-2}) and the mean winter temperature at 10 m depths for inshore stations (stations inshore of CalCOFI station 100 in the core area) from 1984–2004 [357]. While the data are variable, and the relationship could be further investigated, the data do support the idea that the degree of winter convective overturn affects the subsequent level of phytoplankton production in the nearshore SCB. This has considerable implications for the spring spawning of small pelagic fish in the SCB. Recent models of sardine and anchovy spawning habitat incorporated this idea by including a proxy for phytoplankton production based on the depth of the maximum oxygen concentration as a predictor in the models [580]. Subsurface variables improve the Weber and McClatchie (2010) [580] spawning habitat model for anchovy, but not for sardine (Sect. 4.2.2.3).

Wind Stress Curl in the SCB

Winds are upwelling-favorable all year-round in the California Current System south of San Francisco, which contributes to the nutrient enrichment and productivity of the region [107]. However, in the SCB, upwelling occurs primarily around Point Conception. Classical wind-driven upwelling is restricted to a very narrow band along the coast ([107] attributed to [593]), on the order of 20–40 km, so large-scale upwelling must be driven by wind stress curl [107].

Wind stress curl controls vertical advection through “Ekman pumping” in regions offshore from the effects of coastal boundaries [43, 593], and so controls a wide range of physical, chemical and biological effects on ecosystems. The mechanisms for these effects include changes in current flows, the generation of baroclinic Rossby waves, and association between cyclonic wind stress curl and the formation of poleward coastal undercurrents. Vertical transfer of physical and chemical properties by Ekman pumping can have major biological effects on production (see Sect. 2.4.2 and references in [43]). Until the advent of satellites with scatterometer sensors, the finest-scale calculations of wind stress curl in the California Current System were 2° latitude or longitude [414]. Bakun and Nelson (1991) [43] were able to interpolate these computations to 1° latitude or longitude using objectively filtered mapping.

While the dominant signals of variability in the California Current are not related to the local wind field, there are secondary aspects of physical variability that are related to wind forcing [107]. Chelton (1982) [107] argued that the earlier studies by Bernal, Chelton and McGowan [58,59,108] could not detect the smaller scales of variability across the shelf because they used large-scale averaging to determine the larger scales of variability. Chelton (1982) pointed out that if coastal wind-driven upwelling was the only driver for production, then zooplankton production should be highest at the coast, decreasing toward the offshore.[9] In fact this is only the case to the south of CalCOFI line 100 [107], off Ensenada (32°N) (Fig. 1.7).

To the south of Ensenada and the Ensenada Front, the peak in zooplankton is near to the coast [53, 107]. However, Chelton (1982) used the CalCOFI survey data to show that there is a peak in spring and summer mean zooplankton displacement volume[10] at about 50–150 km distant from the coast along CalCOFI lines 60 (off San Francisco), 70 (south of Monterey), 80 (off Point Conception), and 90 (off San Clemente, CA) (Fig. 2.45). In short, from San Francisco to northern Baja California, zooplankton abundance is greatest about 100 km offshore, but further south the zooplankton are more abundant near the coast. Chelton (1982) argued that while phytoplankton production is greatest at the coast due to upwelling, and while an associated peak in zooplankton biomass might have been missed due to the CalCOFI sampling pattern (which at that time, in the early 1980s, lacked very nearshore stations), the offshore peak in biomass is still a significant feature of the California Current System.

The offshore peak in zooplankton displacement volume to the north of Ensenada occurs in the region of highest current shear, where the mean integrated current reverses between an equatorward 0–500 m integrated offshore flow and poleward flow nearer to the coast (Fig. 2.46). The 50–100 km offshore area between San Francisco and Ensenada is an area of very low flow, where zooplankton populations would not be dispersed [107].

Further to the south, there is still a region of flow reversal 50–100 km offshore, but coastal upwelling appears to control zooplankton production, since the peak zooplankton abundance occurs near the coast [107]. Off northern Baja California, relationships between cross-shore chlorophyll-a structure and the seasonal wind forcing are weakest despite

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[9] The assumption that zooplankton production would be highest at the coast might not be true if the time lag for zooplankton production was long enough for zooplankton to be transported away from the coast. Nevertheless since upwelling is is restricted to about 40 km from the coast (approximately one Rossby radius), the peak in zooplankton production would still be expected nearer to the coast than the observed maxima that is found approximately 50–150 km offshore.

[10] Chelton (1982) [107] referred to zooplankton displacement volume (DV) as zooplankton biomass which, strictly speaking, it is not since the units of DV are mL 1,000 m^{-3} (Chelton used mL 10 m^{-3}) rather than Carbon or dry weight m^{-3}. DV has been used a rough proxy for biomass in many studies, but see [297, 298].

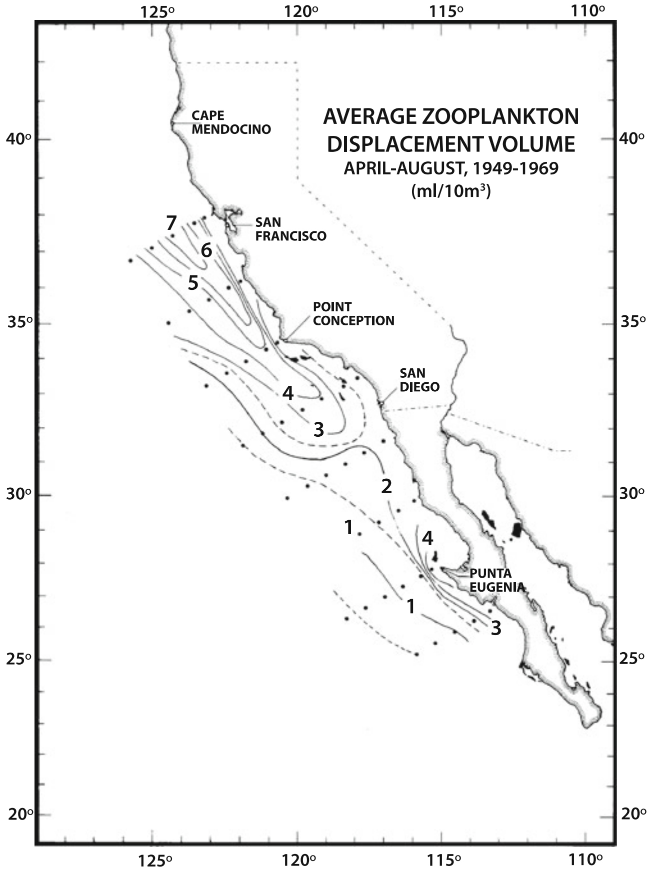

Fig. 2.45 Spring and summer distribution of zooplankton displacement volume in the California Current System. April–August means were computed at 200 km (along-shore) and 65 km (cross shore) resolution (From [107])

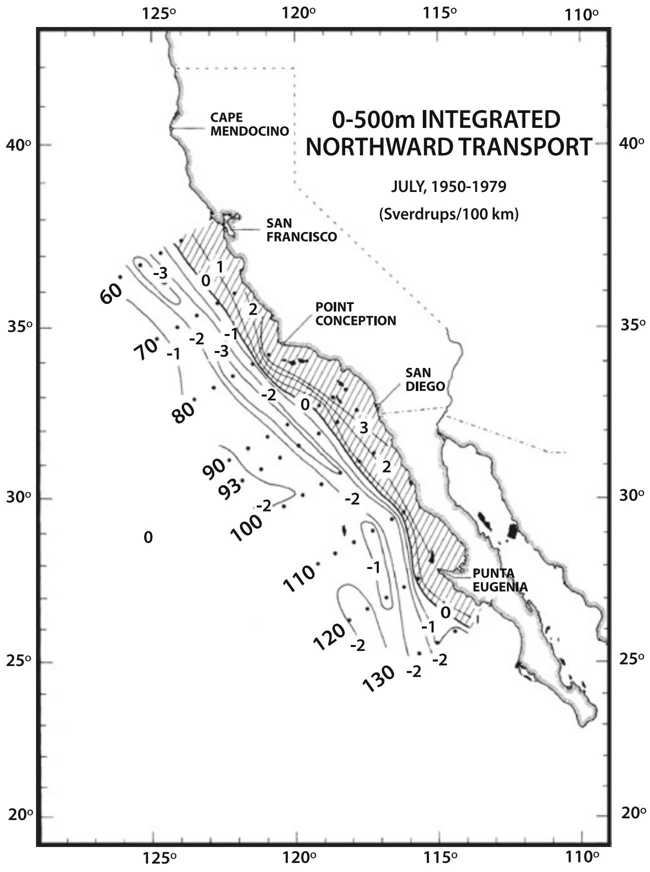

Fig. 2.46 Seasonally averaged along-shore geostrophic transport for the month of July for 1950–1979 referenced to 500 m. *Shaded region* indicates poleward transport. *Numbers* at the left of the figure are CalCOFI lines (Modified from [107])

upwelling-favorable wind stress all year around (although there is a maximum period of upwelling-favorable wind stress in spring and early summer) [556]. Southern Baja California has the same seasonal peak in wind forcing as northern Baja California, and year around upwelling-favorable wind stress, but wind stress is stronger than off northern Baja California. Similar to northern Baja California, there is no consistent relationship between cross-shore chlorophyll-a structure and wind forcing off southern Baja California [556].

Chelton (1982) described the flow of the California Current as having two modes: the nearshore, poleward counter flow and an offshore equatorward flow. This nearshore flow is called the California Countercurrent, and north of Point Conception it is called the Davidson Current. Both flows extend from the surface to a depth of 500 m but differ in their seasonality. The nearshore, poleward flow varies weakly with the seasons, whereas the offshore mode has strong seasonal variability. The offshore mode is weakest in the late fall and early winter, and in those seasons the nearshore, poleward mode is evident from Ensenada to San Francisco from the surface to 500 m depth (Fig. 2.47). When the offshore mode is strong in late spring and early summer, the nearshore, poleward counterflow is reduced or disappears in the surface layer, but remains evident as a deep poleward flowing current (the California Undercurrent) [107].

The reversal in geostrophic current flow is associated with changes in sea-surface slope that affects the depth of the thermocline, and Chelton (1982) used a theoretical two-layered system to illustrate the pressure gradients (Fig. 2.48). Northward geostrophic flow implies sea surface sloping upwards toward the coast, while equatorward geostrophic flow implies sea surface sloping down toward the coast. The net effect is a trough in sea surface heights between the two flows. To compensate for reduced pressure, the thermocline domes upwards beneath the trough in sea-surface height, bringing nutrients closer to the surface, which increases primary production and the energy flow to secondary producers. Consequently enhanced zooplankton displacement volume is associated with this region of maximum vertical displacement of the isotherms or deep-water upwelling 50–150 km offshore (Fig. 2.48). Although there is some seasonal variation, deep-water upwelling is present all year. The upwelling due to uplift of the isotherms at 50–150 km offshore is distinct from wind-driven coastal upwelling which is restricted to distances 20–50 km offshore [107].

The time rate of change of thermocline depth is related to the instantaneous wind stress curl with the dynamic balance referred to as "Ekman pumping" [107]. Positive wind stress curl depresses sea surface elevation and correspondingly elevates the thermocline, so positive wind stress curl causes upwelling of nutrients from deeper in the water column. This can be seen in the uplift of the nitrate isopleths in Fig. 2.49.

The relationship between wind stress curl and sardine production was explored by Rykaczewski and Checkley (2008) [482]. Areas of positive wind stress curl are as much as 18–22 times larger than the areas of coastal upwelling, and upwelling caused by wind stress in the lee of major headlands off southern California [482] (Fig. 2.50). Mean vertical flow velocities in the smaller areas of wind-driven coastal upwelling are an order of magnitude larger than mean vertical velocities over the extensive areas of curl-driven upwelling [482]. Small areas of intense cyclonic curl with vertical flow velocities of 3–7 m d^{-1} are common in summer in the lee of prominent headlands off California. Coastal upwelling with vertical flow velocities of 7–12 m d^{-1} also occur at these headlands. In contrast, the large offshore areas of positive wind stress curl have slower vertical flow velocities of 1–4 m d^{-1} [482] (Fig. 2.50, and see also Fig. 4.41). These velocities are similar to those reported in earlier studies ([269, 450] cited in [482]).

The differences in vertical flow velocities in different areas off southern and central California have important implications for the pelagic food web. Phytoplankton cell sizes are related to the speed of upwelling because small cells have high surface area to volume ratios and more efficient nutrient uptake. Thus small phytoplankton have a competitive advantage in lower nutrient conditions associated with less vigorous upwelling and slower vertical flow velocities. Consequently the size structure of phytoplankton tends to be smaller in waters with slow curl-driven upwelling such as the large open ocean areas of the California Current System. Compared to the open ocean, the size structure of phytoplankton is larger in coastal areas with vigorous upwelling, higher vertical flow velocities, and higher nutrient concentrations (Fig. 2.51). The effect of phytoplankton particle size propagates up the food chain because smaller phytoplankters tend to be eaten by smaller zooplankton (and microzooplankton). This affects the feeding environment of small pelagic fish, for example, because sardine eat small zooplankton more effectively than anchovy. Sardine can capture small particles more effectively than anchovy because sardine have finer gill rakers than anchovy. The effect of upwelling velocities on the food web helps to explain why sardine can effectively exploit the oligotrophic offshore waters in the California Current System.

During late spring and early summer (May to July), sardine surplus production is correlated with curl driven upwelling, but is not correlated with coastal upwelling[11] (Fig. 2.52) [482]. Rykaczewski and Checkley (2008) [482] used this insight to develop an environmental index based on curl-driven upwelling that they incorporated into a surplus

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[11] Addition of coastal upwelling to a stepwise regression model predicting surplus production per unit sardine biomass from curl driven upwelling did not improve the fit of the model [482].

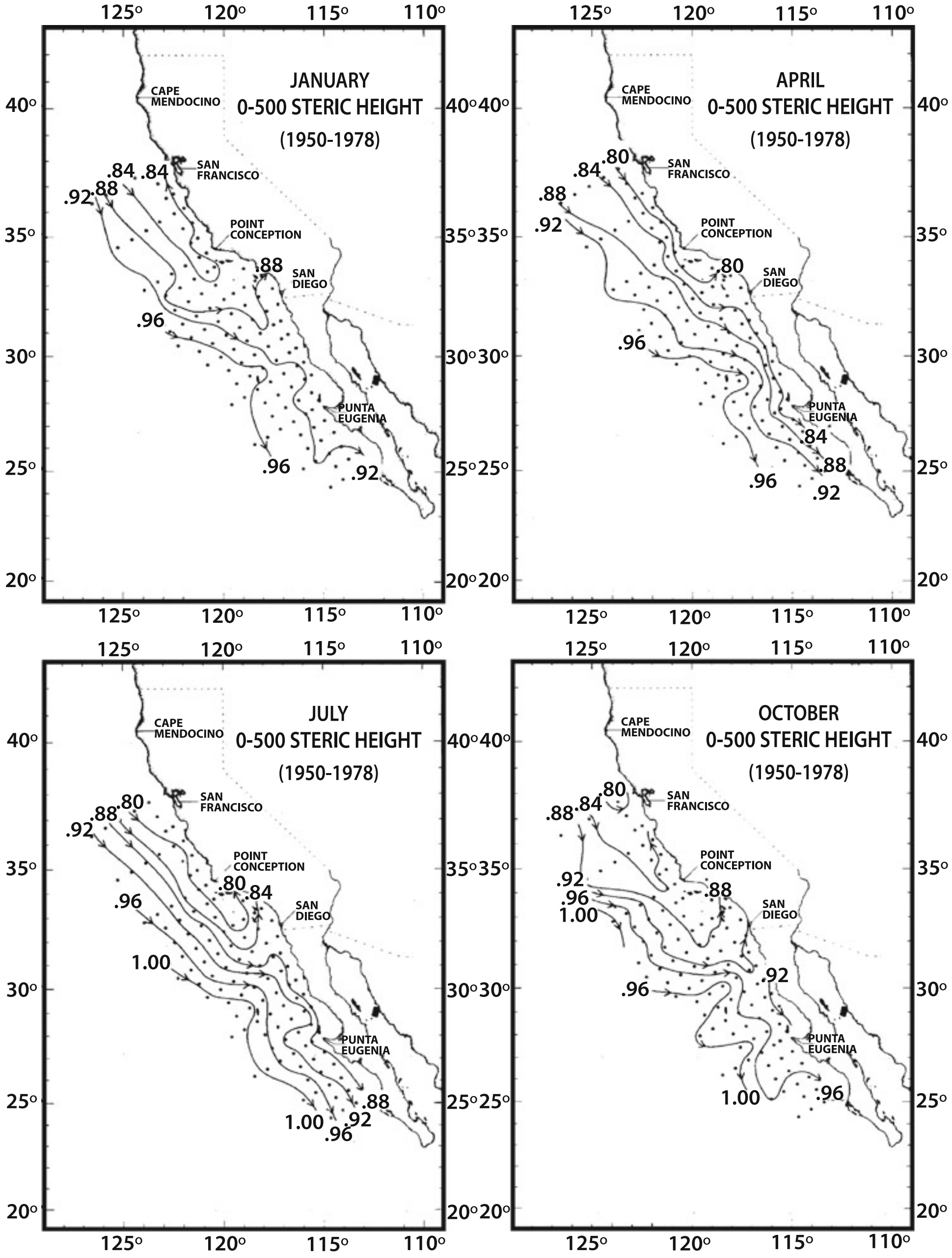

Fig. 2.47 Seasonal variability in mean steric height of the sea surface relative to 500 db. *Arrows* show the direction of geostrophic flow computed from steric height gradients averaged over 30 years (1950–1980) using harmonic analysis. Note that flows go from high to low steric height, deflected to the right by Coriolis force (Modified from [107])

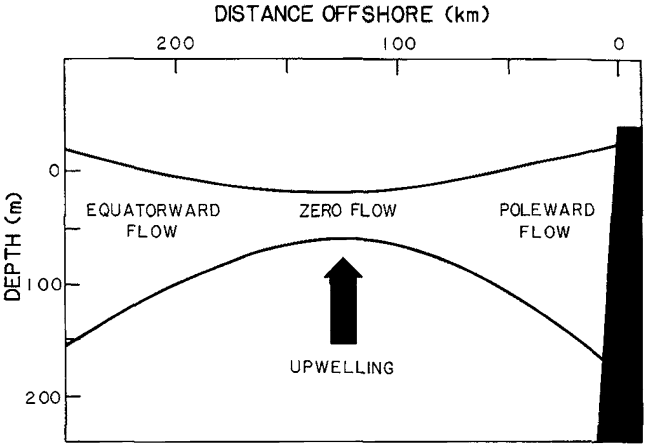

Fig. 2.48 Schematic showing how sea-surface slope differences produced by current flow reversal results in uplift of the thermocline in an idealized two-layer system (From [107])

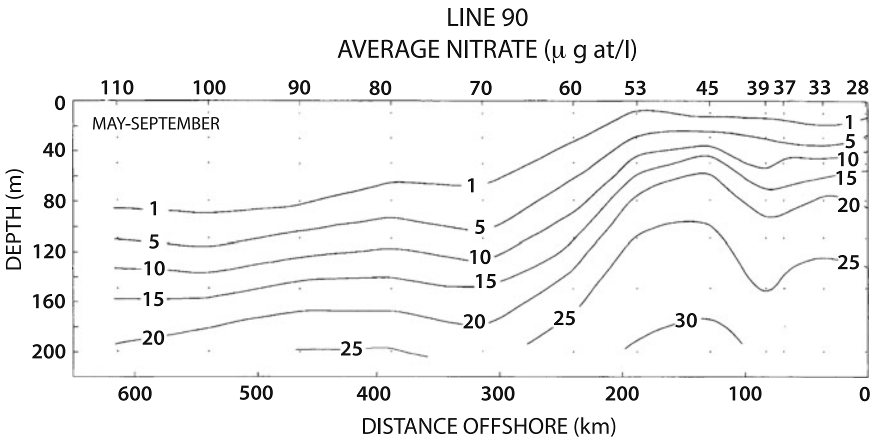

Fig. 2.49 Vertical distribution of nitrate in the spring-summer seasons of 1969, 1972 and 1978 showing the curl-driven uplift of isopleths approximately 50–150 km offshore along CalCOFI line 90 in the Southern California Bight (Modified from [107])

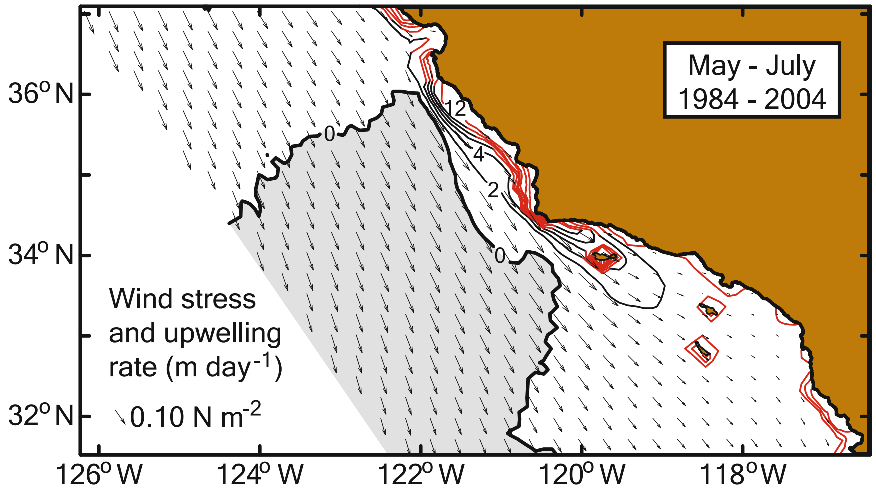

Fig. 2.50 Modeled wind stress off central and southern California for May–June 1984–2004 overlaid on contours of vertical upwelling velocities. *Black contours* indicate the region of curl-driven upwelling. *Red contours* denote coastal upwelling. Areas of anti-cyclonic curl (downwelling) are *shaded* (From [482])

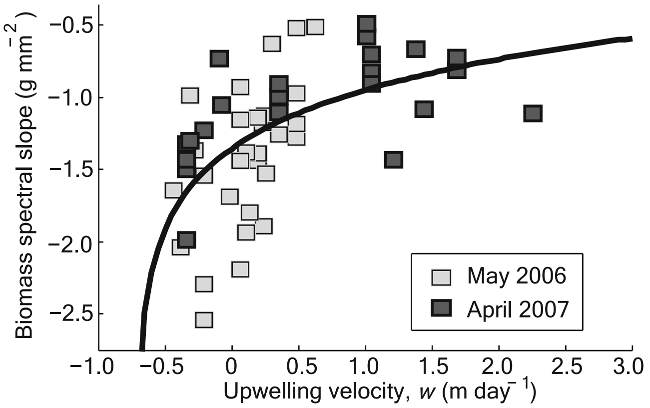

Fig. 2.51 Relationship between zooplankton size spectrum and upwelling rate. A steeper slope of the biomass spectrum occurs when there is a higher proportion of large particles in the spectrum. Data are from zooplankton collected during two cruises in May 2006 and April 2007 at LTER sampling locations near CalCOFI lines 80 and 77, from nearshore to approximately station 120 (From [482])

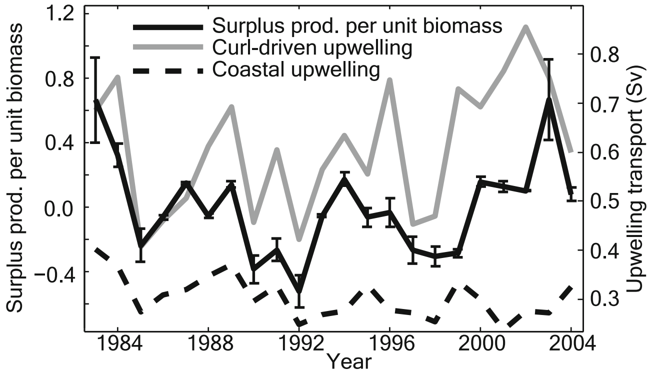

Fig. 2.52 22-year time series of coastal and curl-driven upwelling and surplus production per unit biomass of Pacific sardine. Error bars are one standard deviation of the sardine production estimates (From [482])

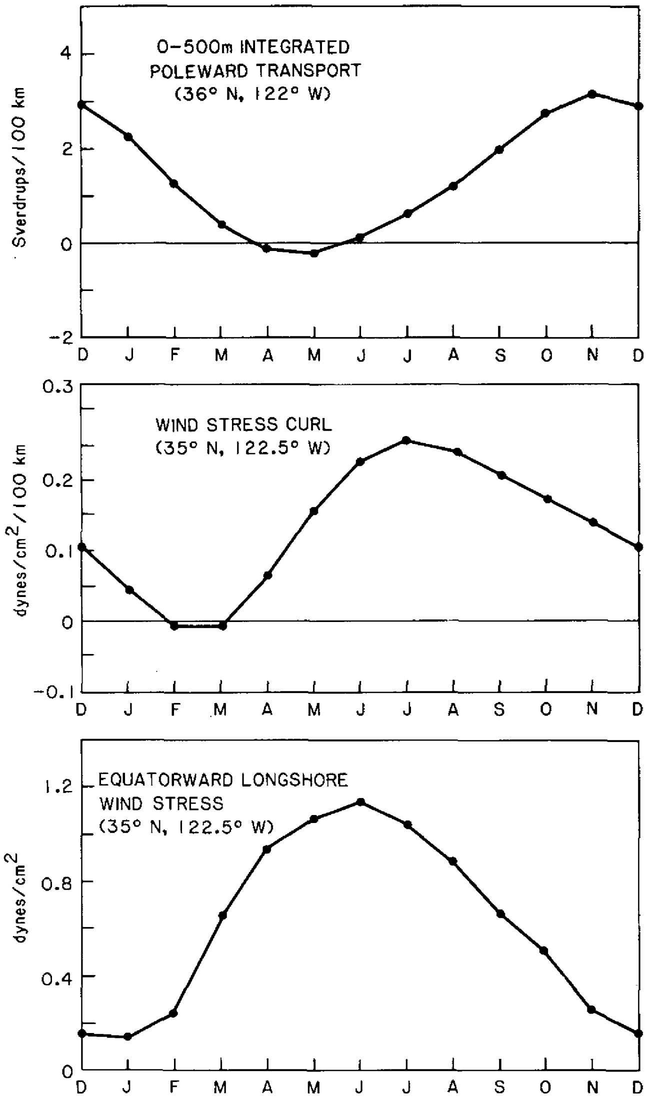

Fig. 2.53 *Upper panel*: Seasonal variation of the along-shore integrated geostrophic transport in the upper 500 m between stations 55–60 (i.e. relatively nearshore) along CalCOFI line 70. *Middle panel*: seasonal variation of the wind stress curl. *Lower panel*: Seasonal variation of equatorward along-shore wind stress (From [107])

production equation to model environmental forcing on sardine surplus production (Sect. 6.1.1.8). Interestingly, they found that the surplus production model incorporating the environmental parameter fit best when the curl-driven environmental index was averaged over May to July during 1983–2004, but fit better when averaged over October to December for the period 1948–1962 [482]. The explanation proposed for this change is that early life history stages are most strongly influenced by environment, and the southern population that spawns in the fall rather than the spring season was more dominant in years when the population size was low [482].

Sverdrup Transport in the Nearshore

The counterflow associated with increased zooplankton production offshore of southern California is opposite what would be expected from the overlying winds [107]. Chelton (1982) investigated the driving forces for the counterflow. The winds in the Bight increase to a maximum offshore, such that a jet produces a change in sign of the wind stress curl, from positive values inshore of the jet to negative values offshore of the wind jet [43, 107, 414]. The change in sign of the wind-stress curl occurs from 200–400 km offshore, roughly parallel to the coast [107]. Chelton (1982) [107] used Sverdrup's (1947) [542] equation for the steady-state response to wind-stress curl to show that nearshore positive wind-stress curl in the California Current leads to nearshore, vertically integrated, poleward "Sverdrup transport", despite the prevailing equatorward winds. The integrated transport in the upper 500 m is positive nearshore at CalCOFI line 70, stations 55–60, south of Monterey (Fig. 1.6), in all months except April-May when there is no net transport (Fig. 2.53, upper panel). Interestingly, April-May is the sardine spawning season. The poleward transport lags the wind stress curl by 3–4 months (Fig. 2.53, middle panel), and is in opposition to the equatorward wind stress

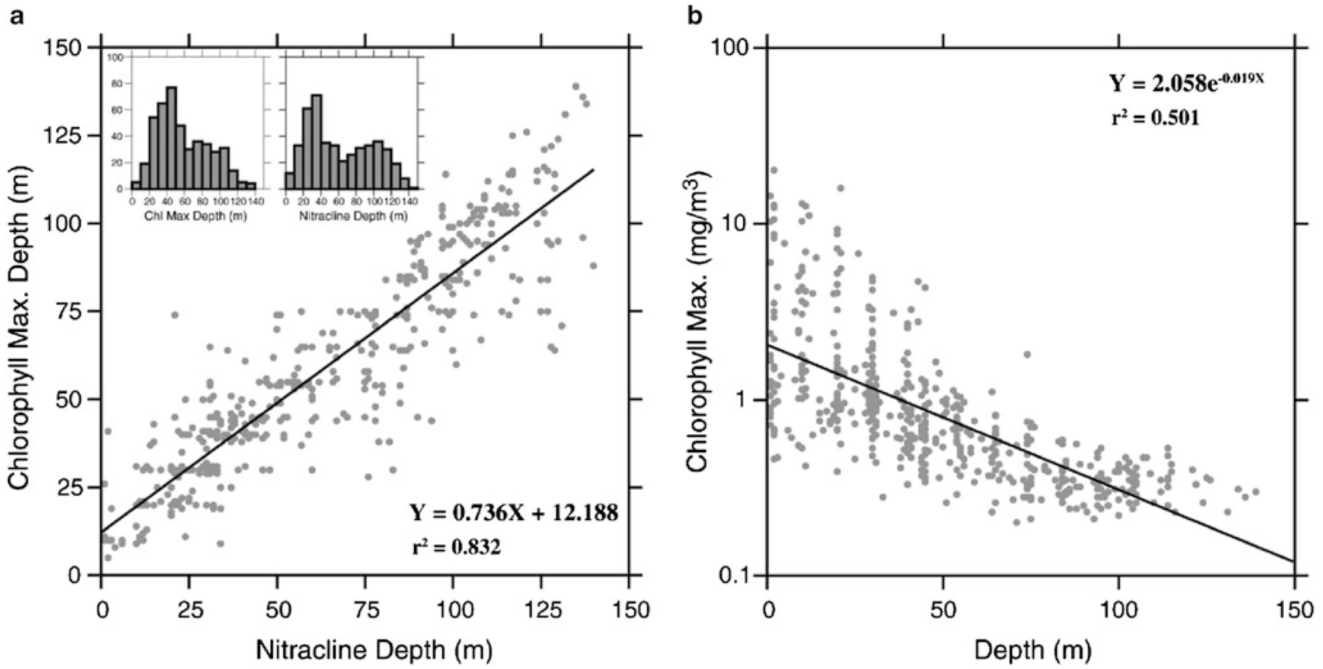

Fig. 2.54 (**a**) Relationship between depth of the chlorophyll maximum and depth of the nitracline defined as $1.0\,\mu$M NO_3. *Insets* show the frequency distribution of the depth of the chlorophyll maximum and the nitracline. (**b**) Negative exponential decline in the concentration of chlorophyll in the chlorophyll maximum with depth (From [357])

(Fig. 2.53, lower panel) [107]. The 3–4 month time lag arises from the time required for the ocean to adjust to seasonally changing wind stress curl forcing ([107] attributed to [593]).

The Deep Chlorophyll Maximum

The vertical distribution of chlorophyll reflects a balance between light and nutrient availability, although at the extremes of low and high light, the phytoplankton response to light dominates the response to nutrients [357]. A subsurface chlorophyll maximum layer is common off southern California, and its depth is closely related to the depth of the nitracline (where nitrate begins to increase) (Fig. 2.54a). Mantyla et al. (2008) [357] reported that 450 out of 528 core CalCOFI stations sampled on 8 cruises (two per season) in 1998 and 1999 had a deep chlorophyll maximum. Chlorophyll maxima tend to be shallower (~20–60 m) in the more productive area off Point Conception, and deeper (60–110 m) in the Central Pacific Water offshore [357]. The relation between the concentration of chlorophyll in the chlorophyll maximum and depth of the chlorophyll maximum can be approximated by a negative exponential fit (Fig. 2.54b), which is consistent with the exponential decline of light with depth [357].

2.6.2.2 Fronts

Although remote sensing revealed that the California Current System encompasses areas with high mesoscale variability, there are surprisingly few studies of frontal features. Off southern California, the Ensenada Front is the best studied front. Scripps Institution of Oceanography launched two studies, in 1985 and 1988, that targeted the Ensenada Front. The publications originating from these cruises remain the core references 25 years later ([114, 178, 196, 406, 417, 443, 566]). Recently the NSF-funded Long Term Ecological Research (LTER) California Current program has turned their attention to fronts in the SCB, and is expected to produce a new generation of research results. The following is a summary of the studies on the Ensenada Front. I do not review the new LTER results here.

The Ensenada Front

Approaching the Ensenada Front from the north, the south-eastward, surface flow leading into the front is cool and relatively fresh, with a high velocity core ([114]) (Fig. 2.55). This south-eastward flow originates from the California Current. A shallow salinity front separates fresher water offshore from more saline water inshore. Surface salinity contours follow dynamic topography in this region and the tracks of satellite tracked drifters followed the property contours ([114]) (Fig. 2.56). Solar heating affects the surface temperatures, so salinity is a better indicator of flow ([114]). Drifters followed the surface minimum of the spiciness anomaly, which was nearly identical to the surface salinity minimum, both of which trace the flow of the California Current ([114]).

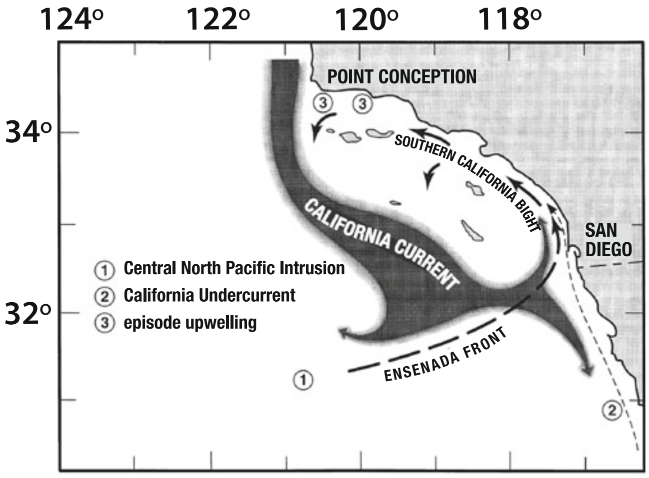

Fig. 2.55 The Ensenada Front and some of its source waters. There is considerable variation in the spatial arrangement and location of the flows shown (Redrawn from [566])

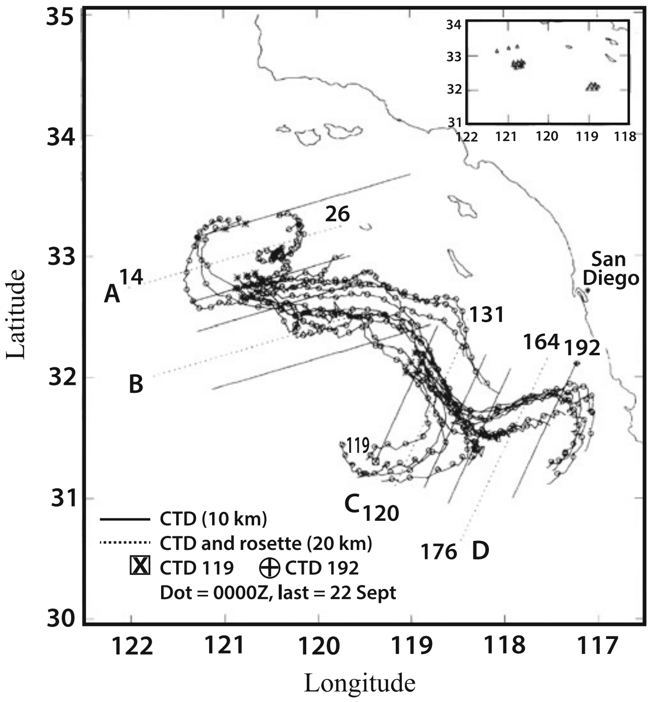

Fig. 2.56 Trajectories of 21 mixed-layer drifters from deployment (*asterisks*) until the last day of the experiment in September 1988. Interpolated daily positions fit midnight GMT are marked by *open symbols*. *Inset* shows drifter deployment pattern (Redrawn from [114])

Approaching the Ensenada Front from the south, the flow of warm, salty Equatorial Pacific Water of southern origin into southern Californian waters is complex [114, 340] and extends both inshore and offshore of the south-eastward flowing filament of the California Current. The inshore flow may be an extension of the California Undercurrent bringing Equatorial Pacific Water into the Southern California Bight (SCB), flowing northwards and exiting the SCB through gaps in the Santa Rosa ridge [114]. At depth, on the σ_t 26.5 surface, the high spiciness anomaly of the California Undercurrent is evident, especially in the south-eastern part of the SCB ([114]). At the deeper σ_t 26.8 surface, the California Undercurrent is evident offshore of the SCB except in the northwest ([114]) (Sect. 2.4.1). Offshore waters appear to be transported by mesoscale eddies. Chereskin and Niiler (1994) report that an eastward flowing filament aligned with the Ensenada Front flows directly into a mesoscale eddy field off northern Baja California where it meets the warm, salty Equatorial Pacific Water. The surface waters of the eddies originate from Pacific Subarctic Water, and the deeper layers of the eddies originate from Equatorial Pacific Water [114].

South-eastward flowing California Current waters turn inshore at ~32°N and flow eastward for about 200 km at the Ensenada Front ([114]) before splitting at the coast into two branches, one flowing northward along the coast in the Southern California Bight and the other flowing southward along the coast of northern Baja California ([114, 566]). The eastward-flowing current is persistently visible in the surface geostrophic streamlines, and forms the southern edge of the Southern California Eddy, which is a permanent cyclonic

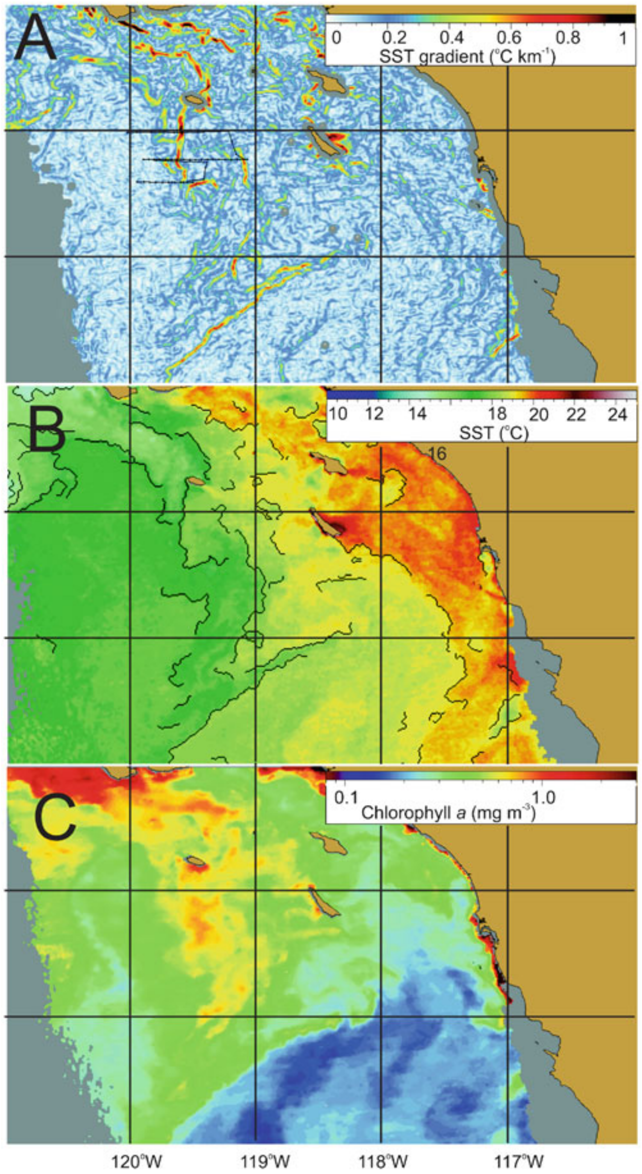

Fig. 2.57 Single pass remote sensing images from the Modis Aqua sensor for October 10, 2010. (**a**) Fronts detected from gradients in sea surface temperature (SST) using the Sobel edge operator. Linear features with higher temperature gradients show the front locations. (**b**) SST image for the same area with fronts overlaid derived from an improved Cayuga-Cornillon algorithm [416] showing that fronts primarily were found at the meeting of cooler offshore water with warmer water nearer to shore and to the south. (**c**) Ocean color image for the same area showing enhanced chlorophyll in the broader frontal zone (From [368])

(counter-clockwise) gyre ([339, 544, 590]). The east-west frontal zone can clearly be seen in satellite SST ([62, 302]) and ocean color imagery ([443,555]) (Fig. 2.57 [368]). After the flow turns shoreward, it appears to be strongly influenced by mesoscale features. Mesoscale eddies are associated with the eastward flow along the front, and have been observed rotating in opposite directions on either side of the front ([417, 467]). During the 1988 frontal study, counter-rotating eddies located to the southwest and northeast of the jet may have caused the flow to bifurcate ([114]). The eastward flow constitutes a divergent, upwelling filament with convergent flow along the edges. The filament embedded within the 100 km-wide, along-front, east/southeast (i.e. onshore) flow was 60 km wide, with surface velocities > 30 cm s^{-1} and most of the velocity shear was in the upper 100 m ([114]). This filament differs from the downwelling, offshore directed filaments observed off northern California ([114]), but the dynamics could be modeled in the same way using wind blowing over a mesoscale jet [437]. Chereskin and Niiler (1994) used such a model to show that the relatively weak wind stress measured during the cruise, blowing along the jet, could account for upwelling on the order of 5 m d^{-1} over scales of 10–50 km near the center of the jet.

3 Classic CalCOFI

Abstract

The CalCOFI program produced a library of reports including important refinements to sampling methodologies that resulted in manuals for the surveys. The spatial and temporal distributions of measured physical variables (such as temperature, salinity, nutrients and oxygen) and derived physical variables (such as density, dynamic height anomalies, and geostrophic flows) were analyzed and published as a series of atlases. Biological variables including chlorophyll and zooplankton displacement volume were mapped and compiled, as were the occurrence and distributions of zooplankton and ichthyoplankton species, especially with regard to the spawning seasons of fishes. The taxonomic knowledge of ichthyoplankton was improved over the years and the depth and detail of taxonomic information improved with time. Methods were developed for estimating the biomass of commercially important fish and for tracking relative trends in abundance to facilitate more accurate and useful stock assessments for use by management. Researchers used the hydrographic and ichthyoplankton databases, and the sample collections, to underpin numerous peer-reviewed publications that are now the "classic papers" from the CalCOFI program. Virtually all of these publications, atlases and reports are publicly available on the Internet. In addition, the entire hydrographic and ichthyoplankton databases are available to the public either through web forms or by email request.

Keywords

California Cooperative Oceanic Fisheries Investigations sampling • California Cooperative Oceanic Fisheries Investigations atlases • Ichthyoplankton taxonomy

> History is important!
>
> (Nancy Lo, repeatedly)
>
> Please reply to Cushing and tell him you have the data but to extract it would require and inordinate amount of time which you can't spare at this moment.
>
> (Memo to Paul Smith from Reuben Lasker, February 25th, 1977)

3.1 Sampling

One of the hallmarks of CalCOFI is that sampling gear has been improved with time and experience. A variety of nets were devised and modified over the years as part of the process of improving sampling during CalCOFI surveys. Standard protocols were developed, incorporated into the surveys (and into procedures for sample processing), and protocols were published in detailed technical reports [281, 522]. In many cases reports or papers were written that documented potential sources of error or variability associated with the net deployments. Protocols were developed to ensure quality control of the sampling was maintained at known and acceptable levels [203, 323, 517, 519, 522]. Wherever the innovations led to changes in sampling protocols, the effects of these changes were assessed by comparative studies to ensure that the continuity of the time series would be maintained. Sea-going experimental studies with different gear were an integral component of the CalCOFI survey program. In some cases

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the experiments led to the application of correction factors [5, 323, 426].

Classic CalCOFI net sampling continues to use three categories of nets and tow types, deployed to sample different assemblages of micronekton, mesozooplankton, and ichthyoplankton, over different depth ranges, and for distinct but related purposes. Unlike the zooplankton and ichthyoplankton, phytoplankton are not sampled with nets. The three tow types are oblique tows for micronekton, mesozooplankton and ichthyoplankton, vertical tows for ichthyoplankton and mesozooplankton, and surface tows for neuston. Oblique tows are currently made with bongo nets (Sect. 3.1.2.1), but previously were done with ring nets. Vertical tows are done with PairoVET nets (Sect. 3.1.2.2), which are the successor to CalVET nets, and with the PRPOOS net (Sect. 3.1.3.4). Neuston tows are made with a manta net. Details for each of these nets are given below.

Supplementary CalCOFI net sampling focuses on fish, and includes three different types of trawls. The Modified Isaacs Kidd net (Sect. 3.1.3.2), which is not currently in use, was designed to sample juvenile small pelagic fishes. Other supplementary nets currently in use at the time of writing include the Matsuda Oozeki Hu trawl (MOHT) (Sect. 3.1.3.3) used to capture mesopelagic fishes, and the Nordic rope trawl (Sect. 3.1.3.1) used to sample near-surface small pelagic fishes.

The following descriptions draw on the more detailed material that is presented on the CalCOFI web pages (www.calcofi.org). These pages also present detailed methods for oxygen, nutrient, primary productivity, and size fractionation measurements, and much more that is not repeated here.

3.1.1 Hydrographic Sampling

Hydrographic profiles are collected at each station using a Sea-Bird Electronics 911plus temperature, conductivity, oxygen system fitted with a transmissometer, fluorometer, underwater Photosynthetically Active Radiation (PAR), and Surface PAR meters, altimeter, nitrate and pH sensor (Fig. 3.1a). The electronic carousel water sampler is normally lowered to 515 m, or to within a few meters of the bottom, depending on which is shallower. On each cruise, four deeper CTD casts are done at station 90.90 (line.station) (3,500 m), 80.90 (3,500 m), Santa Monica Basin (770 m), and Santa Barbara Basin (570 m). The package is lowered at a slower rate (~30 m min^{-1}) for the first 100 m to ensure that physical and biological gradients are well sampled, and then lowered faster (~60 m min^{-1}) for the remainder of the profile. Seawater samples are collected with 24, 10 l Niskin bottles at ~20 target depths and analyzed aboard the research vessel for salinity, oxygen, nutrients, and chlorophyll. Bottle sampling depths are determined by the profile data collected on the downcast, distributing higher resolution 10 m spaced bottle samples around the chlorophyll maximum.

3.1.2 Standard CalCOFI Nets

3.1.2.1 Oblique Tows for Sampling Ichthyoplankton and Zooplankton

The bongo net (Fig. 3.1b) is towed obliquely from 212 m to the surface at one to two knots [281, 522], collecting two samples with a 505 μm mesh nylon net. The mouth diameter of each side of the bongo is 0.71 m. The right side of the net is preserved in buffered 5 % formalin and the left side in 90 % ethanol to permit genetic analyses. The bongo net collects mesozooplankton, and its catches are also critical for determining egg and larval mortality curves used in the Daily Egg Production Method for estimating the spawning stock biomass of sardine [317, 320, 323]. The bongo net catches euphausiids more efficiently at night. Due to issues of net avoidance, it is common practice to only include night-time samples for analyses of zooplankton [297, 426].

Ohman and Smith (1995) [426] wrote that "a hallmark of CalCOFI measurements is the attention given to calibration of biological, physical, and chemical methods, and the rigor with which different methodologies have been compared." There have been three changes in oblique net tows during the CalCOFI time series that involve one or more of tow depth, net configuration or mesh size and material. The very early oblique net tows on CalCOFI surveys in 1949 and 1950 were made with a 1-m diameter ring net with 550 μm (0.55 mm) silk mesh towed from a depth of 70 m with a 45° wire angle [17, 426]. From the first cruise of 1951, the tow depth was increased to 140 m, probably because the diversity and abundance of zooplankton was low above 70 m in the daytime.[1] The net type, mouth diameter, mesh size and mesh material remained the same when the depth was changed to 140 m [426, 523]. The next change was made from the first survey of 1969. The net remained the same (1-m ring net), but in 1969 both the mesh and the tow depth were changed. 550 μm silk mesh was replaced with 505 μm (0.505 mm) nylon and the tow depth was extended to 210 m [281, 426]. The deployment depth was deepened to encompass the depth distribution of larval hake.[2] The mesh of the ring net was changed to nylon to take advantage of better durability, lower cost and more efficient filtration compared to silk [281, 426]. In 1978 the 1-m ring net was abandoned in favor of a 0.71 m mouth diameter bongo net that captured active zooplankton more effectively [377, 426].

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[1] The exact reason was not recorded [426].

[2] In contrast to hake, sardine larvae are largely found in the upper 40 m of the water column [6].

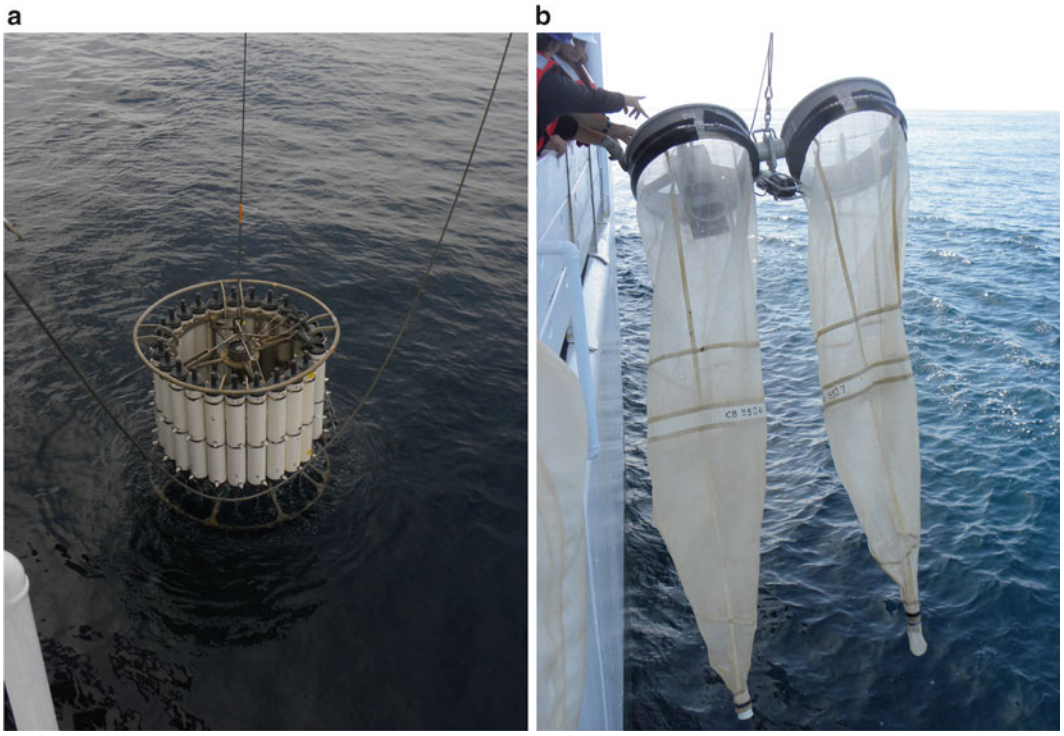

Fig. 3.1 (**a**) CTD rosette being recovered after a cast from NOAA Ship Bell M. Shimada. (**b**) Bongo net being recovered after a tow from Bell M. Shimada The Laser Optical Plankton Counter (LOPC) is mounted in the mouth of the port net (Photos: S. McClatchie)

Ohman and Smith (1995) [426] made several detailed comparisons between nets towed at different depths and nets of different configuration. They found that the shallower 70 m depth 1 m-ring net tows yielded significantly greater abundance of zooplankton per unit volume than the deeper 210 m tows. The lower catches per volume in deeper tows is likely due to the commonly found decline in the abundance of oceanic zooplankton with depth [426]. They also found no diurnal effect on the ratios of catch between the nets [426]. The ratio of catch per volume in the shallower to the deeper tows was 0.731 ± 0.091 (mean ± 95 % confidence interval). When Ohman and Smith (1995) [426] compared the 0.71 m diameter bongo net with the 1 m diameter ring net they found that the bongo net collected more zooplankton. The explanation is probably because zooplankton are less able to avoid a bridle-less bongo net than a ring net, although there is some evidence that, at least for euphausiids, catchability of the bongo net may be stage-specific. Again there was no diurnal effect on the ratio of catches per volume between the nets [426]. The ratio of catch per volume between the bongo and ring net was 1.366 ± 0.156 in favor of the bongo net [426]. To express the pre-1969 catches per volume in terms of the post 1978 net catches, the two ratios could be multiplied (0.731 × 1.366) which coincidentally yields a value of almost unity, indicating that no correction for catchability is required to compare the oblique tows from these years. However, the ring net catches from the intervening years 1969–1977 do need to be corrected by multiplying by the ratio of bongo net to ring net catches (1.366 ± 0.156) in order to compare these years with earlier or later years [426].

Rebstock (2002) [461] compared the catches of calanoid copepods caught by a 0.71 m or 0.6 m diameter bongo net with a 1-m ring net, and concluded that there was no difference between the catches (after correction for multiple comparisons). In this study, the copepods were enumerated by species and stages, whereas Ohman and Smith (1995) [426] made their comparison of nets on the basis of zooplankton displacement volume. The difference between the nets may be more due to the lack of a bridle in front of the bongo net than to the difference in the mouth area of the two nets. For zooplankton as small as copepods, the presence of a bridle may not be important, but for euphausiids, the bridle can cause them to avoid the net. The difference between Ohman and Smith (1995) [426] and Rebstock's (2002) [461] results may simply be that the displacement volumes contained euphausiids, and the bongo net was more effective than the ring net at catching euphausiids, so there was significantly higher displacement volumes caught by the bongo net.

3.1.2.2 Vertical Tows (CalVET and PairoVET) for Sampling Ichthyoplankton

The PairoVET net is used to collect ichthyoplankton in vertical tows from 70 m to the surface using paired 0.05 m^2, 150 μm mesh nets (Fig. 3.2a). The net is deployed only to

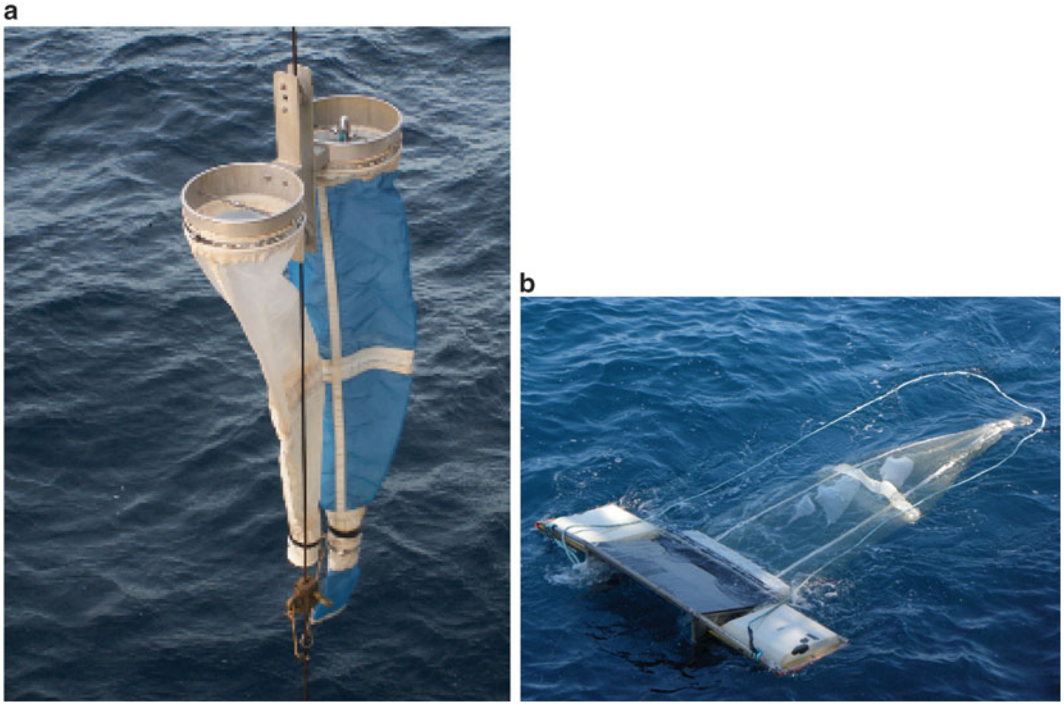

Fig. 3.2 CalCOFI plankton nets (**a**) PairoVET net from NOAA Ship Miller Freeman. (**b**) Manta net deployed from Bell M. Shimada (Photos: S. McClatchie)

70 m because earlier studies indicated that most fish eggs are found in the upper 70 m of the water column [6, 404]. The net is raised and lowered at 70 m min^{-1}, and the wire angle is monitored to ensure that the tow is sufficiently vertical to be usable. The aim is to sample a constant volume of water over all depths while towing the net vertically. The main causes of variation from this ideal are horizontal ship motion and water currents, net clogging, and vertical heave due to vessel pitch and roll [203]. If the vessel rolls heavily during net recovery, and forces the net downward faster than the recovery rate, water could be forced through the meshes from outside the net, and eggs could be pumped out the mouth, causing sample loss [203]. Alternatively if the vessel rolled away from the net during recovery and accelerated water flow through the net, then eggs could be forced against the meshes which might cause loss due to rupture [203]. Another potential source of variance is time in the neuston which can have high concentrations of fish eggs, so the net must pass through the neuston layer quickly and at right angles to the surface [519]. A set of protocols is followed to require a net tow to be repeated if the tow is judged to be unsatisfactory for any of these reasons (wire angle, vessel heave, or dragging in the neuston layer).

The net was designed to collect anchovy eggs with 100 % efficiency, but its small mouth area means that it probably does not effectively collect active larvae larger than 5 mm [519]. The mouth area was also designed small to collect fewer eggs, and thereby reduce sample sorting time in the laboratory [519]. The net shape was designed with a cylindrical portion (rather than being tapered evenly from the mouth) to reduce clogging and permit the mesh size to be as small as possible, while minimizing clogging [519]. For efficient filtering, the net needs to have an open mesh area exceeding three times the area of the mouth of the net, which was achieved by using a truncated conical end to the net behind a cylindrical cone [519]. While calculations showed that the net was unlikely to clog on a single tow, the possibility of sequential tows leading to progressive clogging of the meshes remained, even though the net is rinsed on recovery. As a check on this, the net was fitted with a flow meter. In the PairoVET design, the nets are paired, with the flowmeter in one of the nets to permit checking for sequential clogging, and the sample is collected from the other net (note that this is not the configuration shown in Fig. 3.2a). The original CalVET net was a single mouth configuration, where a flowmeter would have partly obscured the small diameter (25 cm) mouth of the net. The paired net configuration also permitted precision between the two nets to be checked [519].

3.1.2.3 Manta Net Surface Tows for Sampling the Neuston

Curiously, the manta net (Fig. 3.2b) takes its inspiration from the shape of the mouth of a manta ray [86]. An efficient surface sampler should remain at the surface over a range of sea states, should veer away from the side of the vessel during towing to avoid ship wake, and should have a mouth unobstructed by a bridle that might cause avoidance by organisms [86]. The bridle of the manta net is weighted by a sinker so that it hangs vertically for several meters below the net, thereby avoiding interfering with the mouth of the net during towing [86]. The manta net is used to collect animals of the sea surface, referred to as neuston. Many fishes that have a prolonged transformation between larval and juvenile stages of development, develop features that are suited to a period in the neuston [392], and these stages would be collected by the manta net. Some species are neustonic throughout their larval stage, e.g. silversides, saury, and sablefish after their yolk sac stage (William Watson, SWFSC, personal communication). Manta net samples have been collected on CalCOFI cruises using a 505 μm nylon mesh net since 1977 [426].

3.1.3 Supplementary CalCOFI Nets

3.1.3.1 Nordic 264 Rope Trawl for Sampling Pelagic Fishes

The Nordic surface trawl has been used to collect adult coastal pelagic species since July 2003 [187]. Unlike the MIK and MOHT trawls (Sects. 3.1.3.2 and 3.1.3.3), the Nordic trawl mouth is opened by low-drag, wide-spreading trawl doors, and has a much larger 600 m^2 mouth area. Juvenile and even large larval fish are retained by the 8 mm mesh liner in the codend [187]. The net is constrained to fish at the surface by attaching floats to the rigging (Fig. 3.3). Since 2008 the net has been fitted with a marine mammal excluder device (MMEL) [143] designed to allow mammals that become trapped in the body of the net to escape, hopefully minimizing unwanted mortality (Fig. 3.4).

The rope trawl is used to obtain sardines for histological analyses that are necessary for the estimation of sardine spawning stock biomass using the Daily Egg Production Method [292, 320]. The catches are also used to obtain species composition and size structure required for calculation of acoustic biomass estimates of sardine and other small pelagic fish [598].

3.1.3.2 Modified Isaacs Kidd (MIK) Frame Trawl for Sampling Juvenile Fishes

The development of a new trawl to sample late larval and juvenile (age-0) small pelagic fish that can avoid plankton nets, but are too small to be captured by large mid-water trawls, was part of the recruitment studies at the SWFSC in the 1980s [391] (see comments by John Hunter in Sect. 8.15 for a perspective on why pre-recruit surveys were not subsequently pursued). A similar net was used in Scandinavia to sample herring. The primary target for the MIK net was 15–60 mm anchovy.

Fig. 3.3 Nordic 264 rope trawl being deployed from Bell M. Shimada, October 2010. Normally this trawl is fished near the surface at night to obtain dispersed small pelagic fishes (Photo: S. McClatchie)

The bridle design, mouth area, mesh size, and tow speed were designed to facilitate sampling a large volume, while minimizing avoidance by larger organisms, reducing the catch of plankton and being easy to handle. The net needed to be capable of sampling surface-associated late larvae and juveniles as well as fishing at depth, and also ideally should have an opening-closing mechanism [391].

Methot (1986) [391] referred to the MIK net as a “frame trawl” (Fig. 3.5). It had a hard-frame mouth with an area of 5 m^2, a two-point bridle attachment at the middle of the sides of the frame, a 2 × 3 mm mesh to retain 15 mm larvae but to extrude most plankton, and a routine tow speed of 2 ms^{-1}(~4 knots), but it lacked an opening-closing mechanism [391]. The frame could be rigged with floats to fish at the surface, or rigged with an IKMT-type depressor deployed back from the mouth (to minimize turbulence and associated avoidance at the net mouth) to fish at depth (Fig. 3.5). The target volume to sample the rarer organisms was 10,000 m^3 [391]. The frame net filters about 7,000 m^3over a 3 km tow, or over 100 times as much water per tow as a bongo net [391].

Fig. 3.4 Marine Mammal Excluder Device (MMEL) sewn into the Nordic 264 rope trawl to permit escape of inadvertently entrained bycatch such as seals, sea lions and dolphins (Photo: D. Griffith)

Experience with the frame trawl indicated that larval herring are easier to capture than anchovies and sardines of the same size. Daytime trawls were not successful and the net needed to be towed at 5 knots to capture juvenile anchovy or sardine (P.E. Smith, personal communication). However, the frame trawl effectively caught larval anchovy larger than 15 mm that were poorly sampled by plankton nets due to both avoidance and low volumes filtered.

3.1.3.3 Matsuda-Oozeki-Hu (MOHT) Trawl for Sampling Mesopelagics

The Matsuda-Oozeki-Hu trawl (MOHT) [430] is a hard-mouth square-framed trawl with a 5.5 m^2 mouth opening with a cambered V-type depressor that can be towed at speeds up to 4.5 knots (Fig. 3.6). It is designed to capture a variety of organisms including krill, late larval and juvenile fishes, and micronekton. The net has been used to collect samples of the mesopelagic assemblages as well as juvenile small pelagic fish on selected stations of the 75-station CalCOFI pattern. This net was introduced to the survey in 2008. The trawl samples are used in conjunction with multifrequency acoustics to estimate the distribution and biomass of micronekton on CalCOFI surveys. The MOHT net samples the mesopelagic community better than a bongo net or the rope trawl, and as such fills a gap in the net sampling of the CalCOFI program.

3.1.3.4 PRPOOS Net for Sampling Zooplankton

A Planktonic Rate Processes in Oligotrophic Ocean Systems (PRPOOS) net, formerly known as the Soutar-Hemingway Animal Trap or "SHAT" (see Fig. 5 in [281]), is a 202 µm mesh ring net that has a 50 cm diameter single frame opening and is 3 m in length. The PRPOOS net is deployed vertically from a depth of 210 m to the surface. This net was incorporated into the CalCOFI sampling in 2005 and has been used to sample mesozooplankton at stations on CalCOFI lines 90.0 and 80.0, and stations inshore of station 70 on CalCOFI lines 86.7 and 83.3 (see Fig. 1.4).

3.1.4 Continuous Underway Fish Egg Sampler (CUFES)

The Continuous Underway Fish Egg Sampler or CUFES has become an essential tool for CalCOFI and ichthyoplankton surveys in general. It was developed in the mid-1990s [102, 105] and originally incorporated automated identification of fish eggs using either video or an optical plankton counter (Fig. 3.7) [102]. Early studies attempting automated identification of pelagic fish eggs obtained promising results with menhaden [102], but 15 years later, purely automated egg identification has not become routine, and the CUFES still requires manual identification of the samples. Part of the problem is that menhaden eggs, and presumably many other pelagic fish eggs, have optical properties that are similar to much more abundant copepods of smaller diameter. While the egg concentrating device serves to reduce this problem by increasing the density of eggs relative to zooplankton [102], the misidentification probability remains unacceptably high without a person to check the samples.

Despite its limitations, CUFES has been an invaluable addition to ichthyoplankton surveys. It was used in early efforts to better define sardine and anchovy habitats [105]. Checkley et al. (2000) [105] used egg-temperature-salinity plots to describe differences in the water mass characteristics where sardine and anchovy spawned, based on two cruises in 1996 and 1997 off southern and central California (Fig. 3.8). As more years of data were collected, it became clear that the habitat bounds were more complex [32, 580, 599], but the CUFES data from cruises are still routinely sent back to shore and overlaid on sea surface temperature imagery to show the sardine, anchovy and jack mackerel spawning habitat in near real time (see Fig. 4.47). CUFES data were used to develop the sardine spawning habitat model by Zwolinski et al. (2011) [599] (Sect. 4.2.2.3).

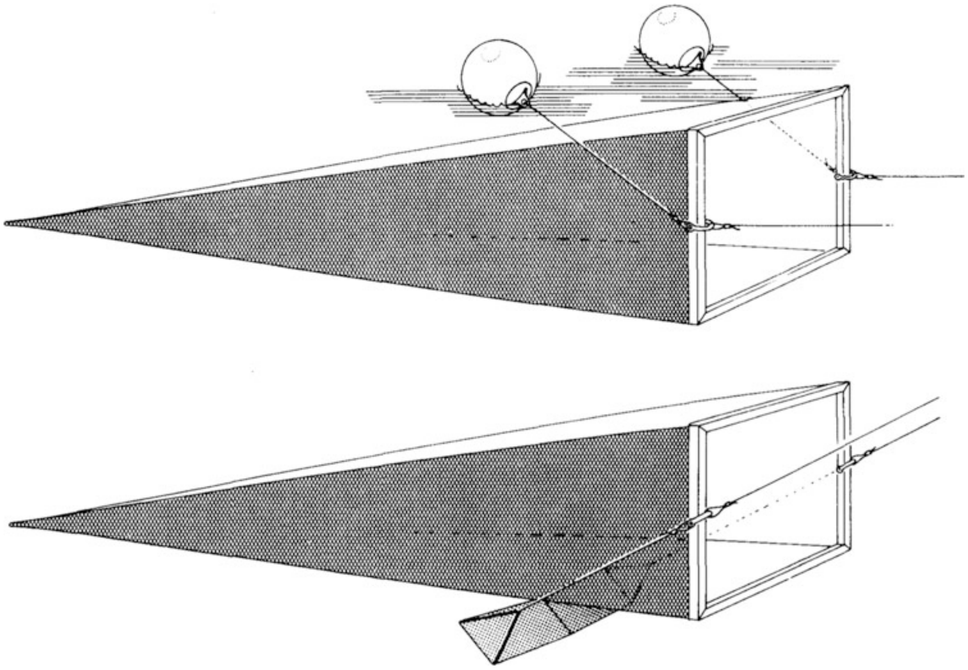

Fig. 3.5 MIK (Modified Isaacs-Kidd) Frame trawl with a 5 m^2 mouth area designed to collect large larvae or juvenile anchovy and sardine showing the surface tow configuration with floats (*above*) and the deeper tow configuration with a 2.4 × 0.6 m depressor (*below*). Note the extended support lines for the depressor designed to reduce turbulence and associated avoidance at the mouth of the net (From [391])

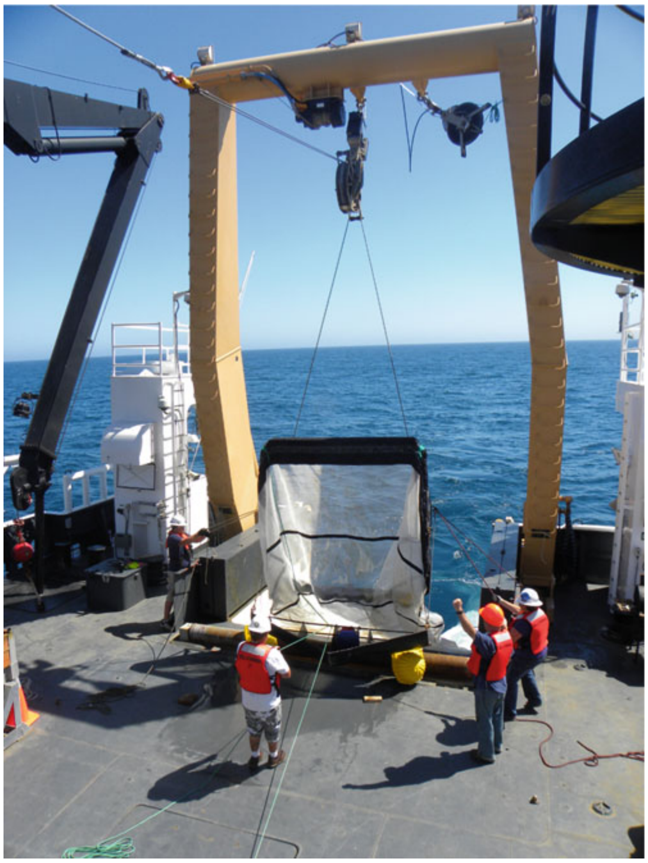

Fig. 3.6 Matsuda-Oozeki-Hu trawl (MOHT) being deployed from NOAA Ship Bell M. Shimada (Photo: S. McClatchie)

An important use of CUFES is to inform adaptive sampling of sardine eggs by vertical (formerly CalVET, now PairoVET) net tows [322]. Sardine egg counts from PairoVET samples collected on the spring cruises between San Diego and San Francisco (the 113 station CalCOFI pattern) are currently used to estimate sardine spawning stock biomass using the Daily Egg Production Method (DEPM)[3] [211, 320]. The procedure prior to the advent of CUFES required net tows every 4 km to achieve the acceptable confidence level of egg production estimates from uncorrelated egg samples. Lo et al. (2001) [322] compared field surveys (using only CalVET net in 1994, and both CalVET net and CUFES in 1996 and 1997) to determine how CUFES could be used to reduce the effort required to obtain an acceptable DEPM estimate of egg production. As a first step, they used variograms to determine that the decorrelation length scale[4] for all stages of sardine eggs combined was 22 km [322] (Fig. 3.9). Decorrelation length scales were 15 km for 1-day old eggs, increasing to 22 km for 3-day old eggs [322], consistent with dispersal of sardine egg patches [511].

Lo et al. (2001) [322] compared egg densities from CUFES (eggs min^{-1}) with egg densities from vertical CalVET tows (eggs 0.5 m^{-2})[5] and found that the conversion constant was "ephemeral" [322]. Using 91 paired samples

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[3] The DEPM is only one of three biomass estimation methods that go into the sardine assessment as of 2012. The others are derived from acoustic-trawl and aerial surveys.

[4] i.e. the variogram range, or the separation distance between samples beyond which samples are not correlated.

[5] 0.5 m^2 was the mouth area of the CalVET net.

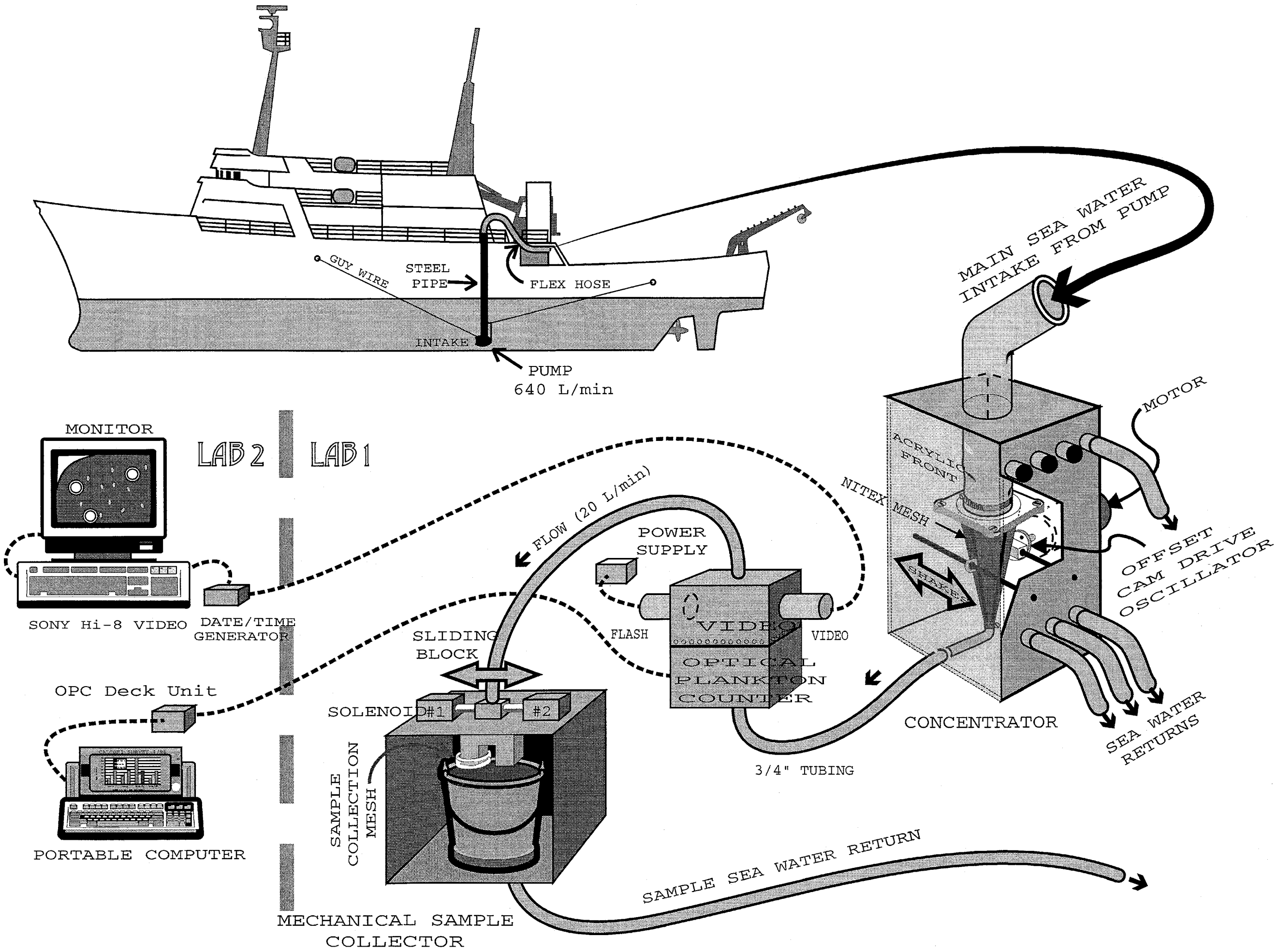

Fig. 3.7 Schematic of the Continuous Underway Fish Egg Sampler (CUFES). Current systems used on CalCOFI and Southwest Fisheries Science Center cruises do not incorporate the video or optical plankton counter. The instrument is used as a sophisticated egg collector, and the eggs are identified manually at sea under a microscope and subsequently resorted and checked for species identification in the SWFSC ichthyoplankton laboratory (From [102])

from the spring 1996 cruise, they found that for one egg min^{-1} from CUFES there were 1.5 eggs from the CalVET vertical tow. In contrast, from the spring 1997 cruise, they compared 110 paired samples and found that for one egg min^{-1} from CUFES there were four eggs from the CalVET vertical tow. The different ratios between cruises for egg densities in CUFES and CalVET samples is likely due to differences in mixing affecting the distribution and availability of eggs to CUFES which samples only at 3 m depth [322]. The variable ratio between samplers is contradictory to earlier findings that the CUFES produced egg counts that were comparable to the vertical CalVET net tows. Based on the same 91 paired samples from the 1996 cruise, Checkley et al. (1997) [102] previously reported a correlation between logarithmically transformed egg counts from CUFES and CalVET tows of 0.85 for anchovy and 0.62 for sardine. Checkley et al. [102] recognized that there were unquantified sources of variance in the CUFES data, and considered that these were likely related to ontogenetic changes in the buoyancy of pelagic fish eggs that could potentially be quantified by measurements of the density profile of the upper water column, and modeling the egg development [102].

Lo et al. (2001) [322] also found that CUFES undersampled the early stage sardine eggs. They used a chi-square analysis to compare the abundance of 11 stages of sardine eggs in 91 paired CUFES and CalVET samples from the spring 1996 cruise. They concluded that there were significantly fewer stage I, III, V, and VI eggs in the CUFES samples and that the distribution of sardine egg stages caught by the two samplers was not the same [322]. The distribution of egg stages sampled by CUFES in the upper three meters did not match the distribution sampled over the full water column (i.e. the upper 70 m) where the eggs occur, and "egg production computed from the CUFES survey would be biased" [322]. Earlier work indicated there was no difference

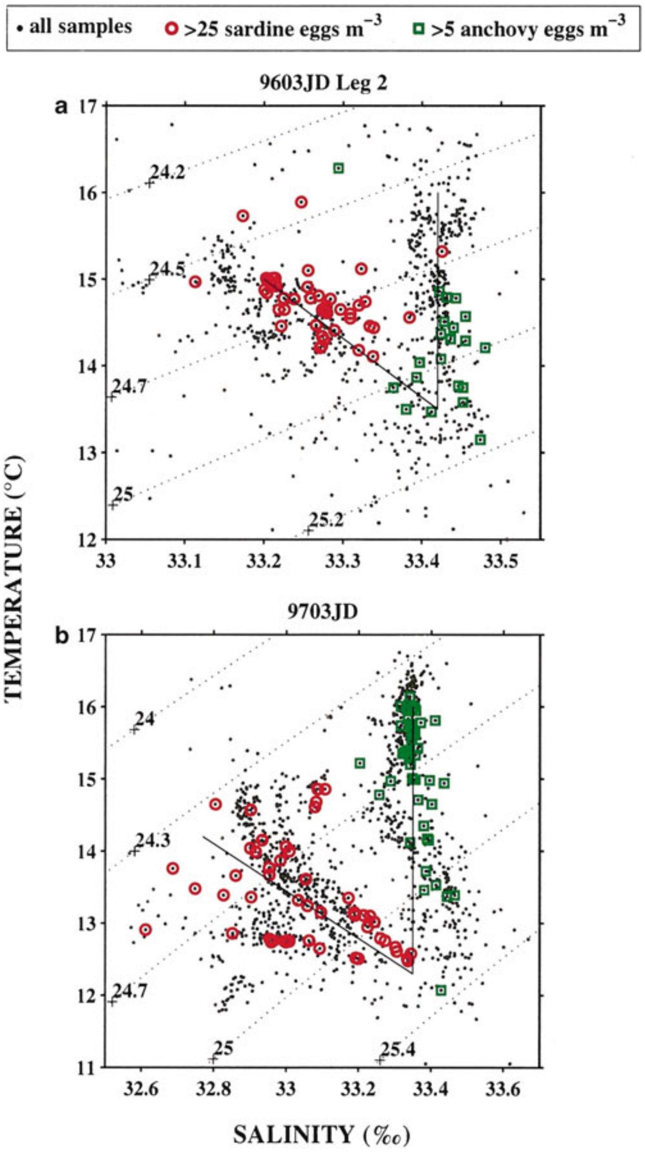

Fig. 3.8 Fish eggs collected on two spring cruises (March 1996 and 1997) off central and southern California using the Continuous Underway Fish Egg Sampler (CUFES) and plotted in temperature-salinity space to illustrate separation of sardine and anchovy eggs by water characteristics. These patterns tend to vary considerably from year to year, but this is an early example of the application of CUFES to understanding the spawning habitat of small pelagic fish in the California Current System (From [105])

in the sampling of sardine egg development stages between CUFES and the CalVET net, except for stage I eggs which were undersampled by CUFES [102].

The comparisons between CUFES and the vertical CalVET net tows by Checkley et al. [102] and subsequently by Lo et al. [322] led to the conclusion that the CUFES data alone cannot be used for DEPM estimates of spawning stock biomass. The CUFES is nevertheless an essential tool for adaptively allocating extra vertical PairoVET net sampling when sardine eggs are present above a threshold of 2 eggs min^{-1} in the CUFES samples[6] [322]. Based on the real-time CUFES data, the survey is stratified into a "high egg density area" where PairoVETS are taken every 4 km, and a "low density area" where PairoVET samples are only taken at the regular CalCOFI stations. For the DEPM estimate of spawning stock biomass, mortality (z) and egg production (P_0) are only estimated from the high density area [322]. Estimating P_0 from the low density area is not done because there is a low density of eggs and yolk sac larvae (which makes estimating z difficult) and there is a possibility of stage-specific bias due to low densities. Instead, P_0 is estimated by scaling P_0 from the high density area by the ratio of egg densities from CUFES in the high and low density areas [322].

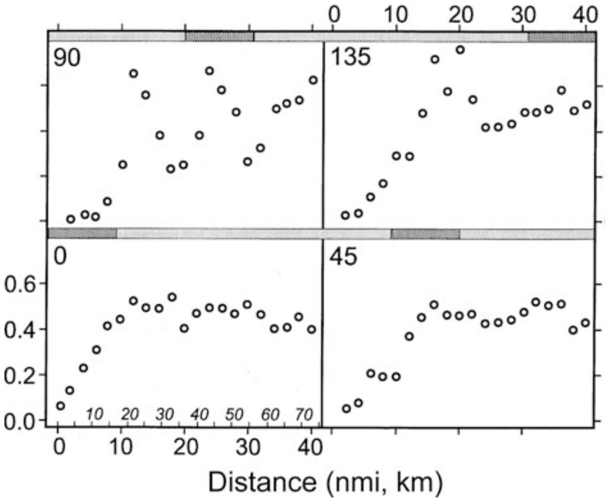

Fig. 3.9 Directional variograms constructed from detrended ln-transformed, egg counts from the Continuous Underway Fish Egg Sampler (CUFES). Graph shows all egg ages (days 1–3) combined. Degree 0 is perpendicular to the coast, and Degree 90 is oriented along the coast. The abscissa shows separation distances in nautical miles (*outer ticks*) and kilometers (*inner ticks*). Note that the clearest variogram is obtained from the along-transect data and the model that was fitted to the data is not shown (From [322])

3.2 The CalCOFI Atlases

The CalCOFI atlases are now quite old, and readers should note that in many cases taxonomy has been revised, many more samples have been counted, and tables showing the relative abundance of species are likely to have been superseded and should no longer be regarded as completely accurate.

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[6] Two sardine eggs min^{-1} in the CUFES is equivalent to three to eight eggs per 70 m vertical PairoVET tow depending on the conversion factor. The critical or threshold value defining the high density sampling would likely differ with both species and the survey area [322].

The atlases are online at the CalCOFI web site (www.calcofi.org), and in many cases there are comments and references to current taxonomic web sites, and to more recent related literature provided for each atlas.

The CalCOFI atlases comprise 35 volumes that were published between 1963 and 2002. Seventeen volumes, or approximately 50 % of the total collection, were published in the first decade of the series, and 13 more volumes were published in the second decade. The remaining five volumes were published in the fourth decade of the series, after a 10 year gap between 1983 and 1992 when no CalCOFI atlases were published. These last five atlases, all written by Geoff Moser and his colleagues, focused on the distribution of the ichthyoplankton assemblages. No atlases were published after 2002. The pattern of publication of the atlases reflects the development and completion of mapping studies focused on the descriptive physical oceanography and plankton biogeography of the California Current System.

The approach taken by the SWFSC to the CalCOFI ichthyoplankton atlases was well organized. First they studied key commercial species, then moved on to selected coherent groups of species, and then, as the taxonomic knowledge became more highly resolved, they broadened investigations to cover the wider ichthyoplankton assemblages. Twelve of the atlases focused on ichthyoplankton. The earlier volumes addressed the distribution of commercial species: anchovy [280] (later updated by Hewitt [206]), jack mackerel and hake [8], and sardine [279]. After the major commercial species, attention turned to the mesopelagic fishes [9], the flatfishes [13], and rockfishes [16], and later to the broader ichthyoplankton assemblages [394, 398–401]. The taxonomic work culminated in the publication of the massive 1,517 page volume number 33 edited by Moser (1996) entitled "The early stages of fishes of the California Current region" [394] (see vignettes by both Geoff Moser and Bill Watson in Chap. 8).

The approach taken by Scripps scientists to the CalCOFI zooplankton atlases differed from the SWFSC approach to ichthyoplankton, and to some degree reflected the taxonomic expertise of staff at SIO at the time. Nine of the CalCOFI atlases addressed different zooplankton groups. Of these, three volumes focused on calanoid copepods [73, 169, 170], three volumes focused on euphausiids [80, 81, 83], one volume was on chaetognaths [20], and another on thaliaceans (mostly the salps and doliolids) [61]. This reflected the fact that copepods, euphausiids, chaetognaths, and tunicates[7] are the four most abundant zooplankton groups in the California Current System (see Fig. 4.21). Among those describing zooplankton groups, the remaining volume covered pelagic molluscs [375], which although fascinating, are not nearly as abundant as the copepods, euphausiids, chaetognaths, and tunicates.

3.2.1 Krill in the Atlases

Brinton's (1962) [79] monograph on the Pacific euphausiids was based on 10 years of data, collected using oblique tows with the standard 1-m ring net used in the early CalCOFI years. In areas of particular interest, samples were also collected with an Isaacs-Kidd midwater trawl, and in some cases with opening-closing 1-meter nets [79]. Samples were collected from 16 cruises and were supplemented by CalCOFI cruises (1949–1958) covering the broader eastern Pacific. Samples from the north Pacific including the California Current System were collected mainly between April–October. This was not considered a problem because the seasonal coverage available in the CalCOFI series in the 1950s revealed that the faunal boundaries of euphausiids were not strongly affected by the seasonal variability [79].

Brinton listed species characteristic of the Baja California coast as *Euphausia eximia*, *Nyctiphanes simplex*, *Nematoscelis difficilis*, and *Stylocheiron affine*. Several vertically migrating species are important components of the deep scattering layer, namely *Euphausia pacifica*, *Nyctiphanes simplex*, *Thysanoessa gregaria*,[8] and *Nematoscelis difficilis* off San Diego [67]. *Euphausia pacifica* and the decapod *Sergestes* are found in the scattering layers off Monterey [47].

Brinton (1962) [79] described *Nyctiphanes simplex* as the classic nearshore, warm water, relatively shallow living krill of the California Current System. This species can be contrasted with *Euphausia pacifica* which is a cool water species, extending further offshore and vertically migrating over a greater depth range. The contrast between these krill is the basis for the often pictured graphic showing *N.simplex* dominant off southern California during the warm phase Pacific Decadal Oscillation (PDO) but almost absent during the cool phase of the PDO [82, 427] (see Fig. 4.28).

Brinton referred to the California Current as a transition zone region because there were no clear faunistic boundaries for krill along the axis of the California Current [80]. This transition zone was penetrated by species with their centers of distribution in the Pacific Subarctic Water (*Euphausa pacifica* and *Thysanoessa spinifera*), the North Pacific Central Water (*Euphausia hemigibba* and *Nematoscelis atlantica*), and Equatorial Pacific Water (*Euphausia distinguenda* and *E. tenera*) [80]. In contrast to these species of the margins,

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[7] Tunicates include salps, doliolids, appendicularians and pyrosomes. Thaliaceans only include include salps, doliolids, and pyrosomes, but not the appendicularians (which include larvaceans).

[8] Brinton [83] states that *T. gregaria* does not vertically migrate, which is in contrast to what is reported by Boden [67].

there are krill species that occupy the entire extent of the California Current, and are not found in the marginal areas. These resident krill species include *Nematoscelis difficilis*, *Thysanoessa gregaria* and likely *Euphausia gibboides*, as well as *Nyctiphanes simplex. N. simplex* is "the coastal element of the assemblage" [80].

Brinton (1967) [80] cautioned that the maps in his atlas were based on both daytime and night samples, and so should be regarded as potentially affected by net avoidance. To offset this problem, he provided distributions based on nighttime samples as insets to his maps, and suggested that although they were constructed from fewer data points, the night-based maps may show more reliable species distributions. Plankton net avoidance problems are severe enough with krill that many researchers now use only nighttime samples in their analyses, since the krill are less able to avoid nets at night.

3.2.2 Chaetognaths in the Atlases

Alvariño (1965) [20] listed warm and cold-water associated species, as well as neritic and mesopelagic chaetognaths in the California Current System. Cold-water northern species include *Sagitta scrippsae* in the upper layers, and *S. maxima* and *Eukronia hama* deeper than 100 m [20]. *S. scrippsae* is most common in the north of the California Current and gradually decreases as the California Current mixes with waters to the south [20,23]. A typical warm water and central species is *S. pacifica*, and *S. euneritica* is a typical neritic species. I will not list the tropical or mesopelagic species named by Alvariño (1965) [20] here.

Alvariño (1965) [20] considered that net avoidance by large chaetognaths and loss of small chaetognaths through the meshes of the standard oblique ring net tows used prior to the publication of her atlas [20], affected the species composition in the CalCOFI samples. *Sagitta hexaptera*, *S. maxima*, and *S. scrippsae* were likely to be able to avoid the net [20]. Immature specimens of *Krohnitta pacifica, Pterosagitta draco, S. minima, S. pseudoserratodentata, S. neglecta, S. regularis* and *S. robusta* were likely to pass through the meshes [20]. This selectivity problem would likely also affect size distributions estimated from samples. Although the bongo net replaced the ring net used for CalCOFI oblique plankton tows in December 1977, there is probably little difference in the species selectivity of the two nets for chaetognaths (see Sect. 3.1.2.1). This suggests that the catchability bias for chaetognaths still exists in the more recent samples.

3.2.3 Copepods in the Atlases

Based on four CalCOFI cruises from April, July and October 1958 and January 1959[9] Fleminger [169, 170] mapped the distributions of 176 species (and 57 genera) of Calanoid copepods found in the California Current System. Fleminger (1967) [170] listed the species that fall into quite a number of major biogeographical-habitat groups, including Subarctic species, Transitional species, Central species, Equatorial oceanic species, and Coastal neritic species comprising Endemics and Non-endemics, amongst which he distinguished boreal-temperate, temperate-subtropical, and tropical Non-endemics [170]. Interestingly Fleminger (1967) [170] commented that any single CalCOFI oblique tow is unlikely to yield representatives of only one faunal assemblage or biogeographic region, but rather a mixture of Transitional and Subarctic, or Transitional and Central assemblages, or less commonly and only in the south, the Transitional and Equatorial assemblages. In addition, it is common to see mixtures of inshore and offshore assemblages, as well as mesopelagic representatives in any one sample [170]. Fleminger (1967) attributed this to two factors. First the California Current System is one of "relatively weak physical and chemical gradients, seasonally variable winds, countercurrents and semi-permanent eddies, all of which enhance advection and faunal mixing" [170]. Secondly, the CalCOFI oblique net tow "obscures vertically zoned habitat or faunal groupings ... as well as [those associated with] layering or interleaving of water masses".

3.2.4 Ichthyoplankton in the Atlases

Tremendous effort has been applied to identify the ichthyoplankton and cephalopods collected by nets on the CalCOFI surveys [398–400, 429]. As of 2010, 490 species of fish larvae and 22 species of cephalopod larvae had been identified in the CalCOFI samples by the NOAA SWFSC ichthyoplankton laboratory staff. Most of the ichthyoplankton fauna are now being identified, as shown by the fact that the guide to the ichthyoplankton of the California Current region, produced by Moser's group, includes 25 orders, 158 families and 586 species [394].

The process of refinement in taxonomic resolution continues, retroactively updating identifications to current standards from 1951 to the present. Identifications of all larvae have so far been updated from 1966 to the present. Identification of hake (whiting), jack mackerel and Pacific mackerel eggs collected in bongo nets is now complete back to 1984.

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[9] The study covered 20–40°N and west to 130°W [170].

Market squid paralarvae have been identified from manta net samples back to 1981, and all cephalopod paralarvae have been identified since 2008 (Watson writing in [271]).

Genetic techniques with the capacity to process large numbers of samples hold considerable promise for the molecular identification of ichthyoplankton. Such techniques potentially could provide accurate, near real-time identification for species that are either difficult or impossible to identify using conventional morphological characters, such as *Sebastes*. The techniques are likely to be applied to hake, Pacific mackerel, white seabass and California barracuda eggs to develop a time series back to 1997 based on ethanol preserved samples in an effort to develop more automated identification methods (Watson writing in [271]).

3.3 Biogeography, Ichthyoplankton and ENSO

Plankton biogeography of the eastern Pacific is well beyond the scope of this book, and is only briefly covered here with reference to ichthyoplankton. Community and distribution studies of plankton in the North Pacific revealed distinct faunal characteristics with broad-scale patterns that are often related to the distribution of water masses [20, 79–81, 154–156, 375, 379–381]. The California Current System is referred to as a transitional region due to the mixture of species, including endemics, that occur in adjacent water masses. Several studies used the ichthyoplankton species abundance data collected by CalCOFI to examine assemblage structure and the regional differences in ichthyoplankton in the California Current system. Of these studies [188, 328, 406, 407], two focused on a wider range of years [406, 407], and so are discussed in more detail here.

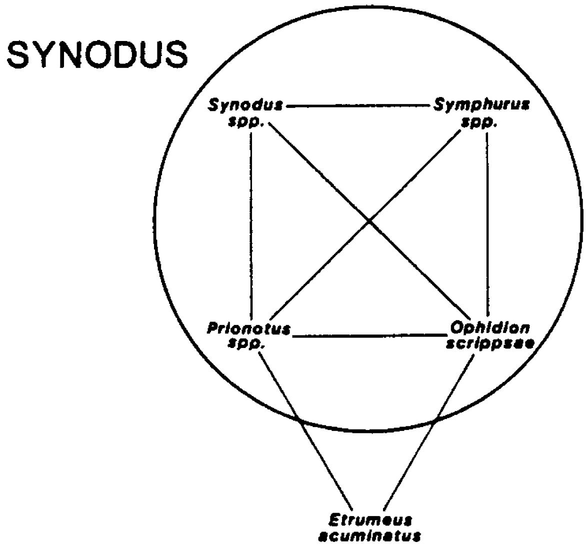

Fig. 3.10 Southern Coastal complex of ichthyoplankton taxa showing groups and associations derived from a recurrent group analysis based on 7 years of CalCOFI data (1954–1960) (From [407])

Moser et al. (1987) [407] analyzed 7 years of CalCOFI surveys (1954–1960) for the area between Point Conception to Punta Eugenia, Baja California, and identified nine recurrent groups of ichthyoplankton. Recurrent groups identify taxa that consistently occur together and experience the same environmental conditions. Moser et al. (1987) combined the recurrent groups into northern and southern super-groups or complexes, plus a southern coastal complex that did not clearly fit into either the northern or southern complexes (Fig. 3.10). The northern complex had primarily cold-water affinities (Fig. 3.11), and the southern complex had mainly warm-water affinities (Fig. 3.12).

The numbers of recurrent groups obtained was different for different years, ranging from 8 groups in 1955 to 14 groups in 1956 and 1960 [407]. In four of these years, group members of one complex later became group members of a different complex [407]. Inter-annual variability was greater in the southern complex than in the northern complex. Despite this variability in the recurrent groups, Moser et al. (1987) [407] considered that the northern, southern and southern coastal complexes were conserved and less affected by variability.

The taxa comprising the complexes were strongly influenced by the 1957–1958 ENSO event. In general members of the northern complex (Fig. 3.11) declined in abundance, and their southern distributional limits shifted northward during the El Niño. For example, *Leuroglossus stilbius* decreased by 16–33 % in both inshore and offshore areas of the Southern California Bight (CalCOFI lines 80–97) and northern Baja, California (CalCOFI lines 100–117) [407]. *Stenobrachius leucopsaurus* decreased by 18–23 % in the Southern California Bight and inshore northern Baja, California. *Sebastes* spp. decreased by 14–28 % in all areas, while hake, *Merluccius productus* decreased mainly off Baja, California. The flatfish *Citharichthys* spp. decreased by 3–15 % off northern Baja, California, as did the anchovy, *Engraulis mordax*. However the anchovy also increased in the offshore southern California area indicating a northern and seaward expansion of anchovy spawning during this El Niño [407]. The change in sardine distributions was difficult to determine due to the reduction of the stock in the 1950s.

Southern complex species (Fig. 3.12) increased in abundance, and their northern limits shifted northward [407]. Among the southern species, *Triphoturus mexicanus* expanded by 15–30 % in the Southern California Bight during this El Niño, although this species is not usually found north of northern Baja, California. *Vinciguerria lucetia* showed the greatest change of any species, with a 52–54 % increase in the offshore areas of the Southern California Bight and northern Baja, California, respectively. *V. lucetia* is abundant in the eastern tropical Pacific. Even though *V. lucetia* is normally not found north of CalCOFI line 100, near Ensenada, Baja California, it expanded north of Point Conception during this El Niño (see Fig. 1.5) [407]. This species only increased in the offshore and not in the inshore areas of the Southern California Bight.

Moser and Smith (1993) [406] performed another community analysis on CalCOFI data, this time basing their conclusions on the entire dataset available to them at the time (1951–1984). In this study they examined the data using recurrent group analysis, cluster analysis and principal component analysis. From these data they again found a northern complex, a southern complex and a southern shelf complex. There were also a small number of isolated species that did not show any association with other species or the broader species complexes [406] (Fig. 3.13). They concluded that the results from the longer time series were consistent with those from shorter parts of the series, and that the recurrent group, cluster and principal components analyses gave similar species groupings. They also concluded that the species groups were associated with particular water masses. Their results in regard to oceanography were quite general because they did not perform any detailed water mass analysis based on characteristic properties such as potential temperature, salinity, oxygen or nutrients. However, this is not surprising because the focus of these papers is on the ichthyoplankton assemblages rather than the oceanography.

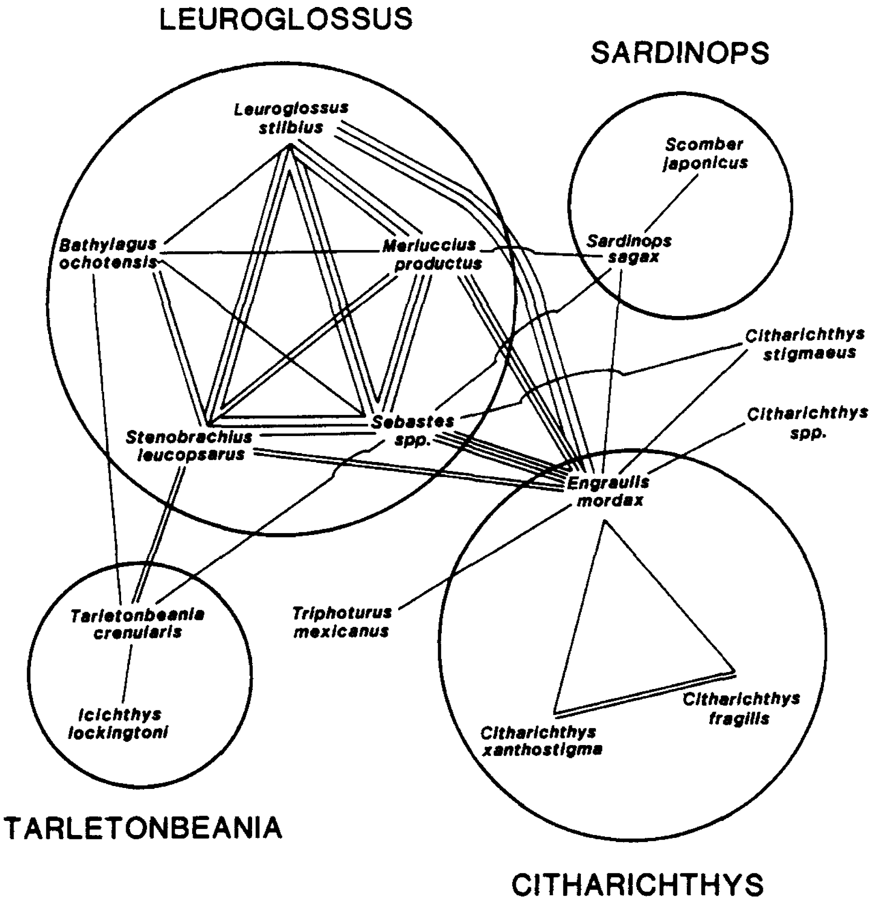

Fig. 3.11 Northern complex of ichthyoplankton taxa showing groups and associations derived from a recurrent group analysis based on 7 years of CalCOFI data (1954–1960) (From [407])

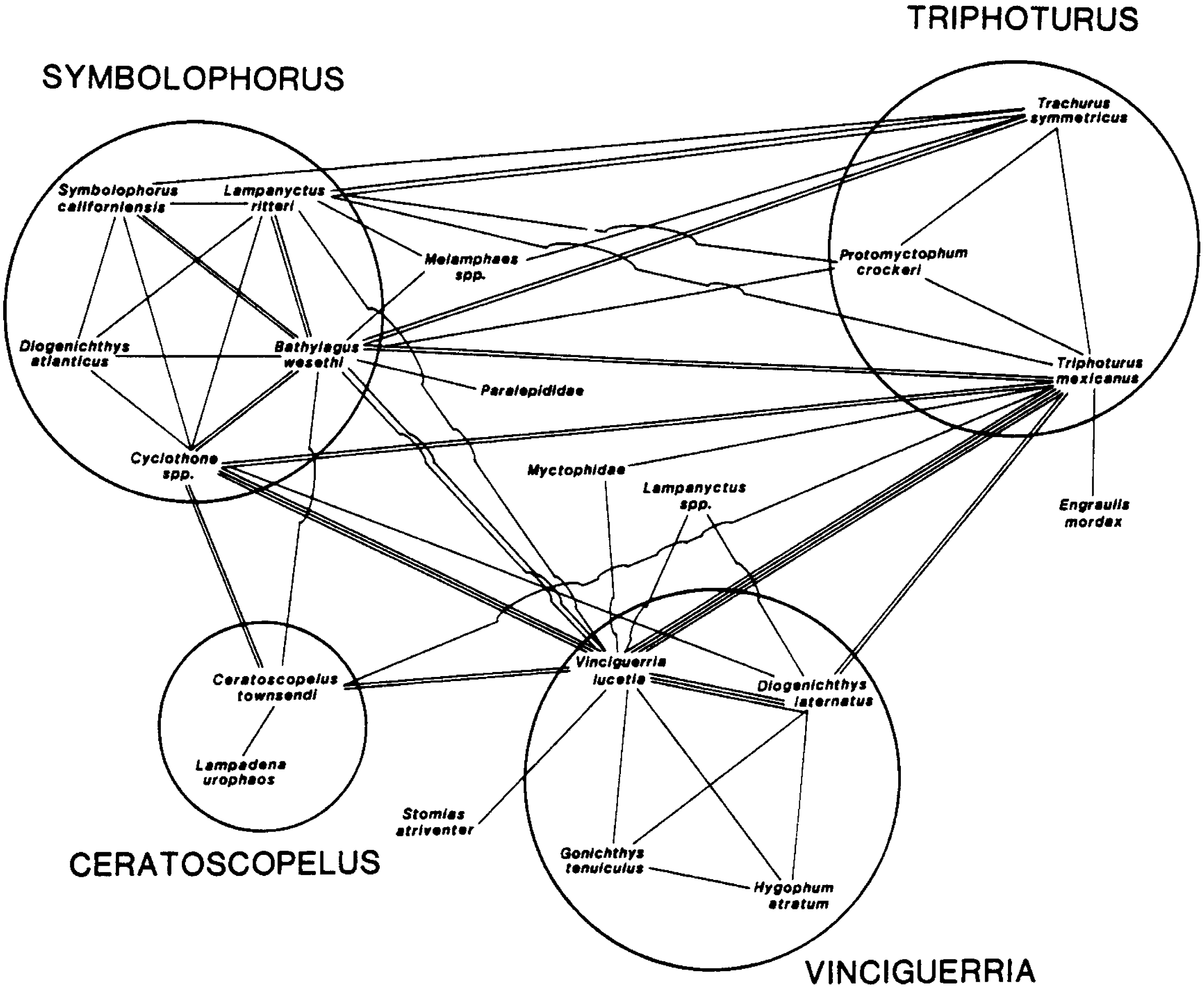

Fig. 3.12 Southern complex of ichthyoplankton taxa showing groups and associations derived from a recurrent group analysis based on 7 years of CalCOFI data (1954–1960) (From [407])

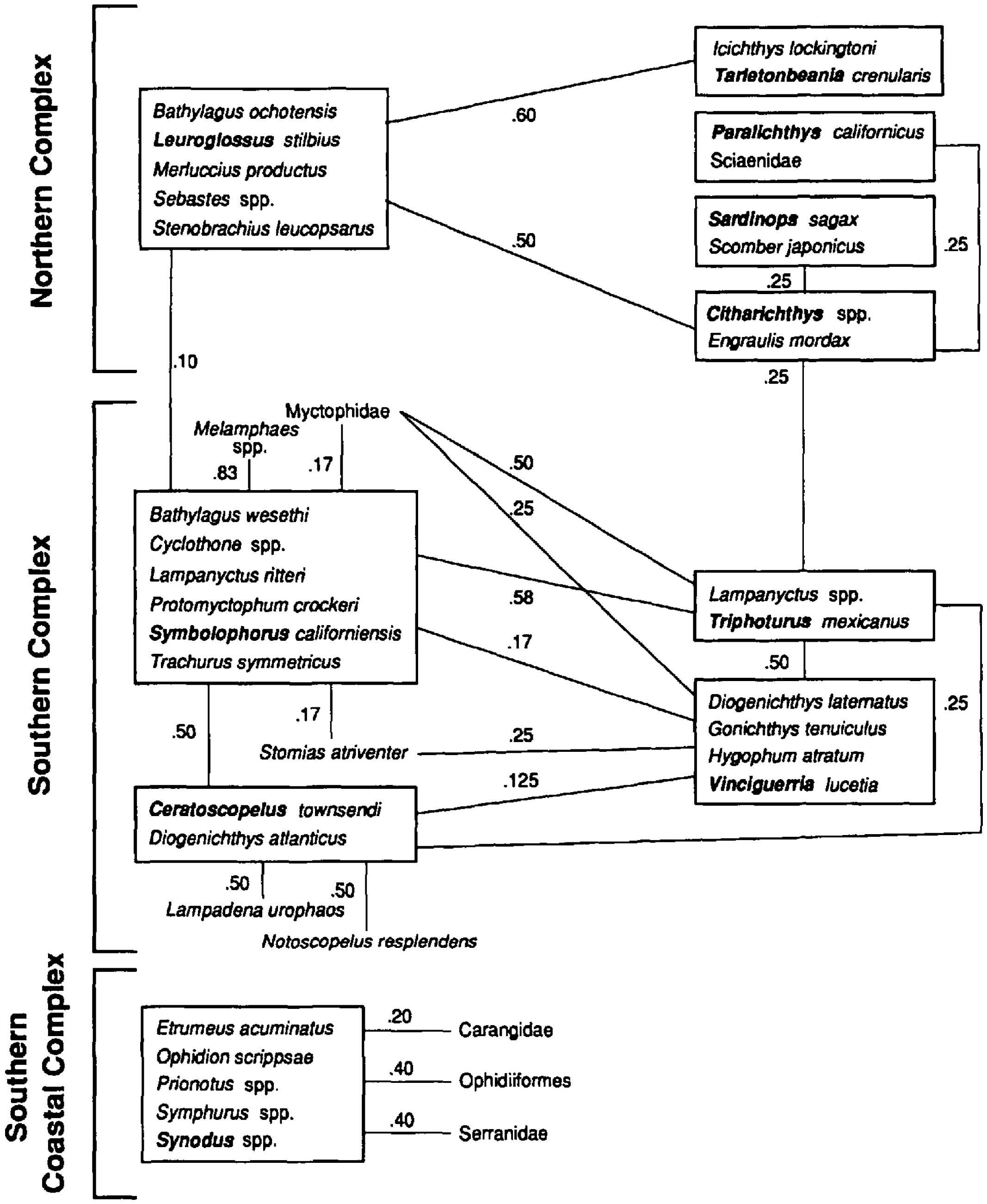

Fig. 3.13 Composition and interrelationships of recurrent groups of larval fishes (in boxes) and their associates (not enclosed) in the CalCOFI area, based on 34 years of data (1951 to 1984). A line connecting recurrent groups to other recurrent groups or to associate taxa indicates there are inter-group pairs with significant affinity indices (≥0.3). The value associated with each line represents the number of significant inter-group affinity pairs divided by the total possible pairs (From [406])

Scales of Variability Relevant to Fisheries in the Southern California Current System

4

Abstract

The concepts that have received considerable attention by researchers and that have guided trends in the interpretation of research results relevant to CalCOFI can be organized according to the temporal scales that they encompass, notably the decadal (10–100+ years), inter-annual (1–5 years), seasonal (1 month to 1 year) and weather (less than 1 month) scales. At the decadal scale are regime shifts, the basin hypothesis of range contraction and expansion, cycles in fish and plankton assemblages, the alternation of dominance in small pelagic fish populations, and geographical shifts of assemblages with secular trends in climate. Inter-annual scales are dominated by the effects of El Niño-Southern Oscillation events and by mesoscale variability and associated advection. At seasonal scales, I discuss upwelling and production, the spring transition and phenology (in Chap. 2), fish migration, and variability in small pelagic fish spawning habitat. At the shortest daily to weekly time frames, or weather scale, the key concepts include mixing, stability and recruitment, mortality and patchiness.

Keywords

Decadal-scale variability in the California Current System • Regime shifts in the California Current System • Inter-annual variability in the California Current System • El Niño-Southern Oscillation in the California Current System • Seasonal variability in the California Current System • Weather-scale variability in the California Current System

> The spawning area surveys were based on the conventional view of sardines as being a relatively nearshore species. Indeed, the historical fishery had been conducted in nearshore waters, and the early CalCOFI ichthyoplankton surveys suggested a coastal affinity. The nearshore view was shattered in 1991 due to the chance discovery of large concentrations of Pacific sardine far offshore. While conducting exploratory trawling for jack mackerel (*Trachurus symmetricus*) the Russian survey vessel *Novodrutsk* encountered surprising abundances of Pacific sardines as well as chub mackerel, a.k.a. Pacific mackerel (*Scomber japonicus*) – at the furthest edge of the range covered by standard CalCOFI surveys.
>
> (Alec MacCall [346])

> The assumption is that there are some normal statistics to all kinds of conditions. Rather, there are probably a great number of possible regimes and abrupt discontinuities connecting them, flip-flops from one regime to another; multifarious regimes involving biology or climate, or oceanography, or migrations, temperature, or weather, or combinations of these, etc. Sardines, for example, are either here or not here. Rainfall follows these persistent trends, in periods of years during which it is high and others during which it is low, etc. There are internal, interactive episodes locked into persistence, and one is entirely fooled if one takes one of these short intervals of a decade or so and decides there is some sort of simple probability associated with it.
>
> (John Isaacs [242])

> If the underlying process [contributing to the PDO] were more cyclic and deterministic, then there would be more possibility to say when a future shift might occur. But with red noise, the large shifts occur when the different contributions add together in a random manner, with little potential predictability. Thus if the true underlying climate process was close to red noise, predictions from extrapolation by curve fitting of twentieth century data would be a misleading and dangerous exercise.
>
> (Jim Overland [431])

Fisheries oceanography is essentially biological oceanography relevant to fisheries. This definition is rather loose and

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DOI 10.1007/978-94-007-7223-6_4,

in this chapter I cover research results that might better be categorized as biological oceanography. Nevertheless, these works are core to CalCOFI and the findings are relevant to understanding the fluctuating biomass and recruitment of fisheries, and so their inclusion here seems reasonable. More formal definitions of fisheries oceanography can be found in the literature. For example, Kendall and Duker [262] distinguish operational fisheries oceanography from recruitment fisheries oceanography and also from fisheries oceanography focused on production processes in the ocean. Operational fisheries oceanography uses the relationships between environmental variables and the distribution and abundance of resources to facilitate their effective exploitation. In contrast, recruitment fisheries oceanography focuses on understanding the fluctuations in year class strength that determine abundance, and is primarily directed to studies on the planktonic egg and larval stages [262]. Fisheries oceanography of production processes examines how spatial and temporal productivity of the oceans affects the fluctuations in abundance of fishes on a range of scales [262]. The CalCOFI program has largely been concerned with these last two types of fisheries oceanography as well as with the broader aspects of biological oceanography relevant to fisheries in the widest sense.

I use temporal scales of variability to structure the following discussion of themes in fisheries oceanography of the California Current System. I grouped the temporal scales into low-frequency decadal scales (10–100+ years) which includes climate variability, inter-annual scales (1–5 years) including ENSO-driven variability, seasonal scales (1 month to 1 year), and what I have termed weather-scale variability, which pertains to shorter than seasonal time scales.

4.1 Decadal-Scale Variability (10–100+ Years)

Climate indices are diagnostic quantities that are used to characterize geophysical systems. They can be used to characterize a circulation pattern in the ocean or atmosphere, or to summarize modes of variability of selected variables such as surface atmospheric pressure, pressure at 500 db, or surface temperature, for example. Climate indices are calculated in a variety of different ways (see Sect. 4.2.1.2 for examples). Some indices can only be properly applied in certain regional contexts.

There are some persistent misunderstandings in fisheries oceanography about the use of climate indices. First, many climate indices are correlated and so should not be used as independent time series when selecting predictive variables in models such as a GAM or GLM predicting recruitment. The various sea surface temperature based indices of ENSO are correlated, and there is little value in using both the MEI and NINO3.4 time series (see Sect. 4.2.1.2) as predictors in a model, for example. The PDO is also correlated with ENSO (see Sect. 4.1.1.1), and it is redundant to include both PDO and ENSO indices in a GLM or GAM as predictors. Another common misconception is that an observed relationship between a climate index like the PDO and a variable of interest to fisheries oceanographers, such as sardine recruitment success, has any generality when the PDO can be modeled as a red noise spectrum (Sect. 4.1.2). The appearance of a relationship between the PDO and recruitment success does exist for the period of interest, but it is not general beyond the short time period being examined (Sect. 4.1.3.3). Further, climate indices like the PDO and NPGO (Sects. 4.1.1.1 and 4.1.1.2) are created from detrended, standardized time series, and the EOFs are rotated to maximize the variance explained by single variables. By definition, the seasonality that is inherent in the variables has been removed. To then take a subset of monthly values of a climate index and treat it as a seasonal index in a model is to create indices on indices, and interpretation of such a predictor value is obscure.

Finally, climate indices provide a catch-all for environmental variables, and this is why large-scale climate indices predict ecological processes better than local weather [191]. In their illuminating study, Hallet et al. [191] showed that the mortality of Soay sheep in the Outer Hebrides Islands of Scotland could arise from various combinations of weather variables (e.g. cold temperatures, heavy precipitation, strong winds) at any time of year, that mortality had a spatial component, and could also occur at different lags from the weather events. Climate indices aggregate these factors and so provided a useful predictor variable, while the predictive power of the weather variables was obscured by the variability or noise. However, examination of the weather variables in relation to mortality was essential to disentangle the various mechanisms causing mortality events. This study is very relevant to fisheries oceanography where we want to understand the mechanisms driving successful recruitment, but often fail to think clearly about the variables that should be used to predict recruitment in models. Either climate indices or appropriately averaged or integrated weather variables should be used, but not both.

4.1.1 Climate Variability and Teleconnections

In the northern hemisphere there are persistent patterns of low and high pressure in the atmosphere that are constrained to certain latitude and longitude ranges by global atmospheric circulation and by the topography of land masses and the shape of ocean basins. Although they are largely spatially locked, the pressure patterns do change with inter-annual variations of heating and cooling over the land and oceans, combined with random processes [431]. The pressure differences are referred to as “stationary waves”, and they are caused by heating contrasts between the continents and the oceans [431]. The large scale pressure patterns impose large scale coherence on seasonal, inter-annual and decadal variations in climate [431]. Overland et al. [431] explain that these “simultaneous variations in climate, often of opposite sign [i.e. wetter vs drier, warmer vs. cooler], over distant parts of the globe are commonly referred to as teleconnections”.

The dominant teleconnections in the northern hemisphere are the North Atlantic Oscillation (NAO) and the Pacific-North American pattern (PNA). Both show largest amplitude in the winter when variability in atmospheric pressure fields is also greatest [431]. The PNA teleconnection is comprised of four centers of high and low pressure aligned in an arc from the Central Pacific to the Gulf of Alaska, through western Canada, and ending over the southeastern United States [431]. Variations in pressure over western Canada and the northwestern U.S. are positively correlated with the subtropical Pacific [431]. The PNA and the NAO are internal modes of atmospheric variability [431] that represent about 35 % of the monthly variability in sea level pressure, and provide conceptual models for a considerable portion of the large scale climate variability in the northern hemisphere [431] (but see Sect. 4.1.1). I will not discuss the NAO further here. The PNA is closely related to the North Pacific index, which is the sea level pressure in a region near the Aleutian Islands, and to the Pacific Decadal Oscillation (PDO), which is based on variability of sea surface temperature in the North Pacific [431].

4.1.1.1 The Pacific Decadal Oscillation (PDO)

The Pacific Decadal Oscillation (PDO) has been used to model variability in climate patterns in the North Pacific over the last century [72,356,431,432].[1] The PDO is derived from the first principal component of monthly sea surface temperature (SST) anomalies in the North Pacific Ocean, poleward of 20°N. While the monthly values of the PDO anomalies vary considerably (Fig. 4.1), the shift from predominantly negative to predominantly positive anomalies is referred to as a shift from the negative or cool phase (PDO$^-$) to the positive or warm phase (PDO$^+$) of the PDO in the California Current System. A key feature of the PDO time series is the shift in the sign of the PDO that occurred in 1976/1977, that was interpreted as a “regime shift” in oceanographic and atmospheric conditions [192, 356]. The regime shift was clearly reflected in changes in ecological assemblages and regional patterns of production. There was a period of considerable discussion in the literature ([101, 186, 448]) as to whether a second shift in the phase of the PDO was occurring when PDO$^+$ shifted to PDO$^-$ in 1999–2002 (Fig. 4.1). Subsequent data showed that the PDO in the following decade (2000–2010) was not stable in either phase, fueling doubts about the validity of the regime shift concept.

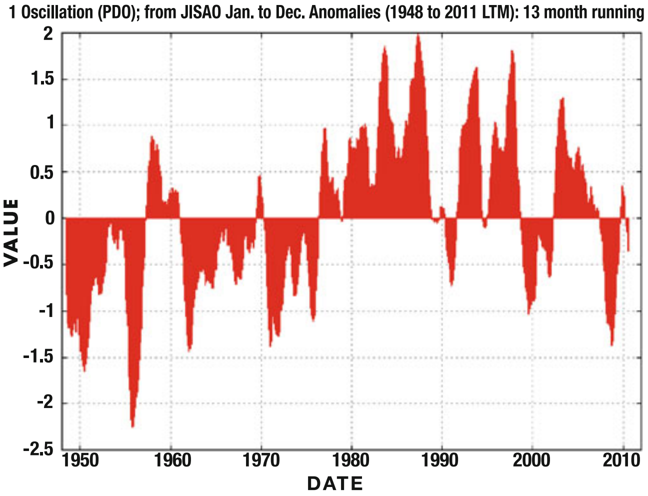

Fig. 4.1 Pacific Decadal Oscillation anomalies from 1948 to 2011, plotted as a 13-month running average. The PDO index is “derived as the leading principal component of monthly sea surface temperature (SST) anomalies in the North Pacific Ocean, poleward of 20 °N. The monthly mean global average SST anomalies are removed to separate this pattern of variability from any “global warming” signal that may be present in the data” (Data provided by the Joint Institute for the Study of the Atmosphere and Ocean at the University of Washington, and the plot was generated using the NOAA Earth System Research Laboratory web page)

It has now been shown that the PDO, which is the leading pattern of climate variability in the North Pacific, incompletely characterizes North Pacific climate [72]. This can be illustrated by comparing the canonical patterns of sea-level air pressure (SLP) and sea surface temperature (SST) anomalies before and after the 1976/1977 regime shift with recent patterns measured in 1999–2002, when it was thought that a second regime shift might have occurred [72].

The canonical pattern for PDO$^-$ is shown by the average SLP anomalies over five winters prior to the regime shift (1972 through 1976), characterized by a northwest-southeast aligned high pressure anomaly extending from eastern Siberia to the coast of California (Fig. 4.2, panel 2a [72]). A warm SST anomaly in the central Pacific, especially north of Hawaii was associated with this pattern [72], and a cold SST anomaly extended along the west coast of North America (which leads to PDO$^-$ being referred to as the cold phase of the PDO in the California Current System) (Fig. 4.2, panel 2b). The pattern is similar, but in the reverse sense for the canonical PDO$^+$condition, as Bond et al. [72] showed by averaging five winters after the regime shift (1977 through 1981). The central North Pacific is dominated by a low SLP anomaly and cool temperatures, while the west coast of the North America showed warmer than average SST (Fig. 4.2,

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[1] PDO time series data are available from the Joint Institute for the Study of the Atmosphere and Oceans, University of Washington.

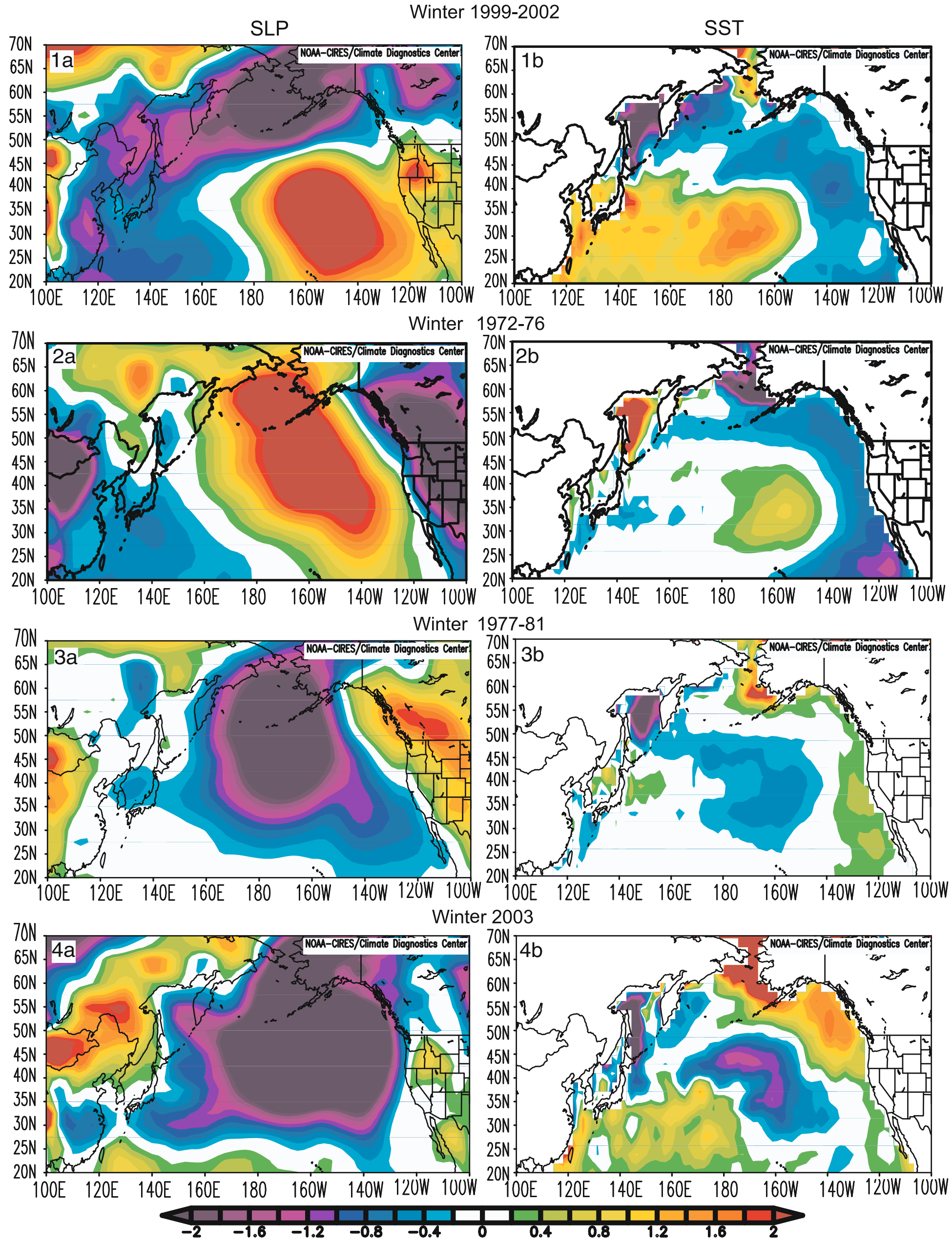

Fig. 4.2 Spatial anomalies of sea-level pressure (SLP, on *left*) and sea surface temperature (SST, on *right*) for November–March of 4 recent years (1999–2002), 5 years before the PDO regime shift of 1976/1977 (1972–1976), 5 years after the regime shift (1977–1981), and the winter of 2003 which was influenced by El Niño (From Bond et al. [72])

panel 3a and b [72]), leading the condition to be referred to as the warm phase of the PDO in the California Current System.

Bond et al. [72] showed that patterns of SLP anomalies and SST anomalies in the North Pacific during the winters of 1999–2002 "bore little resemblance to those … of the [canonical] Pacific Decadal Oscillation" (Fig. 4.2, panel 1a and b [72]). There was no indication that North Pacific climate was shifting from PDO$^+$ to return to PDO$^-$, and he could find no evidence supporting a second regime shift. Furthermore, the pattern in 2003 differed from both the canonical PDO regime patterns, and from the pattern of 1999–2002 (Fig. 4.2, panel 4a and b [72]), due to the influence of El Niño.

Despite the uncertainties concerning the validity of regimes, there are some detectable differences between the cool phase PDO$^-$ (1950–1976) and the warm phase PDO$^+$ (1977–1999) in the CalCOFI survey data. For example, surface dynamic heights were generally higher during the warm phase PDO$^+$, likely due to thermal expansion [69]. Links between inter-annual variability of seasonality and decadal-scale variability may drive the observed "regime shift". Seasonal upwelling showed considerable inter-annual variability between 1967–2007, but there were extended periods of either high seasonally-integrated upwelling (1970s, 1998–2004) or low seasonally-integrated upwelling (1980–1995) [70]. The periods of high or low upwelling do not correlate well with the phases of the PDO (see Fig. 4.1). Schwing and Mendelssohn [498] suggested that long-term changes in seasonal upwelling may have been responsible for ecosystem shifts in the California Current ecosystem, again suggesting that the mechanisms underlying climate variability are more complex than can be explained by the PDO alone.

Modulation of ENSO Teleconnections by the PDO

The spatial patterns of sea surface temperature anomalies and wind fields over the Pacific are quite similar between PDO$^+$ and El Niño, or between PDO$^-$ and La Niña. Correlation between unfiltered indices of ENSO and PDO is about 0.3–0.4 [356]. The principal difference between the PDO and ENSO is that the time scale of ENSO variability is an order of magnitude shorter (2–7 years) than the time scale of the PDO (40–76 years). In addition, ENSO variability is driven by processes in the equatorial regions in contrast to the PDO which is driven by dynamics in the North Pacific. More La Niñas occur during PDO$^-$, while more El Niños occur during PDO$^+$. The similar spatial patterns between ENSO and PDO suggests that the PDO modulates ENSO stability and magnitude [182]. Typical El Niño pressure anomalies occur in the North Pacific when the PDO is positive (PDO$^+$), and typical La Niña pressure anomalies occur when the PDO is negative (PDO$^-$), according to Gershunov and Barnett [182], leading them to refer to this as the constructive ENSO-NPO[2] phase relationship. In contrast, they find that ENSO signals are distorted when ENSO and PDO phase pairing takes the opposite, or destructive, sense (i.e. El Niño during PDO$^-$ or La Niña during PDO$^+$).

Gershunov and Barnett [182] hypothesize that the mechanism by which the PDO modulates ENSO acts through the influence of the Aleutian low pressure center (see Fig. 4.2, winter of 1977–1981) on the tracks of storms. The strength of the Aleutian low is the dominant atmospheric manifestation of the PDO [356]. The Aleutian low is less intense during negative (PDO$^-$) conditions and, when paired with La Niña, cyclonic storms are steered further to the north, increasing precipitation in the northwest United States, but bringing fewer storms and drier conditions to the southwest [182]. In contrast, a deeper Aleutian low shifts the storm track further south, which when combined with El Niño conditions bringing moist air from the eastern tropical Pacific, results in wetter conditions in the southwest United States. The modulation of ENSO teleconnections by the PDO [182], the complex relationship between upwelling, secular climate trends and ecosystem shifts [498], and the uncertainties in detecting regime shifts in the face of observed changes in the ecosystem (see Sect. 4.1.2), all indicate that the relationships between the PDO and regime shifts are considerably more complex than was initially thought.

4.1.1.2 The North Pacific Gyre Oscillation (NPGO)

The fact that that the Pacific Decadal Oscillation (PDO) was poorly correlated with many components of the planktonic ecosystem in the north-eastern Pacific led Di Lorenzo et al. [138] to re-examine basin scale patterns of sea surface temperature anomalies (SSTa) and sea surface height anomalies (SSHa), two fields that are highly correlated ($R \approx 0.85$). Based on an Empirical Orthogonal Function (EOF) analysis (also called Principal Components Analysis) over 180–110°W and 25–62°N, they described a new basin scale pattern that they called the North Pacific Gyre Oscillation (NPGO). Di Lorenzo et al. [138] characterized the PDO as the first EOF of SSHa[3] and they characterized the NPGO by the second EOF of SSHa [138]. The PDO and the NPGO are statistically independent since they are represented by different EOF axes that are orthogonal in terms of variability. The NPGO exhibits a very similar pattern to the previously described "Victoria mode" [72] that is represented by the second EOF of SSTa (rather than SSHa), but the NPGO shows stronger low frequency oscillations than the Victoria mode pattern [138].

Di Lorenzo et al. [138] used a Regional Ocean Modeling System (ROMS) model combined with a nutrient-phytoplankton-zooplankton-detritus (NPZD) model to determine the correlations and coherence between time series of the PDO and the NPGO with averaged time series of physical and biological variables from both the model output and from CalCOFI surveys. They reported that "The numerical model has significant skill in reconstructing the regional oceanic biological and physical conditions between 1950–2004, and tracks the observed temporal fluctuations of SSTa, sea surface salinity anomaly (SSSa), Chl-a, and subsurface 150 m NO_3 in the CalCOFI region". The model essentially provides a large scale interpolation regime for the variables, while the CalCOFI data provide an observational reference for the model time series. The model is also used to hind-cast the time series for variables like nitrate and chlorophyll that have only been measured since 1984 (Fig. 4.3).

Consistent with previous studies, the PDO mode (i.e. the first EOF of the monthly model SSTa or SSHa field) is the dominant mode of variability in the model, and accounted for 34 % of the variance in SSTa and 22 % of the variance in SSHa [138]. The NPGO mode explained 22 % of the

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[2] Gershunov and Barnett [182] use the term NPO, or North Pacific Oscillation, to refer to the same phenomena that Mantua et al. [356] call the PDO, or Pacific Decadal Oscillation.

[3] The PDO was described from sea surface temperature anomaly (SSTa) field by Mantua et al. [356] in contrast to Di Lorenzo et al. [138] who described the PDO in terms of the sea surface height anomaly (SSHa) field, but both these fields are highly correlated.

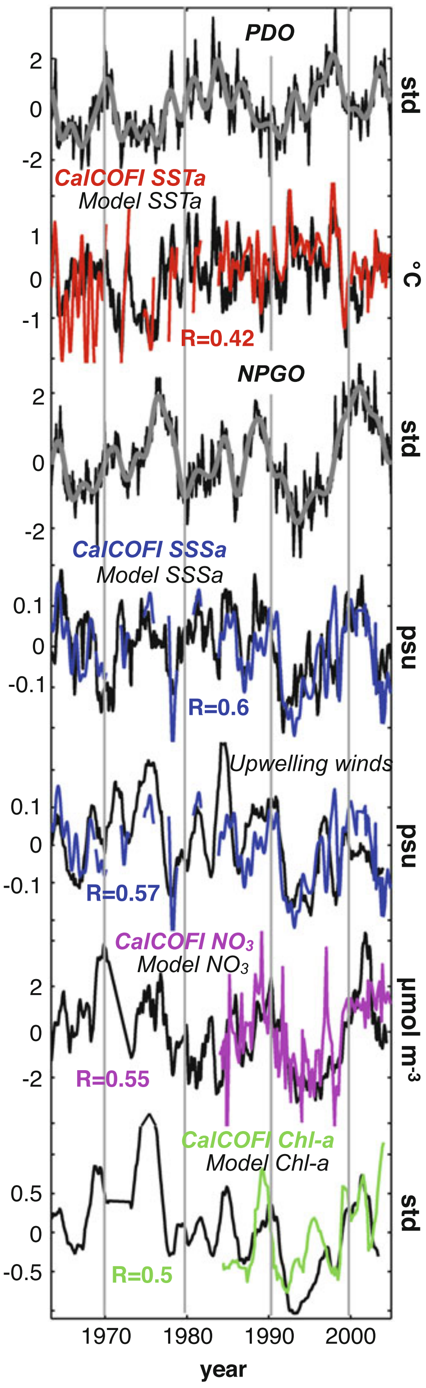

Fig. 4.3 PDO and NPGO compared to the model and CalCOFI observations. The PDO and NPGO indices (*black*) are plotted in standard deviation units with their 2 years low-pass filtered time series (*grey*). All other time series are spatial averages from the Southern California Current System model (*black*) or data (*color*). Correlations of raw monthly data between the model and data are given below each time series pair in color. All correlations are significant at the 95 % level or greater. The nitrate timeseries uses samples from 150 m. The Chl-a anomaly data have been smoothed with a 2 years running average, and normalized by their standard deviation. The upwelling winds are calculated from NCEP reanalysis data, smoothed with a 2 years running average, and standardized to psu units for comparison to CalCOFI SSSa. Positive winds are directed equatorward, implying upwelling favorable conditions (From Di Lorenzo et al. [138])

SSTa field and 8 % of the SSHa field [138]. The PDO was significantly correlated with sea surface temperature anomalies (SSTa) ($R = 0.42$), but not with other variables. The PDO was also correlated ($R = 0.4$) with detrended, 12-month running mean SSTa at the Scripps Institution of Oceanography pier [138]. However only the NPGO was significantly correlated with sea surface salinity anomalies ($R = 0.6$), upwelling winds ($R = 0.57$), average chlorophyll a ($R = 0.5$) and subsurface (150 m depth) mean nitrate ($R = 0.55$), phosphate ($R = 0.35$), silicate ($R = 0.53$) and oxygen ($R = -0.5$) in the CalCOFI region [138].

The NPGO is strongly correlated with wind-stress and in particular with wind-forced coastal upwelling (Fig. 4.4), so Di Lorenzo et al. [138] suggest that the NPGO is a "primary of indicator of upwelling strength [and] nutrient fluxes … in the CalCOFI region". These authors appear to interpret the high correlation of the NPGO with modeled and observed chlorophyll as evidence of nutrient-driven bottom up forcing by coastal upwelling (but see Sect. 2.4.2).

Regime shifts occur when there are strong reversals of both the PDO and the NPGO but of opposite sign. Understanding the basin scale changes in the North Pacific may depend partly on determining the effect of the phase relationship of these teleconnection modes [138]. The spatial patterns of the PDO and NPGO are distinct and exhibit different dynamics. Based on sea surface pressure maps, the PDO shows a single large wind gyre north of 25°N and anomalously strong poleward flow along the west coast from 25°N to 55°N (Fig. 4.4) [138]. A positive PDO strengthens the Alaskan Gyre and weakens the California Current. The pattern of the positive NPGO differs from the PDO in showing two counter-rotating gyres separated by the eastward flowing North Pacific Current (Fig. 4.4). Positive NPGO results in open ocean wind stress curl anomalies driving intensification of the North Pacific Current, as well as strengthening of the Alaskan Coastal Current and the California Current (see Sect. 2.3), and strengthening of coastal upwelling south of 38°N [138]. The effect of positive phase NPGO on the California Current is opposite to the effect of positive phase PDO. The spatial pattern of wind stress anomalies of the positive NPGO resembles the spatial pattern of the positive North Pacific Oscillation (NPO), which is a dominant atmospheric mode of variability in the North Pacific (Sect. 4.1.1), and the NPGO may be the oceanic expression of the atmospheric NPO [138].

4.1.2 Defining Regime Shifts

Changes in climate indices such as the PDO in the mid-1940s and in 1976/1977 that were associated with synchronous changes in ecosystems over extensive geographic areas have

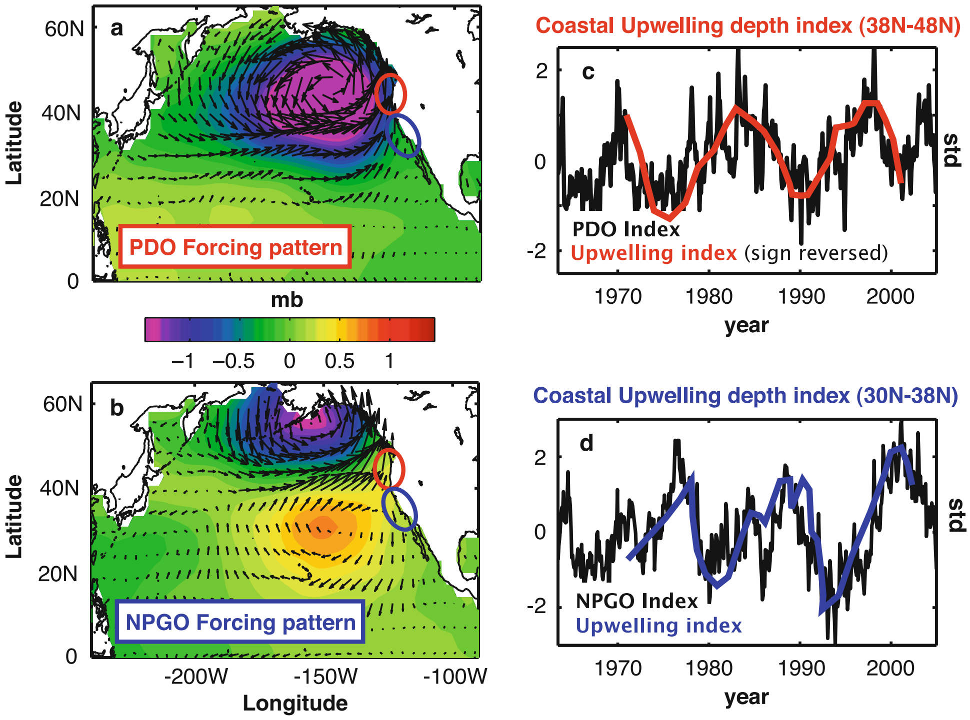

Fig. 4.4 Regression maps of (**a**) PDO and (**b**) NPGO indices with National Center for Environmental Prediction (NCEP) wind stress vectors and sea level pressure (*color scale*). (**c**) Coastal upwelling depth index from inverse model calculations averaged from 38°N to 48°N (area denoted by *red circles* in the maps) compared to PDO index. (**d**) Coastal upwelling depth index averaged from 30°N to 38°N (area denoted by *blue circle* in the maps) compared to NPGO index. A positive upwelling index implies a deeper upwelling cell (From Di Lorenzo et al. [138])

suggested the existence of "regime shifts" [356, 431, 432]. The term "regime shift" has been rather loosely used to refer to persistent changes in multiple variables over large areas, and there are various definitions of the term in the literature (reviewed by [433], see also [256, 431, 432, 479]). Overland et al. [431] distinguishes between regime shifts that are defined as a "displacement" of the mean state [355, 356], regime shifts that imply the existence of "multiple stable states", and regime shifts defined by external forcing such as climate or fishing [144].

Displacement regime shifts are based on analysis of relatively short (50 years or less) time series where there are periods with mean values that are significantly different. The differences may have important implications for fisheries management [433]. Significant displacement of the mean is determined by considering the variance of the series before and after the regime shift, using the methods of Rodionov [473], for example (see review by Mantua [355]). Over the twentieth century, Rodionov's [473] method detects displacements in the mean value of the PDO in the mid 1940s and late 1970s. However, Overland et al. [431] pointed out that "One can have large local displacement regime shifts even if the time series of the underlying physical process on hundreds of years were from a Gaussian statistical distribution (i.e. without multiple equilibria) but with a large variance". Further to this, Overland et al. [433] showed that when the selectivity parameter for Rodionov's [473] method is relaxed, additional regime shifts were detected in 1934 and 1999, indicating that the analysis is sensitive to changes in the analysis parameters.

The second type of regime shift depends on identifying processes driving time series into discrete states. In these different states, the temporal variation of key biotic and abiotic variables are "concentrated near distinct dynamical attractors in a limited dimensional phase space" [433]. Rudnick and Davis [479] limit regimes to multi-modal states originating from non-linear/ deterministic processes, implying but not requiring, multiple states. They distinguish such regimes from relatively random processes yielding more Gaussian distributions of variables [433]. This is a much more demanding definition of regimes which requires long times series that can be analyzed with statistical rigor. It also assumes a sufficient understanding of the processes leading to the development of discrete biological and physical states. It seems apparent that for many regions, these conditions will not be met.

The third definition of regimes is inconsistent with the first two described here [433]. Duffy-Anderson et al. [144] refer to changes in external forcing, such as climate or fishing, as regimes, but call changes within an ecosystem "phase changes". We will not discuss their concept further here.

Rudnick and Davis [479] showed that the kind of steps in time series that have been interpreted as regime shifts by Hare and Mantua [192] and others are likely to be detected in stationary time series with the same frequency content as the PDO. They calculated that "given 100 independent and stationary time series of identical frequency content as the PDO, the composite analysis applied to a randomly selected 20-year span will detect a regime shift comparable to that found by Hare and Mantua about half the time" [479]. Their simulations indicated that using many short time series in a composite analysis was an excellent way to create large and easily detectable shifts that would be interpreted as "regime shifts" [479]. They argue that while genuine regime shifts may occur, due to the relationship between biological and physical variables in a changing climate, their analysis shows that the detection methods used by Hare and Mantua [192] were flawed, and would produce steps even in a stationary Gaussian red noise[4] time series [479].

Overland et al. [432] also concluded that a 104-year long record of the PDO was insufficient to distinguish underlying processes, and cautioned against attempting to predict future state based on curve fitting methods. They [432] found that a first-order autoregressive red noise model, a long-memory red noise model and a periodic model all fit a century-long time series of the PDO equally well.

4.1.3 Regime Shifts and the Biota

The idea of "regimes" in the California Current System was first advanced in the 1970s, 20 years before Mantua et al's. [356] seminal paper. The concept goes back to Isaacs [242] who considered regimes to be "distinct environmental or climatic states" [344]. However, the general idea was advanced considerably earlier. For example, based on the incidence of tropical fishes caught off central and southern California, Hubbs concluded that 1850–1870 was an anomalously warm (i.e. warmer than average) period ([344] attributed to [226][5]). MacCall [344] further elaborated the concept and used temperature as a proxy for a suite of environmental variables that changed as the regimes changed. Thus MacCall [344] considered that "the Scripps Pier record consists of three conspicuous temperature regimes: a moderate and highly variable period from the beginning of the time series [in 1916] to about 1940, a cold period from 1940 to 1976, and a warm period since 1976" [344]. The temperature proxy for regimes is not necessarily coherent between southern, central and northern California [344]. Small pelagic fish populations show some currently unexplained long-term fluctuations in abundance that appear to be related to changes in "regimes" [344], but see Sect. 4.1.3.3.

4.1.3.1 Long-Term Changes in Atmospheric Forcing, Hydrography and Circulation

Much of this section pertains to changes in the core CalCOFI area rather than the entire California Current System. There is strong regional variability in the California Current System, briefly reviewed in Sect. 2.1.

Geostrophic flows off southern California were described in Sect. 2.4.1. When these flows are averaged over the period 1949–2000 [137], the pattern appears considerably simpler than described in that section, both at the surface and at depth (Fig. 4.5). At the surface, the averaged offshore flow appears dominated by a broad, slow, equatorward California Current bringing cold, fresher water of northern origin into the region. In the nearshore, the averaged current is narrower and poleward directed, bringing warm, saline water from the south. The northward flowing current below the thermocline is called the California Undercurrent. Connecting these two currents is a cyclonic circulation called the Southern California Eddy (SCE) ([115, 135, 339] cited by [137]). When the mean depths of the 26.4 isopycnal[6] are plotted (Fig. 4.5b) the core of the averaged California Current remains well-defined below the thermocline, and the signature of the SCE is stronger [137] (Fig. 4.5).

Both observational data and models show intensification of the Southern California Eddy [137]. A Hovmöller plot of wind stress curl (Fig. 4.6) over the last 50 years in the core CalCOFI area shows more negative curl in the coastal region before 1980, followed by a transition to stronger positive wind stress curl after the 1980s [137]. When a ROMS model is forced with these changes in the winds, results show intensification of southward surface currents after 1980 [137]. Model results are consistent with observations from CalCOFI surveys, but the effect is stronger in the observations [137]. The spatial structure of the observed response from EOF analysis shows that after 1980, the alongshore velocity is more southward in the offshore part of the recirculation region and more northward inshore [137].

Changes in steric height (relative to 500 decibar) off southern California are largely due to thermal expansion [474] (Fig. 4.7b). The time series of steric height shows "large positive offsets during major El Niño episodes … [that] subsequently decreased after each episode but never fully returned to the pre-El Niño values" [474]. The change in steric height from 1950 to 1992 is equivalent to a trend of 0.9 ± 0.2 mm year^{-1} (Fig. 4.7a), and the total rise over that period was nearly 3 cm [474]. The change of slope of the

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[4] Climate "noise" comes from the realization of random processes created from the sum of individual sinusoids of different frequencies, amplitudes and phases. A red noise spectrum is one where the power (i.e. the average-squared amplitude) increases as frequency decreases (or wavelength increases). In contrast, for a white noise process, the power is constant as a function of frequency [432]. Different realizations of a stationary red noise process can produce "runs" where a time series anomaly will have the same sign (i.e. be either above or below the mean) for extended periods [479].

[5] Hubb's conclusions were based on the Pacific Railroad Survey off San Diego between 1853–1857 and more extensive collections off Monterey Bay and southern California conducted by Gilbert and Jordan around 1880 (MacCall [344] attributed to Hubbs [226]).

[6] The 26.4 isopycnal is used to show the influence of the California Undercurrent or flows of southern origin (see Sect. 2.3).

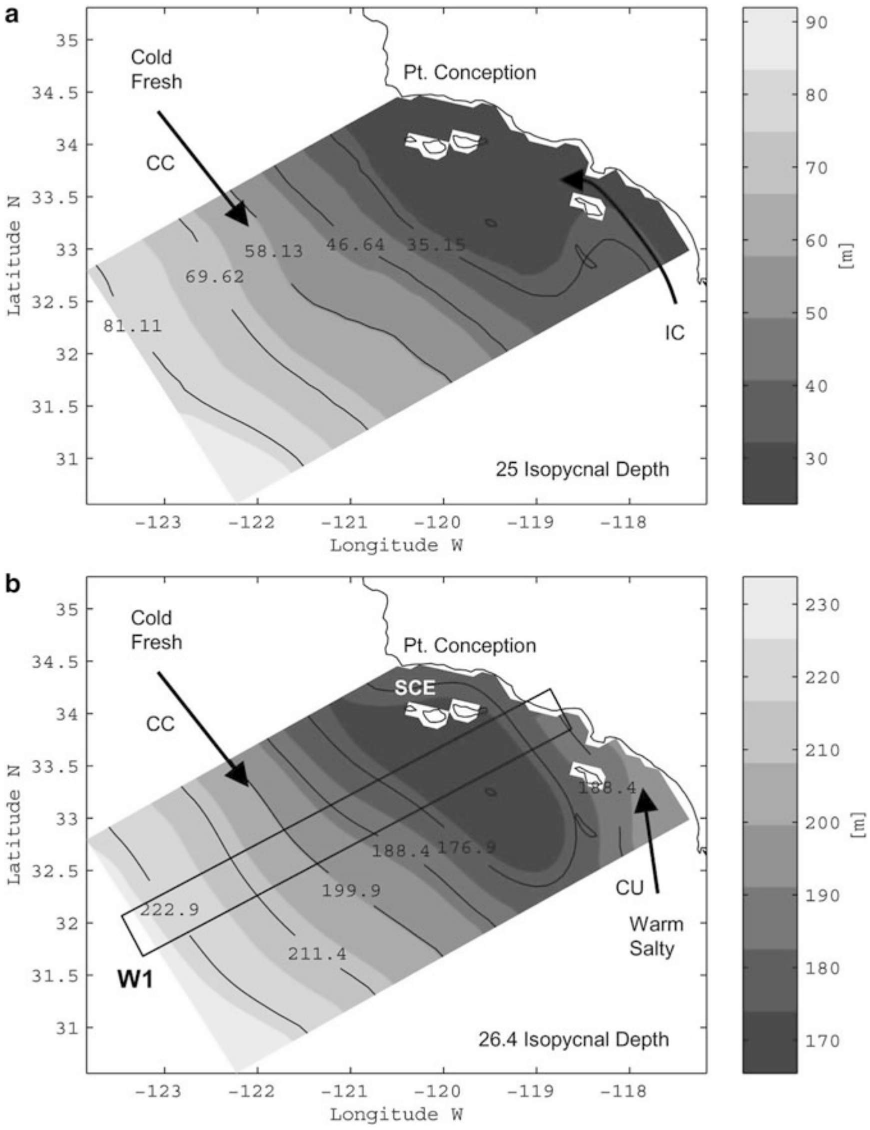

Fig. 4.5 Average depths of isopycnal (**a**) 25 and (**b**) 26.4 based on CalCOFI survey data collected from 1949 to 2000 to indicate surface and deeper flow fields (From Di Lorenzo et al. [137])

steric height curve with distance offshore in Fig. 4.7 reflects the change in current direction with distance offshore. See the footnote[7] for a brief explanation.

Temperature and salinity anomalies on the 26.4 isopycnal, the depth of which varies seasonally from 180 to 220 m always below the thermocline, show prominent low frequency variability (with periods longer than 3-years) [137]. Temperature anomalies are highly correlated with climatic indices such as ENSO and the PDO, and show strong inter-annual variability. In contrast to temperature, salinity anomalies vary on decadal rather than inter-annual time scales and are not well correlated with climate indices [137]. Time series of salinity do not show any trend at any depth [474]. Temperature and salinity are not correlated at time scales longer than a few years.

Sea surface temperature (SST) is better correlated in space than wind stress on inter-annual (1–5 year) time scales [388] (Figs. 2.2a, b). Temperature trends also show an obvious warming trend after the 1976 climate shift, a feature not shown in the wind stress (Figs. 2.2a, b). This suggests that

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[7] At the sea surface, the geostrophic velocities can be calculated from time-averaged sea surface heights at two measurement locations relative to an assumed level surface (which is generally 500 m or 200 m in the CalCOFI atlases). The mass of water at a given measurement location is a function of both the sea surface height and the density of the water. The total mass of water determines the pressure difference at a given depth. The geostrophic velocity is proportional to the difference in pressure at two locations. Near the coast, the water column stands higher at the surface relative to the geoid, and the greater mass of water creates higher pressure. The geostrophic balance between pressure and Coriolis forces (i.e. no flow relative to the earth) causes the current to flow to the right of the down-pressure gradient, i.e. creates a northward flowing current. Further offshore, sea surface height is greater toward the west, and the geostrophic balance again deflects flow to the right of the down-pressure gradient, which in this case, is a southward-flowing current (see [546] for detail).

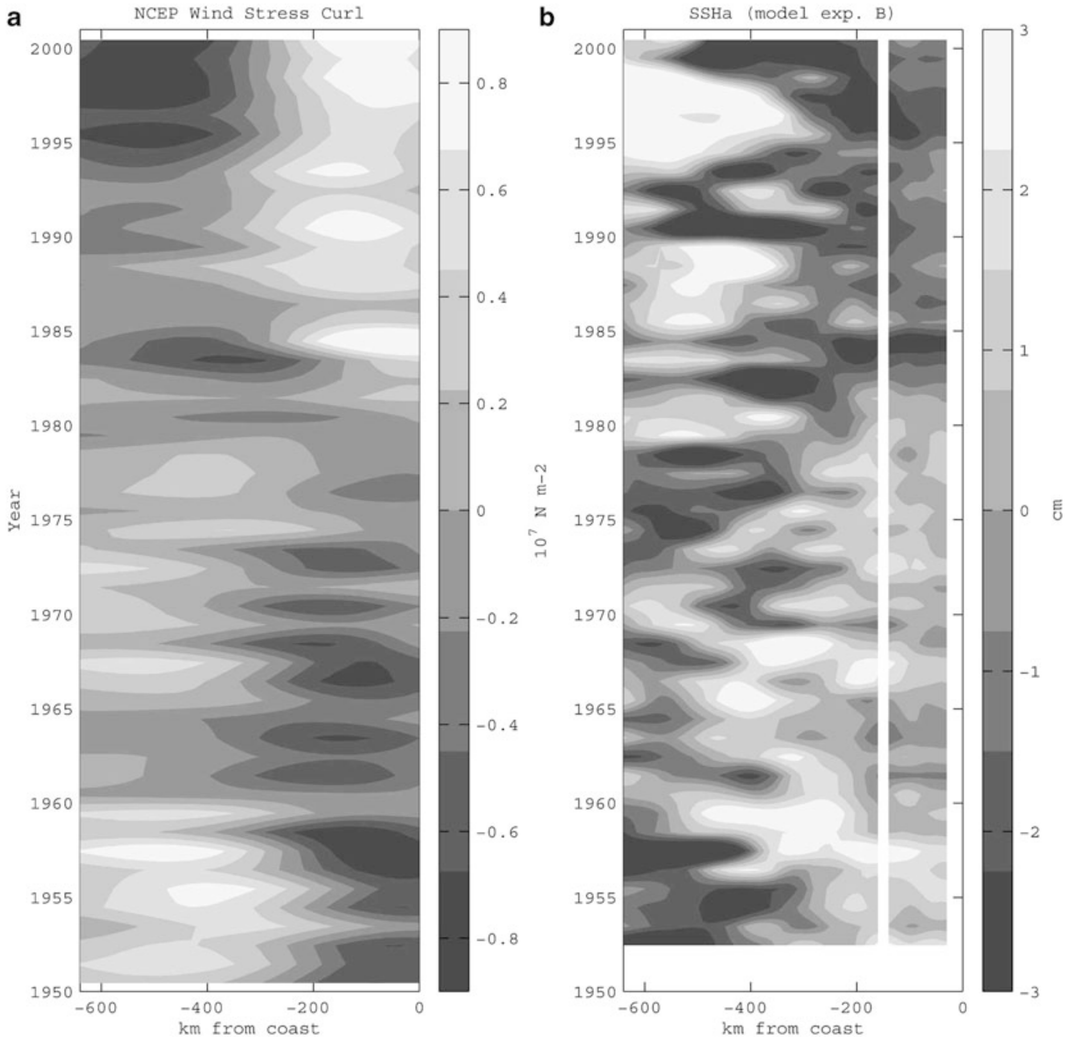

Fig. 4.6 Hovmöller plots showing the 50-year trend in NCEP reanalysis (**a**) wind stress curl anomalies and (**b**) modeled sea surface height anomalies along a CalCOFI line (86.7) in the middle of the Southern California Bight (From Di Lorenzo et al. [137])

SST trends are influenced by the basin-scale pressure and wind fields, rather than by local wind forcing [388].

Temperature off southern California showed a secular warming of 1.3 °C over 52 years (1949–2000) according to Di Lorenzo et al. [137], or 0.025 °C year^{-1} on average. This compares to warming of 0.8 °C in the upper 100 m over 42 years (1950–1992), or 0.019 °C year^{-1} on average, estimated earlier by Roemmich for waters 50–315 km offshore off southern California [474]. Roemmich found evidence of warming down to 300 m depth at some stations (Fig. 4.7b) [474]. Warming at Scripps pier (0.024 ± 0.007 °C year^{-1} on average) was greater than in the offshore waters [474] (see also [369]). Palacios et al. [438] found that thermocline temperatures increased by 0.6–1.3 °C over 44 years (1950–1993) at 8 locations in the central and southern California Current System (Fig. 4.12). Heat content integrated over the upper 200 m increased by 6.2–9.1 % at the coast and 2.4–7.1 % offshore during this same period (Fig. 4.8). These results are consistent with a 1 °C warming trend at both surface and sub-surface depths in the entire California Current System over the last 50 years [389, 475, 498].

Increased heat content of the upper water column due to warming trends is related to changes in stratification, which has implications for biological production. Long-term changes in stratification within the southern California Current System are quite subtle in the sense that the thermocline temperature anomaly increased from 1950–2005, but the depth of the thermocline did not increase in and offshore of the Southern California Bight [264]. Kim [264] showed that a section along CalCOFI line 80 off Point Conception was dominated by alternating periods of positive and negative thermocline and pycnocline depth anomalies (i.e. alternating periods when the thermocline and pycnocline depth was shallower or deeper than the means), with no trend, nor obvious response to the 1976/1977 regime shift (Fig. 4.9a, b). She also found that the pattern along line 80 was representative of other CalCOFI stations. In contrast to the thermocline and pycnocline depth anomalies which show no trend, the

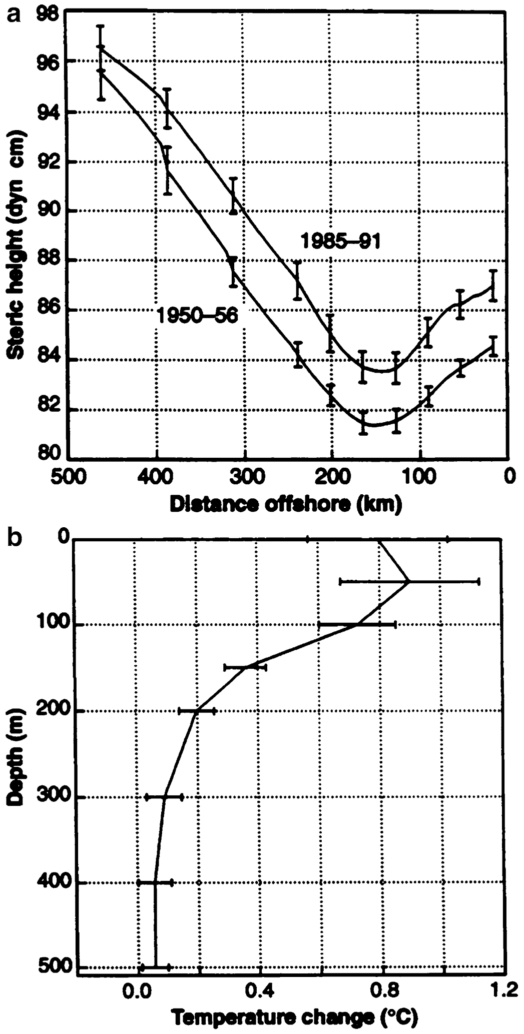

Fig. 4.7 (**a**) Steric height relative to 500 decibar as a function of distance offshore along CalCOFI line 90 off southern California for two time periods, 1950–1956 and 1985–1991. *Vertical bars* are the standard error of the mean for each time interval. Note that these two time periods contain no major El Niño episodes. (**b**) Temperature change as a function of depth for the same two time periods as in (a). Bars are the sum of the standard errors for the two time intervals (From Peterman et al. [474])

thermocline temperature anomaly was more positive during the warm regime (1977–1998) (Fig. 4.9c) [264]. The thermocline temperature was defined as the temperature at the depth of the maximum temperature gradient. Positive thermocline temperature anomalies reflect the increased stability of the water column during the warm regime (1977–1998), shown by the prevalence of positive buoyancy frequency anomalies (Fig. 4.9d) [264]. These trends are shown even more clearly by plotting the probability density functions of the thermocline and pycnocline depth anomalies, the thermocline temperature anomaly, and the buoyancy frequency anomaly (Fig. 4.10). There was no difference in the distributions of either thermocline or pycnocline depth anomalies in either the Southern California Bight or in offshore waters (Fig. 4.10a, b). In contrast, the temperature anomaly at the thermocline was warmer, and water column stability anomaly was greater during the warm regime (1977/98) than during the cool regime (1950–1976) (Fig. 4.9c, d) [264]. The implications of increased stratification for production in the southern California Current System are important. Despite the fact that there are far fewer data available during the cool regime than the warm regime, Kim [264] was able to show that for a given temperature, nitrate levels were higher during the warm regime in the upper 200 m of the water column (Fig. 4.11). There was no difference at depth because the increased heat content does not penetrate to greater depths [264]. This is intriguing, but bears further investigation since Fig. 4.11 is based on a single nearshore station (line 90, station 37) in late winter-spring (January–March), which is when the most appropriate data were available to compare the warm and cool regimes.

Kim's [264] results are somewhat different than those Palacios et al. [438] who reported that the coastal thermocline strengthened and deepened, while the offshore thermocline weakened and shoaled from 1950 to 1993. Palacios et al. [438] modeled trends in the thermocline at eight locations in the central and southern California Current System (Fig. 4.12) and Kim [264] argued that Palacios et al. [438] locations 1 and 4 in the Southern California Bight (Fig. 4.12) showed no trend in the depth of the thermocline, in agreement with her results. In contrast, Palacios et al. [438] maintained that the thermocline deepened at nearshore stations 2, 6 and 8 by 9–18 m, while the offshore stations 3, 5 and 7 shoaled by 5–10 m (Fig. 4.12) [438]. These authors reported temperature gradient strengthened by 30–44 % and deepened by 35–82 % at coastal locations, but weakened by 7–23 % and shoaled by 10–17 % offshore [438]. An important result from Palacios et al. [438] is that the trends over time in the thermocline depth differ both with latitude and between inshore and offshore in the central and southern California Current System. The regional differences show that local processes influence the amplitude and phase of the seasonal thermocline [438]. Since stratification depends upon the balance of heat inputs and losses as well as on the degree of mixing, these differences are not surprising given the regional variability in the wind stress. Seasonal trends in both thermocline strength and depth also show 3–5 year periods of weakening and strengthening annual cycles, in addition to decadal trends [438]. Some, but not all, of these variations in the annual cycles are related to ENSO events [438].

Bakun postulated that land masses would warm faster than the ocean with climate change, resulting in stronger pressure gradients between atmospheric low pressure over the warmer land, and higher pressure over the cooler ocean [40]. The more intense pressure gradient should

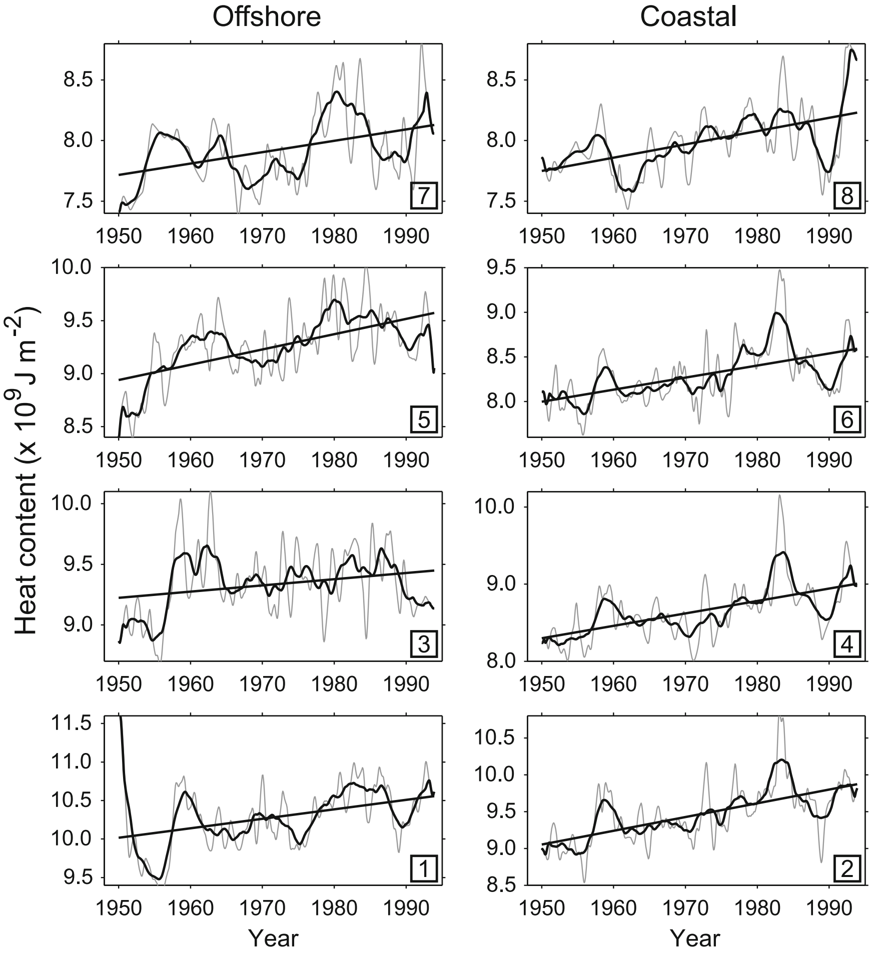

Fig. 4.8 Time series of 0–200 m heat content (10^9 J m^{-2}) showing the trend component derived from state space modeling at eight locations in the California Current System (shown in Fig. 4.12), 1950–1993. *Light gray* curves are the monthly series, and *black curves* are the 37-point running averages. The regression of heat content on year is indicated by the *black line* (From Palacios et al. [438])

produce stronger equatorward wind flows at eastern ocean boundaries, driving more intense upwelling. Based on an index of wind stress, Bakun found that seasonal upwelling favorable winds showed a long-term increasing trend in the California Current System, except at 24°N and 27°N off Baja California[8] [40]. For this study, wind stress was calculated from ship observations of wind and barometric pressure, using geostrophic constraints. Bakun used interpolated fields of wind stress to produce monthly indices at different locations along the coast. Spring-summer wind stress off Point Arena–Cape Mendocino (39°N) was used to describe the California trend (Fig. 4.13), since this latitude represents the "highest intensity core of the California upwelling system" [40].

Based on a linear trend in these data, Bakun concluded that equatorward along-shore wind stress intensified over the 42-year period between 1946–1988 (Fig. 4.13), although there was substantial variability at scales ranging from inter-annual (1–5 years) to the decadal [40]. Further, Bakun found that there was increased intensity of upwelling favorable wind stress during the upwelling seasons at widely separated locations around the world (Fig. 4.13) [40]. However, when these regional series were differenced to remove linear trends, the correlations between widely separated regions was lost. This suggested that the only coherence in wind stress between the regions was the long-term secular trend [40] (Fig. 4.13). The coherence in secular trends between widely separated regions with similar dynamics, such as the upwelling regions off Peru and California was independently supported by state-space analyses of SST and wind stress [388]. Mendelssohn and Schwing [388] suggested that a "more global process rather than regional dynamics, may be underlying the climate variability in both these eastern boundary current regions. These results imply that climate change will affect geographically disparate ecosystems having a common physical and ecological structure in a like manner" [388].

Bakun suggested that intensification of upwelling along eastern ocean boundaries resulting from the increased wind stress would lead to more cool foggy weather along the

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[8] Bakun considered that the locations off Baja California were influenced by the Gulf of California waters to the east which changed the ocean-atmosphere interactions that create the upwelling favorable winds, so that these areas did not experience the same conditions as locations further to the north which have continental land mass to the east.

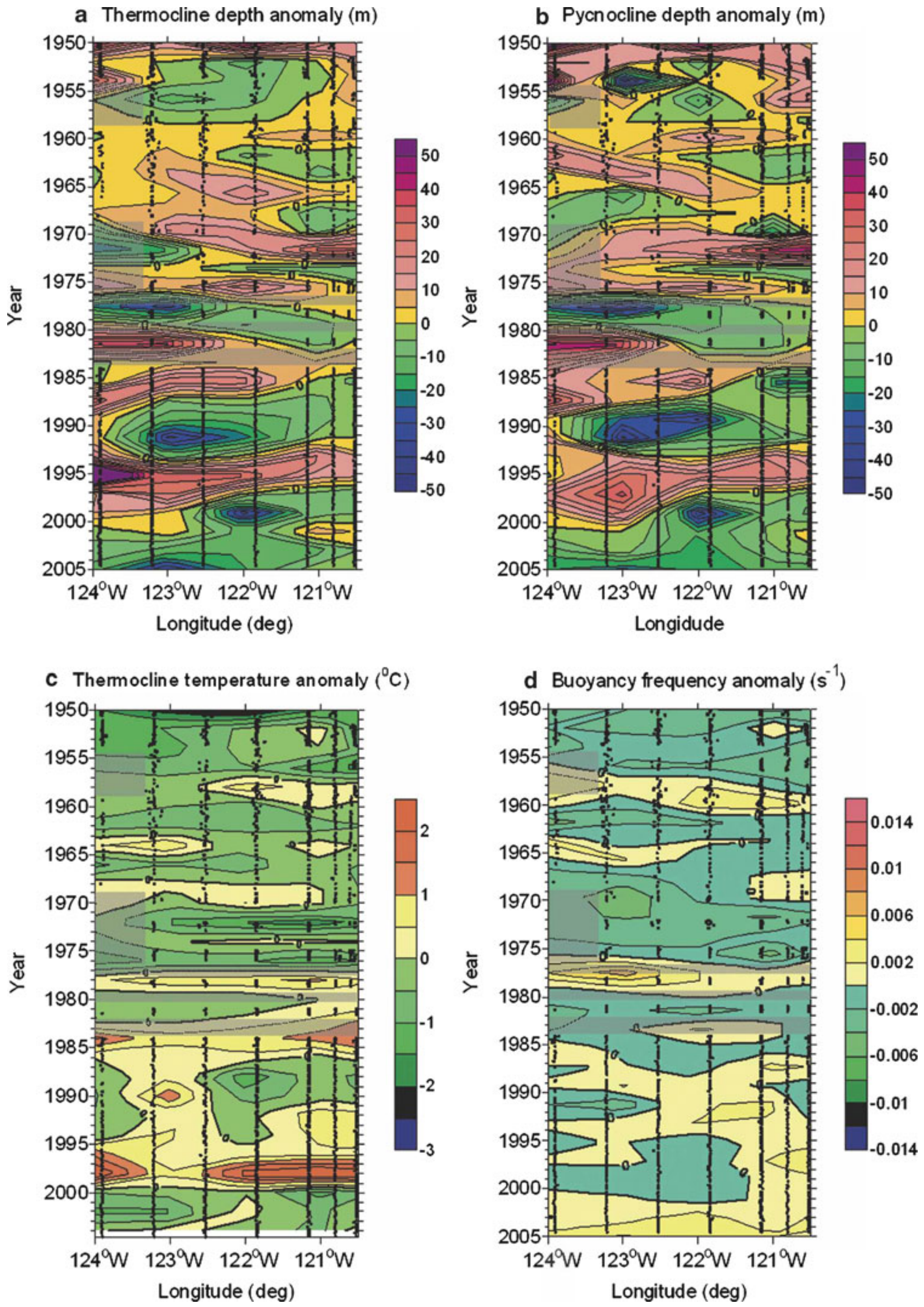


Fig. 4.9 Hovmöller diagrams for CalCOFI line-80 (**a**) thermocline anomalies, (**b**) pycnocline anomalies, (**c**) thermocline temperature anomalies, and (**d**) buoyancy frequency anomalies at the pycnocline between 1950 and 2005 (From Kim [264])

coast, and stronger winds blowing from the coast through coastal mountain passes to the hotter interior valleys. He also suggested that increased heat transfer to the cooler coastal ocean might increase atmospheric stability, and lead to drier conditions inland of the coastal fog zone. Bakun was less certain about the effects of increased upwelling on the marine ecosystem. While increased upwelling might lead to greater primary production, how this production would be used in the food web was uncertain [40].

There are strong regional differences in wind stress in the California Current System, and the trends in wind stress differ between regions. Mendelssohn and Schwing [388] found that the wind trends can be separated into three distinct regions: south (22–32°N), central (32–40°N) and north (42–48°N). The central region has the strongest wind stress and showed a long-term trend to stronger equatorward wind stress over the period 1946–1990 (Fig. 2.2a). The central region shows large inter-annual variability [388]. As

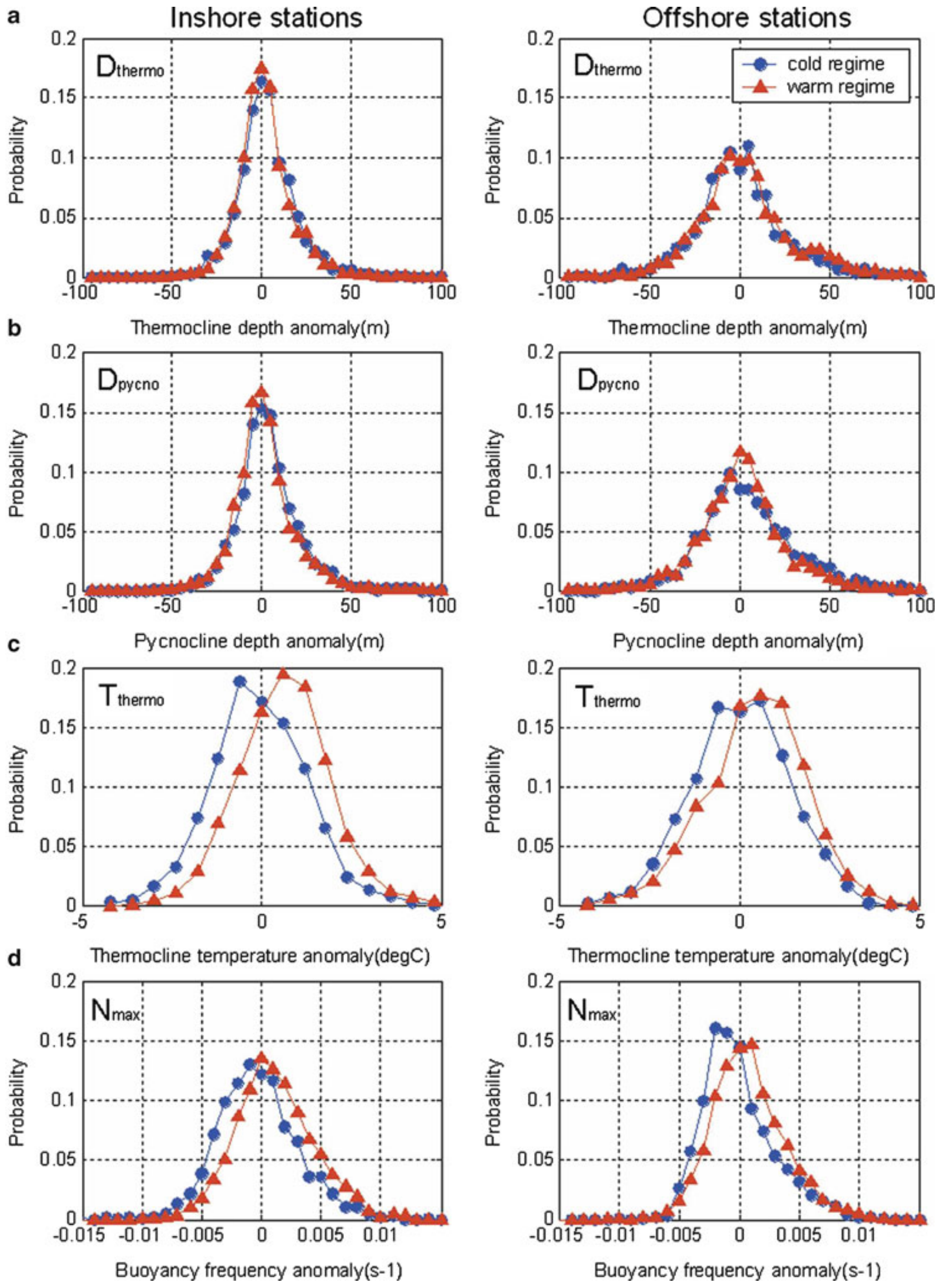


Fig. 4.10 Probability density functions of the four variables as in Fig. 4.9. (*Left*) Inshore stations and (*right*) offshore stations. Offshore stations are defined as deeper than 2,000 m bottom depth (i.e. west of the Santa Rosa Ridge and outside the Southern California Bight). *Blue lines* represent the cool regime (1950/76), and *red lines* represent the warm regime (1977/98) (From Kim [264])

for the central region, long-term trends in wind stress in the southern region showed intensified equatorward winds over the same period. Winds offshore of the Southern California Bight (at 33°N) in the southern region are actually similar to the central region wind stress series [388]. In contrast to the winds in the central and southern regions, equatorward wind stress decreases rapidly north of 40°N, and wind stress in the northern region showed a mean northward trend (Fig. 2.2a). The northern region showed long-term strengthening of poleward wind stress, contrasting with the direction of the trend in the central and southern regions (Fig. 2.2a) [388].

Evidence indicates that long-term trends in SST, excluding seasonal events like upwelling, are not related to local wind forcing [498]. Winds are much more variable than temperature, with more regional differences and local behavior [388]. Upwelling also has a complex spatial and temporal structure, such that within any upwelling season there are periods of variable upwelling and downwelling intensity, and there are also regions along the coast that are more or less favorable for upwelling. This level of variability is additional to the considerable inter-annual variability in upwelling. This complex spatial and temporal structure of

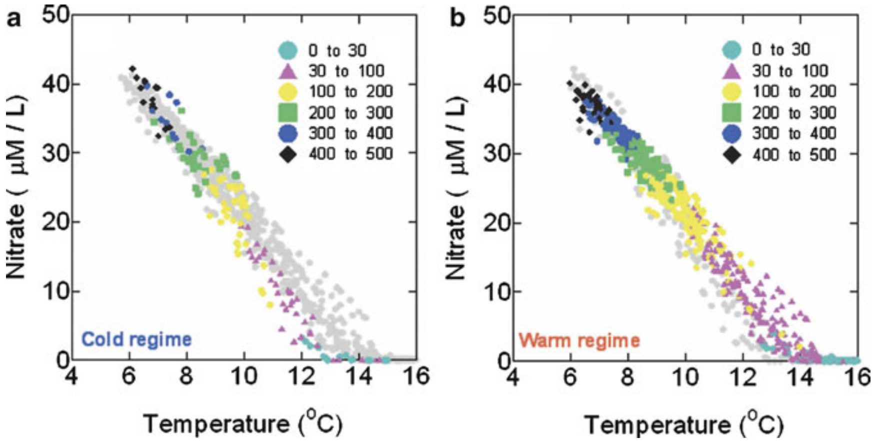


Fig. 4.11 Nitrate–temperature scatter plots in the (**a**) cool regime and (**b**) warm regime. *Gray background dots* are plotted to compare with the other regime. Data are from a single nearshore station (line 90, station 37) in late winter-spring (January–March) from 1977 to 1998 (From Kim [264])

upwelling means that trends cannot be quantified by spatially integrated indices, nor by indices from a single locale along the coast [498].

In summary, off southern California, temperature shows a secular warming trend from 1949 to 2000, despite strong inter-annual variability. Temperature trends are well correlated with the PDO and ENSO climate indices. The temperature warming trend is stronger inshore than offshore. Thermal expansion is the major influence on a secular trend in steric height, and steric height has increased off southern California from 1950 to 1992. The long-term increasing trend in steric height is overlain by a positive response to strong El Niños. The Southern California Eddy has strengthened over the last 50 years (1949–2000), in part due to changes in wind stress curl forcing of currents. Salinity shows no consistent trends over the same period, but appears to vary on decadal scales as a function of the intrinsic variability of the California Current System. Upwelling-favorable wind stress shows a long-term increase along the central California coast, indicating increased upwelling from 1946 to 1988. Equatorward wind stress has also increased offshore of the Southern California Bight from 1946 to 1990. Temperature at the depth of the thermocline increased, at least up to 1998, with consequent increase in stability due to stratification of the water column. Increased stratification and reduced mixing implies lower nutrient flux into the surface layers and reduced production. At the same time, increased stratification appears to be associated with a change in the nitrate-temperature relationship, such that more nitrate is available at a given temperature off southern California, which should partially offset the effect of increased stratification. Deepening of the coastal thermocline and shoaling of the offshore thermocline implies a flattening of the isotherms and slowing of geostrophic equatorward flow between 40°N and 31°N [438].

4.1.3.2 Trends in Hypoxia

Analysis of data has shown widespread changes in the concentration of dissolved oxygen in virtually every basin of the world's oceans (see references in Deutsch et al. [134]. In biogeochemical terms, the change in concentration of oxygen in the ocean is a function of exchange with the atmosphere, ventilation of deeper waters, biological production and respiration, and advection, which can be expressed as the sum of anomalies of each of these processes: $\Delta O_2 = \Delta O_2^{sat} + \Delta O_2^{vent} + \Delta O_2^{bio} + \Delta O_2^{circ} = \Delta O_2^{sat} - \Delta AOU$. Apparent Oxygen Utilization ($AOU = O_2^{sat} - O_2$) integrates the effect of ventilation, biology, and circulation. ΔO_2^{sat}reflects thermodynamic changes in the saturation or air-sea disequilibrium of oxygen in the surface waters. ΔO_2^{vent} is the change in the ventilation of deeper waters through sinking of oxygen rich waters. ΔO_2^{bio} is the change in the subsurface biological oxygen consumption, and ΔO_2^{circ}reflects changes in the speed or pathway of advection through the oxygen field [134].

The largest and best documented changes in oxygen have been observed in the North Pacific ([147] cited in [134]). Evidence indicates that the changes are due to changes in AOU, i.e. to physical and biological mechanisms, rather than to shifts in the thermodynamic equilibrium between the surface waters and the atmosphere, ΔO_2^{sat} [134]. Circulation and biogeochemical models are necessary to quantify the spatial and temporal changes in oxygen and associated physical and biological variables [134]. Deutsch et al. [134] used such models to characterize and isolate the ventilation, biological utilization and circulation components contributing to changes in Apparent Oxygen Utilization between the 1980s and 1990s in the North Pacific [134]. At basin scales in the North Pacific, Deutsch et al. [134] showed that oxygen decreases seen throughout the mid-latitudes are primarily driven by reduced exchange between the atmosphere and the ocean interior, ΔO_2^{vent}.

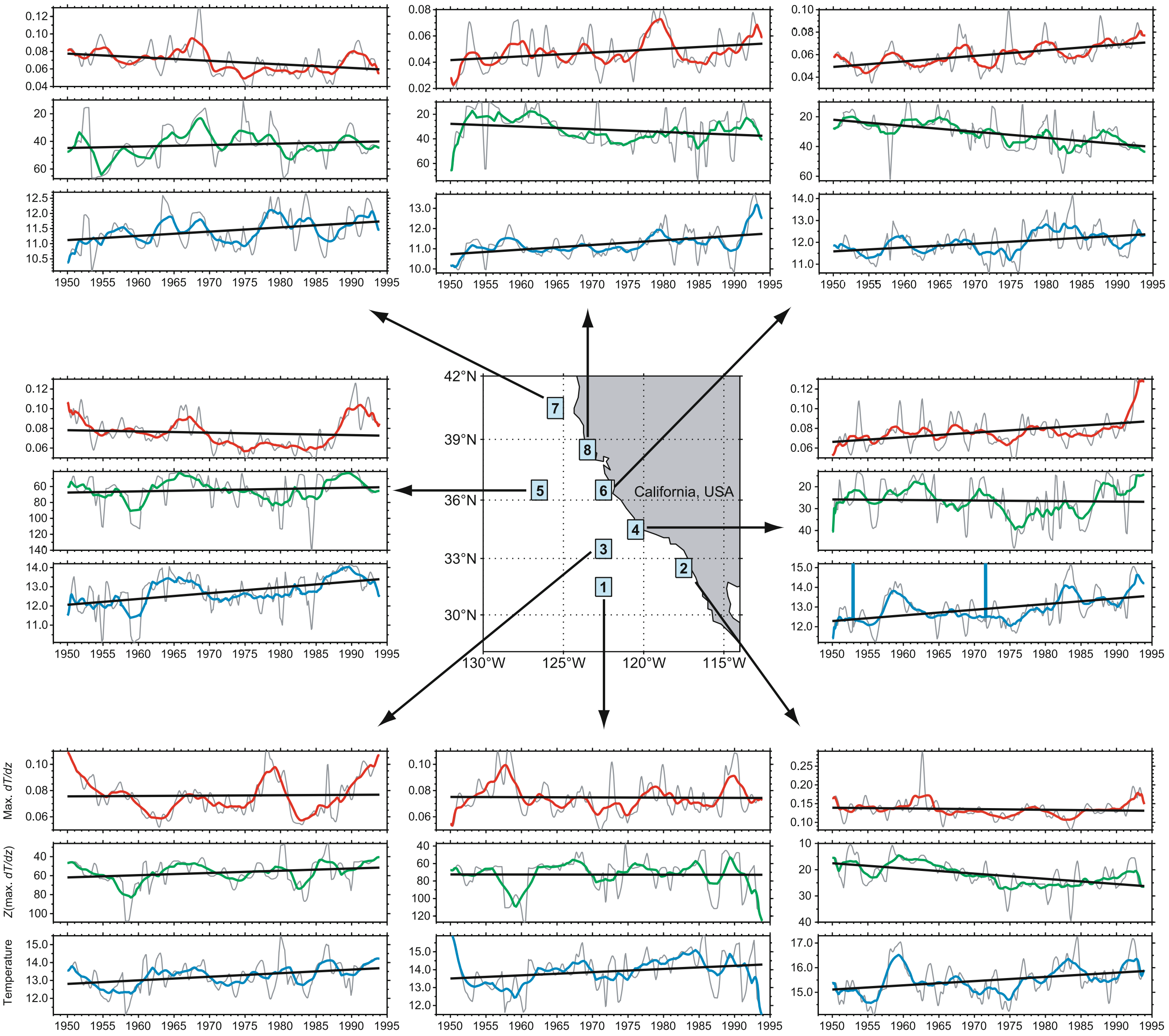


Fig. 4.12 Time series of the trend component derived from state space modeling of temperature-related variables at eight locations in the California Current System, 1950–1993. At each location, the (*top panel*) maximum vertical temperature gradient (°C m^{-1}), (*middle panel*) depth of the maximum temperature gradient (m), and (*bottom panel*) temperature at the depth of the maximum temperature gradient (°C) are shown. *Light gray curves* are the monthly series, and *colored curves* are the 37-point running averages. The linear regression of each variable on year is indicated by the *black line* (From [438])

A recent study [71] of trends in dissolved oxygen concentrations off southern California based on CalCOFI data showed that dissolved oxygen declined at most CalCOFI stations over the period 1984–2006. The trend could be described as linear at most stations down to 500 m (Fig. 4.14). Bograd et al. [71] tested the significance of linear trends for each station at 50, 100, 200, 300, 400 and 500 m depths, and used significant fits to calculate the absolute and relative declines in dissolved oxygen over the 23 year period. While the largest absolute declines in oxygen levels occurred in the upper water column (Fig. 4.14), the greatest relative declines occurred at greater depths. Over the 23-year period, dissolved oxygen declined by $< 10\,\%$ at 50–100 m depths, but by 10–30 % at 200–300 m depths [71]. Declines were greatest below the thermocline, with a mean decline of 21 % at 300 m depths.

CalCOFI water bottle measurements are generally taken only in the upper 500 m, so the estimated declines in oxygen represent shoaling of the deeper layers. The hypoxic boundary (defined in Bograd et al. [71] as $\sim 60\mu Mol.kg^{-1}$) has shoaled by 41 m on average, and shoaled by up to 90 m at CalCOFI station 93.30 (i.e. nearshore close to San

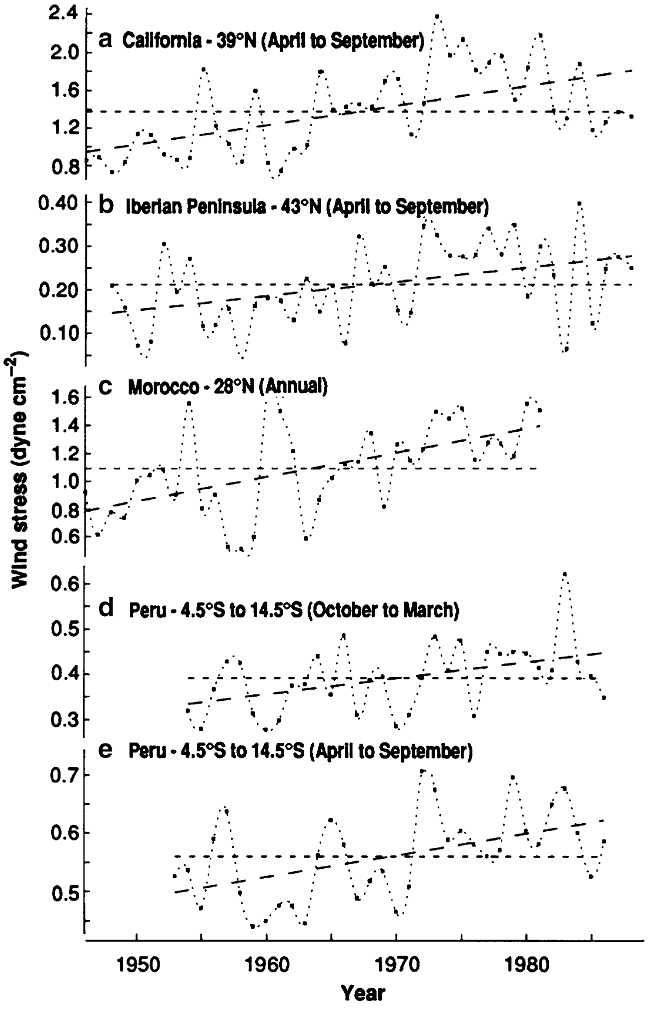


Fig. 4.13 Average monthly wind stress from five different coastal upwelling regions showing the short-term variability and the long-term secular increase in wind stress, fitted as a linear trend (From Bakun [40])

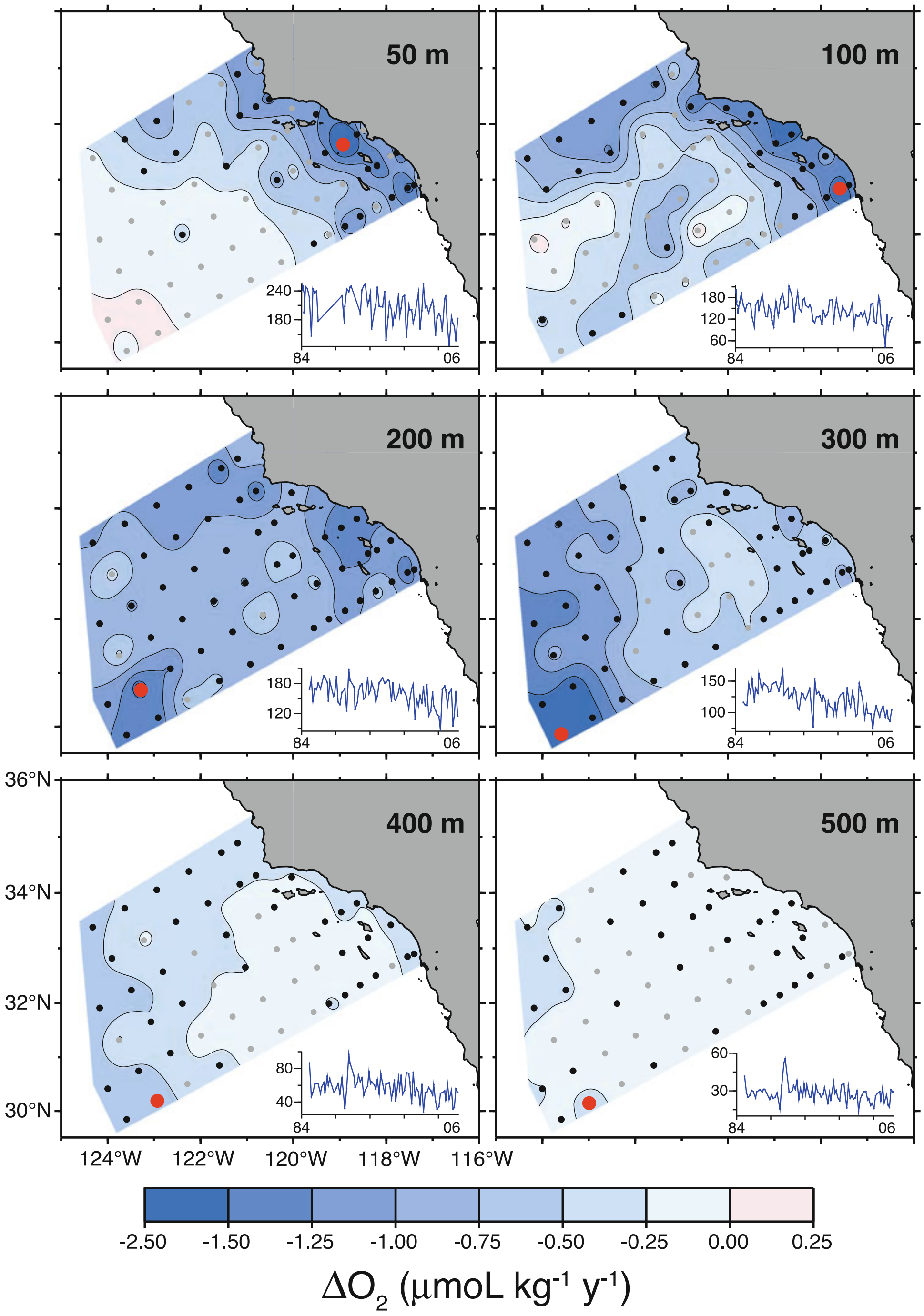
Diego) from 1984 to 2006 [71] (Fig. 4.15). Bograd et al. [71] reported that the magnitudes of declines in dissolved oxygen estimated from the CalCOFI data were comparable to declines reported for several areas of the western and eastern sub-Arctic Pacific. This fact, combined with reports of hypoxia driven by upwelling off Oregon [98, 185], suggest a basin-wide decline in oxygen.

Bograd et al. discussed several possible causes of the decline of dissolved oxygen off southern California. They were not able to distinguish between local and advective processes, and considered that the cause was likely a combination of stratification, advection and the local balance of respiration and production [71]. General circulation models predict that secular warming trends will reduce the efficiency of the biological pump, leading to reduced oxygen concentrations at mid depths, primarily attributed to the effects of stratification ([260, 486] cited in [71]). Secular trends in warming and associated increases in stratification (see Sect. 4.1.3.1) would reduce the vertical flux of dissolved oxygen from surface waters to deeper layers ([260, 486] cited in [71]). This mechanism is consistent with the observation that greatest relative declines in dissolved oxygen have occurred below the seasonal thermocline off southern California [71]. Advective processes may also play a role. The greatest relative decreases in dissolved oxygen occur at 200–300 m depths. Source waters of the California Undercurrent influencing these depths also show reduced oxygen (Table 2.1). Further support for the influence of southern waters comes from experiments with ROMS models, that suggest increased advection of subtropical waters with warmer temperatures and low oxygen into the southern California region [71]. Furthermore, the offshore areas of the CalCOFI region, that are influenced by Eastern North Pacific Central Water of the Subtropical Gyre (see Sect. 2.3), show declines that are consistent with observed thickening of the oxygen minimum layer in the eastern Equatorial Pacific [535, 536]. The inference is that advective processes both from the south, mediated by the California Undercurrent, and from offshore mediated by the influence of the Subtropical Gyre, contribute to the observed declines of dissolved oxygen off southern California.

Using circulation and biogeochemical models, Deutsch et al. [134] examined the causes of decadal shifts in North Pacific oxygen in the 1980 and 1990s. Model biological productivity in the North Pacific shows shifts on the order of 50 % of the mean between these decades. However, the changes in biologically driven Apparent Oxygen Utilization in the lower ventilated thermocline are very small in the North Pacific because respiration of sinking organic matter attenuates rapidly with depth [134]. Deutsch et al. [134] concluded that the decadal differences must be driven by physical processes, and the specific causes of changes in AOU can be traced both to circulation trends and to decadal-scale episodic perturbations of the physical state of the North Pacific. The model shows that changes in the outcropping of the $\sigma_\theta = 26.6$ isopycnal reduces the ventilation rate, which creates the long-term declining trend in oxygen. The long-term declining trend in the area of the winter-time exposure of the $\sigma_\theta = 26.6$ isopycnal "reduces the communication of atmospheric properties to the lower ventilated thermocline" [134].

However, episodic physical perturbations also contribute to the decadal scale variability of oxygen in the North Pacific [134]. The model shows two perturbations in the 1970s in the Kuroshio Extension and in the Eastern Tropical North Pacific that generate oxygen anomalies of sufficient geographical extent (~20 ° longitude) and sufficient intensity ($\Delta O_2 \sim 50 \mu Mol.kg^{-1}$) that they "remain coherent features for over a decade" [134]. The multi-decadal trend in reduced ventilation is punctuated by episodic increased ventilation in the early 1970s. This episodic event injects a bolus of high

Fig. 4.14 Linear trends in dissolved oxygen ($\mu Mol.kg^{-1}$) at six standard depths (50, 100, 200, 300, 400, and 500 m) on the CalCOFI survey grid over the period 1984–2006. Stations with significant linear regressions ($p < 0.05$) are marked *black*. Dissolved oxygen time series at stations with the greatest absolute declines in oxygen (marked *red* on the maps) are shown in the insets for each standard depth (From Bograd [71])



oxygen water into the thermocline that subsequently travels east and then south into the Subtropical Gyre. The result in the model is an increase in oxygen from the 1970s to the 1980s, followed by a decrease in oxygen from the 1980s to the 1990s.

Five years after Deutsch et al.'s [134] modeling results were published, McClatchie et al. [370] independently obtained evidence for episodic decadal-scale oxygenation from CalCOFI survey data. They [370] were unaware of Deutsch et al.'s [134] explanation for episodic forcing of fluctuating oxygen in the subtropical North Pacific at the time their paper was published. While McClatchie et al. [370] found the same decline in dissolved oxygen reported by Bograd et al. [71] in the period 1984–2006, they were able to justify using the longer time series back to 1950 (see [370] Supplementary material for details). They compared trends in a fisheries conservation area off southern California (the Cowcod Conservation Area), with trends in a 15 km nearshore strip along the Southern California Bight. Based on the 57-year time series (1950–2007), oxygen anomalies increased

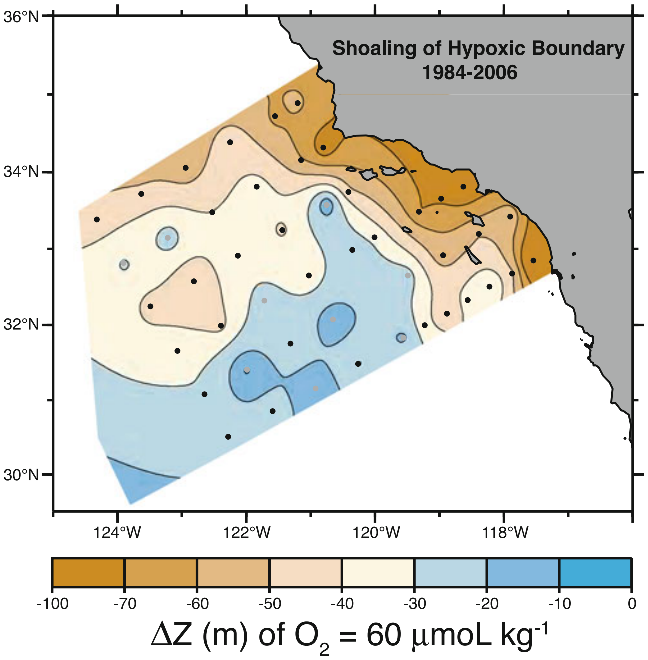


Fig. 4.15 Total change in the depth (m) of the $O_2 = 60 \mu Mol.kg^{-1}$ surface on the CalCOFI survey grid over the period 1984–2006. Stations with linear slopes different from zero ($p < 0.05$) are marked *black* (From Bograd [71])

by 0.15 ml L^{-1}during 1950–1990 but decreased by 0.3 ml L^{-1}during 1990–2007 in both areas [370]. The depth of the hypoxic zone deepened by 40–45 m from 1950 to 1985–1990 in both areas. In contrast, since 1990, the hypoxic zone shoaled by 45 m in the Cowcod Conservation Area, which is further offshore, compared to shoaling of 65 m inshore (Fig. 4.16). The pattern of periods with increased oxygenation and decreased oxygenation resembles the pattern described by Deutsch [134], but the timing is out of phase. Deutsch described an increase in oxygen in the Subtropical Gyre from the 1970s to the 1980s, followed by a decrease in oxygen from the 1980s to the 1990s. The CalCOFI region showed increased oxygenation from 1950 to 1990, followed by a decrease in oxygenation from 1990 to 2007 [370]. In both cases, the system seemed to be returning to an earlier oxygenation state. " … part of the [oxygen] increase in the center of the subtropical gyre reflects a return to background [oxygen] levels following the passage of a transient low-[oxygen] anomaly transported westward from the Eastern Tropical North Pacific in the early 1970s" [134]. In the case of the CalCOFI region, the early (1950–1957) and recent (2000–2007) vertical profiles of oxygen anomalies were indistinguishable, but clearly distinct from the higher oxygenation levels of the intervening period (e.g. 1980–1987) in both areas studied (Fig. 4.17), indicating a return to previous oxygenation conditions [370].

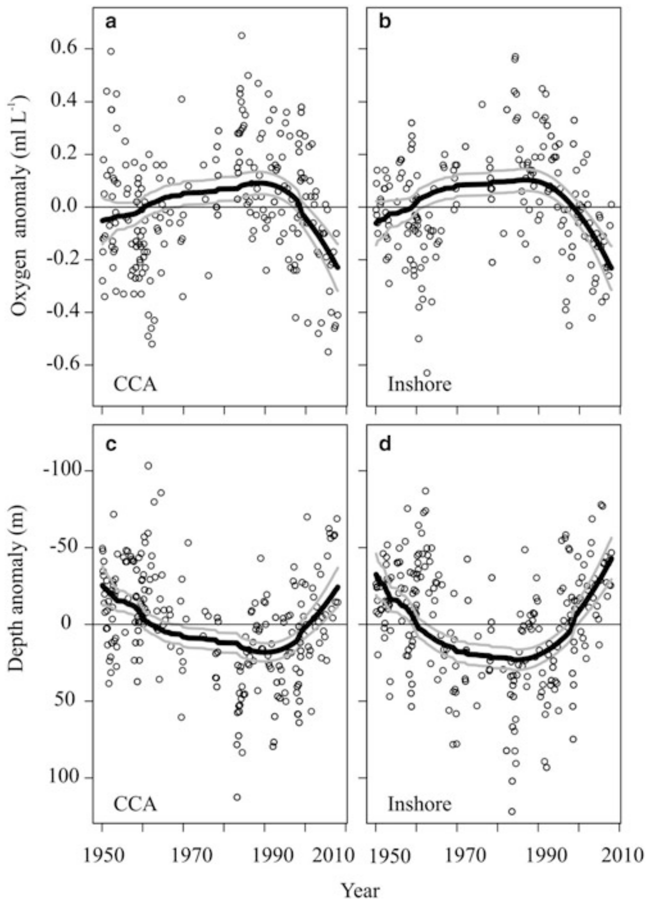


Fig. 4.16 Time series of oxygen concentration anomalies at $\sigma_t = 26.6$ between 1950 and 2007 for (**a**) the Cowcod Conservation Area and (**b**) the Inshore Area. Time series of the depth anomaly for oxygen concentrations of 1.5 ml L^{-1}during the same time period for (**c**) the Cowcod Conservation Area and (**d**) the Inshore Area. The *horizontal line* represents the long-term average, which in the case of anomalies, is zero. Note the reversed axis for depth anomalies. *Fitted lines* are lowess smooths ±2 CI (From McClatchie et al. [370])

The decadal-scale shifts in the volume of the ocean below a critical oxygen threshold (ΔV_{O_2}) is correlated with decadal shifts in the depth of the thermocline, as shown from both global circulation models and the CalCOFI data [133]. Deutsch et al. [133] showed that ΔV_{O_2} changes more rapidly at low oxygen concentrations, so that "a hypothetical warming of 1°C throughout the upper ocean would expand the reach of hypoxic conditions by 10 % while sub-oxic zones would nearly triple in volume". Simulated fluctuations in the scale of hypoxia show that ΔV_{O_2} is prone to large expansions and contractions on decadal time scales. Large inter-annual changes can also occur, but are strongly modulated by the decadal scale changes. The principal spatial pattern of thermocline variation across the North Pacific includes coherent rising and falling of thermocline depth, which is highly correlated ($r^2 = 0.67$) with the Pacific Decadal Oscillation, that alone explains 24 % of ΔV_{O_2} of sub-oxic water [133].

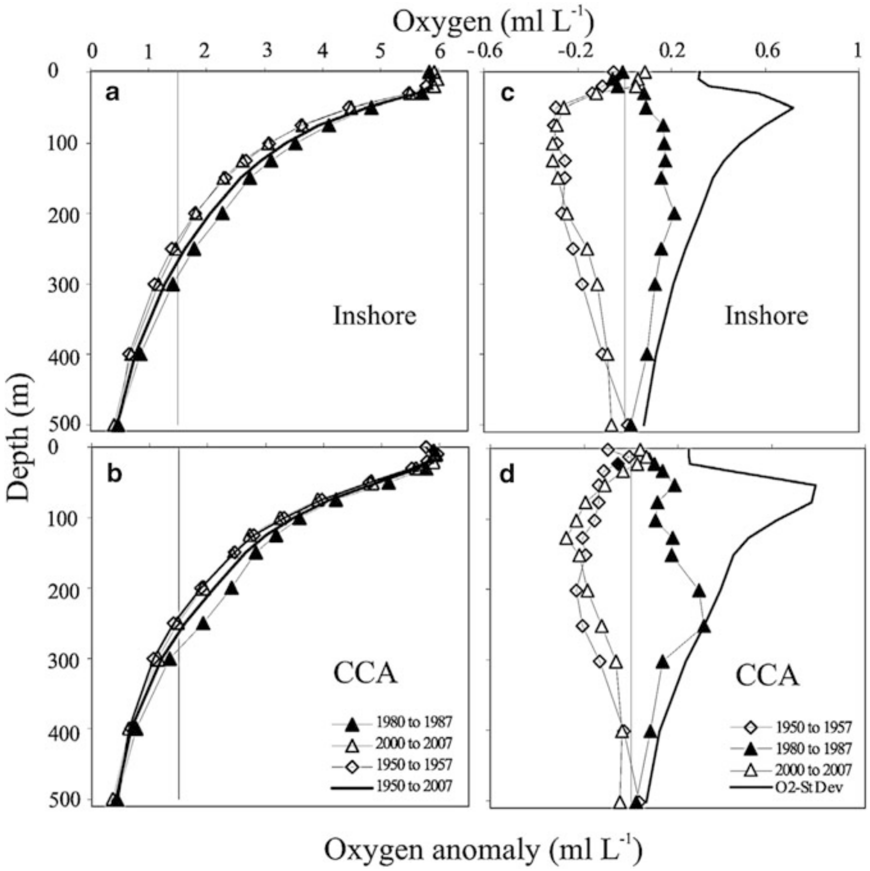


Fig. 4.17 Depth profiles of oxygen concentrations at standard CalCOFI depths for (**a**) the Inshore area and (**b**) the Cowcod Conservation Area (*CCA*). Corresponding depth profiles of oxygen concentration anomalies for the data for (**c**) the Inshore area and (**d**) the CCA. Anomalies are defined as deviations from the average concentrations at that depth using the time periods 1950 – 2007 as a base (From McClatchie et al. [370])

Nam et al. [413] used data from a mooring off Del Mar, near San Diego (Fig. 4.18) to show that ENSO also has a marked effect on dissolved oxygen in the Southern California Bight on inter-annual time scales. El Niño is associated with positive oxygen anomalies because thermocline depression brings oxygenated water to greater depths from the surface layers, leading to warmer temperatures, reduced densities, and higher dissolved oxygen (Fig. 4.18b, c, f) [413]. In contrast, during La Niña or during seasonal upwelling, oxygen anomalies are negative because an elevated thermocline brings sub-oxic water nearer to the surface associated with cooler temperatures, higher densities and lower dissolved oxygen concentration (Fig. 4.18b, c, f) [413].

Depression of cross-shelf isopycnals during El Niño and uplift during La Niña is normally expected. Nam et al. [413] showed that the effect of ENSO on oxygen concentrations was larger than the average seasonal cycle that is generally driven by the seasonal upwelling. The ENSO effect on dissolved oxygen is two to three times larger than that expected from the depression of isopycnals during El Niño, or uplift of isopycnals during La Niña. For example, in the summer and fall seasons of 2009 during El Niño conditions, dissolved oxygen at 88 m depth was 0.75 ml L^{-1} higher than the mean seasonal climatology, and only about half of this could be explained by depression of the isopycnals bringing oxygenated water to these depths. The additional effect of ENSO on the dissolved oxygen, beyond that expected from elevation or depression of the isopycnals, appears to be related to differences in primary production, combined with changes in the nearshore, poleward flow of the California Undercurrent [413]. During La Niña, the nearshore primary production at 35 m was enhanced (Fig. 4.18e), and the nearshore poleward flow of low oxygen water in the California Undercurrent intensified (Fig. 4.18d), both of which add to the effect of uplifted isopycnals in enhancing negative oxygen anomalies (Fig. 4.18F) [413]. Nam et al. [413] caution that their results may not be representative of all ENSO events and the flows may differ between Eastern Pacific and Central Pacific El Niños, so the effect of ENSO on oxygen in the California Current System requires more study.

Hypoxia and California Fisheries

The implications for fisheries of the trends in hypoxia described in Sect. 4.1.3.2 and the trends in temperature described in Sect. 4.1.3.1 are considerable. The decadal-scale shifts in the volume of the ocean below a critical oxygen threshold indicate that the current trend toward

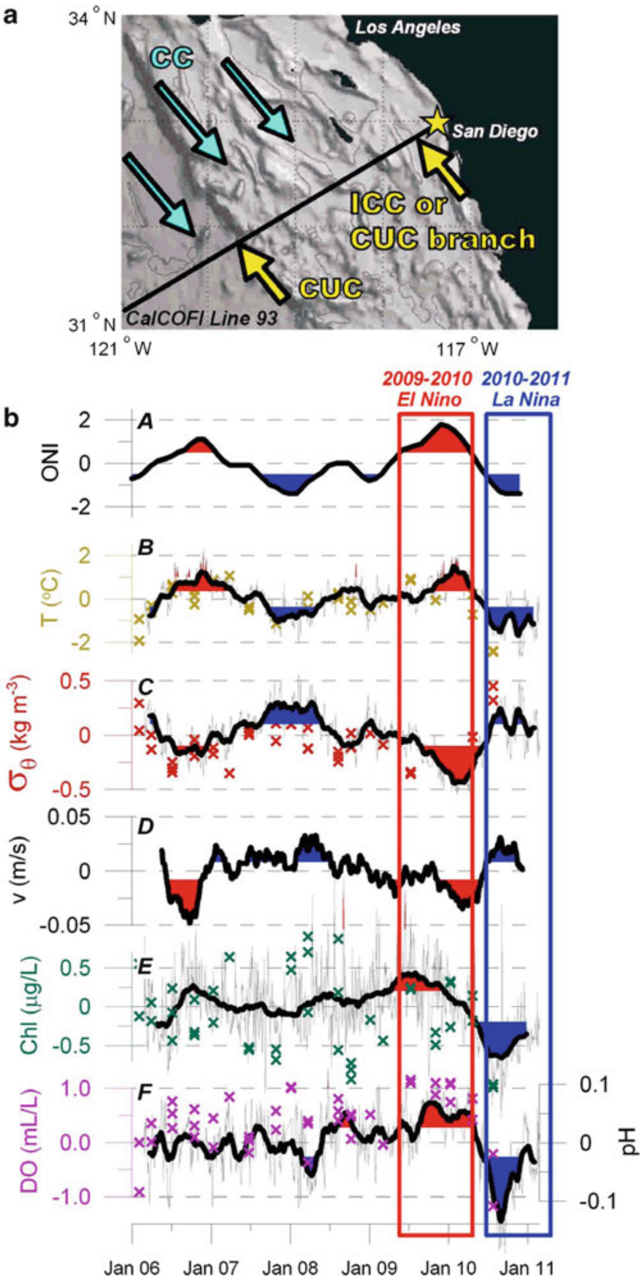


Fig. 4.18 (**a**) Map with mooring location (*yellow star*), CalCOFI Line 93 (*black line*), bathymetry and the California Current (*CC*) and California Undercurrent (*CUC*) or Inshore Countercurrent (*ICC*). (**b**) Time series of (*A*) Oceanic Niño Index (*ONI*), and anomalies from the average seasonal cycle of (*B*) water temperature, (*C*) density, (*D*) alongshore current, (*E*) chlorophyll, and (*F*) dissolved oxygen (*DO*), at 35 m depth on the mooring between 2006 and 2011. Values exceeding half a standard deviation (0.5 for ONI) are filled in *red* (El Niño) or *blue* (La Niña). Anomalies from CalCOFI observations at the nearby station (line 26.7, station 93.3) at 30–40 m depth are shown by x symbols. *Thick lines* in B, C, E, and F are smoothed time series, whereas daily values are shown in *gray* (From Nam et al. [413])

increased hypoxia in the CalCOFI area described by Bograd et al. [71] are likely to reverse at some stage. Such reversals have happened in the past [370], and appear to be a general basin-scale characteristic of the North Pacific [133, 134] (Sect. 4.1.3.2). On the other hand, secular warming trends in the California Current System, combined with the temperature sensitivity of the volume of the ocean below a critical oxygen threshold, would strengthen the current trend toward increased hypoxia. It is not yet entirely clear what the secular trend will be, but widespread warming in the North Pacific suggests that increasing hypoxia is likely over multi-decadal time scales.

Continued shoaling of the hypoxic zone over the Cowcod Conservation Area off southern California would be expected to impact the 100–350 m rockfish habitat around Tanner Bank and San Nicolas Island [370]. Unlike typical continental shelf systems, the availability of specific depth habitats is extremely limited in the Southern California Bight due to narrow shelves and/ or steep slopes. The fish on these banks may ultimately be at risk from intrusions of low-oxygen water into the Southern California Bight. In summer months about 37 % of the Cowcod Conservation Area at depths of 240 – 350 m is affected by hypoxia [370]. If current trends continue for 20 years, the top of the hypoxic zone would shoal by 60 m to a depth of 180 m, and the area affected by hypoxia would increase to 55 % of the total habitat, placing an additional 18 % of habitat under oxygen stress in the 180–240 m depth range [370]. About 45 % of the habitat is never impacted by hypoxia (historical data spanning 60+ years), and this habitat in the 100 – 180 m depth range constitutes a refuge from oxygen stress [370].

The highly diverse rockfishes (*Sebastes*) are the dominant benthic fishes of the SCB. The tissue oxygen demands and downward oxygen cascade from water to hemoglobin to ovary may put brooding females at particular risk of hypoxia. Consideration of habitat quality in the Southern California Bight should take potential exposure to hypoxia into consideration. Consequently it is important to monitor future levels of oxygen off southern California to determine whether trends will continue in the current direction as climate continues to change. Continuation of current trends toward increasing hypoxia would have detrimental impacts on rockfish fisheries [370].

Declining oxygen in the southern California Current System would also likely affect the forage base for fisheries [275]. Mesopelagic fishes are a poorly quantified and potentially very large assemblage exploited by many levels of the food web, including commercially exploited fish. They are considered an important component of the

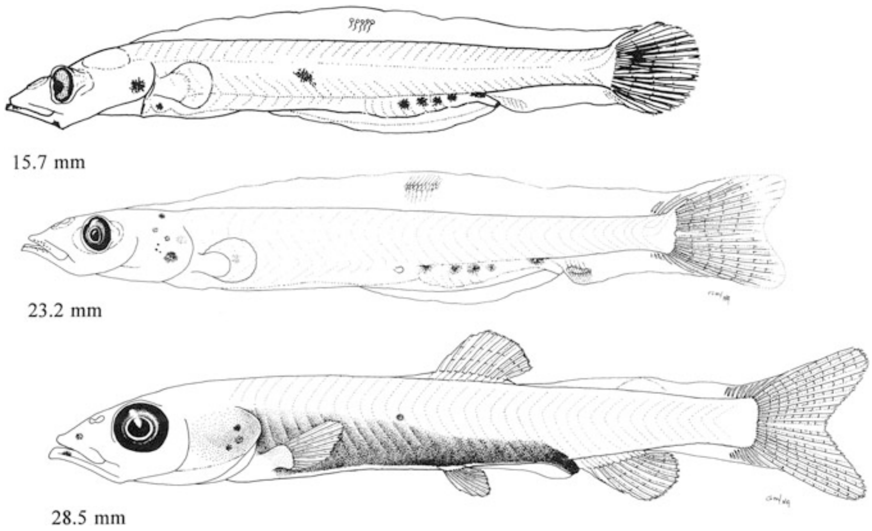


Fig. 4.19 *Leuroglossus stilbius* or California smoothtongue (family Bathilagidae) is one of the mesopelagic species that declined in numbers with declining oxygen (From Lasker et al. [395])

forage community. Numerically dominant families of the mesopelagic assemblage off southern California include the Bathylagidae (blacksmelts and smoothtongues) [395] and Myctophidae (lanternfishes) [396]. Bathylagids are particularly abundant in the CalCOFI ichthyoplankton time series (Fig. 4.19) [394]. Larvae of the bathylagids *Leuroglossus stilbius*, *Bathylagoides wesethi*, and *Lipolagus ochotensis*, are among the most abundant species in the CalCOFI time series, ranking 5th, 12th, and 13th in overall abundance [395].

Koslow et al. [275] used multivariate statistics to create a synthetic time series representing the aggregate potential mesopelagic forage community combined with representatives of the demersal ichthyoplankton assemblage of the shelf and slope. They applied a principal components analysis to 86 individual ichthyoplankton species time series, and then selected 49 species where the individual time series correlated with the first principal component at a correlation greater than 0.29 to create their synthetic time series (PC1 in Fig. 4.20). I will call their refined synthetic time series the "mesopelagic/ demersal time series". Twenty-seven of the 49 species comprising the mesopelagic/ demersal time series were more highly correlated (≥ 0.5) with the first principal component in this analysis, and of these, 24 of the species were mesopelagic species from eight families [275].

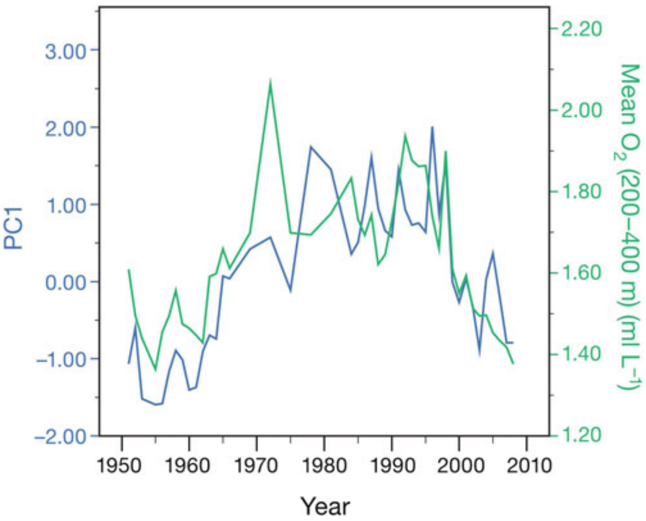


Fig. 4.20 Time series showing the relationship between a synthetic mesopelagic/demersal ichthyoplankton time series (first principal component, *PC1*) and mean mid-water oxygen concentrations from the consistently sampled 66-station CalCOFI pattern at 200–400 m depths, 1951–2008 (From Koslow et al. [275])

Koslow et al. [275] examined how temporal trends in their mesopelagic/ demersal time series were related to the measured changes in mid-water (200–400 m depth) oxygen from 1951 to 2008 (Fig. 4.20). Mid-water oxygen shared a common temporal trend with temperature at the surface and at 200 m, but oxygen was not correlated with temperature when the time series were detrended [275]. They found that mid-water oxygen was correlated with three climate indices (PDO, NPGO, and MEI), even after detrending (See Sects. 4.1.1.1, 4.1.1.2, and 4.2.1.2 for discussion of these indices, and Sect. 4.1.3.2 for an explanation of the relationship between the PDO and oxygen in the North Pacific). Their key finding was that the mesopelagic/ demersal time series was correlated with the multidecadal trend in oxygen off southern California (Fig. 4.20). We now know from the studies of Deutsch et al. [133, 134] that trends in oxygenation at mid-depths in the North Pacific are correlated with trends in the depth of the seasonal thermocline and with the PDO, but that the secular trends are overlain by episodic events that can last a decade or more, and that ENSO events add to high frequency variability [413]. The correlation shown in Fig. 4.20 appears to be better at low frequencies, suggesting that the mesopelagic/

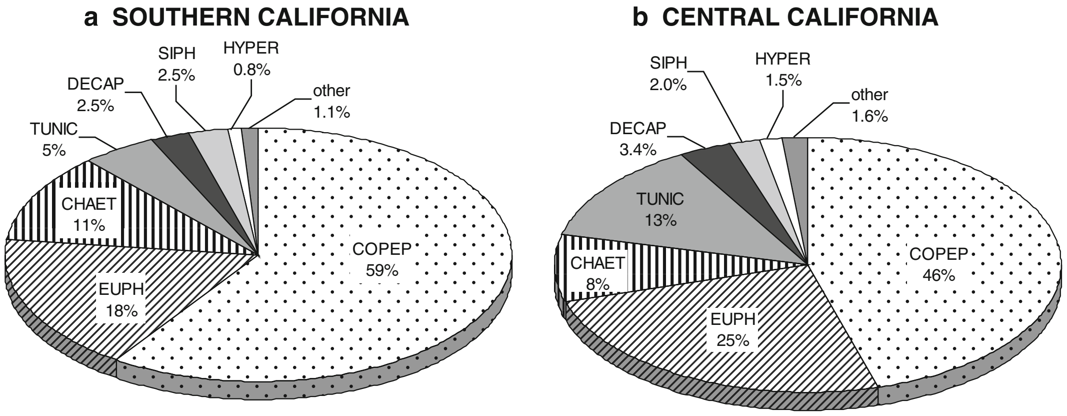


Fig. 4.21 The relative proportions of carbon-based biomass of different zooplankton groups off (**a**) southern and (**b**) central California in springtime (based on geometric means). *COPEP* copepods, *EUPH* euphausiids, *CHAET* chaetognaths, *TUNIC* tunicates comprising salps, doliolids, appendicularians and pyrosomes, *DECAP* decapods, *SIPH* siphonophores, and *HYPER* hyperiid amphipods (From Lavaniegos and Ohman [298])

demersal time series of ichthyoplankton is tracking the secular trends in mid-depth oxygen, thermocline depth and the PDO. Essentially the mesopelagic/ demersal time series is indicating the large-scale, low frequency physical state of the system.

The abundance of 24 species of mesopelagic larvae has declined by approximately 63 % in the period 1999–2010 according to Koslow et al.'s analysis [275] (see Sect. 4.1.3.3 for trends from 1951 to 1999). The correlation between this decline in abundance and the decline in dissolved oxygen and associated shoaling of the sub-oxic layers off southern California led Koslow et al. [275] to conclude that the mechanism for the decline may have been increased vulnerability to predation. They suggested that shoaling of sub-oxic layers has been associated with shoaling of the Deep Scattering Layers (DSL) containing visually oriented predators. This would increase the vulnerability of the mesopelagic fishes to visual predators, and possibly cause their decline. This is an intriguing hypothesis, but would need more extensive sampling of the DSL than that presented in Koslow et al. [275] to quantitatively test whether DSL have shoaled significantly.

4.1.3.3 Long-Term Changes in Zooplankton and Fish Assemblages Relevant to Fisheries

Four groups of zooplankton dominate the carbon biomass off southern and central California, notwithstanding the fact there are significant regional differences in the relative proportion of zooplankton groups, as well as in the total biomass in the two regions [298]. In both regions, the dominants in order of biomass measured as carbon, are copepods, euphausiids and chaetognaths. Tunicates occupy fourth place in biomass proportion off southern California, and outweigh chaetognaths to take third place off central California [298] (Fig. 4.21).

Lavaniegos and Ohman estimated[9] that copepods, euphausiids and chaetognaths comprised 90 % of the biomass off southern California, while salps, doliolids, appendicularians and pyrosomes (collectively grouped as tunicates) accounted for a further 3.4 %, and all other zooplankton made up the remaining 6.9 % [298] (Fig. 4.21). Copepods and chaetognaths showed no regional difference in carbon biomass between southern and central California, in contrast to euphausiids and tunicates. Euphausiid biomass off central California was double the biomass off southern California, while salp biomass was three times higher, and doliolid biomass was ten times greater off central California [298]. The proportions described here are indicative only of the overall mean values and there is considerable inter-annual variability. The mean zooplankton biomass off central California was 57 % higher on average than the biomass off southern California [298].

Zooplankton Displacement Volume

In 1995 Roemmich and McGowan [475,476] used zooplankton displacement volume data[10] from CalCOFI lines 80 and 90 (see map in Fig. 1.4) to estimate that there had been a large decrease in zooplankton over 43 years (1951–1993) off southern California. The declining trend in zooplankton displacement volume was consistent for both line 80 and line 90, but volume was consistently higher on line 80 off Point Conception than further south off southern California on

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[9] Based on springtime samples collected over 32 years in the period 1951–2005 when both southern and central California were surveyed.

[10] Roemich and McGowan [475, 476] do not state in their methods whether they used total zooplankton displacement volume including larger individual organisms with biovolumes > 5 ml, or whether they used small plankton volumes which exclude these larger individuals. Lavaniegos and Ohman [298] stated that they used total zooplankton displacement volumes.

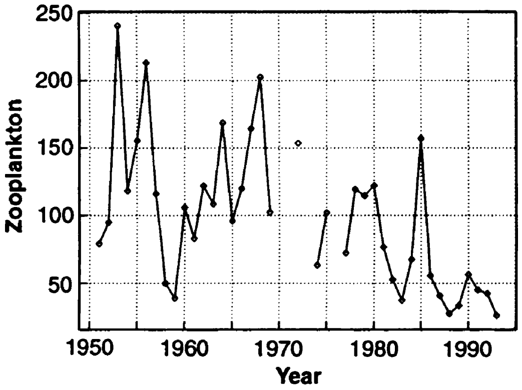

Fig. 4.22 Annual averages of zooplankton displacement volume (ml 1,000 m^3) for all stations on CalCOFI line 90 (see map in Fig. 1.4) (From Roemmich and McGowan [476])

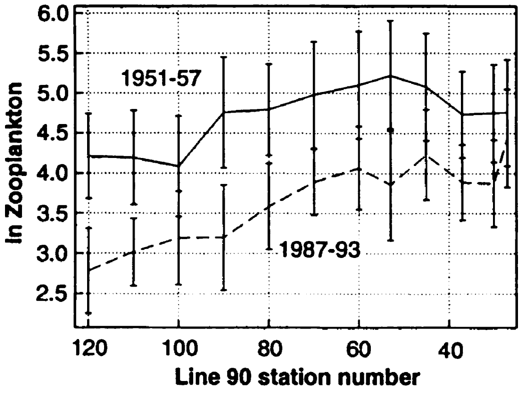

Fig. 4.23 Mean log$_e$ transformed zooplankton displacement volumes for all stations on line 90 (see map in Fig. 1.4) with ± one standard deviation for two 7-year periods early in the CalCOFI time series (1951–1957) and a period recent to the time of the paper's publication date (1987–1993) (From Roemmich and McGowan [476])

line 90. Displacement volume was also consistently higher inshore compared to offshore (Fig. 4.23). The rate of the decrease in displacement volume was two orders of magnitude smaller than the advective flux of zooplankton displacement volume from the north estimated by Chelton et al. [108]. Nevertheless, this small effect was substantial when accumulated over 43 years [475, 476] (Figs. 4.22 and 4.23).

The decrease in zooplankton displacement volume was correlated with the warming trend of the surface waters in the region [474]. Based on observations that warming was 25 % greater in surface waters than at 200 m, Roemmich and McGowan [475, 476] argued that the decline in displacement volume was associated with increased stratification. The proposed mechanism derives from the inverse relationship between upwelling and stratification. For a given upwelling-favorable wind stress, upward displacement of the thermocline is inversely related to the degree of stratification. Warming waters become more stratified, resulting in less displacement of the thermocline, so that nutrients in the surface waters come from shallower depths. The reduced nutrients would produce less new production, and presumably less zooplankton displacement volume [475, 476] (see Sect. 4.1.3.1).

Roemmich and McGowan suggested that the effect of decadal scale warming on stratification, reduced nutrient flux to the surface layers, and consequently reduced new production could offset the expected effects of increased wind stress driving more intense upwelling, which was expected to increase production. They took issue with Bakun's prediction that secular warming would lead to increased upwelling-favorable winds [40], arguing that there were potential biases in the analysis of the smoothed wind stress climatology [475, 476]. They pointed out that a secular trend of intensified wind-driven upwelling in this region of the California Current System was inconsistent with their observations of a secular warming trend [474] and declining zooplankton displacement volumes [475, 476].

The decline in mean zooplankton displacement volume reported by Roemmich and McGowan [475], was confirmed by Lavaniegos and Ohman [298] who showed significant declines in the spring means of zooplankton displacement volume for both southern and central California between 1951 and 2005 (Fig. 4.24). Mean displacement volumes declined by 64 % off southern California and 68 % off central California from 1951 to 2005 [298]. Roemmich and McGowan had earlier reported approximately 70 % decline in mean zooplankton displacement volume off southern California between 1987–1993 relative to 1951–1957 [475, 476]. There were also transient decreases in mean zooplankton displacement volumes during El Niño periods and transient increases during La Niñas [298]. Lavaniegos and Ohman [298] discovered that the decline in zooplankton displacement volumes was due to decline in the numbers of cold-water associated salps in the later half of the time series (see Sect. 4.1.3.3). While there was little controversy about whether the decline in zooplankton displacement volume was real, disagreement arose concerning both the cause of the decline and whether displacement volume was useful to detect climatic effects on the zooplankton in the California Current System.

Pelagic Tunicates and Salps

Lavaniegos and Ohman [297] identified ten species of salps in the 66-station CalCOFI sampling area (Fig. 1.4) as far offshore as station 70, but there may be other species. Among the species of salps that were present throughout the 56-year period (1951–1998), *Salpa fusiformis* and *Salpa aspera* were numerically dominant [297], and both these species formed large blooms in some years. They did not find any relationship between the abundance of either individual species or total areal biomass of salps and ENSO. On longer time scales they noted that the "cool-phase species" *Salpa maxima*,

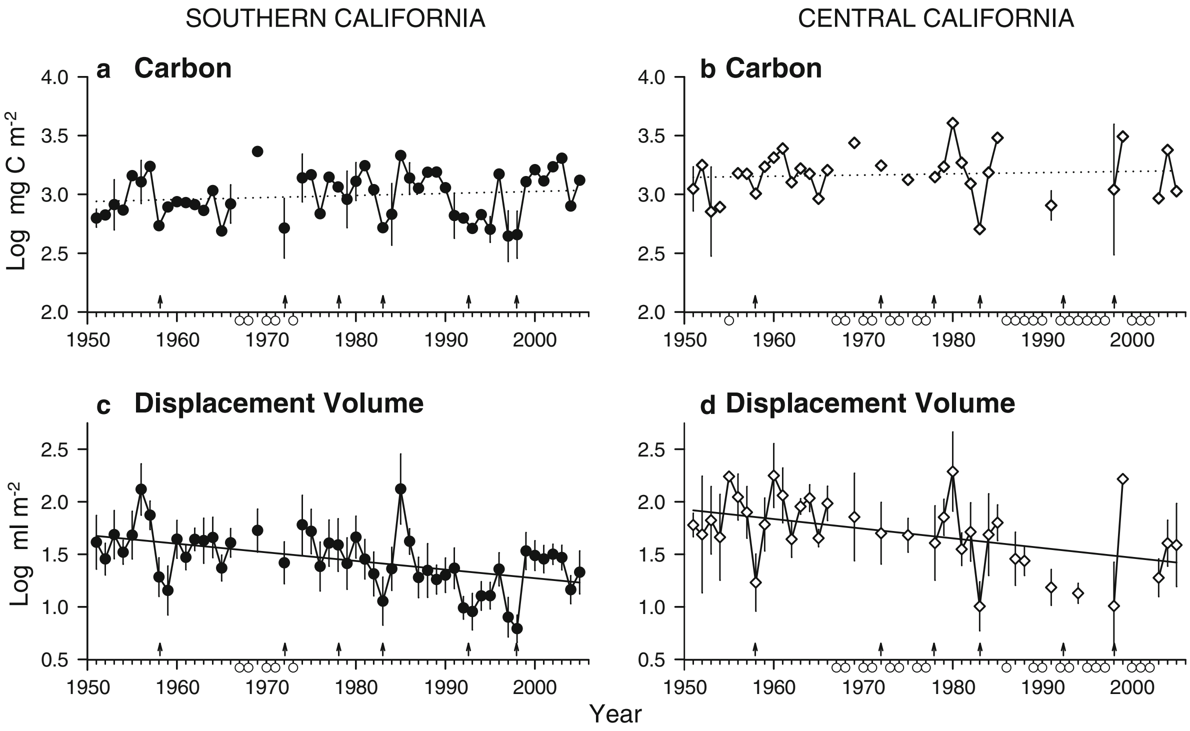

Fig. 4.24 Time series of total zooplankton biomass in terms of carbon (**a**, **b**) and total displacement volume including organisms with individual biovolume > 5 ml (**c**, **d**) for spring (March–May) CalCOFI cruises separated by region (southern and central California). *Vertical arrows* mark El Niño years. *Open circles* below the x-axis indicate no data (From Lavaniegos and Ohman [298])

Pegea socia, *Cyclosalpa bakeri*, and *Cyclosalpa affinis* were entirely absent during the warm PDO$^+$ period between 1977–1998, although they had been present during the earlier, cool PDO$^-$ period between 1951–1976 (Fig. 4.25) [297].

Lavaniegos and Ohman [297] presented the case that more detailed species-specific measurements of zooplankton are likely to be more sensitive to climate effects than are measurements of zooplankton displacement volume, which has always been the default measurement made on CalCOFI bongo net samples. Their argument clearly has a lot of merit, but it should be borne in mind that much valuable scientific work has been achieved using zooplankton displacement volume [58, 59, 107, 108, 477] (see Sect. 2.4.2). Some provocative hypotheses have also been based on displacement volume measurements [378, 475, 476] (see Sect. 4.1.3.3), and these analyses led directly to further understanding of zooplankton production [297, 298] and stratification [264, 388, 438] in the California Current System (see Sect. 4.1.3.1). The labor and expense necessary to count plankton samples to species made it necessary to pool many (but not all) of the zooplankton sub-samples for analyses, which results in loss of valuable spatial information [297, 298, 425, 460, 462, 463]. Nevertheless, Lavaniegos and Ohman point out that zooplankton displacement volume is an aggregate measure of zooplankton that includes up to four trophic “levels”, widely different morphologies and sizes, volume to biomass ratios, growth rates, life histories and biogeographic affinities [297]. As such, it is not equivalent to zooplankton biomass and must be used with caution.

Most of the zooplankton taxa examined by Lavaniegos and Ohman [298] showed no long-term trend in carbon biomass over the 56 years (1951–2005) of their study. Total zooplankton carbon biomass also showed no trend over time (Fig. 4.24), and this result clearly illustrates the different trends obtained by using zooplankton displacement volume as a proxy for biomass, or actually measuring biomass in terms of carbon.

In contrast to copepods, pelagic tunicates and especially salps, showed a long-term decline. Pelagic tunicates have a very high volume to carbon ratio due to their high water content, and consequently have a disproportionate effect on trends expressed as zooplankton displacement volume. The regression relationship between zooplankton carbon and displacement volume derived from spring means off Central and southern California contained a strong trend in the residuals over time (Fig. 4.26b). The residuals of the carbon-displacement volume regression show that carbon was lower than predicted from the regression before the late 1970s, but higher than predicted from the regression after the late 1970s (Fig. 4.26b). The displacement volumes were dominated by high volume-low carbon zooplankton in the early years (before the late 1970s), but not in the more

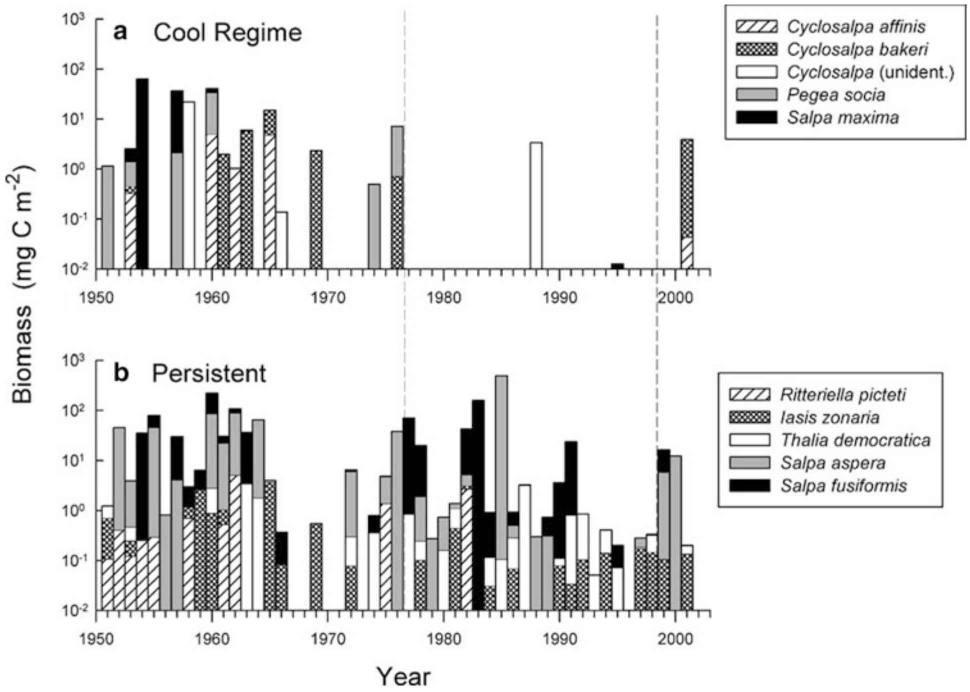

Fig. 4.25 Summed biomass, as organic carbon of: (**a**) salp species that were present primarily during the earlier, cool PDO$^-$ period (1951–1976), and (**b**) salp species that were present through both the earlier, cool PDO$^-$ period and the later, warm PDO$^+$period (1951–1998). Note that the ordinate is logarithmic (From Lavaniegos and Ohman [297])

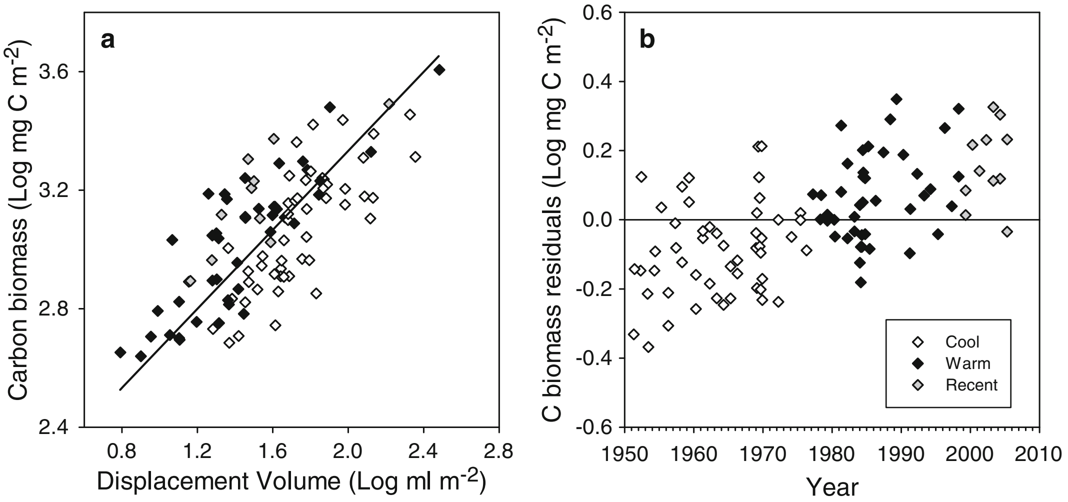

Fig. 4.26 (**a**) Model II regression between zooplankton carbon and zooplankton displacement volume based on spring means from southern and central California. (**b**) Residuals from the regression in (a) plotted against year. The cool period was defined as 1951–1976, warm period as 1977–1998, and recent period as 1999–2005 (From Lavaniegos and Ohman [298])

recent years. When the evidence from the residuals and from species counts of the salps were considered together, the conclusion was that pelagic tunicates, and particularly the "cool-phase" salp species, were more abundant during the earlier, cool PDO$^-$ period (1951–1976) prior to the 1976–1977 regime shift, and declined in abundance during the more recent, warm PDO$^+$ period (1977–1998) (Fig. 4.25) [297, 298]. This analysis indicated that the observed multidecadal decline in zooplankton displacement volume was due to the decline in pelagic tunicates and salps that are disproportionately represented in the volume measurements in the earlier years. Combined with the lack of trend in total zooplankton carbon over the same period, it is apparent that zooplankton biomass has not declined off southern California, but that that a decadal scale shift in the gelatinous plankton occurred that appears to be related to the large scale, low frequency variability of the North Pacific that is reflected in the phase of the PDO (see Sects. 4.1.1.1 and 4.1.3.2). These results underscore the importance of resolving different groups of zooplankton when studying the effects of climate because the responses of different groups may vary considerably [297].

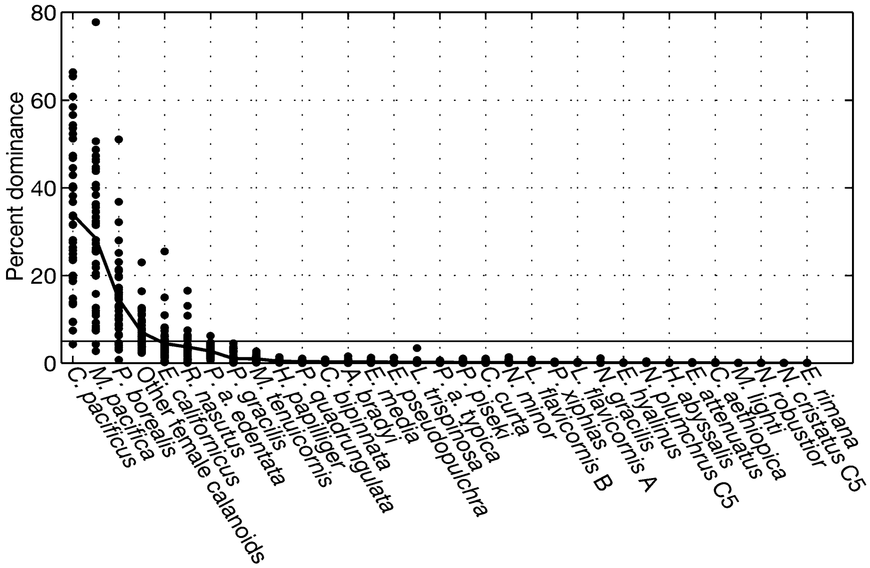

Fig. 4.27 Percent dominance by copepod species or category for spring cruises, sorted by mean percent dominance. Curve connects mean percentages. Each column of *dots* represents the percentage contribution to the total for that category in the 41 spring cruises. The *solid horizontal line* marks 5 % (From Rebstock [460])

Copepods

The stability of copepod species composition off southern California was described by Rebstock [460] using CalCOFI samples spanning 1951–1999. She found, on average, that three species (*Calanus pacificus, Metridia pacifica* and *Pleuromamma borealis*) accounted for 77 % of calanoid copepods. Together with *Eucalanus californicus, Rhincalanus nasutus, Pleuromamma abdominalis edentata*, these seven species make up about 95 % of the calanoid copepods [460] (Fig. 4.27). The dominance by *Calanus pacificus* and *Metridia pacifica* off southern California is so strong that changes in the abundance of other species has relatively little effect on the dominance structure [462]. Rebstock [460] reported that copepod species composition was stable over the 49 years of study, except for six anomalous years, five of which were either associated with strong El Niño events during the warm PDO$^+$ period (see Sect. 4.1.1.1), or occurred immediately after 1976–1977 regime shift [460]. This is an interesting finding, differing from McGowan and Walker [380] who found low similarity between copepod samples in the California Current System, and from Venrick [565] who reported no stability, on any time scale, for a 20 years time series of diatom species collected at Scripps pier. Both Venrick [565] and McGowan and Walker [380] reported that samples from the Central Gyre were much more stable on time scales of years to decades with respect to copepod and diatom assemblage composition than were samples from the California Current System. Rebstock [460] pointed out that stability should be referenced to a time scale, since there is evidence from studies in the North Atlantic that plankton assemblage structure can change, and then return to a former state over about 40–60 years. There may be decadal-scale periods of stability in assemblage structure during the intervening periods.

Copepod assemblages off southern California may be relatively stable but they nevertheless show some changes over time that appear to be related to either ENSO events or to regime shifts. Rebstock was able to distinguish these real changes from artifacts caused by changes in the depths of sampling that were implemented in the 1960s [461, 462]. It appears that the strong El Niño of the late 1950s caused changes in the abundance of some species that lasted up to a decade or longer. Rebstock [462] viewed this as evidence that relatively short-term extreme events can lead to much longer term shifts in species. For example, abundance of *Eucalanus californicus* and *Calanus pacificus* declined after the strong El Niño in the late 1950s and remained low for a decade. On the other hand *Labidocera trispinosa* increased after the warm event and remained at higher abundances until the 1980s [462]. The evidence seems stronger for *E. californicus* and *L. trispinosa,* than it is for *C. pacificus,* because the temporal trends for *C. pacificus* are more variable [462].

Changes in species abundance off southern California related to the 1976/1977 regime shift were more difficult to detect clearly, in part due to much reduced CalCOFI sampling between 1966 and 1977, combined with possible effects of sampling depth changes between 1966 and 1969 [462]. Seven out of twenty-five copepod species increased after the regime shift, and of these, five were warm water associated species (*Pleuromamma gracilis, P. abdominalis typica, Neocalanus gracilis, Nannocalanus minor* and *Lucicutia flavicornis*). These warm water species may have been responding to the warmer conditions following the regime shift. However, two other cool water associated species typical of the California Current System (*Eucalanus californicus* and *Pleuromamma abdominalis edentata*) also increased after the regime shift, despite the warm conditions. Rebstock [462] concluded that there was no simple pattern in the way that warm water or cool water associated species responded to the same climate shifts.

Many taxa including calanoid copepods undergo large fluctuations in the California Current System and yet manage to persist on long time scales. Rebstock [463] used this observation to underline the need for multidecadal time series such as CalCOFI if we are to understand the relationships between the biota and the environment. Life history of species has a major influence on their response to environmental forcing [463]. Long-term stability of assemblages in a strongly fluctuating system may arise from averaging the phases of component species with different temporal trends, as for example in alternation of species within an assemblage. Long-term stability also presupposes some form of compensatory mechanism when species decline in abundance. In the California Current System this mechanism may be the large-scale, equatorward flow that could replenish Transition Zone copepod populations by advective transport [463].

Euphausiids

The relationship between the sub-tropical coastal euphausiid (or krill) *Nyctiphanes simplex* and the PDO has become a poster child for illustrating the effects of regime shifts in the California Current System on the pelagic biota [82]. *N.simplex* is a largely near-shore, but not exclusively neritic species, reported to be "a conspicuous element of the plankton where coastal upwelling is a characteristic feature" [79]. Brinton reported that *N.simplex* was found as far north as ape Mendocino in warm years, but that its range rarely extended north of Point Conception in cooler years [79]. The species is a vertical migrator, generally confined to waters shallower than 140 m, and found in the upper 50 m at night. In some cases this species may be found in the upper 10 m during both day and night [79]. *N.simplex* was present in the core CalCOFI area (see Fig. 1.4) at lower than average abundances during the PDO$^-$ "cool regime" from 1951 to1976, and showed a dramatic shift to abundances greater than the mean following the "regime shift" to PDO$^+$ in 1976–1977 (Fig. 4.28). Brinton and Townsend used a regression analysis (corrected for autocorrelation) to test for significant changes in the abundance anomalies of eight species of krill in relation to anomalies of the PDO. They detected slopes significantly different from zero for five of the eight species, with positive slopes for four warm-water species and a negative slope for only one cold-water species [82] (Fig. 4.29). This indicates that warm-water krill (*N.simplex, E.eximia, E.gibboides* and *E.recurva*) were more common than their mean abundance during PDO$^+$, while one cold-water species (*E.pacifica*) was less abundant during the same warm period.

The response to decadal scale variability shown by the sub-tropical krill *N.simplex* contrasts with the response of the cold water krill *Euphausia pacifica*. *E.pacifica* is the most widely distributed krill species in the California Current System, and has its heaviest concentration in the east-west axis of the North Pacific Drift and Aleutian Current, which feed into the origin of the California Current [79]. *E.pacifica* is found off central California all year round [79]. Brinton reported that seasonal variability in distribution, mainly regression to the north and toward shore after the upwelling season, was less marked than inter-annual variability in the distribution of this species. Intriguingly, Brinton also reported localized higher abundance in "upper layers where waters were cool in a divergent eddy off mid-Baja California" [79]. These krill are found from the surface to 400 m depth off California and are generally in the upper 80 m at night [79]. The abundance of *E.pacifica* is depressed during El Niño periods, as indexed by the MEI (see Sect. 4.2.1.2) (Fig. 4.28b). They used a non-quantitative analysis to point out that the density of *E.pacifica* peaked during La Niña events and then declined by an order of magnitude over 1–2 year periods following transition to El Niño conditions.

Brinton and Townsend [82] classified the krill that reproduce in the California Current "transition zone"[11] as "inhabitant" species, including *Euphausia pacifica* (cold water and widespread), *Thysanoessa spinifera* (cold water and coastal), *Nematoscelis difficilis* and *Thysanoessa gregaria* (both transition zone, cool water species), *Euphausia recurva* and *E. gibboides* (transition zone, warm water species), and the sub-tropical species, *Euphausia eximia* and *Nyctiphanes simplex* (see Sect. 3.2.1). Their study is a graphic illustration that different species respond very differently to climatic variation.

Long-Term Changes in Fishery Catches

Norton et al. used Empirical Orthogonal Function (EOF) analysis to study the long-term changes in commercial fishery catches off California from 1930–2000 [419–421] and 1877–2004 [422]. They found characteristic associations between species in the commercial landings data during particular time intervals, and they used these associations to graphically depict an evolving "ecospace" of fish assemblages over 70 years. By plotting the loadings for the first two principal components of an EOF analysis of the time series of commercial catches of 29 taxa they showed what appears to be a cycle in the fish assemblages of southern and central California [419, 422]. For each 5-year period from 1930 to 2000 they grouped taxa that showed a "near maximum"[12] catch in that period. What appears to be a cycle on first inspection of their graph is actually not a perfect

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[11] Their study area was the regions from San Francisco to south-central Baja California, extending offshore to about CalCOFI station 80 (their figure 1 [82]).

[12] It is unclear what a "near maximum" as opposed to a maximum is.

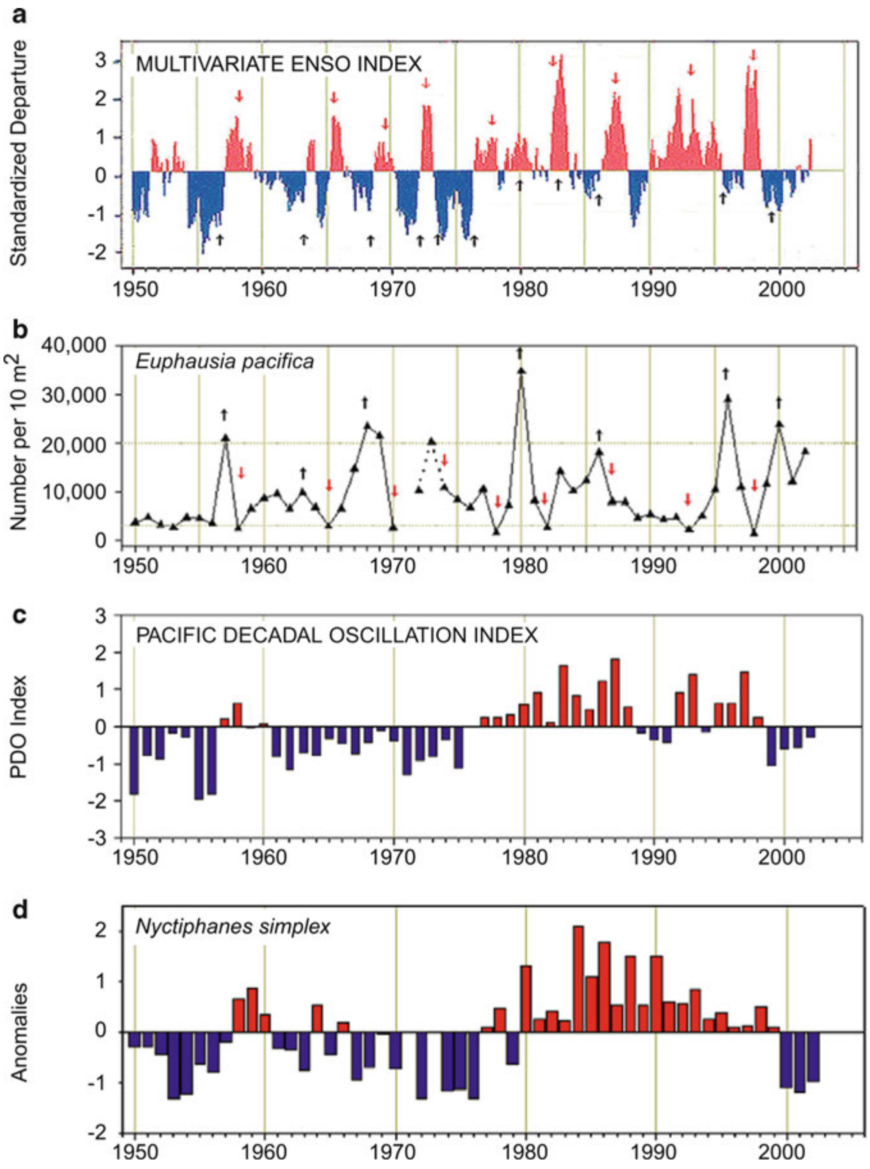

Fig. 4.28 Comparison of the MEI (Multivariate ENSO Index) anomalies with euphausiid abundances. (**a**) *Black arrows* highlight selected MEI anomalies, and *red arrows* highlight selected positive MEI anomalies. (**b**) *Black* and *red arrows* align peaks and troughs of *Euphausia pacifica* abundance with MEI anomalies in (a). (**c**) PDO (Pacific Decadal Oscillation) anomalies. (**d**) *Nyctiphanes simplex* annual abundance anomalies (From Brinton and Townsend [82])

cycle as shown by their tables (Fig. 4.30). For example, in both the 1930–1935 period ("1930" in Fig. 4.30) and the 1995–2000 period ("2000" in Fig. 4.30), the same species showed "near maxima", closing the cycle. The characteristic species in both periods were Pacific sardine (*Sardinops sagax*), Pacific halibut (*Hippoglossus stenolepus*), barracuda (*Sphyraena argentea*), ocean whitefish (*Caulolatilus princeps*) and sheephead (*Semicossyphus pulcher*). However the total catch in 1930 was approximately 240,000 t compared to approximately 180,000 t in 2000, and the value in year-2000 U.S. dollars of small pelagics (sardine, northern anchovy (*Engraulis mordax*) and Pacific herring (*Clupea pallasii*)) was \$18.2 million in 1930 compared to only \$8 million in 2000 [422].[13] Although the species assemblage groups were similar in 1930 and 2000 (Fig. 4.30), the value of the catches had increased from \$75 million to \$124 million, while the relative contribution of small pelagic fish had decreased from 24 to 6 % of the total value, and the total tonnage landed declined by about 25 % (Fig. 4.30). This suggests that the proportion of the species in the landings had changed, and the most obvious difference is that the proportion of sardine was lower.

Another notable point arising from their analysis is that the total fishery catches from southern and central California did not vary as widely as might be expected. Catches were 0.24 Mt[14] (in 1930), 0.54 (1940), 0.43 (1945), 0.3 (1950), 0.15 (1960), 0.11 (1965), 0.14 (1970), 0.21 (1975), 0.2 (1980), 0.16 (1985), 0.17 (1990), 0.18 (1995), and 0.18 Mt in 2000 [422]. The lowest species-aggregated catches in 1965

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[13] Dollars are not inflation adjusted.

[14] 0.24 million or 240,000 metric tons

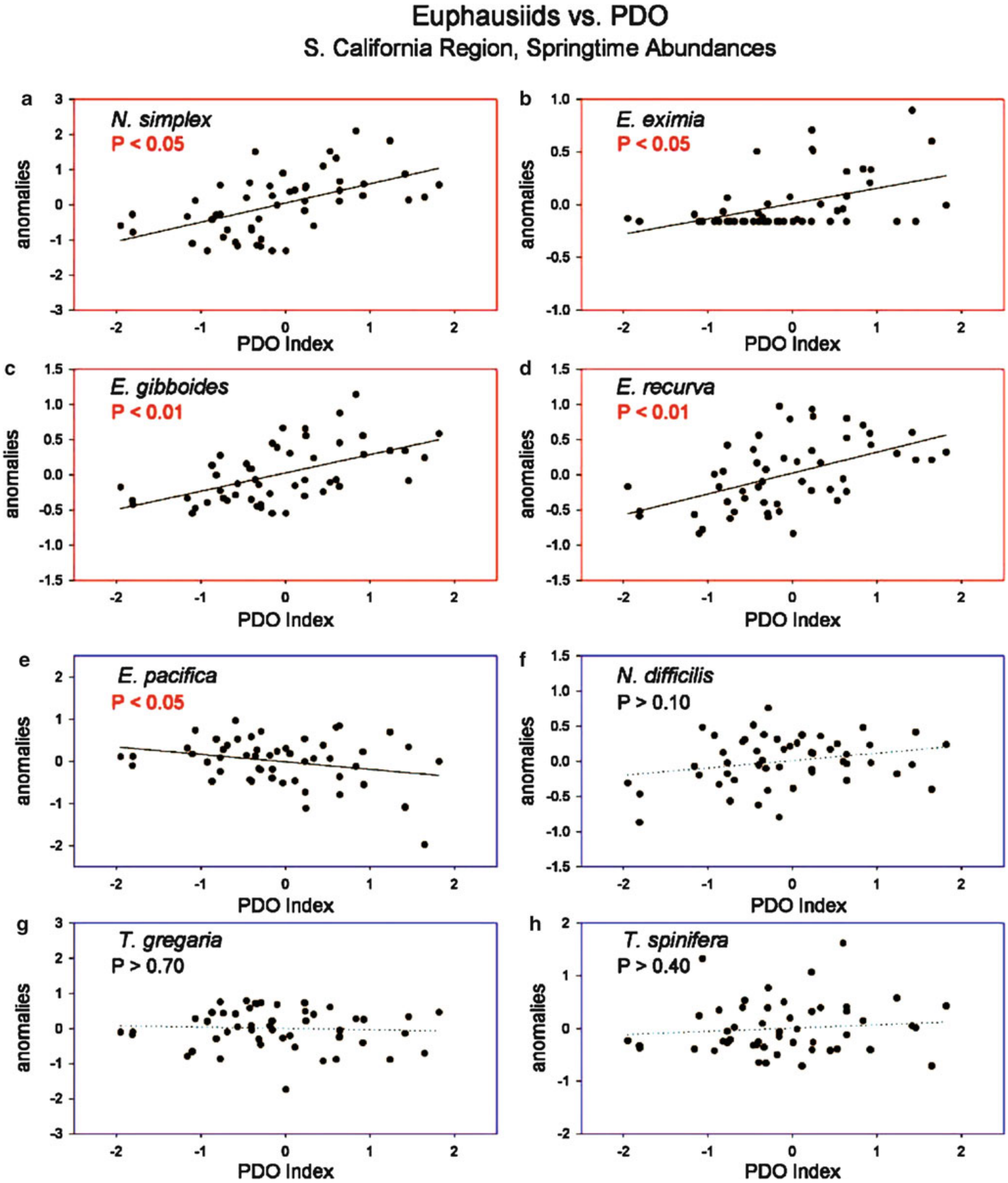

Fig. 4.29 Relationships between anomalies (deviations from the series mean) of krill abundances and anomalies of the PDO, for four warm-water associated species (**a**–**d**) and four cold-water associated species (**e**–**h**). *P*-values (corrected for autocorrelation) test for significant differences from zero-slope of the regressions. Note that these relationships cannot be tested over more appropriate lengths of the time series (i.e. 2–4 times the periods of the PDO which are 40–76 years) and so should be not be regarded as generally true outside the time period tested (see Sect. 4.1.3.3) (From Brinton and Townsend [82])

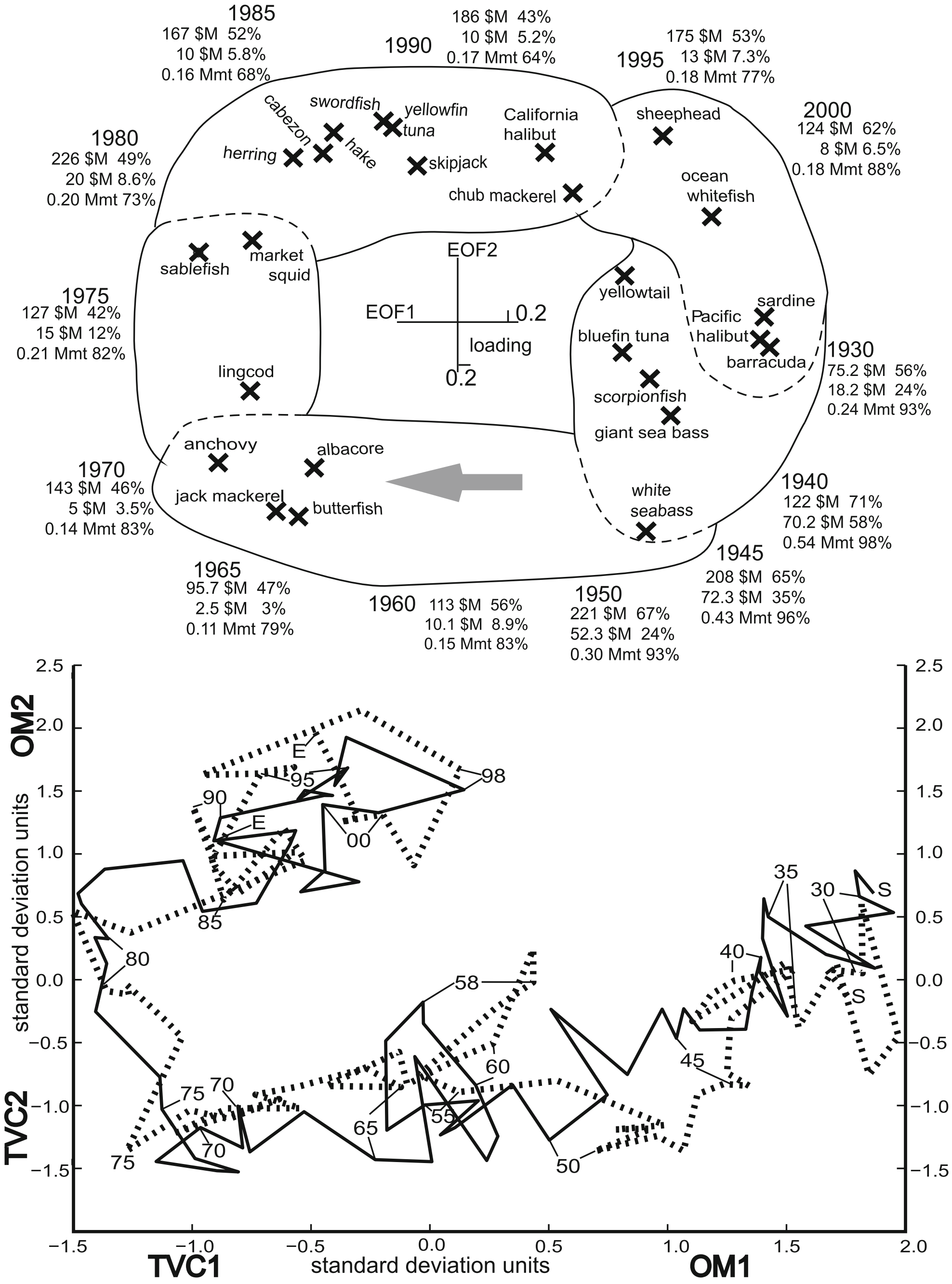

Fig. 4.30 *Upper panel*: Fish assemblages describing an "ecospace" created by plotting the loadings for each taxa from EOF1 (*horizontal*) against the loadings from EOF2 (*vertical*). The small tables under each date show the 5-year mean of commercial fishing statistics where the *top line* gives the total value of US landings. Norton et al. [422] suggest that changes in the position of fish taxa in this ecospace reflect changes in the state of the California Current ecosystem. *Lower panel*: Another representation of changes in the system shown by plotting (*solid line*) the time-variable coefficients (*TVC*) of EOF1 (*horizontal*) against EOF2 (*vertical*). See Norton et al. [422] for further detail (From Norton et al. [422])

reported in their analysis were about 20 % of the highest catches in the early 1940s. Aggregate catches in 2000 were 33 % of the highest catches. However part of the reason for this relative stability in total aggregated catches is likely to be related to increasing catch efficiencies. Another contributing factor will be adjustment of targeted species by fishers to optimize their yield. As is well known, fish catches should not be interpreted as abundance.

Small Pelagic Fish

Low-frequency fluctuations of small pelagic fish populations in relation to climate variability are important for planning commercial fishing investment [267], for developing environmental indices for stock assessment [250, 369], and for integrated ecosystem assessments [310]. Several studies concluded that there are environmentally driven fluctuations in small pelagic fish populations with periods of 40–70 years [52], 50–75 years [571], 65 years [267] and 100–120 years [244]. Sardines fluctuate widely in abundance over inter-annual to multidecadal time scales [52, 346, 496]. For sardines, there have been repeated attempts to link biomass fluctuations to indices of climatic variability, like the Pacific Decadal Oscillation (PDO) [18, 101, 496, 597]. Correlations between the PDO with periods of 40–76 years [433], and sardine biomass with periods of 40–70 years [52], have been inferred using 90-year time series (e.g. 1920–2010) [101, 344, 345, 374, 597]. These correlations cannot be tested because the long-period fluctuations are outside the observation window that can be analyzed statistically, i.e. the period (40–76 years) is greater than half the length of the series 45 years) [303]. Using 370 years of paleoclimatic data, McClatchie (2012) [367] showed there is no significant correlation between the PDO and sardine biomass.

On longer time scales the paleoclimatic record from fish scales in sediment cores shows that large fluctuations in sardine and anchovy off California, including extreme events (outbreaks and crashes) of the order of 3 standard deviations from the mean, occur in the absence of fishing [52, 527]. The mechanisms driving these fluctuations are poorly understood. Modern sardine abundance is affected by environment, biological interactions, and commercial fishing. Modern data show that forces driving abundance fluctuations are primarily environmental and strongly influenced by ENSO (El Niño-Southern Oscillation) events [344, 421, 526]. Key factors include temperature, level of production, large scale advective flow, mesoscale variability and predation pressure. Although alternation of species, or species groups (e.g. sardine, anchovy and mackerels) may also play a role in determining abundance [344], there appears to be little evidence for alternation of species in the paleoclimatic record [164]. In addition to environmental influences, fishing pressure also has an influence on population abundance, but simulation showed that fishing intensity affects the magnitude, but not the period, of fluctuations [342].

Long time series are needed to statistically test for correlation between the PDO and sardine abundance. McClatchie [367] used a 370-year record of paleoclimatic proxies [52, 180] to show that fluctuations in sardine biomass off California are not related to the PDO, despite the appearance of correlation in the 90-year record from 1920 to the present day [101, 344, 345, 374, 597]. The proxy for the PDO (henceforth referred to as 'paleo-PDO proxy') was derived from tree ring data along the west coast of North America [180]. The proxy for sardine biomass (henceforth referred to as 'paleo-sardine proxy') was derived from fish scales in sediment cores from the Santa Barbara Basin (SBB), southern California [52]. By using paleoclimatic series [52, 180] McClatchie [367] overcame the statistical limitations of short time series that prevent quantification of any relationship between the PDO and low-frequency variability of sardine biomass.

One potential problem with interpreting the paleo-sardine proxy as biomass is that the fluctuations in the series may reflect a shift north or south along the west coast of the center of the fish population, rather than a change in biomass. Ideally one would compare time series from two or more spatially separated sites and test for coherence between the series to address this issue. Unfortunately, there are few locations with anoxic sediments that produce varved layers, and the SBB core data are the only series available on the Pacific west coast.

Another problem is that the Santa Barbara Basin may not be representative of the broader region. However, Field et al. [163] noted: "Although the Santa Barbara Basin lies within an upwelling environment, regional- and basin-scale processes are considered more influential than high-frequency, local processes. The major inter-annual, decadal, and secular variations observed in sea surface temperature (SST) and zooplankton abundance at or near the SBB clearly follow the same patterns of variability observed coherently throughout the California Current." [163].

The PDO is derived from the spatial field of sea surface temperatures using a common method of reducing the dimensionality of spatio-temporal climate data, and is the first principal component of sea surface temperature in the North Pacific, north of 20°N [356] (Sect. 4.1.1.1). Low-frequency oscillations in northeast Pacific sea surface temperatures and along-shore winter wind stress have dominant periodicities of about 25 and 50 years [571]. Variability occurs at all scales in these environmental time series, but Ware [571] determined that there were dominant periodicities at 2–3, 5–7, 21–25 and 50 years. The ENSO-scale periodicities (5–7 years) were particularly prominent in the time series of winter wind stress. In contrast the very-low-frequency component (50 years) dominated the variability in sea surface temperatures. Ware's work [571] indicates that the dominant periodicities for variation in sea surface temperatures (50–75 years) are the same order as the low-frequency fluctuations in sardine abundance (40–70 years [52]. However, the low-frequency component of the temperature series was difficult to resolve [571] because of the relative lengths of the period and the time series, as mentioned above.

One might argue that correlating the paleo-PDO proxy with the paleo-sardine proxy from the SBB in southern California may not be informative. However, sardine seasonally migrate along the coast from a spawning ground off southern and central California to the Pacific Northwest, as far north as northern Vancouver Island (Sect. 4.3.1). As such, the mature fish that migrate effectively integrate the environmental

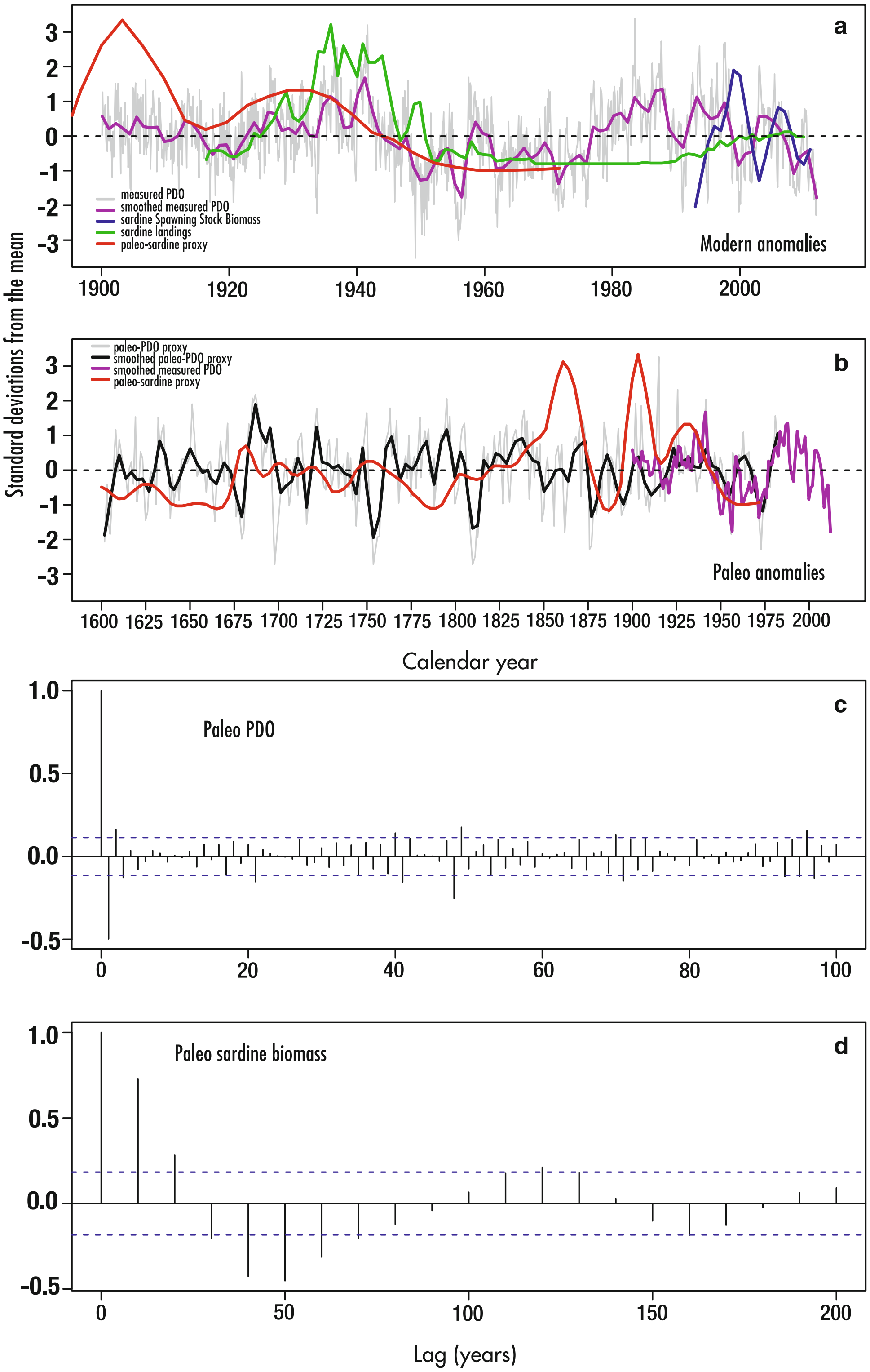

Fig. 4.31 Time series of climate indices and sardine biomass. (**a**) Time series of the PDO based on sea surface temperatures for the last 111 years overlaid on three independent time series indices of sardine biomass. (**b**) Time series of the paleo-PDO proxy and paleo-sardine proxy over 370 years. The PDO based on sea surface temperatures is overlaid on the paleo-PDO proxy in the last 111 years to show the coherence between the modern and paleoclimatic indices. Smoothed curves are fitted by locally weighted robust regression (LOWESS).(**c**) Auto-correlation of the detrended annual paleo-PDO proxy derived from tree rings. (**d**) Auto-correlation of the detrended decadal (10-year resolution) paleo-sardine proxy. *Dotted lines* indicate significance level ($p = 0.05$) (From McClatchie [367])

conditions along the Pacific west coast, rather than just in the southern California area, so relating their biomass to the PDO is reasonable.

The historical trend of the sardine fishery and sardine biomass off California shows similarity to the fluctuations in the PDO (Fig. 4.31a). The PDO has been used to model variability in climate patterns in the North Pacific [72, 356, 431, 432]. While the monthy values of PDO anomalies vary considerably, the shift from predominantly negative to positive anomalies in the California Current System, referred to as a shift from the cool phase (PDO$^-$) to the warm phase (PDO$^+$), occurred in phase with the collapse of the sardine fishery in the 1930s, and subsequent recovery in the 1980s (Fig. 4.31a). A key feature of the PDO time series is the shift from PDO$^-$ to PDO$^+$ in 1976/1977, interpreted as a "regime shift" in oceanographic and atmospheric conditions. About 7–8 years after the 1976/1977 "regime shift" from cool to warm conditions in the California Current System, the sardine population off California began to increase rapidly inshore [577], as a recovery from its collapsed state began (Fig. 4.31a). The population continued to increase, although with considerable variability in rate of growth, for the next ≈15 years, but began a declining trend after 2000 (Fig. 4.31a). There was controversy [101, 186, 448] as to whether a second phase shift of the PDO occurred when PDO$^+$ reverted to PDO$^-$ in 1999–2002, coincident with the shift to a downward trend in the sardine abundance (Fig. 4.31a) (Sect. 4.1.1.1).

Subsequent data showed that the PDO during 2000–2010 included fluctuations between positive and negative phases, fueling doubts about the regime shift concept, and methods for detecting regime shifts [432, 433, 479]. It is now known that the PDO, which is the leading pattern of climate variability in the North Pacific, incompletely characterizes North Pacific climate [72]. Overland et al. pointed out that: "If the underlying [climate] process [of the PDO] were more cyclic and deterministic, then there would be more possibility to say when a future shift might occur. But with red noise, the large shifts occur when the different contributions add together in a random manner, with little potential predictability. Thus if the true underlying climate process was close to red noise, predictions from extrapolation by curve fitting of twentieth century data would be a misleading and dangerous exercise." [431].

Recently Zwolinski and Demer [597] inferred, from earlier studies and recent surveys, that sardine are currently showing trends similar to the fishery collapse of the 1940s. They suggested that a cold regime, described as a predictable phase of a cyclic PDO, combined with fishing pressure on the larger, more fecund fish, and increasing abundance of mackerels (a likely competitor and predator, Sect. 5.3) was driving another collapse of the sardine fishery [597]. The implication drawn from their review of the literature, is that the "cold regime" of the PDO is unfavorable to sardine. McClatchie (2012) [367] questioned whether the PDO is the correct index of environmental variability to relate to sardine varability.

For the period of overlap between 1900 and 1970, the paleo-PDO proxy shows anomalies of approximately the same magnitude (approx. 2 standard deviations from the mean) as the modern PDO derived from SST (Fig. 4.31b). The phase of the two series is also coherent during the 70 years when they overlap (Fig. 4.31b). The coherence between the modern PDO and the paleo-PDO suggests that the paleo-PDO is a reasonable approximation to the actual PDO series. A full validation of the chronology for this paleo-PDO proxy was published by Gedalof and Smith [180].

Comparing the paleo-sardine proxy with the paleo-PDO proxy, there was no extreme fluctuation in the paleo-PDO series at the time when the extreme events occurred in the paleo-sardine record, nor at reasonable lags given a maximum lifespan of about 8 years for sardine (Fig. 4.31b). Unfortunately there is no overlap between the paleo-sardine proxy, which ends in 1973, and modern estimates of sardine spawning stock biomass that begin in 1993 (Fig. 4.31a). Fishery landing data do overlap with the paleo-sardine proxy, but the relationship between fishery landings data and sardine biomass is complicated by the development phase of the sardine fishery, as well as by subsequent changes in effort. The rising arm of the sardine landings curve reflects increasing exploitation of the resource as the fishery developed in the 1920s, rather than increasing biomass of sardine (Fig. 4.31a). In fact, contrary to appearance given by the fishery landings data, the paleo-sardine proxy indicates that sardine biomass was greater than the mean in the years (1920–1930) immediately prior to the development of the fishery in California. These data show that the lead up to the peak in fishery landings does not reflect an increase from low sardine biomass (Fig. 4.31a).

Autocorrelation of the detrended (first-differenced) paleo-PDO proxy shows no significant periodicity over lags up to one-third the length of the time series (Fig. 4.31c). McClatchie [367] noted that Gedalof and Smith [180] reported intervals when there is no evidence of regime shifts, e.g. 1840–1923, and there are other periods where most of the inter-decadal activity (periods 30–70 years) is concentrated, e.g. prior to 1840. Given these qualifications, it is reasonable to say there is no consistent periodicity in the series. McClatchie [367] showed that the paleo-PDO proxy has no dominant periodicity, which is a conclusion consistent with analyses of the modern PDO summarized by Overland et al. [431–433]. In contrast to the paleo-PDO proxy, the paleo-sardine record shows significant negative autocorrelation at lags of 40–60 years (Fig. 4.31d), indicating a period of 80–120 years, partially supported by the positive autocorrelation at 100–120 years. This periodicity is somewhat longer than that found by Baumgartner et al. [52], who reported peaks in the power spectra of the paleo-sardine proxy at 40, 60 and 70 years.

The detrended PDO and indices of sardine biomass were not correlated at any of the three scales tested. These three scales were 370 years from 1600 to 1970 (Fig. 4.32a), 92 years from 1920 to 2012 (Fig. 4.32b), and 18 years from 1993 to 2011 (Fig. 4.32c). There is no significant

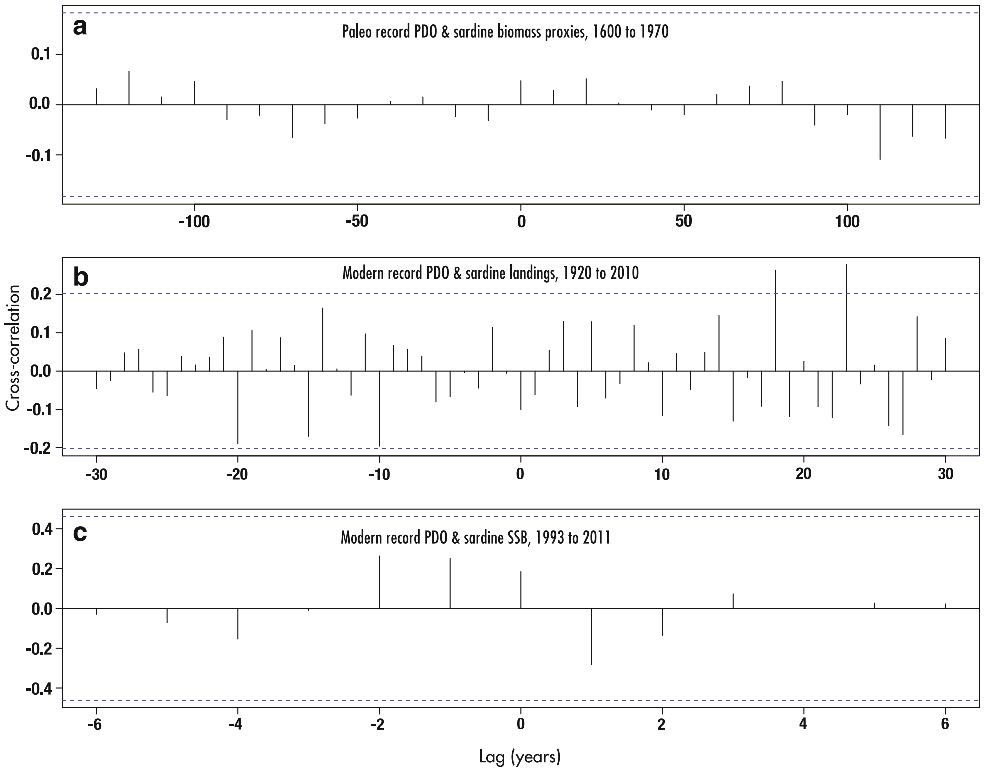

Fig. 4.32 Cross-correlation between detrended paleo-PDO proxy and paleo-sardine proxy at three different time scales. (**a**) At a ≈370-year time scale, paleo-PDO proxy is derived from tree rings and the paleo-sardine proxy is derived from fish scales in sediment cores. The paleo-PDO proxy was averaged over 10-year periods to match the resolution of the paleo-sardine proxy (see Fig. 4.31). (**b**) At a ≈90-year time scale, the PDO is derived from sea surface temperatures (SST) and sardine abundance is represented by commercial landings. (**c**) At ≈20-year time scale, the PDO is derived from SST and sardine biomass is presented as Spawing Stock Biomass (SSB). *Dotted lines* indicate significance level ($p = 0.05$) (From McClatchie [367])

correlation between the PDO and indices of sardine biomass on either longer or shorter time scales, based on either paleoclimatic proxies or modern data. Although we know that climate variability affects fisheries, inferring causality from apparent coincidence of change is not proper science. ENSO affects the PDO on all scales [415] so the lack of significant correlation between the paleo-PDO and paleo-sardine biomass probably reflects the greater importance of mechanisms operating on time scales of a few years (ENSO) rather than mechanisms operating on the slow multi-decadal time scales of the PDO (Sect. 4.2.1.4).

Sardine range contraction and expansion

The effect of environment on sardine at decadal scales is confounded by changes in population size and the spatial extent of their habitat. Expansion and contraction of sardine habitat as the population expanded and contracted has been modeled using a density-dependent habitat selection model [343]. MacCall [343] developed several variations of his population model for habitat selection, one of which was the "basin model". In common with other population models of habitat selection, fitness is loosely defined. In MacCall's model, optimizing fitness through the process of habitat selection, is defined as maximizing per capita growth rate, where per capita growth rate is taken as an analog of reproductive value. In other words the habitat that optimizes the contribution to reproductive success of the population, regardless of how the selection of habitat is achieved, is assumed to be the habitat where per capita growth rate is maximized. Mathematically the model is formulated to describe the change in abundance ($\triangle N$) at a given location as:

$$\triangle N = G - H + D + (I - E)$$

where G is the *in situ* population growth rate (births - deaths), H is the harvest, D is diffusion in or out of the area, and $(I - E)$ is the difference between immigration and emigration [343]. Diffusion reflects a tendency for the population to even out spatially, so that areas of high population density flow into areas of low density. Consequently, the population tends to expand into areas of marginal habitat with lower realized growth rate or reproductive value (r^*) (defined below). The model assumes that local population growth rate ($^{dN}/_{dt}$) is a function of habitat suitability, r, and declines in a linear fashion with population density, such that

$$\frac{dN}{dt} = rN(1 - bN)$$

where b is the coefficient for density-dependent decrement in per capita growth rate [343]. Habitat suitability, r, was visualized as the profile of the geographic fitness topography of the basin model.

The full model is:
$\frac{\delta N}{\delta t} = r^* N - FN + \kappa \frac{\delta^2 N}{\delta x^2} - V^{-1} \frac{\delta r^*}{\delta x} \frac{\delta N}{\delta x}$ where $r^* = r(1 - bN)$, N is abundance, F is the per capita death rate (representing harvest, H), κ is the coefficient of diffusivity,

x is a location along a continuum, and V is a constant determining the rate of flow per unit gradient in realized habitat suitability which depends on viscosity [343]. MacCall [343] argued that a retracting population might not follow the same path as an expanding population. He used the concept of viscosity to explain such hysteresis. Basically, an expanding population can be envisioned as expanding from a domed, high density center towards less suitable habitat on the periphery. When the same population retracts, resistance due to viscosity, preventing a return to an ideal free distribution, could lead to reduced density at the center and residual population at the periphery.

The model is necessarily idealized but offers some intriguing explanations for the observed changes in sardine populations as they have retracted into a collapsed state, and later expanded their geographic range when the population recovered. Density dependence is a key feature of the basin model. To date, the evidence for density dependence in sardine populations, such as shifts to smaller sizes, to poorer adult condition, or to reduced reproductive output at higher population densities, remains equivocal.

Ichthyoplankton

The ichthyoplankton data collected by CalCOFI provide a useful way to examine long-term changes in fish assemblages off California. Long-term trends in fish larval abundance reflect trends in adult abundance, in contrast to short-term fluctuations that are more related to annual fluctuations in adult reproductive output, or to shifts in the geographic distribution of adults [402]. The CalCOFI larval fish time series can be considered representative of the fish assemblages that produced them (see Sect. 6.1 for specific examples).

Smith and Moser [521] presented 50-year long trends of larval abundance for 14 taxa derived from the CalCOFI surveys from 1951 to 2000. They examined the fluctuations in larval abundance in relation to changes in temperature and zooplankton displacement volumes. By examining each time series in turn they determined whether the fluctuations in larval abundance were related to the PDO or to ENSO variability. They found that the mesopelagic larvae of southern offshore species showed the greatest response to both decadal and ENSO-scale variability [521]. In contrast, the subarctic-transitional mesopelagic species and nearshore species did not respond to the 1976/1977 regime shift. Their conclusions were later confirmed by Hsieh et al. [224], with the difference that Smith and Moser emphasized that the climate sensitivity of the assemblages had a regional as well as an oceanic-coastal component. The greatest sensitivity to climate was shown by the southern offshore assemblages, likely because the larvae of these fishes are associated with distinct water masses at the northern edge of their range, and so shifts in the boundaries between subarctic, transitional and equatorial waters (see Sect. 2.3) would be reflected in their abundances [521].

Hsieh et al. [224] proposed that unexploited taxa would track climate trends more closely than exploited species because the trends in exploited species would be confounded by the effects of fishing on adult abundance. They grouped the species into assemblages that live in the same biogeographic region and habitat, and combined this information on habitat with the life history trait of age at maturation, which was available for most species, in order to test their hypothesis. Their analysis was based on 67 taxa that occurred frequently over 30–40 years of sampling, and that could be considered representative of oceanic, coastal-oceanic and coastal assemblages [224].

Hsieh et al. [224] used correlation and regression analyses to investigate the effects of five correlated climate variables[15] on the abundance of oceanic, coastal-oceanic and coastal taxa during the cold PDO$^-$ period (1951–1976) and the warm PDO$^+$ period (1977–1998). They concluded that fluctuations in the abundance of oceanic taxa were strongly associated with the temperature pattern of the Northeast Pacific. However, the fluctuations were somewhat surprising. Larvae of tropical/ sub-tropical oceanic species consistently increased in abundance in the warm period, but so also did all but one taxon of larvae of sub-arctic/ transitional species. Four more widely distributed species also increased in the warm period (see also Sect. 4.1.3.3). Furthermore, only three of the taxa in the coastal-oceanic species group exhibited any significant correlation with environmental variables: these were chub mackerel (*Scomber japonicus*), jack mackerel (*Trachurus symmetricus*) and medusafish (*Icichthys lockingtoni*). Notably, neither sardine (*Sardinops sagax*) nor anchovy (*Engraulis mordax*) were correlated with any of the climate variables tested [224]. Sardine were among the species that increased significantly in the warm period, but the lack of correlation with the three climate indices or the average surface temperature in the 75-station CalCOFI sampling domain is consistent with recent studies ([367, 369], but see [309]).

Changes in abundance of oceanic species seem to be more closely related to climatic variables than is the case for coastal-oceanic or coastal species. Abundance of 24 out of 34 oceanic species (71 %) were correlated with climate variables [224]. Oceanic fish species are known to be associated with specific water masses [401, 407, 521]. Hsieh et al. [224] suggested that incursion of central gyre waters

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[15] The environmental variables used by Hsieh et al. [224] were surface temperatures averaged over the 75-station CalCOFI pattern, the upwelling index anomaly from the central Southern California Bight (33N, 119W) [40], and three climate indices: the Southern Oscillation Index [561], the Pacific Decadal Oscillation Index [356], and the North Pacific Index [562].

(presumably North Pacific Central Water in the upper 200 m and Equatorial Pacific Water below 200 m, Table 2.1) could bring oceanic species into the CalCOFI sampling domain. As a result they suggested that oceanic fishes would be useful to detect climatic effects on the California Current System [224] (see also Sect. 4.1.3.2). Based on co-variation among species within and between assemblages, Hsieh et al. [224] concluded that vertically migrating species responded differently than mesopelagic species to climate variables. This is consistent with the distinction between Equatorial Pacific Water below 200 m that mesopelagic oceanic species live in, and the presence of North Pacific Central Water in the upper 200 m that vertically migrating oceanic fishes would also encounter during their diel migrations. Vertically migrating oceanic species showed a stronger response than non-migrating species to decadal-scale climatic changes off southern California [225].

In contrast to oceanic species, the abundance of only 3 out of 10 coastal-oceanic species (30 %) were correlated with climate variables, and there was no difference in the correlations on the basis of whether species were exploited or not. The response to climate variables was even weaker for coastal fishes than for coastal-oceanic species; only 3 out of 23 species (13 %) were significantly correlated with the climate variables, with no differences between fished and unfished species [224]. Hsieh et al.'s [224] results differ somewhat from Koslow et al. [270] who applied a multivariate analysis (PCA) of species abundances to relate ichthyoplankton assemblages to environmental time series, building on their earlier study [275] (Sect. 4.1.3.2). Koslow et al. found that a group of mostly pelagic species were strongly correlated with their second principal component (PC2). The species were Pacific sardine (*Sardinops sagax*), Pacific hake (*Merluccius productus*), northern anchovy (*Engraulis mordax*), *Sebastes* spp., and two of the most abundant midwater fishes, *Leuroglossus stilbius* and *Stenobrachius leucopsarus.* All of these species except sardine were positively correlated with the PC2 in Koslow et al.'s analysis. Their detrended second principal component was significantly negatively correlated both with temperature at lags of 1–3 years, and with sea surface height at San Francisco at a 1 year lag [270]. The difference in sign of the correlation between sardine and PC2 means that sardine abundances were positively correlated with temperature and with positive sea level anomalies that imply weaker flow in the California Current.

An important consideration when evaluating these results is to bear in mind that Hsieh et al. [224] stated clearly that "In constructing the time series, we assumed that spatial heterogeneity and sampling errors are insignificant after the averaging process". While averaging was necessary for their analysis, Hsieh et al. [224] pointed out at the end of their paper that "the CalCOFI time series have high variance [consisting of] spatial heterogeneity and sampling errors". As Paul Smith repeatedly pointed out, this type of variability has been a thorn in the side of researchers working with these data.

The effect of secular warming trends on the centers of distribution, and the latitudinal range limits, of oceanic mesopelagic fish appears to differ with species. Hsieh et al. [225] found the median latitudinal distribution of 8 mesopelagic species in their peak spawning season were positively correlated with mean annual temperatures.[16] These eight species (*Aristostomias scintillans, Chauliodus macouni, Nannobrachium* spp., *Notoscopelus resplendens, Protomyctophum crockeri, Stenobrachius leucopsarus, Symbolophorus californiensis*, and *Tarletonbeania crenularis*) shifted their median latitudinal distribution northward by 29 ± 11 km per °C with warming off southern California [225]. In addition to shifting median latitudes of their distributions, 9 mesopelagic species significantly shifted their northern range limits, and 5 species shifted their southern range limits. Hsieh et al. [225] suggested that most oceanic mesopelagic fish species have shifted northward in the PDO^+ period relative to the PDO^- period (see Sect. 4.1.1.1), although the distance moved is statistically significant in only about 25 % of species. In addition, the abundance of 25 out of 34 mesopelagic species increased in the PDO^+ period relative to the PDO^- period [225], but subsequently decreased from 1999 to 2010 [275] (Sect. 4.1.3.2).

4.2 Inter-annual Scale Variability (1–5 Years)

4.2.1 Effect of ENSO off Southern and Central California

The effects of El Niño in the California Current System originate from processes in the western Pacific. Sea surface temperatures were above average in the central and western Pacific prior to El Niño episodes of 1982–1983, 1986–1987 and 1991 (see references cited in [99]). Chavez [99] described how strong westerly wind bursts over the warmer than normal "warm pool" in the western tropical Pacific generated planetary Kelvin waves ([263, 386, 592] in [99]), that propagated eastward along the equator to the coast of South America. After reaching the coast, the waves continued both to the north and to the south as coastally-trapped waves ([151, 238] in [99]), propagating at speeds of 200–250 km day^{-1}. Wind bursts lasting approximately

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[16] Temperature was from 6 core CalCOFI lines on the quarterly surveys including stations as far offshore as station 90, and all standard depths (0, 10, 20, 30, 50, 75, 100, 125, 150, 200, 250, 300, 400, and 500 m). Quarterly means were calculated and the long term quarterly averages removed to create anomalies, which were then averaged to create annual "SST" anomalies. It is unclear whether Hsieh et al. [225] used all of these depths, or just some of these depths to estimate "SST".

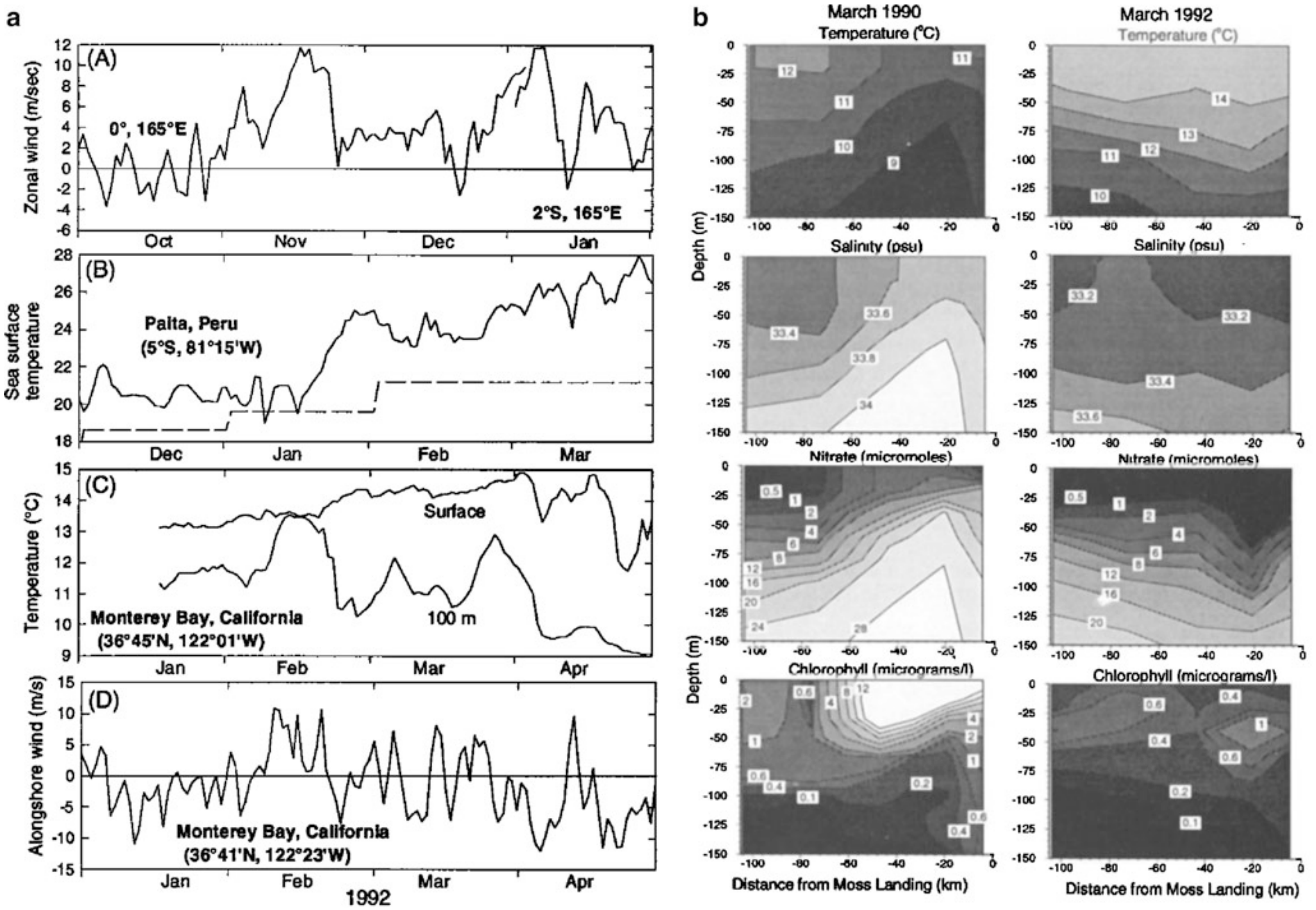

Fig. 4.33 **Panel (a):** (*A*) Time series of the zonal (i.e. east-west) wind from the TOGA-TAO buoy array where westerly winds (i.e. from the west) are positive. (*B*) Sea surface temperature measured at a pier in Paita, Peru (dashed line is the long-term (1961–1982) climatological mean. (*C*) Temperature time series at the surface and 100 m measured at a mooring in Monterey Bay, California. (*D*) Time series of along-shore wind measured at NODC buoy 46042, 27 nm west of Monterey Bay, California (From Chavez [99]). **Panel (b):** Sections of temperature, salinity, nitrate and chlorophyll along a transect in the center of Monterey Bay comparing March 25, 1990 with March 27, 1992 during the El Niño (From Chavez [99])

2 weeks were measured in November 1991 and December 1991–January 1992 (Fig. 4.33(a) A). Warming at Paita, Peru (located at 5 °5'S), which is the most westerly instrumented location on the Peruvian coast (Fig. 4.33(a) B) was consistent in timing with the arrival of a Kelvin wave generated at 165°E by the November 1991 wind burst, traveling along the equator at 205 km day^{-1} [99]. This speed is comparable to wave propagation speeds observed in other El Niños [283]. Rapid sub-surface warming (at 100 m depth) was observed off Monterey Bay in February 1992 (Fig. 4.33(a) C), which could have been caused by a wave propagating along the equator and then traveling as a coastally-trapped wave to the north at a speed of 209 km day^{-1} [99] (Note the shift in the dates between panels in Fig. 4.33(a) A, B and C). Chavez [99] notes that the correspondence between local winds and sub-surface warming is much weaker than the correspondence with winds over the western Pacific. Further, he pointed out that local wind reversals deepen isotherms by 10's of meters compared to the deepening of over 100 m that was driven by the remote forcing (e.g. compare March 1990 with March 1992 in Fig. 4.33(b) [99]).

The remotely-forced, coastally-trapped waves deepen the thermocline, raise sea level and produce large, warm temperature anomalies along the eastern equatorial Pacific and Peruvian coastlines [150]. In contrast to the California Current System, local upwelling-favorable winds strengthen during El Niño off Peru, so the deepening of the thermocline, raising of sea level and positive temperature anomalies are attributed to the remotely-forced Kelvin waves ([46, 283] in [99]), since upwelling has opposite effects. At higher latitudes, off California, local atmospheric forces may play a greater role than off Peru [99].

El Niño manifests as changes in many physical, chemical and biological properties and processes in the California Current System. The intensity and timing of these changes varies between ENSO events and in some cases the impacts may be difficult to separate from "normal" inter-annual variability.[17] Strong or moderate ENSO events in the equatorial Pacific do not necessarily produce effects at mid-latitudes [571]. Ware [571] reported that in the twentieth century, "only 42 % of the strong and 25 % of the moderate tropical ENSOs produced large, warm anomalies off [British Columbia]" (see Sect. 4.2.1.1). When temperatures off Indonesia are warmer than average, ENSO effects at mid-latitudes on the west coast are greater [571]. When tropical warmings successfully propagate northward, Rossby waves can be detected along the North American west coast, and there are associated reductions of productivity, shifts in species composition and movements of migratory fish stocks.

The effects of El Niño include an increase in coastal dynamic height, deepening of the mixed layer, broadening and intensifying of northward coastal flow, anomalous temperature and salinity properties, temporary reversal of the net southward flow [337], movement of the core of the California Current further offshore and reduction in the intensity of coastal upwelling. Anomalous warming of surface waters may be caused by El Niño, but this can also originate from other processes. The warming events are caused by large-scale changes in the wind field that inhibit coastal upwelling and produce onshore surface drift that produces greater sea-surface height at the coast [337, 506]. Processes forcing the warming weaken equatorward currents and (or) strengthen poleward currents [238].

Chavez [99] compared two transects crossing the shelf from Monterey Bay, California in March 1990 and during El Niño conditions in March 1992. These transects did not sample the energetic jets that are characteristically found off the central Californian coast. The two sections are strikingly different and serve to illustrate some of the effects of El Niño off central California. Before the El Niño, in March 1990, the isotherms and salinity isopleths domed strongly upward near the coast, indicating upwelling of cool saline water, and a well developed southward flow. Nitrate was enriched at the surface due to upwelling of nutrient rich water, and a bloom of *Chaetoceros* spp. (chain-forming spiny diatoms) with chlorophyll concentrations as high as 15 mg chlorophyll-a m^{-3} developed (Fig. 4.33b [99]). Euphotic zone depth-integrated primary productivity of this bloom exceeded 2.5 gC $m^{-2}d^{-1}$ [99]. In contrast, the section measured in March 1992 during El Niño revealed dipping isotherms and salinity isopleths, indicating downwelling at the coast, and northward surface flow. High nutrient values were deeper than 100 m (Fig. 4.33b [99]). A northward traveling coastally-trapped wave caused changes in circulation, cessation of upwelling, anomalously warm temperatures, and low nutrient levels with primary productivity reduced to levels normally found in the winter [99]. Instead of a diatom bloom, the phytoplankton were dominated by picoplankton (*Synechococcus* spp., a photosynthetic cyanobacterium less than 2 microns in size). Surface chlorophyll during the El Niño period was only about 3 % (0.5 mg chlorophyll-a m^{-3}) of that in March 1990, and primary productivity was 20 % (0.5 gC $m^{-2}d^{-1}$) of that in March 1990 [99].

Biological communities do not respond in the same way to each El Niño - La Niña. During the strong tropical 1926 El Niño event (Fig. 4.34), large numbers of the warm water chondrophore[18] *Velella* occurred from Cape Mendocino to Hecate Strait (Williamson, 1930 unpublished report cited by [571]). In the moderate 1940 event, which had a strong extra-tropical effect in BC, *Velella* were abundant off the Queen Charlotte Islands [571]. Warm-water species were found further north than usual during both the strong tropical 1983 and 1992 El Niños. In the 1997/99 transition, there was a huge shift toward sub-tropical communities off southern California due to advective processes [100, 104, 300]. However, advection of water masses was less apparent in 2009/2010 [559]. There does not seem to be a typical El Niño pattern, and it is now understood that there is more of a spectrum of events between Eastern Pacific El Niños and Central Pacific El Niños (see Sect. 4.2.1.1), which have different effects in the California Current System. Palacios et al. [438] suggested that the manifestation of El Niño in the California Current System may depend upon the conditions prevailing at the time of the impact. For example, the large heat content differences between the surface and 200 m depth during 1972–1973, 1982–1983, and 1986–1987 events indicated that maximum warming occurred below the thermocline. These events were different to the 1957–1958 El Niño where the lower heat content difference indicated warming mainly above the thermocline [438]. In addition the impact is likely to be different and greater in coastal rather than offshore areas because the effects of El Niño in the California Current System are mainly imparted by Ekman processes and oceanic teleconnections that have less impact on the deeper oceanic thermocline [438].

The long time series of CalCOFI measurements provide a baseline for being able to separate different scales of variability, but the lengths of the baselines themselves differ depending upon how often particular measurements were made and when they began. Supplementary CTD surveys helped to resolve the physical impacts of the 1997/98 El Niño that was one of the strongest on record. The intense

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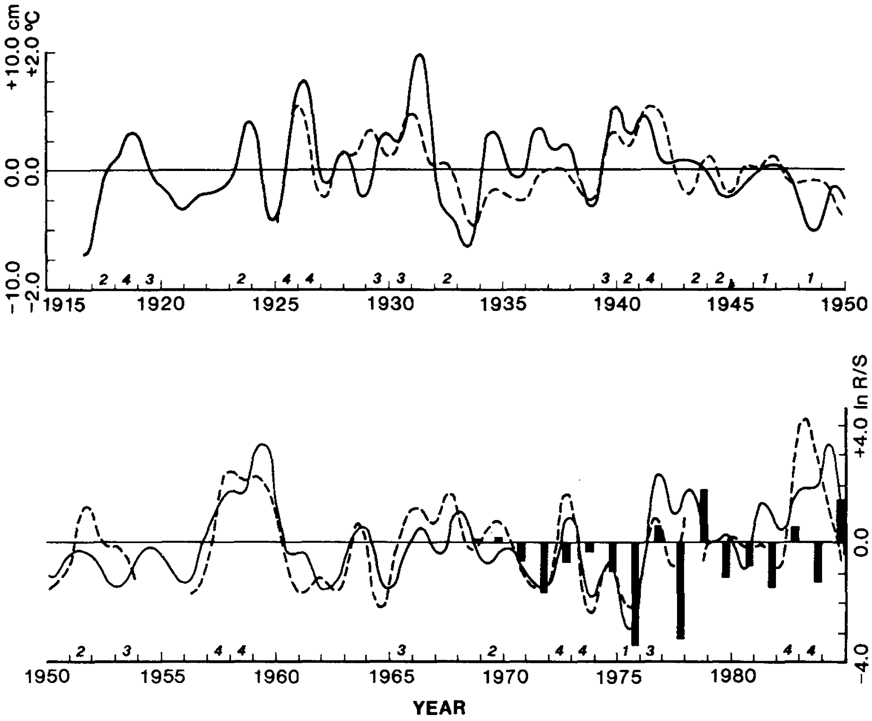
[17] For an example, see the comparison of inter-annual variability in SST anomalies of −0.2 to +2.2°C for April and May 1982 and 1983 versus a temperature anomaly of 4 °C in July 1983 in warm water intruding along the coast of the Southern California Bight attributed to El Niño [160].

[18] Chondrophores are now separated from Siphonophores and are represented by two genera, *Velella* and *Porpita* [459].

Fig. 4.34 Smoothed monthly anomalies of surface temperature (°C, *solid line*) and sea level (cm, *dashed line*) at Scripps Institution of Oceanography pier in La Jolla, California (32.9°N, 117.3°W) from 1915 to 1985. Numbers are rankings of ENSO events ([458] cited by [162]): 1 = weak, 2 = moderate, 3 = strong, 4 = very strong. *Vertical black bars*, $\log_e(R/S)$, are recruitment success for anchovy (From Fiedler et al. [162])



survey effort of 25 cruises mounted over 45 months between February 1996 to October 1999 [337] collected CTD-rosette casts of temperature, salinity, fluorescence and oxygen with associated discrete water samples at 20 depth levels.

Anomalously warm temperatures and high salinities can persist for some time due to El Niños. In 1997/98 anomalies in the temperature-salinity (T-S) plots from stations in the central region of the Southern California Bight (CalCOFI line 90) appeared in September 1997 and persisted through April 1998 (Figs. 4.35 and 4.36). The T-S plots clearly showed the warmer than average and saltier than average water over the whole vertical profile at these times. From May 1998 to September 1998 surface waters became cooler and fresher than normal (Figs. 4.35 and 4.36). The development of the temperature anomaly penetrated from the surface layer to the thermocline, but the anomaly faded faster in the thermocline with transition to La Niña [197]. This means that analysis of surface anomalies and mixed layer depth anomalies will give different impressions of the timing and magnitude of effects [197].

Surface temperature anomalies showed that the winter of 1997/1998 was anomalously warm at both Pacific Grove and the Scripps Institution of Oceanography pier, San Diego due to the El Niño (Fig. 4.37). The seasonal temperature cycle also showed the warming relative to the mean seasonal cycle (Fig. 4.37). The perennial plume of cool water extending south and west of Point Conception that is formed by

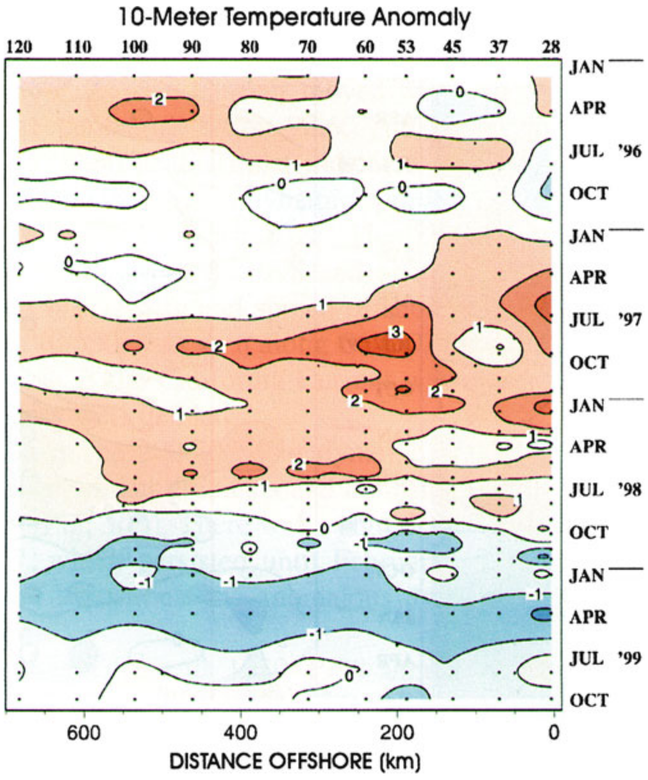


Fig. 4.35 Time–distance plots (1996–1999) of 10 m temperature anomalies for CalCOFI line 90 stations. Anomalies are based on the 1950–1998 annual bi-harmonic means (From Lynn and Bograd [337])

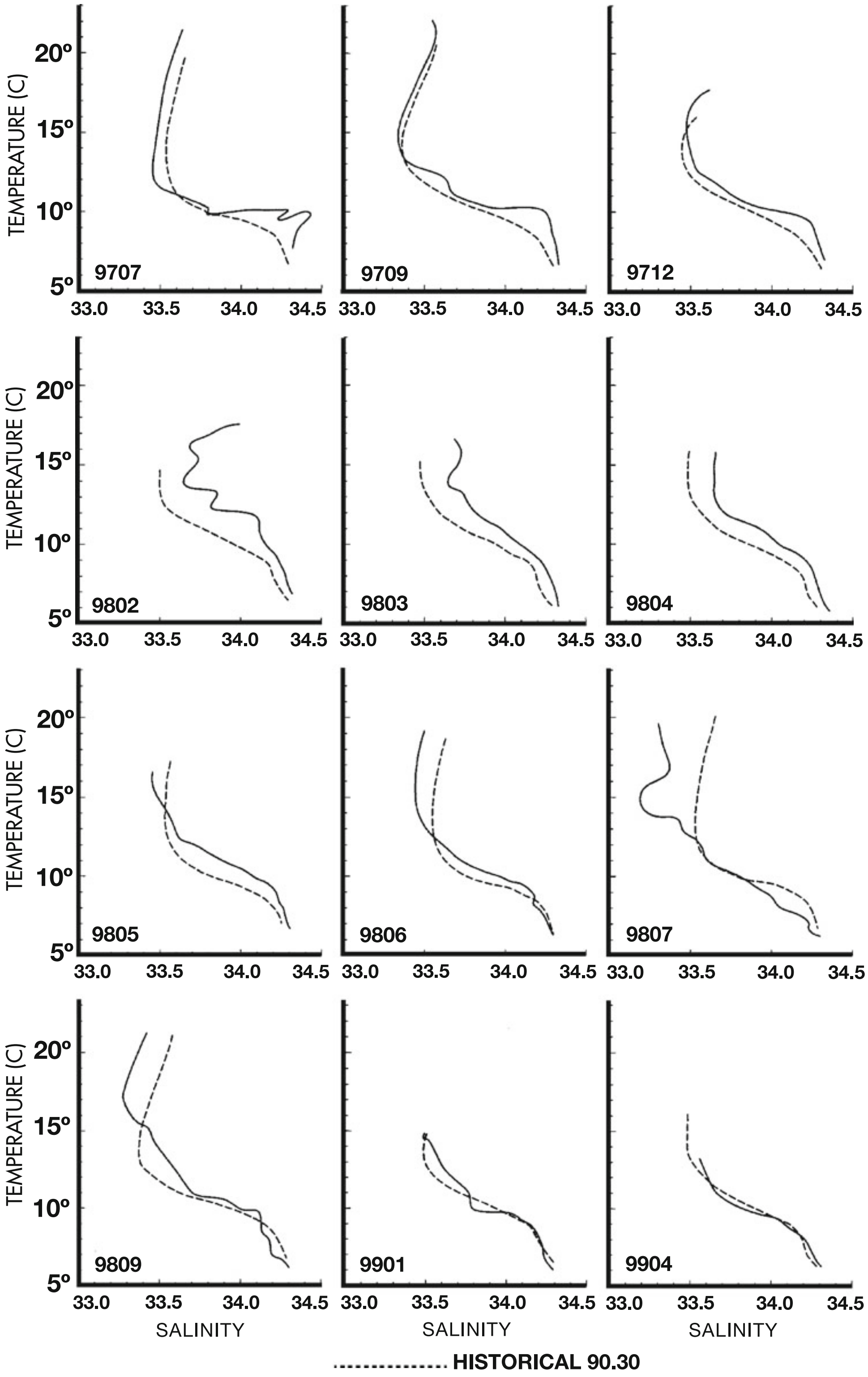


Fig. 4.36 Examples of temperature and salinity anomalies (solid line) from the long-term mean for each month (1950–1992, *dashed line*) from vertical profiles at CalCOFI line 90, station 30 during the 1997–1998 El Niño (Modified from Hayward [197]). Cruise codes, e.g. 9707 refer to year and month of the cruise, which in this example is 1997 July

combined intrusion of California Current water and coastal upwelling was 3 °C warmer in December 1982 compared to 1981 [160]. This mesoscale plume showed the warming effect earlier than the broader area of the coast off southern California and Baja California and by February 1982 the plume had disappeared entirely [160].

The effects of El Niño off southern California and Baja California can disappear and reappear on time scales of months within the one to 2 year time-scale of the entire event. For example during the 1982–1983 event, warming of the surface waters off southern California was not detectable on 16 December 1982 in remote sensing imagery, except in

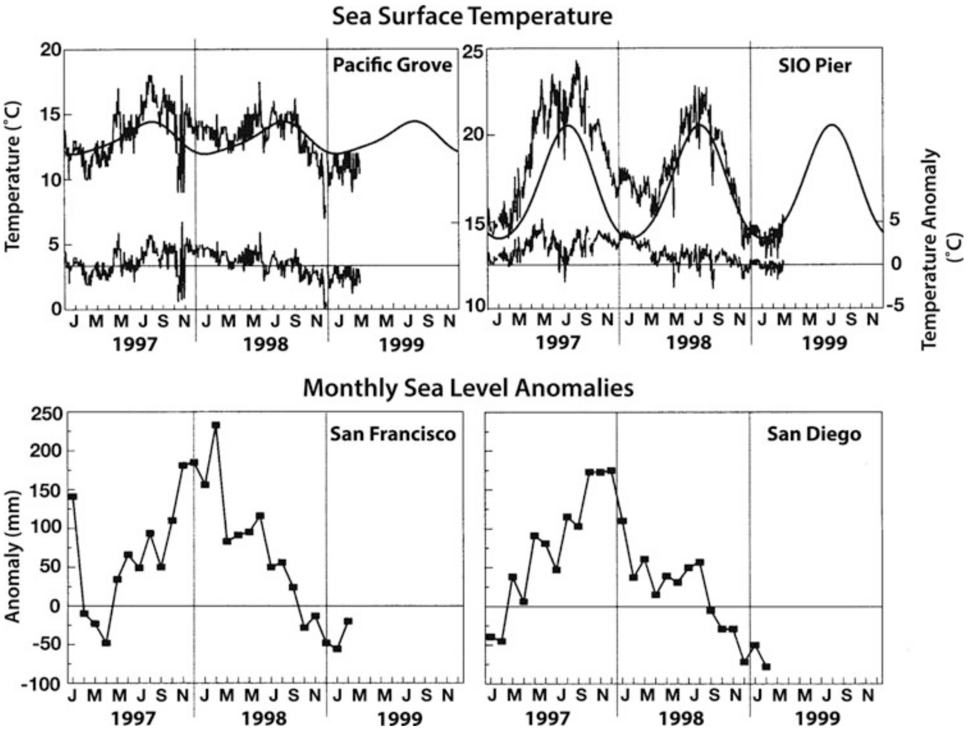


Fig. 4.37 Seasonal cycle of sea surface temperatures in relation to the harmonic mean annual cycle [336], and sea surface temperature anomalies (*upper panel*). Base periods for SST anomalies were 1916–1993 for San Diego and 1919–1993 for Pacific Grove (*lower panel*) (Modified from Hayward [197])

the Point Conception plume. By 10 January 1983 surface temperatures were 0.52–2.92 °C warmer than 1 year earlier and more than 4 °C warmer at the coast [160]. Anomalously warm coastal surface temperature continued in February, but by April and May SST anomalies returned to the "normal" range of inter-annual variability and temperatures in 1983 were not warmer than a year earlier in southern California, although they were up to 5 °C warmer off San Francisco [160]. The moderation of El Niño for several months was also evident in the coastal sea surface height, and followed a decline in the equatorial SST anomalies beginning in January and February [160].

Chlorophyll concentrations during El Niños may not be unusual, although there is evidence of anomalous increase in chlorophyll with the onset of La Niña conditions [197]. Strong inter-annual variability in chlorophyll led Hayward [197] to state that conclusions about whether El Niño brings anomalously lower chlorophyll need to be based on a multi-year baseline rather than on comparisons across only a few years [160, 376, 382]. In fairness to these authors, consistent time series of chlorophyll from CalCOFI series have only been collected since 1984.

Sea surface temperature is a less sensitive indicator of El Niño than is dynamic height at the coast. Anomalously high dynamic height at the coast during El Niño is associated with strengthening of the northward flowing coastal current in the Southern California Bight. Both the offshore extent and the gradient in dynamic height (i.e. the strength of this flow) vary between El Niños [197]. California Current flow is notably weaker during El Niño when trade winds weaken, associated with higher sea level pressure in the aastern equatorial Pacific [108]. Flow of the California Undercurrent is stronger during El Niño.

4.2.1.1 Central Pacific and Eastern Pacific ENSO

In the 1990s a new type of El Niño was detected, variously called the central Pacific (CP)-El Niño, warm pool El Niño, dateline El Niño, or El Niño Modoki (see references in [183]). The CP-El Niño is characterized by maximum warming in the central equatorial Pacific. The CP-El Niño contrasts with the Eastern Pacific (EP)-El Niño, variously referred to as traditional, canonical, conventional, cold tongue or eastern Pacific El Niño, where maximal warming occurs in the eastern equatorial Pacific [183] (Fig. 4.38). According to NOAA's definition there have been 3 EP-El Niño and 4 CP-El Niño events since 1990 [183]. It is worth noting that the number of EP-El Niño and CP-El Niño events differs depending on the how they are defined (Fig. 4.39). For example Singh et al. [508] reported two EP-El Niño events and 5 CP-El Niño events since 1990 based on their analyses of sea surface salinity (SSS).[19]

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[19] Quoting from Singh et al. [508]: "Using EOF and AHC analyses on SSS, and comparing with ENSO-related SST features, we showed that the eastern Pacific (EP) El Niño events in SSS appear in 1982–1983, 1991–1992, and 1997–1998, the central Pacific (CP) El Niño events in 1977–1978, 1986–1988, 1990–1991, 1992–1995, 2002–2003, 2004–2005 and 2006–2007, the EP La Niña events in 1985–1986, 1988–1989, 1995–1996, 1999–2001, 2005–2006 and 2007–2008, and the CP La Niña events in 1983–1984 and 1998–1999. It should be noted, however, that clearly differentiating the two EP and CP El Niño and La Niña

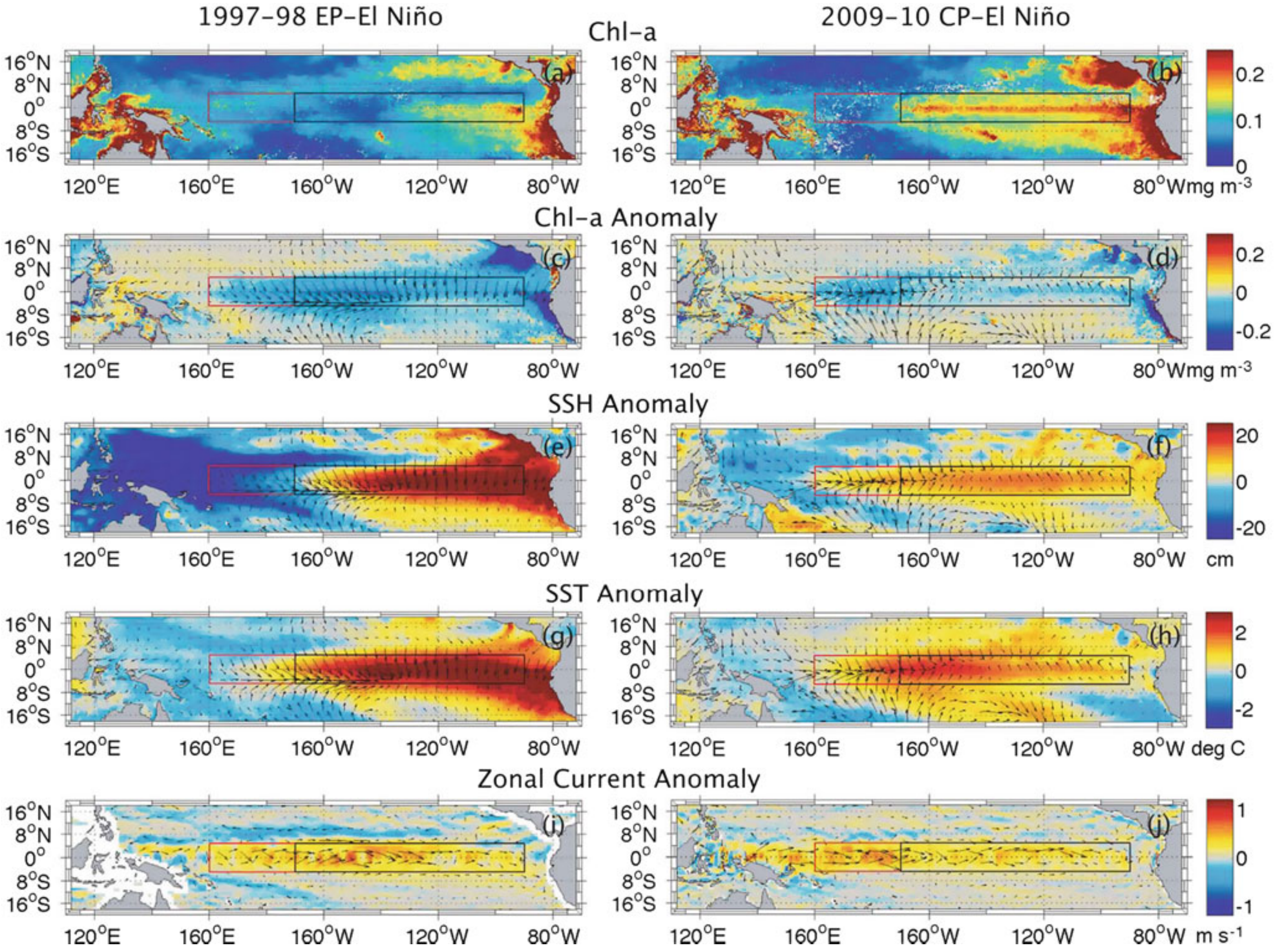

Fig. 4.38 (**a**, **b**) November-December-January (NDJ) averaged SeaWiFS chl-a. NDJ averaged anomalies of (**c**, **d**) SeaWiFS chl-a, (**e**, **f**) AVISO SSH, (**g**, **h**) OISST, and (**i**, **j**) OSCAR zonal ocean surface currents for the 1997–98 EP-El Niño and 2009– 10 CP-El Niño. CCMP wind vector anomalies are overlaid in (**c** to **h**) and ocean surface current vector anomalies in (**i** to **j**). The **black** and **red boxes** denote the EEP (5 S–5 N, 170 W–90 W) and CEP (5 S–5 N, 160 E–170 W) regions (From Gierach et al. [183])

The effects on primary production in the eastern and central equatorial Pacific differ between the EP-El Niño and CP-El Niño. During the period (1997–2010) for which SeaWiFS data are available, the two strongest El Niño events were the 1997–1998 EP-El Niño and the 2009–2010 CP-El Niño [183]. The 1997–1998 EP-El Niño substantially reduced chlorophyll *a* in the eastern tropical Pacific. By comparison, chlorophyll *a* was less reduced and showed patchy increases during the 2009–2010 CP-El Niño [183] (Fig. 4.38). In contrast, the central tropical Pacific exhibited reduced chlorophyll *a* during the 2009–2010 CP-El Niño, and less of a reduction in chlorophyll *a* during the 1997–1998 EP-El Niño [183] (Fig. 4.38).

The biological response in the equatorial Pacific to the EP-El Niño and CP-El Niño was driven by the westerly wind anomalies. The reduction of chlorophyll *a* in the eastern equatorial Pacific during the 1997–1998 EP-El Niño was driven by strong westerly wind anomalies that weakened the easterly trade winds [183] (Fig. 4.40a, b). The weakened trade winds raised sea level and depressed the thermocline, while creating stronger than average eastward surface currents and raising sea surface temperatures in the eastern equatorial Pacific [183] (Fig. 4.38). Areas with low chlorophyll *a* corresponded to areas with higher sea surface height and warmer surface temperatures. Upwelling was weakened in the eastern equatorial Pacific and consequent reduction of nutrients caused lower chlorophyll *a* levels [183]. Gierach et al. [183] used adjoint modeling to show that the effects of the 1997–1998 EP-El Niño in the eastern equatorial Pacific was caused more by suppression of the easterly trade winds and consequent reduction of upwelling and vertical mixing. In contrast the reduction of chlorophyll *a* in the central equatorial Pacific by the 2009–10 CP-El Niño was caused

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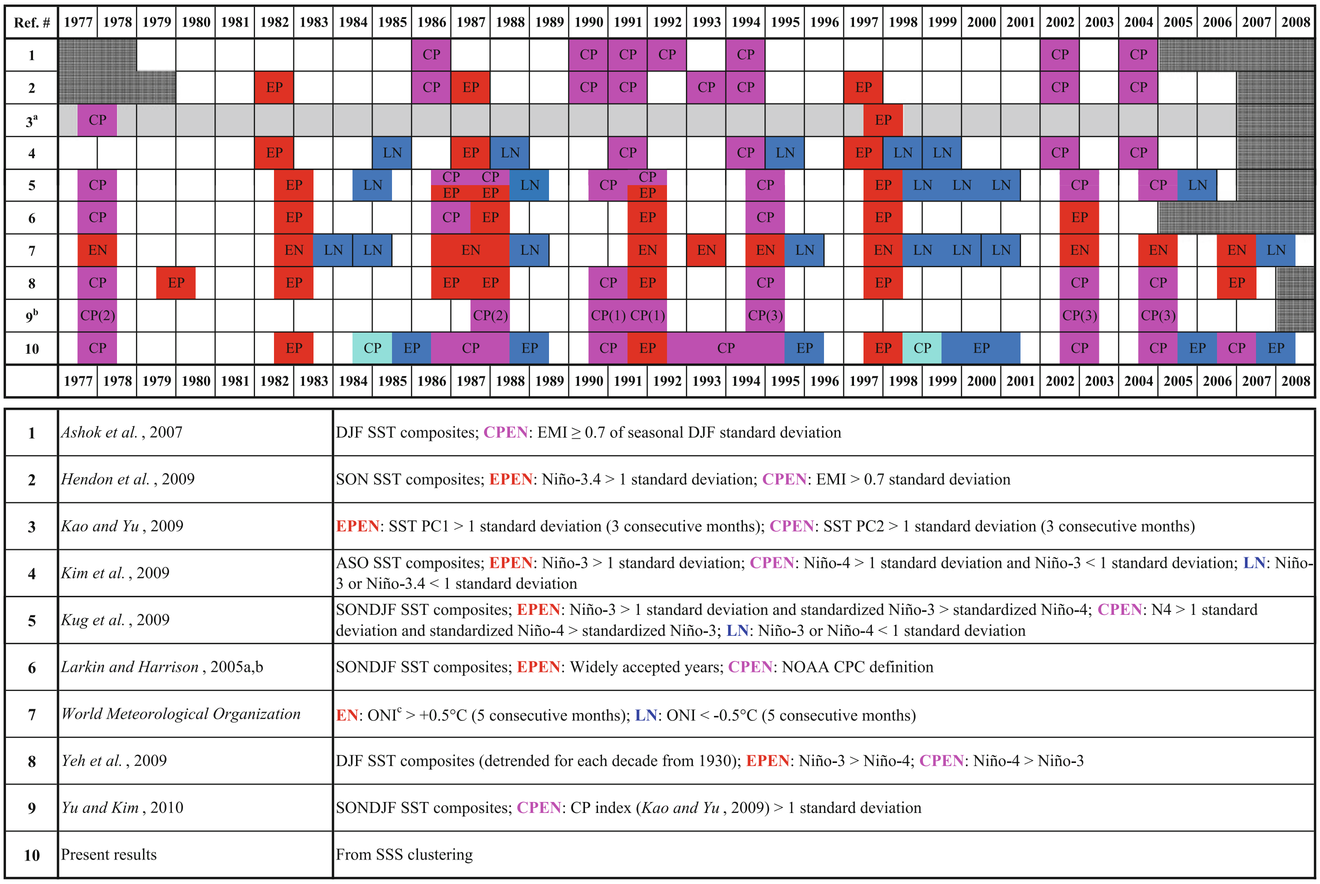
flavors is a difficult exercise, depending on the method used, and noting that some years may even be classified as “mixed events”.



Ref. #	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
1	▨	▨								CP				CP	CP	CP		CP								CP		CP	▨	▨	▨	▨
2	▨	▨	▨			EP				CP	EP			CP	CP		CP	CP			EP					CP		CP			▨	▨
3[a]	CP	░	░	░	░	░	░	░	░	░	░	░	░	░	░	░	░	░	░	░	EP	░	░	░	░	░	░	░	░	░	▨	▨
4						EP			LN		EP	LN			CP			CP	LN		EP	LN	LN			CP		CP			▨	▨
5	CP					EP		LN		CP EP	CP EP	LN		CP	CP EP			CP			EP	LN	LN	LN		CP		CP	LN		▨	▨
6	CP					EP				CP	EP				EP			CP			EP					EP			▨	▨	▨	▨
7	EN					EN	LN	LN		EN		LN			EN		EN	EN	LN		EN	LN	LN	LN		EN		EN		EN	LN	
8	CP		EP			EP				EP	EP			CP	EP			CP			EP					CP		CP		EP		▨
9[b]	CP(2)										CP(2)			CP(1)	CP(1)			CP(3)								CP(3)		CP(3)				▨
10	CP					EP		CP	EP	CP		EP		CP	EP	CP			EP		EP	CP	EP			CP		CP	EP	CP	EP	
	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008

1	*Ashok et al.* , 2007	DJF SST composites; **CPEN**: EMI ≥ 0.7 of seasonal DJF standard deviation
2	*Hendon et al.* , 2009	SON SST composites; **EPEN**: Niño-3.4 > 1 standard deviation; **CPEN**: EMI > 0.7 standard deviation
3	*Kao and Yu* , 2009	**EPEN**: SST PC1 > 1 standard deviation (3 consecutive months); **CPEN**: SST PC2 > 1 standard deviation (3 consecutive months)
4	*Kim et al.* , 2009	ASO SST composites; **EPEN**: Niño-3 > 1 standard deviation; **CPEN**: Niño-4 > 1 standard deviation and Niño-3 < 1 standard deviation; **LN**: Niño-3 or Niño-3.4 < 1 standard deviation
5	*Kug et al.* , 2009	SONDJF SST composites; **EPEN**: Niño-3 > 1 standard deviation and standardized Niño-3 > standardized Niño-4; **CPEN**: N4 > 1 standard deviation and standardized Niño-4 > standardized Niño-3; **LN**: Niño-3 or Niño-4 < 1 standard deviation
6	*Larkin and Harrison* , 2005a,b	SONDJF SST composites; **EPEN**: Widely accepted years; **CPEN**: NOAA CPC definition
7	*World Meteorological Organization*	**EN**: ONI[c] > +0.5°C (5 consecutive months); **LN**: ONI < -0.5°C (5 consecutive months)
8	*Yeh et al.* , 2009	DJF SST composites (detrended for each decade from 1930); **EPEN**: Niño-3 > Niño-4; **CPEN**: Niño-4 > Niño-3
9	*Yu and Kim* , 2010	SONDJF SST composites; **CPEN**: CP index (*Kao and Yu* , 2009) > 1 standard deviation
10	Present results	From SSS clustering

Fig. 4.39 (EN) (in *red* and *pink*) and La Niña (LN) (in *blue* and *turquoise*) events as defined by the various authors. *EP* Eastern Pacific, *CP* Central Pacific. The acronym DJF stands for December-January-February. *Dark hatched boxes* show that the period was not analyzed by the respective authors. *Light hatched boxes* show that the period was analyzed but the authors did not classify the events. See Singh et al. [508] for references to original papers (From Singh et al. [508])

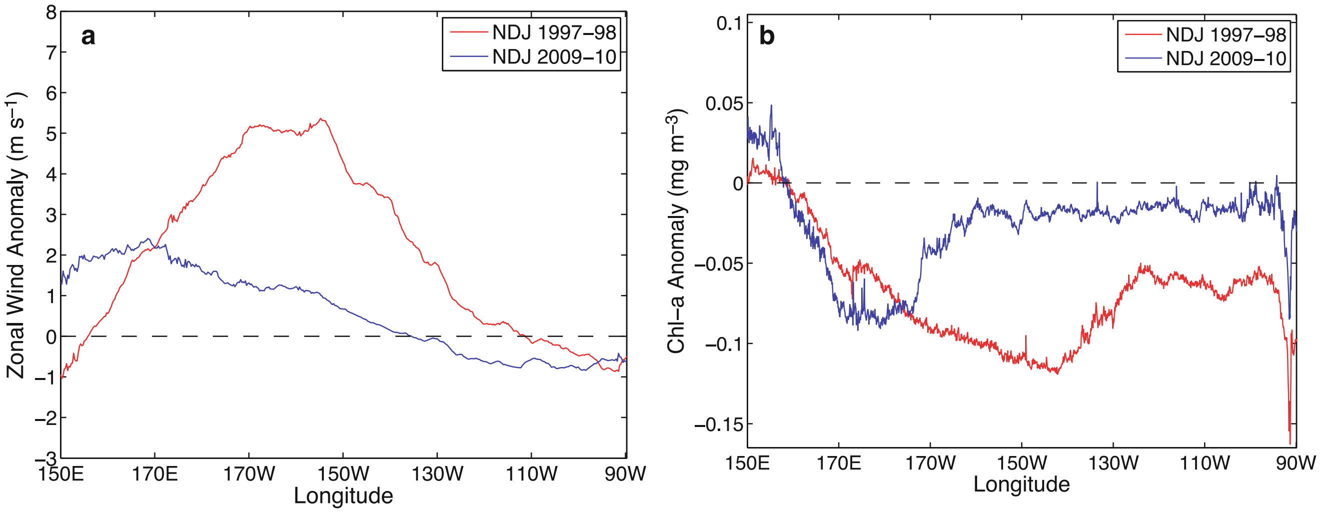


Fig. 4.40 November-December-January 5° S–5° N averaged **(a)** CCMP zonal wind anomaly **(b)** SeaWiFS chlorophyll *a* anomalies in the Pacific (see EEP and CEP areas in Fig. 4.38) during the 1997–1998 EP-El Niño (*red line*) and the 2009–2010 CP-El Niño (*blue line*). Anomalies were calculated as the difference between the individual monthly means and the mean monthly climatology over 1997–2010 (From Gierach et al. [183]). In (a) positive wind anomalies indicate winds from the west

by stronger advection of nutrient depleted waters from the western equatorial Pacific associated with westerly wind anomalies and eastward surface currents [183].

4.2.1.2 ENSO Climate Indices

There are a number of climate indices of El Niño – Southern Oscillation variability. The various ENSO indices include Nino 1+2, Nino 3, Nino 3.4/Oceanic Niño Index (ONI), Nino 4, Trans-Niño Index (TNI), Multivariate ENSO Index (MEI), Bivariate EnSo Time series (BEST), the Southern Oscillation Index (SOI), and the Northern Oscillation Index (NOI). When an author reports that an ENSO index was used in their analysis it is fair to ask which index was used.

The Nino 1+2, Nino 3, Nino 3.4, Nino 4,[20] and Trans-Niño Index (TNI)[21] constitue the Niño SST indices. The ONI is a smoothed Nino 3.4 time series so it is also a Niño SST index. These indices are calculated from surface temperatures in the equatorial Pacific between 0.5°N and 0.5°S, except for Nino 1+2 which is calculated for 0–10°S. Each of the indices is calculated using SST from a different meridional range: Nino 1+2 (90–80°W), Nino 3 (150–90°W), Nino 3.4/ONI (170–120°W) and Nino 4 (160°E-150°W).

An ENSO event (El Niño or La Niña) is considered to occur when selected smoothed climate indices (Niño SST indices) exceed threshold values for 3–5 months. For example, NOAA defines an El Niño as a positive ONI anomaly of 0.5 °C, persisting for 5 consecutive overlapping 3-month periods. For La Niña, a negative ONI anomaly of -0.5 °C must persist for 5 consecutive overlapping 3-month periods.

Not all of the climate indices of El Niño – Southern Oscillation reflect conditions in the region of the California Current during ENSO events. There may also be a significant time lag between the appearance of El Niño conditions and the level of an index in equatorial waters and the appearance of related conditions in the California Current System.

4.2.1.3 ENSO and Geographic Shifts in Assemblages

The El Niño of 1997–1998 had a major effect on the fish community assemblages of the Southern California Bight, as indicated by changes in the species of fishes collected from a wide range of sources [300]. Changes in fish assemblages with changes in temperature had earlier been reported by Hubbs (1948) [226], and with the warming associated with the 1957–1958 El Niño event by Radovich [453], although the impact of ENSO was not recognized at the time. Lea and Rosenblatt [300] reported northern range shifts of 29 families of eastern Pacific tropical (Panamic biogeographic region) fishes into southern Californian waters during the 1997–1998 El Niño. These included new records of species not recorded for almost a century, corroborating the physical evidence that the 1997–1998 event was unusually intense. Surface temperature at the Scripps Institution of Oceanography pier spiked up to 19.55 °C during this El Niño compared to an 82-year mean of 17.0 °C [300]. The authors speculated that many arrivals would have been as ichthyoplankton, or juveniles perhaps associated with flotsam, but that larger fishes may have arrived simply by swimming in suitable water masses. They also suggested that the faunal changes observed during the 1997–1998 El Niño might provide a glimpse of the types of changes in fish assemblages that could occur with warming due to climate change.

4.2.1.4 ENSO and Small Pelagic Fish

Although Fiedler et al. [162] found no consistent relationship between El Niño and recruitment of anchovy in a 17-year record covering three El Niños, their analysis of growth, mortality, spawning distribution and egg production showed that the 1982–1983 Eastern Pacific El Niño had a negative effect on anchovy. The study showed that the effect of this El Niño on anchovy was pervasive, affecting the growth, mortality, size-at-age, fecundity, spawning distribution and the movements of the juveniles and adults. Growth was 47 % slower on average for the 1982 and 1983 year classes during El Niño compared to the 1978–1981 year classes [162]. Both adults and juveniles were smaller by as much as 10–25 mm in El Niño years [162]. Fecundity was lower in 1983 and 1984 compared to 1980–82, and this was attributed to smaller female size-at-age [162]. Lower fecundity did not translate directly into lower egg production due to the interaction between spawning biomass and year class strength that compensated for lower fecundity in 1983. Smaller anchovy moved into the nearshore (shallower than 100 m) Southern California Bight from the south during the 1982–1983 El

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[20] According to a National Center for Atmospheric Research (NCAR) web page (http://climatedataguide.ucar.edu/guidance/nino-sst-indices), these values are computed by following: (a) Calculate the area-averaged total SST from Niño X region; (b) Compute a monthly climatology (e.g., 1950–1979) for area averaged total SST from Niño X region, and subtract the climatology from the area averaged total SST time series to obtain anomalies; (c) Smooth the anomalies with a 5-month running mean; (d) Normalizing the smoothed values by its standard deviation over the climatological period.

[21] According to a National Center for Atmospheric Research (NCAR) web page (http://climatedataguide.ucar.edu/guidance/nino-sst-indices), the TNI computation follows: (a) Compute the area averaged total SST from Niño 1+2 region; (b) Compute area averaged total SST from Niño 4 region; (c) Compute monthly climatologies (e.g., 1950–1979) for area averaged total SST from Niño 1+2 region, and Niño 4 region, and subtract climatologies from area averaged total SST time series to obtain anomalies; (d) Normalize each time series of anomalies by their respective standard deviations over the climatological period; (e) Define the raw TNI as Niño 1+2 normalized anomalies minus Niño 4 normalized anomalies; (f) Smooth the raw TNI with a 5-month running mean; (g) Normalize the smoothed TNI by its standard deviation over the climatological period.

Niño, while larger anchovy moved north and west of Point Conception.

In contrast to anchovy, sardine appear to recruit more successfully in El Niño years. Changes in the distribution and abundance of sardine in Pacific northwest waters off Oregon and Washington have been attributed partly to El Niño. Emmett et al. [149] reviewed reports of catches of sardine in the northwest and reported that while there were commercial catches during 1935–36 in Oregon and in 1937 in Washington, there were generally few sardine caught in the northwest from the 1940s through the 1980s. Sardine numbers then surged in 1992, possibly due to the El Niño of 1991–1992 [193], and they continued to increase in abundance and to spawn in the Pacific northwest. The change in sardine abundance was associated with changes in the entire small pelagic fish community [149]. The 1992 resurgence may not be entirely due to El Niño because there were El Niños in 1957–1958, 1965–1966, 1972–1973, 1977–1978, 1982–1983 prior to 1992, and none resulted in resurgence of sardine in the Pacific northwest. While most of these dates spanned the period of low sardine stock size, the population was recovering rapidly in the early 1980s and yet there was no response in the northwest to the strong Eastern Pacific El Niño of 1982–1983. A possible explanation is that El Niño may not have a detectable effect on the sardine until a population threshold is exceeded.

It was thought that during warm years, such as during El Niño,[22] the spawning habitat of sardine moved further north along the U.S. west coast [3, 42, 149, 317, 374, 514]. Spawning of sardine is generally associated with isotherms of 14–15 °C [149] and sometimes, but not always, shifts northward of San Francisco in El Niño years [66]. Sardine eggs and larvae dominated the ichthyoplankton in the Pacific northwest (off northern Oregon and Washington) in June/July 1994 to 1998 [149]. Presence of juvenile sardine (age-0) in Pacific northwest waters in fall 2003 and 2004 indicated successful spawning in the northwest [317], and high densities of eggs were also reported in 2006 [149]. However, although spawning of sardine does occur in the Pacific northwest, it appears to comprise only a small fraction of spawning along the west coast of North America. For example Lo et al. [317] reported that egg production from the Pacific northwest was only 1.5 and 2.2 % of the total sardine egg production in 2003 and 2004 respectively. Northern spawning of sardine is not just associated with El Niño in the Pacific northwest, but there is somewhat inconclusive evidence for sardine recruitment during El Niño years [149].

The spawning biomass and spawning habitat of sardine vary considerably between years [320, 468, 580] and El Niño/Southern Oscillation (ENSO) events are known to have an important influence, although the mechanisms were not well understood. The strongest ENSO contrast between sardine egg densities, during the period for which CUFES egg data[23] are available (1997 – 2012), was observed between the 2002 La Niña and the 2003 El Niño [66]. Spawning habitat area was larger and daily egg production was lower during the 2002 La Niña compared to the 2003 El Niño [526]. Similarly, spawning habitat area was an order of magnitude larger [468], and daily egg production was lower [66] during the 1999 La Niña compared to the 1998 El Niño.

However, ENSO does not always drive a big contrast in sardine egg abundance. During the 2006 El Niño and 2007 La Niña, the ocean states showed significant differences, but densities of sardine eggs were not as dramatically different compared to the 2002–2003 ENSO transition. During La Niñas in April 2002 (0204LN) and 2007 (0704LN), equatorward winds were stronger than normal (Fig. 4.41). Stronger equatorward winds forced stronger than average upwelling, causing a negative sea surface temperature (SST) anomaly [184, 499]. In contrast, under the influence of the Central Pacific El Niños in April 2003 (0304EN) and 2006 (0604EN) [184, 508], the wind patterns over the North Pacific were anomalously cyclonic, which caused weaker than normal equatorward winds. As a result of weaker than average upwelling, 0304EN and 0604EN showed a warm SST anomaly [184, 567].

Figure 4.41 plots the wind stress and positive wind stress curl during two ENSO contrasts (0204LN, 0304EN, 0604EN and 0704LN). The direction of the wind stress is equatorward along the coast in all periods, but the intensity of the wind stress varies. Equatorward wind drives offshore transport through Ekman transport in the California Current System. The offshore transport is positively proportional to the equatorward wind stress, hence one can expect that anomalous upwelling favorable wind drives more offshore transport.

The averaged offshore transports in the upper 30 m across the black line (approximately 300 km from the coast) in Fig. 4.42 for 0204LN, 0304EN, 0604EN and 0704LN were $-1.2 \times 253\ 10^{-3}$Sv, -0.7×10^{-3}Sv, -0.6×10^{-3}Sv and -1.5×10^{-3}Sv, respectively (negative values represent offshore direction). Thus, anomalous upwelling favorable wind during La Niña conditions results in more offshore transport, and the upwelled nutrient-rich water can be transported further offshore providing a good spawning habitat for sardine. The offshore transport, however, cannot be directly responsible for the horizontal distribution of eggs. Eggs are usually hatched in 72–96 h after spawning in 12–14 °C water [327], so they can travel less than 70 km within a 0.2 m s^{-1} current.

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[22] Note that 2005 was also an anomalously warm year in the northern California Current System with delayed wind-driven upwelling [497]. Conditions were close to ENSO-neutral (Bivariate ENSO index) for much of the year, so warm years are not just associated with ENSO events.

[23] See Sect. 3.1.4

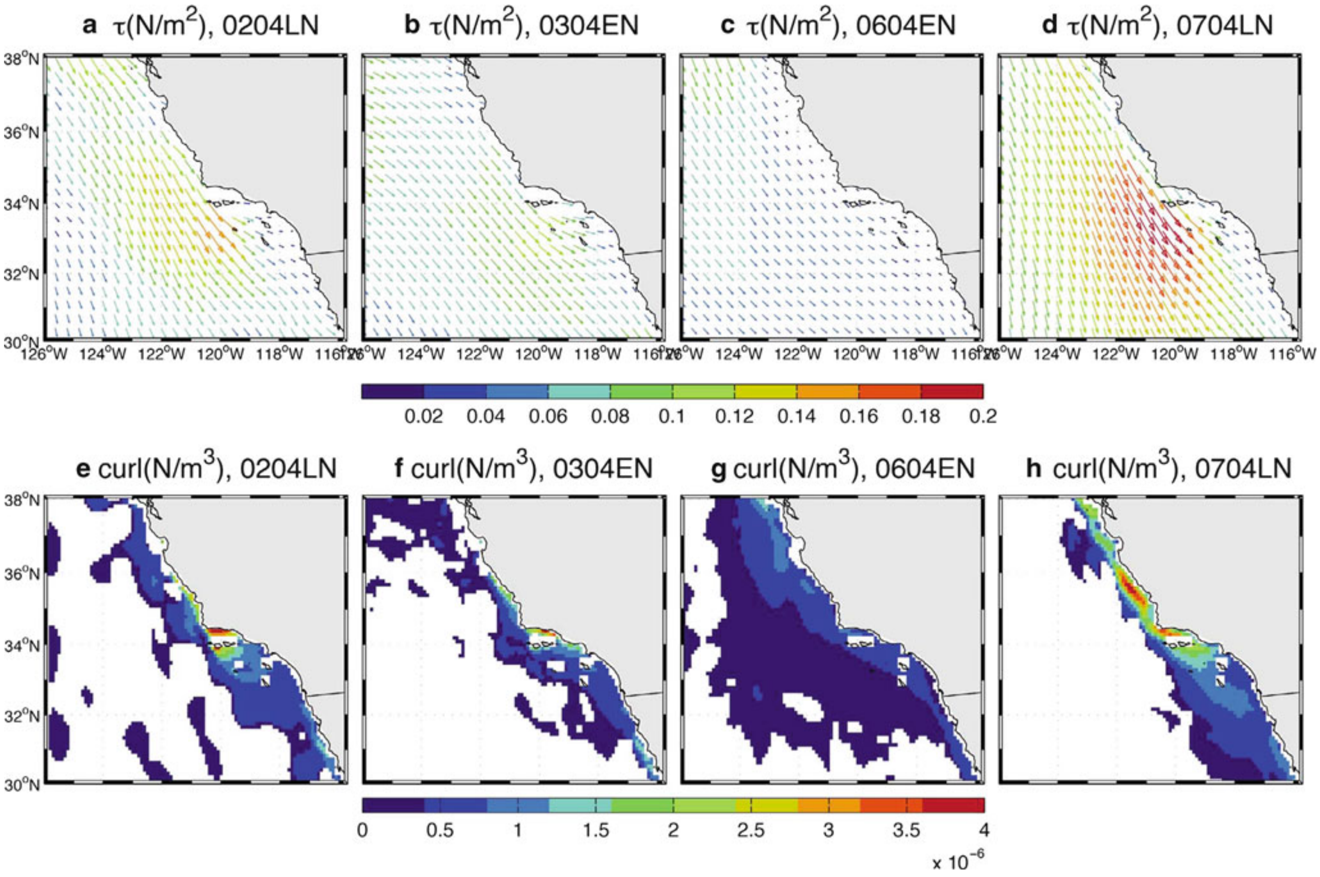

Fig. 4.41 (**a**–**d**) Wind stress and (**e**–**h**) wind stress curl averaged over two El Niños and two La Niñas after data assimilation. In panels (**e**–**h**), only positive values of wind stress curl are plotted in order to indicate the areas of upwelling by Ekman pumping. Codes are year month ENSO, so 0204LN is 2002 April La Niña (From Song et al. [526])

For comparison, the offshore CalCOFI stations are about 74 km apart. From this it is inferred that what was observed is the result of stronger offshore transport in La Niña conditions moving the spawning habitat offshore rather than just moving the eggs. The wind moves the eggs, but they are present only for a short time and so the greater movement is due to a shift in the favorable spawning habitat for the adult fish.

Using either CalCOFI or ROMS data, Weber and McClatchie's [580] spawning habitat model predicted that there would be higher probability of occurrence of sardine eggs during the 2003 and 2006 El Niños, which is consistent with the observations showing higher egg densities (more than 100 eggs m^{-3}) in those years (Fig. 4.43). Spawning habitat model [580] predictions using the CalCOFI surveys (Fig. 4.43, left) clearly show higher probability of occurrence of eggs off southern California during the 2003 and 2006 El Niños with maximum values higher than 0.5, indicating that spawning habitat was better than average in those periods. The predictions using the ROMS data set (Fig. 4.43, right) also show higher probability of occurrence of sardine eggs off southern and central California in the 2003 and 2006 El Niños, which is consistent with the predictions generated from the CalCOFI data. Song et al. [526] inferred from their results that predictions of high probability of occurrence of eggs reflect the potential spawning habitat rather than the actual spawning habitat that will be used by the adult sardine in any given year.

In summary, the "broadening" or "extension" of preferred spawning habitat offshore due to increased wind-driven offshore transport was seen in 2002 and 2007 under La Niña conditions. In 2003 under El Niño conditions, the preferred spawning habitat was not as broad as in other periods, but the spawning habitat was better based on a higher probability of occurrence of sardine eggs. Good spawning habitat was predicted in the 2006 El Niño, but the spawning habitat was not limited to the regions near the coastal areas, partially due to the open water upwelling.

Biological communities do not respond in the same way to each El Niño-La Niña transition. As seen in this study, the responses of the sardine spawning habitat are not the same between 2002–2003 and the 2006–2007 ENSO contrasts. In the 1997/99 transition, there was a huge shift toward sub-tropical communities in the SCB due to advective processes [100, 104, 300], but advection of water masses

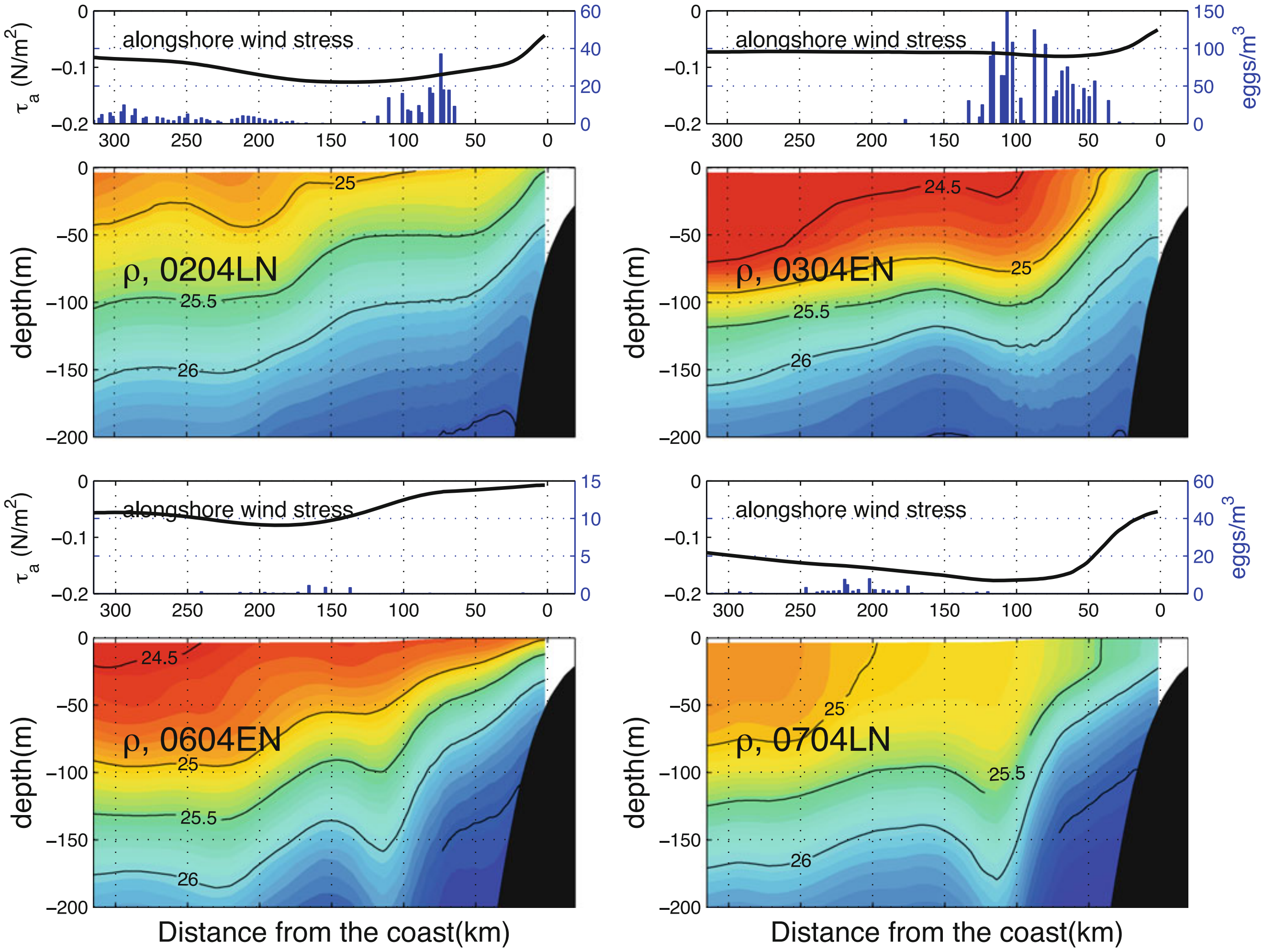

Fig. 4.42 Along-shore wind stress (*black solid lines*), sardine egg counts (*blue bars*) and density (*filled contour*) from the surface to 200 m depth along CalCOFI line 76.7 (Fig. 1.4). The values for wind stress are negative, meaning equatorward, and the egg counts are plotted with different scale. Areas with positive wind stress curl are indicated with *red*, though the saturation of the color does not represent the degree. Codes are year month ENSO, so 0204LN is 2002 April La Niña (From Song et al. [526])

was less apparent in 2009/2010 [559]. Thus the sardine egg distribution may differ between ENSO transitions and the factors controlling sardine spawning behavior are not yet fully understood.

4.2.1.5 ENSO and Market Squid

The market squid, *Doryteuthis* (formerly *Loligo*) *opalescens,* fishery off southern and central California is highly variable and catches have declined to as little as 10 % of the catch quota during El Niño events [247, 568]. The quota was established at 118,000 tons in 2005 by the Fishery Management Plan [26]. Ish et al. [243] suggested that reduced squid catches during El Niño events [360] could be due to reduced krill densities, since krill can make up as much as 65 % of the diet of market squid [259]. However, their theoretical model did not explain the reduced catches in El Niño years, just the effect of variation in a principal prey item, based on the dependence of squid growth rates on prey availability [243]. Reiss et al. [469] emphasized the effect of temperature on the growth rate of squid paralarvae in the month after hatch to explain the effect of El Niño, rather than focusing on the effect of prey availability on the adults. Reiss et al. [469] argued that "monthly mean temperature and mortality rates show that small differences in either [temperature or mortality] create conditions sufficient to rapidly affect the population size."

Subsequent work by Zeidberg et al. [595] showed the "squid landings decreased substantially following large Eastern Pacific El Niño events in 1982–1983 and 1997–1998, but not following small El Niño events of 1987 and 1992" (neither of which are easily classified as either Eastern Pacific or Central Pacific El Niños). Reiss et al. [469] had obtained a different result from Zeidberg et al. [595] for 1992, noting a steep drop in market squid catches in the SCB, but not in Monterey Bay, in that El Niño year. Market squid recover quickly after El Niño-related crashes, especially in

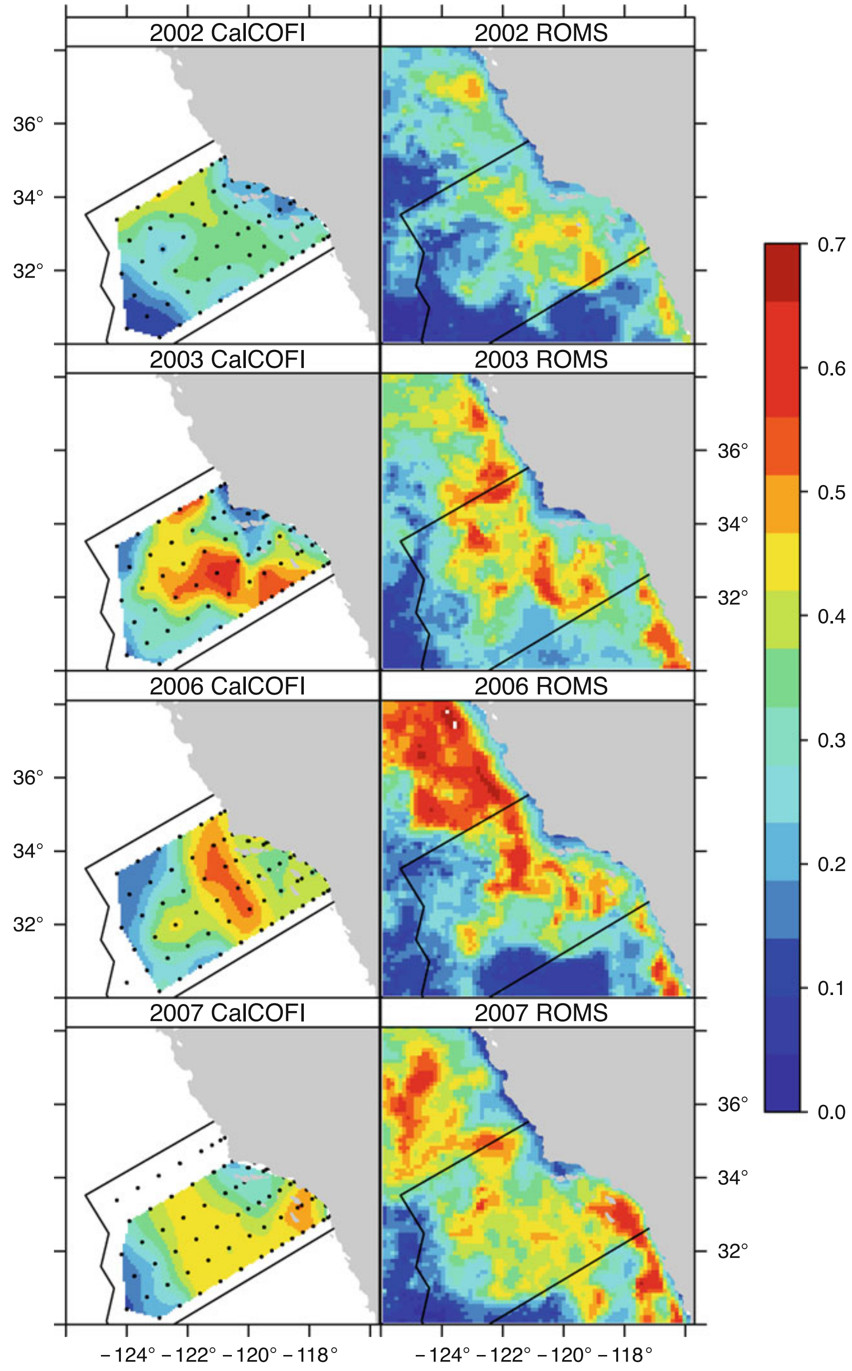

Fig. 4.43 Spawning habitat model [580] predicting the probability of occurrence (0.0–1.0) of sardine eggs in 0204LN, 0304EN, 0604EN and 0704LN. Codes are abbreviated year, month, ENSO phase, so 0204LN is 2002 April La Niña. (*Left panel*): Generated using data from 6 core transects of the CalCOFI surveys as predictors (*black dots* show station positions). (*Right panel*): Environmental variables from the ROMS model were used as predictors in the statistical model. *Red areas* indicate the highest probability of occurrence of sardine eggs (From Song et al. [526])

southern California [243]. However, the rate of recovery has differed between years. Zeidberg [596] reported that “the fishery recovered within 2 years after the large El Niños in 1983 and 1998, but was much slower to recover in Monterey following the small El Niño in 2003”. Market squid are an annual species, with reported lifespan varying from 6–9 months [92, 595] to a maximum of 12–18 months [246, 528]. There is no reserve stock to support recovery following a population crash, so their resilience appears somewhat paradoxical. Despite the lack of a reserve stock which Zeidberg et al. [595] suggested could lead to vulnerability to overfishing, the population can increase orders of magnitude in a few generations during periods of rapid growth [469]. As a result the recovery of the population following El Niño is well within the biological capability of market squid [469].

There is some evidence that squid landings off Monterey Bay, California are positively correlated with warmer than average temperatures 18 months earlier [383]. In contrast, Zeidberg et al. [595] presented data showing a negative

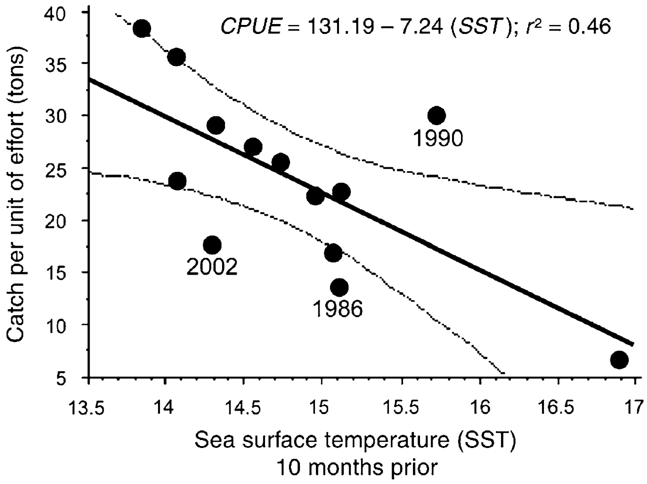

Fig. 4.44 Relationship between catch per unit effort of market squid in November and sea surface temperature during the previous January in the nearshore region off Los Angees (From Zeidberg et al. [595])

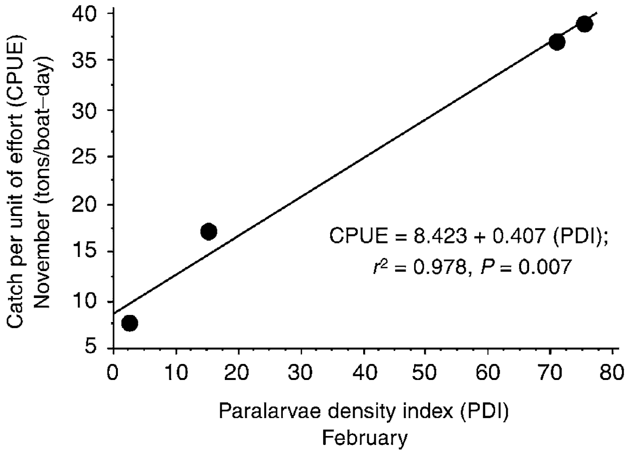

Fig. 4.45 A tantalizing relationship between market squid paralarval density in February and catch per unit effort for the spawning adults in November. Years are 2000–2003 and data were collected from an area approximately surrounded by the Channel Islands, but extending close inshore in the Southern California Bight (From Zeidberg et al. [595])

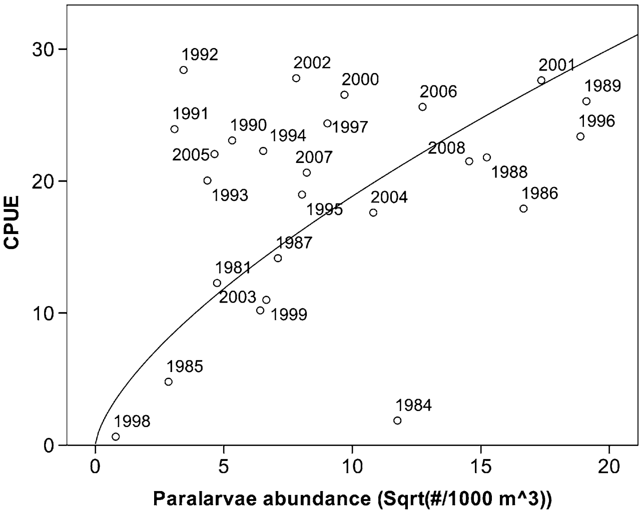

Fig. 4.46 Relationship between catch per unit effort (*CPUE*) of market squid and square root-transformed mean paralarval abundance in the Southern California Bight (From Koslow and Allen [273])

relationship between CPUE of market squid in November and sea surface temperature 10 months earlier (in the previous January) (Fig. 4.44). The 10-month lag corresponds to the time for market squid to become reproductively mature [595]. Koslow and Allen [273] used a principal components analysis followed by stepwise regression to show that mean paralarval abundance could be predicted from one principal component of local environmental variability plus indices of ENSO and the PDO [273]. Temperature and nitrate concentration at 10 m depth, followed by an index of upwelling and oxygen concentration at 10 m contributed most to the principal component. The loading for temperature on the first principal component was negative, consistent with the negative correlation reported by Zeidberg et al. [595]. Koslow and Allen's analysis [273] shows that it is difficult to separate the correlated effects of environmental variables on the abundance of paralarvae. Other *Loligo* spp. (off the U.K., South Africa and Spain) have also been reported to show stronger cohorts, higher landings or more abundant paralarvae correlated with anomalous temperature or upwelling, with the nature of the relationship varying between species and regions (see studies cited in [595]).

Zeidberg et al. [594, 595] found much lower paralarval densities in the SCB in both a "weak" El Niño (2002) and a "strong" La Niña (1999) year, compared to 2000 and 2001. The relationship between mean paralarval densities and market squid catch per unit effort (CPUE)[24] is not yet established in Californian waters. Zeidberg et al. (2006) collected data over 5 years (1999–2003) and fitted a linear regression to 4 points, after excluding the data for 1999, which were from the same areas as the other years, but lacked the sampling nearest to shore (Fig. 4.45). The relationship is tantalizing but should be considered preliminary until it can be tested with more data. However adding more data does not seem to improve the relationship between paralarval abundance and CPUE. Koslow and Allen [273] plotted mean paralarval abundance (January–May) as a function of CPUE (December–April), but the data are highly variable; it is difficult to discern any relationship other than a weak, positive correlation (Fig. 4.46). The reasons for the highly variable relationship between paralarval abundance

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[24] Zeidberg et al. [595] refer to this rather loosely as a "stock recruitment relationship" although CPUE is only a coarse proxy for the biomass of market squid, as they explain in their paper, and they do not measure recruitment.

and CPUE have not been determined, but the imprecision of CPUE estimates, commonly mentioned in the previously cited studies, is likely to be an important contributing factor. Suggestions that the paralarval index can be used to predict market squid CPUE, and to manage the fishery by predicting recruitment the following year, thereby aiding the setting of catch limits [273, 595] is hopeful, but premature at this stage.

4.2.2 Recruitment Dynamics and Environment

McFarlane et al. [374] presented a case for the dominant effect of environment on the recruitment of fishes. They stated that "most fisheries scientists now believe that a fish's environment and changes to that environment play a more important role [… than effects due to fishing]". While this undoubtedly overstates the case, it appears to be closer to the truth for small pelagic fishes than for long-lived demersal fishes like cowcod (*Sebastes levis*) [93], for example. In the case of sardine, environmental effects can lead to reduced numbers of cohorts due to poor year classes, which preceded recruitment failures and rapid reductions in stock sizes, as in the Japanese sardine ([213] cited by [374]). The decline of the California sardine population in the 1940s was associated with a reduction from ten reproductive cohorts to two reproductive cohorts ([411] cited by [374]) due to poor recruitment, to which was added the effects of heavy fishing mortality. Since it is the larger sardine that perform the seasonal migration, loss of the larger cohorts meant the fish could not take advantage of the more productive feeding grounds, ranging from northern California to Vancouver Island. Restricting the range of the population to less productive waters could have affected the resilience of the population [374]. Zwolinski and Demer [597] found some similarity between the condition of the sardine population in 2010–11 and conditions in the 1940s and 1950s when the population was collapsing and the seasonal migration ceased.

Several hypotheses have been put forward to explain recruitment success in sardine off California. One focused on the role of cyclonic mesoscale eddies as survivor habitat for late stage larvae and possibly also juvenile sardine. Another hypothesis focused on how climatic regime shifts affected the suitability of habitat for sardine. Regime shifts were thought to create conditions that were either favorable or unfavorable to sardine recruitment on decadal time scales. The effects of fishing were overlaid on the long-term climatic effects of the environment. A third hypothesis focused on the role of stability and turbulence in creating favorable conditions for early life history stages to grow quickly and survive to recruit. At the time of writing, our current understanding provides a more nuanced view of these hypotheses (see Sects. 4.1.3.3 and 4.2.2.1), but has not revealed any single dominant mechanism controlling sardine recruitment.

4.2.2.1 Mesoscale Eddies and Sardine Recruitment

Understanding of the role of eddies in sardine recruitment is still limited, and the interesting hypothesis that eddies can enhance recruitment of sardine [329–331] is currently unproven. The studies of Logerwell et al. were focused on understanding what constitutes larval survivor habitat, namely the environmental conditions that favor rapid larval growth and high survival. The absence of correlation between recruitment success (recruits per spawner) and spawning stock biomass of anchovy ([330] attributed to [447]) suggested that density-independent environmental effects (rather than density-dependent effects) played a key role in determining recruitment. Similarly for sardine, recruitment was only related to spawning stock at low biomass, and there was no relationship between reproductive success and spawning stock biomass in sardine [250]. Supporting the line of evidence that environmental effects have a great effect on recruitment, Jacobson and MacCall [250] found a positive relationship between a proxy for environmental conditions (the Scripps pier temperature index) and the reproductive success of sardine (but see Sect. 6.1.1.8). Eddies were thought to be an important source of environmental variability that could influence recruitment success.

To date about half a dozen papers have been written on how mesoscale eddies (diameters $> 50\,\text{km}$) affect the distribution and abundance of early life history stages of fish, and their recruitment success off southern California. Studies in the California Current System focused primarily on the effects of eddies on sardine and anchovy [161, 329–331], hake [330], rockfish larvae [547], or the larval and juvenile fish assemblage [418] and subsequent recruitment. It is likely that mesoscale activity has implications for a broad range of species and life history stages.

Eddies can have both positive and negative effects on fish recruitment, as demonstrated by studies in the California Current and other regions. Negative effects include advective transport away from favorable areas for recruitment [161, 171], or succession of the eddy community to one dominated by predators of fish larvae [584], while positive effects are due to enhancement of production providing food resources for larval growth [329, 331]. The effect of eddies on fish depends on the type of eddy and on the time scale for persistence of the feature. Several types of eddies are found in the California Current System. These include fixed eddies that are associated with bathymetric features such as headlands [282], large seasonally intensified recirculation such as the Southern California Eddy, and westward propagating anticyclonic and cyclonic eddies with quite widely varying spatial dimensions [112]. There are several studies documenting increased chlorophyll and zooplankton concentrations in both cyclonic and anticyclonic eddies in the California Current System [198, 443, 477, 507]. Such enrichment could indicate enhanced food availability for larval fish. Logerwell and Smith [331] pointed out the "the large spatial and temporal scale of mesoscale eddies - hundreds of kilometers and hundreds of days [268] - suggests that these features could be large and persistent enough to provide habitat for the 50 day duration of the sardine's larval stage [96]". More recent studies show that the spatial scale of mesoscale eddies is generally smaller than "hundreds of kilometers", but the persistence of larger eddies can certainly be "hundreds of days" [532] (and K. Nieto, unpublished).

The initial work by Logerwell and Smith [330] was largely speculative because the physical data in particular was inadequate to characterize the spatial field of mesoscale variability. They also restricted their analysis to the distribution of large larvae (18.5 mm), because these are survivors, but larvae this large can avoid the plankton nets used to collect the samples [323]. Subsequent work [331] included a day-night ratio correction for escapement of different sized sardine larvae from the nets and modified the larval survivors to be sardine larvae $\geq$ 8.75 mm[25] instead of just the largest larvae, which helped to overcome problems with the earlier larval dataset. Logerwell and Smith (2001) [331] also used remotely-sensed SST gradients above selected thresholds that resembled rounded eddy-like features to define the presence of eddies (i.e. they excluded linear frontal features and filaments).[26] Their work showed that sardine survivors were notably more dense in the core CalCOFI area, both inshore and offshore. The number of survivors was highest in the offshore region, but it was also high in the inshore regions of the Southern California Bight and the southern central California coast [331]. In contrast, the eddies were most common in the offshore region of the core CalCOFI area (which is approximately the "eddy alley" region referred to by Lynn and Simpson [339]). Both chlorophyll and zooplankton displacement volume was greater in the inshore regions, but Logerwell and Smith attributed survival of larvae in the offshore to the presence of eddies that were "expected to produce localized increases in primary and secondary production" [331]. Importantly, Logerwell and Smith [331] noted that their long-term averages of numbers of survivors were biased by four (out of 17) surveys with exceptional numbers of survivors in the offshore habitat. They suggested that "offshore regions may be best characterized as an intermittent habitat producing relatively high numbers of survivors, and the inshore regions as consistent habitat producing moderate numbers of survivors" [331].

Sardine eggs commonly occur near the inshore side of the California Current which is a long distance (more than 150 km) from shore [105, 514] (see Sect. 2.4.1). Adult sardine have been caught more than 450 km outside the 66-station CalCOFI pattern [347]. Offshore eddies were thought to be an important, if rather stochastic, survival habitat for juvenile sardine [329–331]. MacCall (2009) [345] argued that meanders and fronts developing with slower current flow sustain the survival and production of late larval and juvenile sardines. More recent remote sensing work indicates that both may be partly correct in that both cyclonic and anticyclonic eddies entrain streamers of more productive upwelled water, and sardine larvae are more commonly found in the enriched part of the eddies where the meanders have been entrained by the rotation (K. Nieto, SWFSC, in preparation).

The hypothesis that enrichment in eddies is beneficial to larvae assumes that food limitation is important [331]. Early work indicated that starving anchovy larvae [424] and jack mackerel larvae [549] were common off southern California. Laboratory studies on anchovy also indicated that anchovy could not survive at the mean concentration of their food off southern California [233, 288, 289]. Logerwell and Smith admitted that "the current evidence is equivocal regarding eddies as areas of increased sardine prey" [331]. Logerwell et al. [329] followed up on these ideas with a bioenergetic model to estimate sardine pre-recruit growth potential off southern California. They estimated that growth potential was 11–12 % per day in inshore, slope and eddy regions, but was a little lower (9 %) in the offshore region. When the growth potential was multiplied by numbers of larvae found in the eddies (using the same dataset as [331]) the potential production in the eddy was an order of magnitude greater than in other regions. The eddies that appeared to increase sardine larval production were cyclonic according to this modeling study. Rather surprisingly, the postulated effect of these eddies is less due to enhanced growth in conditions of higher production and more due to the higher abundance of sardine larvae in cyclonic eddies [329]. We recall that

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[25] This size threshold was chosen to reflect the size at which larvae are expected to begin schooling behavior, on the assumption that aggregated larvae were those that had occupied suitable habitat and experienced lower mortality than the dispersed early larvae. For the analysis Logerwell and Smith (2001) simulated a Poisson distribution with the same mean as the frequency distribution of larvae (for all surveys combined and for each survey) and then selected larval densities of 8.75+ mm sized larvae that were more abundant than the maximum density from the simulated Poisson distribution (i.e. those larval densities that were considered non-random).

[26] To test the association between larvae and eddies at small scales Logerwell and Smith (2001) selected surveys where more than 10 larvae were caught (17 of 56 surveys) and compared the median density of larvae at stations in eddies and away from eddies using a Mann-Whitney U-test. To test the relationship between survivor abundance and environmental conditions including eddies Logerwell and Smith (2001) divided the survey area into regions, calculated the mean sardine survivor density, egg density, 10 m temperature, chlorophyll *a*, and zooplankton displacement volume for 1983–1998 and eddy density for 1987–1998, and tested for difference between regions using ANOVA.

the earlier study showed that larval densities in eddies were only intermittently higher (4 of 17 cruises). The results are intriguing, but await further study to fully understand how important eddies are for small pelagic fish recruitment. At the time of writing, it is not yet possible to say whether mesoscale features like eddies enhance sardine recruitment or not.

4.2.2.2 Small Pelagic Fish Spawning Habitat

The spawning ground of the sardine currently lies to the west of the Santa Rosa Ridge outside the Southern California Bight, and off the central California coast south of San Francisco (Fig. 4.47). In the 1970s and 1980s, sardine spawned mostly within the Southern California Bight. The anchovy, by contrast, spawned mainly within the Southern California Bight since the mid 1990s. A modern pattern of sardine and anchovy spring and summer distributions was obtained in 2008 (Fig. 4.48). However, there is considerable inter-annual variability in the distribution of spring-spawned small pelagic fish eggs in relation to sea surface temperatures (SST), as shown by data form 1997 to 2012 (Fig. 4.47). The commonly held view of spawning distribution by species has sardine spawning near the eastern edge of the California Current, jack mackerel spawning further offshore, and anchovy spawning nearshore and off central California and Point Conception, in association with wind-driven, coastally upwelled water. There is some acceptance that the center of sardine spawning shifts north in warmer than average years. Additionally, the timing of spawning differs between species, where the northern "stock" of sardine spawn primarily in the spring between March–May, but the anchovy spawn from late winter through spring (January–May). The timing of sardine and anchovy spawning appears to have shifted and narrowed over the CalCOFI sampling period. NMFS and CalCOFI cruises that repeatedly covered the area from San Diego to San Francisco during March–May 1997–2012, admittedly with variable transect spacing and transect lengths, allow us to examine hypotheses about species-specific habitats, the relationship between sardine habitat and temperature anomalies, and to some extent even the timing of spawning.

Comparing years[27] shows that the generalized patterns of egg distributions by species needs qualification. First, jack mackerel do not always spawn further offshore than sardine. Some jack mackerel spawned inshore of sardine in 2000 and 2009, and in 2005 and 2007–2008 their spawning overlapped with the spawning of sardine (Fig. 4.47). Jack mackerel spawned south of the sardine spawning center in 1997, 2000, 2002–2004, and 2006 (Fig. 4.47). Second, anchovy spawning is not always associated with coastal upwelling areas. While anchovy generally did spawn inshore, in 2005–2008 their spawning extended well into the nearshore Southern California Bight south of Point Conception where there is little wind-driven upwelling (Fig. 4.47). Interestingly, anchovy eggs were nearly absent from the spring survey in 2010 and 2011. Third, sardine spawning does not necessarily shift northwards in warmer years. Between 1997–2004 sardine spawning extended strongly northward into the central California region between Point Conception and San Francisco, and in 2004 it was restricted to this northern area. But from 2005–2009 the distribution of sardine spawning was south of Point Conception. In 2010 it again moved north of Point Conception. The north–south–north shift of the sardine spawning along the coast does not appear to be related to warm or cold years, since both the northern and southern spawning distributions encompassed both warm and cool years (Fig. 4.47). The patterns that are briefly described here need to be quantified, and are the subject of current research.

4.2.2.3 Spawning Habitat Models for Small Pelagic Fish

Parrish et al. [441] developed an hypothesis relating sardine and anchovy spawning to environmental variability that was really the precursor to later modeling studies. His study grew out of the International Recruitment Experiment hypothesis that "the biological responses to environmental conditions are similar for separate stocks of closely related species" [441]. Stocks were expected to have a similar functional response to any given environmental variable, but the limiting environmental variable might well be different for different stocks. They identified six variables that were thought to account for most of the biological variability in small pelagic fishes. The variables were temperature, turbulence, transport, food, predation and population density [441]. Of these, temperature, turbulence and transport were considered to be more readily measured and therefore available for use in real-time management applications [441]. Parrish et al. [441] thought that temperature did not have much influence on spawning habitat, as long as the temperature was within the range of physiological tolerance. If temperatures were beyond physiological tolerance, spawning would be precluded, but otherwise temperature would have little influence on reproductive habits [441].

In contrast to temperature, Parrish et al. [441] considered that both turbulence and transport were highly influential on small pelagic fish spawning. Based on data from different eastern boundary current systems, they concluded that spawning of sardine and anchovy was associated with minima in the cube of the wind speed, which is an index of wind-driven turbulence generation in the water

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[27] During spring cruises from 1997 to 2012 fish eggs were collected from 3 m depth with the Continuous Underway Fish Egg Sampler (CUFES), manually identified and counted, and converted to densities (eggs m^{-3}). Sea surface temperature (SST) imagery were gridded to the same resolution [579], and densities of sardine, anchovy and jack mackerel eggs were overlaid on the SST (Fig. 4.47).

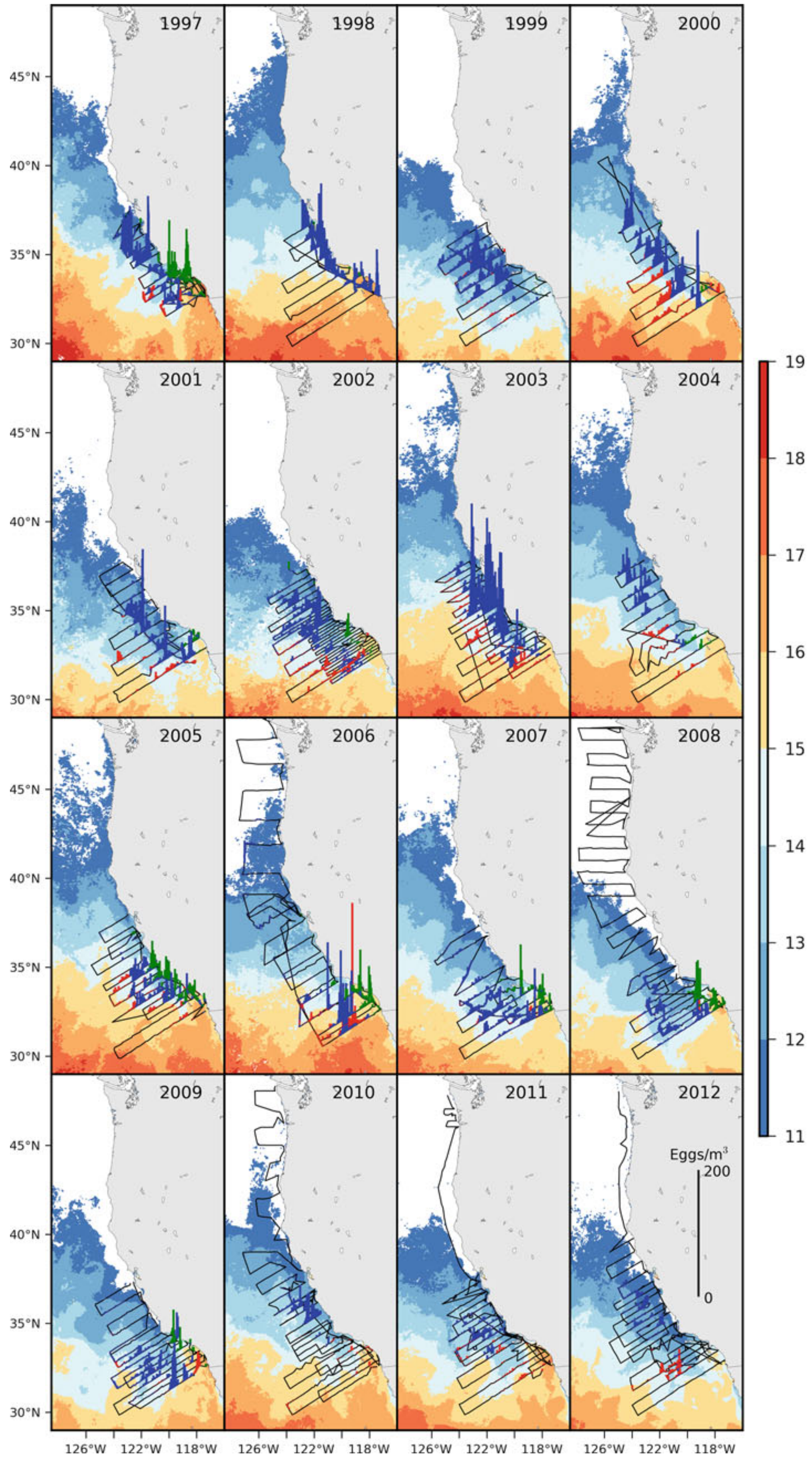

Fig. 4.47 Density of eggs of sardine (blue), anchovy (*green*), and jack mackerel (*red*) collected with the Continuous Underway Fish Egg Sampler (see Sect. 3.1.4) overlaid on satellite sea surface temperatures (°C) derived from a monthly composite of April AVHRR Pathfinder imagery (1997–2008) and a blended SST product (2009–2012). Ship track is shown by the *black line* (Courtesy of Ed Weber, SWFSC)

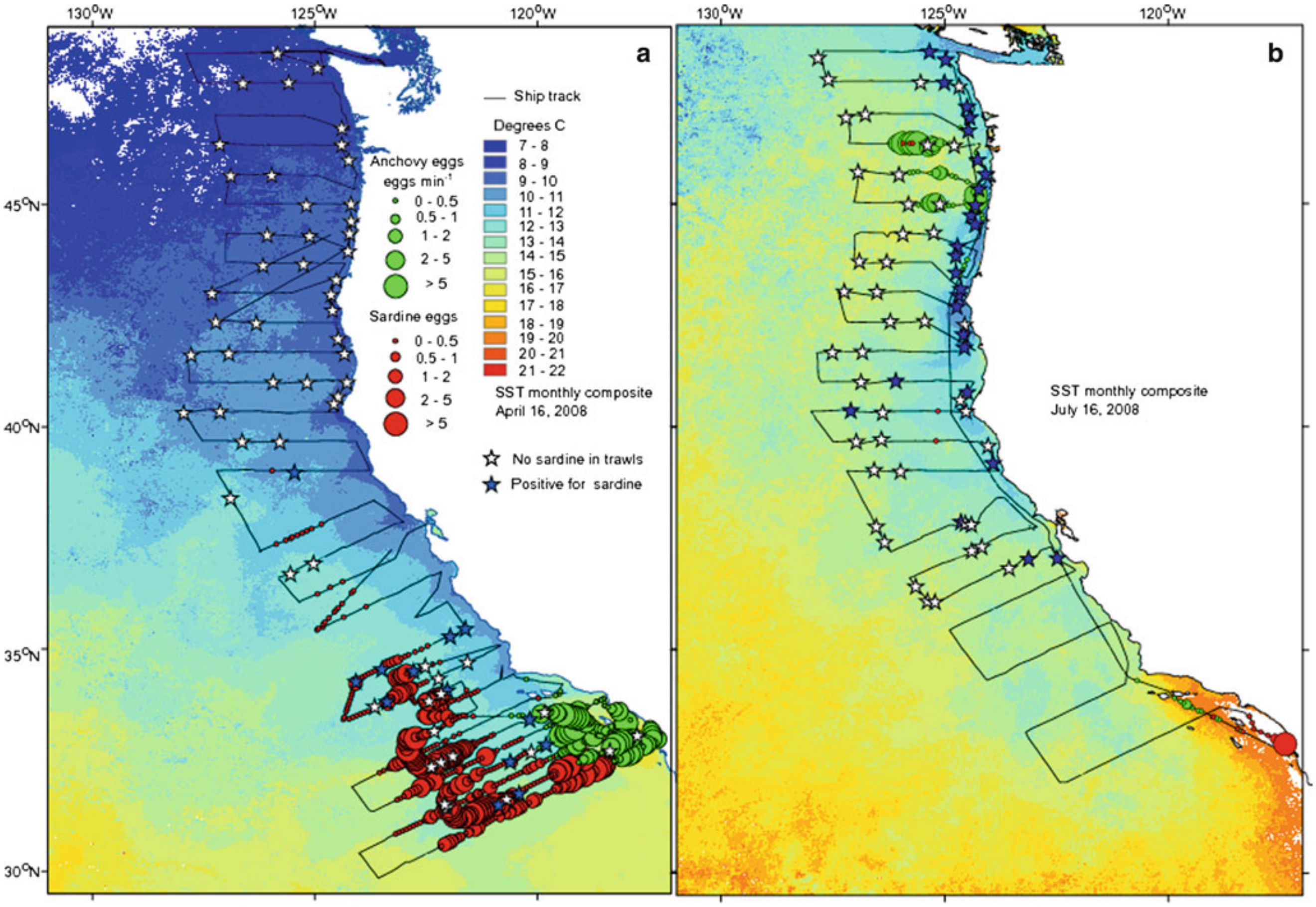

Fig. 4.48 Classic modern pattern of sardine eggs spawned in spring off southern California, followed by movement of the adult fish northwards in the summer where they are found closer to shore. No sardine eggs were observed north of San Francisco in this La Niña year. (**a**) March 24–May 3, 2008, (**b**) July 6–August 20, 2008. Eggs were measured using CUFES (Sect. 3.1.4), trawls collected by the Nordic surface trawl (Sect. 3.1.3.1), and the data are overlaid on a monthly composite of sea surface temperature

column [235]. They also argued that spawning of sardine and anchovy was minimal in areas with strong wind-driven Ekman transport that drives offshore transport [441]. To some extent these variables are confounded in that strong upwelling favorable winds driving offshore transport also tend to mix the water column and break down stratification. Significantly, Parrish et al. [441] stated that “no single feature has overriding control”, and that this also applies to other less easily measured variables of food, predation, and population density.

The first modeling studies sardine or anchovy spawning habitat described the habitat limits in terms of temperature and a measure of production, such as either chlorophyll [159,468] or zooplankton concentrations [335]. Lluch-Belda et al. [316] used temperature and substituted upwelling rate as a proxy for production. Early work with CUFES suggested that sardine and anchovy spawning might be separated by different ranges of temperature and salinity [105] (see Sect. 3.1.4 and Fig. 3.8). For all of these studies there was sufficient unexplained variance that Weber and McClatchie (2010) considered that there might be other explanatory variables that would improve the predictability of spawning habitat [580].

In recent years several statistical models of sardine and anchovy spawning habitat have been published [32,580,599]. These models predict the potential spawning habitat rather than the actual habitat where eggs are found in any given year. They cannot predict the habitat from which successful recruitment originates. As such they provide guides for optimizing sampling, and this was a justification for their development [580, 599]. In reality, the vertical net tow (Pairovet) sampling is adjusted empirically on surveys where CUFES samples are collected and eggs are counted at sea. Additional net tow stations are added when the sardine egg collection rate by CUFES exceeds a threshold (see Sect. 3.1.4). Nevertheless, the near real-time maps derived using remote sensing data showing the probability of occurrence of sardine eggs derived from the Zwolinski et al. [599] spawning habitat model have proven very useful as a guide in cruise planning (Fig. 4.49). The equation developed by Weber and

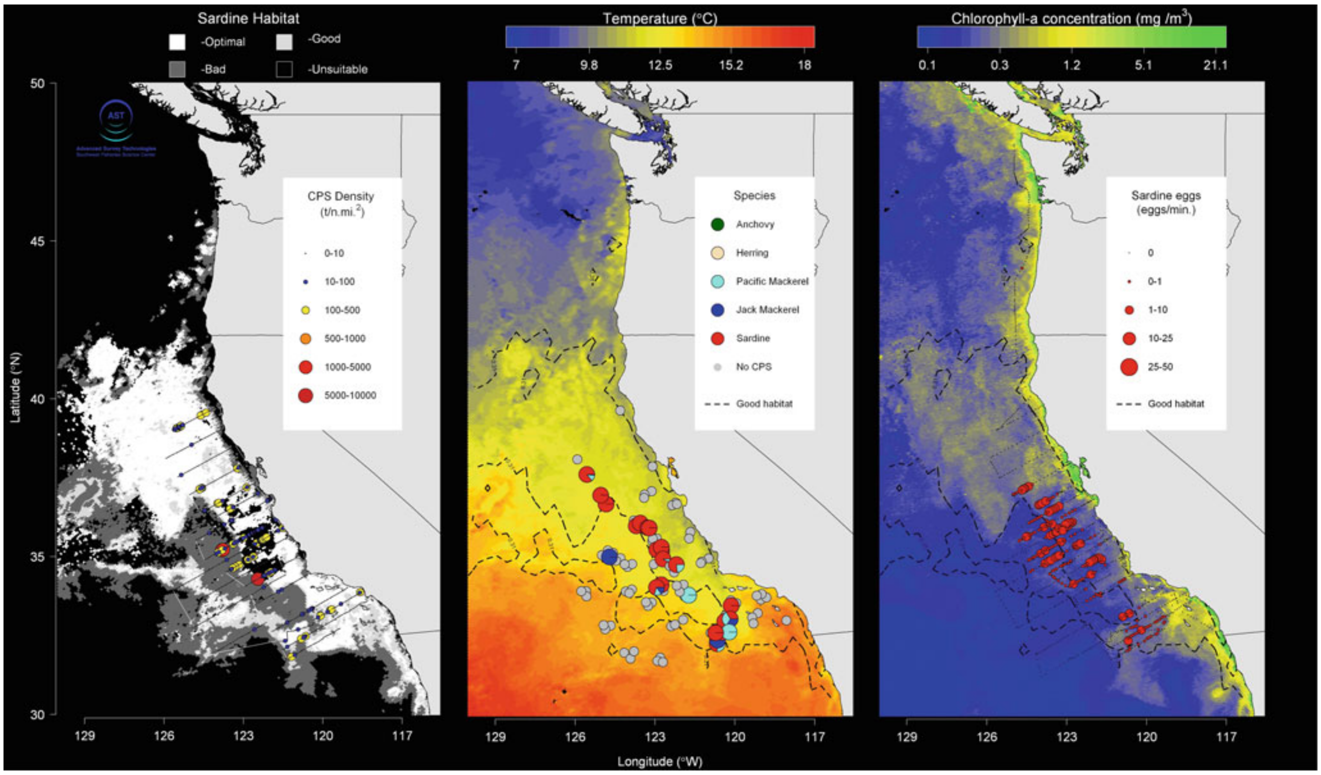

Fig. 4.49 (*Left panel*): Potential sardine spawning habitat during the spring 2012 coast-wide survey with the acoustic biomass of sardine, anchovy and mackerel (labeled CPS) derived from acoustic/trawl data overlaid. (*Center panel*): SST composite from remote sensing overlaid with the abundance of small pelagic fish species derived from acoustic/trawl data. (*Right panel*): Ocean color composite derived from remote sensing overlaid with the abundance of sardine eggs collected in CUFES. This is an example of a real-time map produced during the cruise and data are classed as preliminary at that stage (From Zwolinski et al. [599])

McClatchie [580] does not provide near real-time predictions of spawning habitat, but it has been used in conjunction with ROMS models to extrapolate and interpolate the probability of occurrence of sardine eggs beyond the survey domain by predicting habitat over the model domain (Fig. 4.43) [526].

Weber and McClatchie [580] aimed to develop their model with the longest possible dataset, and for this reason they used egg counts from the CalCOFI oblique bongo net tows collected during 1984–2009. The earlier data were not used because chlorophyll was only sampled after 1984. The model was developed to include potentially important predictors related to the vertical structure of the water column, to horizontal movement of the eggs, primary production and productivity, temperature and salinity. The models were constrained to include variables that could be measured remotely, specifically with gliders in mind, and to include only variables with an hypothesized mechanistic relationship to spawning habitat, apart from a correlation, as for instance with distance from shore. Further, the models were required to be both parsimonious and biologically meaningful [580].

Weber and McClatchie [580] used seven predictor variables to model presence and abundance of anchovy and sardine eggs. They were mean chlorophyll *a* concentration ($\mu g\ l^{-1}$) in the upper 50 m of the water column, depth (m) at which the maximum chlorophyll *a* concentration occurred, mean water temperature (°C) in the upper 50 m, mean salinity (PSU) in the upper 50 m, an index of geostrophic flow, day of the year, and an estimate of the species' stock size the previous year. They used average temperature and salinity in the upper 50 m of the water column because this is the depth range where sardine and anchovy larvae are found [126].[28] The two chlorophyll-related predictors were used in an attempt to incorporate the effects of primary production which is a standing stock (units of mass volume^{-1}) and an index of primary productivity which is a rate (units of mass volume^{-1} time^{-1}). They used depth of the chlorophyll maximum as an index of primary productivity based on the concept that the chlorophyll maximum is shallower when productivity is high and nutrients are sufficient, but deepens progressively through the spring season as phytoplankton balance their need for light and nutrients [357]. They assumed that sardine and anchovy would spawn in areas where primary productivity had continued long enough to support high secondary production, but not so long that productivity

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[28] Ahlstrom [6] found sardine and anchovy larvae in the upper 90 m, but 80–90 % of them were in the upper 50 m.

was low due to light and nutrient limitation.[29] An index of geostrophic flow was included in the model by calculating the slope across dynamic height contours [580].

The logistic model of a two-phase Generalized Additive Model provided the best predictions of spawning habitat of sardine and anchovy because the densities of the eggs are extremely patchy which produced high variance in the second-stage abundance model [580]. The models were more successful at predicting anchovy egg presence (Area Under Curve, or AUC=0.86) than sardine egg presence (AUC=0.77) [580].

The variables predicting spawning differed between sardine and anchovy. Anchovies were most likely to spawn in highly productive areas, increasing with increasing chlorophyll concentrations in the range of 0 to 4 μg l^{-1}. Anchovy continued to spawn in the highest chlorophyll regions and when the depth of the chlorophyll maximum was shallow. The probability of spawning decreased rapidly at water temperatures $<$ 14°C but was relatively stable between 14 and 18°C. Salinity was positively related to the probability of spawning, and spawning was most likely to occur in areas with relatively high geostrophic flow, which generally occurred near the shoreline [580]. The addition of depth of the chlorophyll maximum and geostrophic flow as predictors to the anchovy spawning habitat model provided much greater predictive power than the model described by Reiss et al. [468].

Sardine spawning habitat could be modeled on the basis of chlorophyll, temperature, salinity, and stock size in the previous year. This result is similar to earlier findings by Checkley et al. and Lynn [105,335]. Depth of the chlorophyll maximum and geostrophic flow were not useful in the sardine spawning model, in contrast to anchovy. As for anchovy, the probability of capturing sardine eggs increased with chlorophyll concentration in the range of 0 to 4 μg l^{-1}, but unlike anchovy, sardine eggs were never captured at higher chlorophyll concentrations caused by phytoplankton blooms. One might speculate that the sardines' finer gill rakers might be more readily clogged by phytoplankton blooms, which might cause the sardine to avoid areas with phytoplankton blooms. Sardine eggs were more likely to be found at all locations when stock sizes were higher the previous year (perhaps not surprisingly) [580].

Each of the three spawning habitat models use different variables to predict the probability of presence of eggs. Zwolinski et al. [599] use the probabilities to classify sardine spawning habit as unsuitable, bad, good, or optimal based on satellite SST, chlorophyll derived from satellite ocean color and the gradient in sea surface height derived from satellite altimetry. Single and multivariable habitat models were constructed by fitting a generalized additive model (GAM) to predict the presence of sardine eggs derived from CUFES, sea surface temperature (SST), chlorophyll (CHL), sea surface height, a measure of the gradient of sea surface height (GRAD), and the CUFES sampling interval (CSI) [599]. Zwolinski et al. [599] addressed the problem of spatial autocorrelation in the CUFES data by decimating the along-transect data to greater than the known de-correlation length scale prior to fitting the models.

Zwolinski et al.'s [599] models showed that sardine egg presence was more clearly related to temperature and chlorophyll than to sea surface height or gradient. The final model was: $ln(\hat{p}/1-\hat{p}) = te(SST, ln(CHL)) + te(GRAD, ln(CHL)) + s(CSI)$, where $\hat{p}$ is the predicted probability of occurrence of eggs, *te* and *s* are tensor product and single dimension smoothers respectively, and the other variables are defined above. The final model only contains the gradient of sea surface height rather than sea surface height. Spawning stock biomass was not significant when included in the model, which differs from the model of Weber and McClatchie [580]. They suggested that the inshore limit of spawning was associated with cooler, freshly upwelled water with high chlorophyll concentrations, and that the offshore limit of spawning was associated with warmer, low chlorophyll water. Egg occurrence was greatest between 11.5–15.5 °C and 0.2–3.2 mg chlorophyll *a* m^{-3}, but most eggs were found between 13 and 14 °C [599]. This temperature range for spawning off California was similar to the findings of earlier work [105, 249, 335, 468]. In the temperature range 12–14.5 °C, most eggs were found at moderate chlorophyll concentrations between 0.3–1 mg chlorophyll *a* m^{-3} [599], as found by Reiss et al. [468]. Avoidance of high chlorophyll areas by spawning sardine is also consistent with Weber and McClatchie [580].

An alternative approach to that taken by Weber and McClatchie [580] and Zwolinski et al. [599] is to find a suitable proxy for multiple environmental forcing variables, rather than modeling the variables directly. Asch and Checkley [32] found that dynamic height (relative to 500 m) is a very useful and neglected proxy of sardine spawning habitat and that elevated dynamic height was associated with warmer temperatures, lower chlorophyll, reduced zooplankton volume, lower salinity, and slower geostrophic currents.

Asch and Checkley [32] based their analysis on oblique bongo net samples of sardine, anchovy and jack mackerel eggs and concurrent hydrographic profiles collected on spring cruises over the 113-station CalCOFI pattern between 1998 and 2004 [32]. These authors state that "This [1998–2004] period was sufficient for capturing inter-annual variability in egg distribution, including extreme events observed during El Niño and La Niña." [32]. However, 6 years is

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[29] A reasonable alternative approach when the glider time series is long enough (it is currently only 6–8 years long) would be to revise the model using integrated acoustic backscatter at 420kHz as a direct proxy for secondary production.

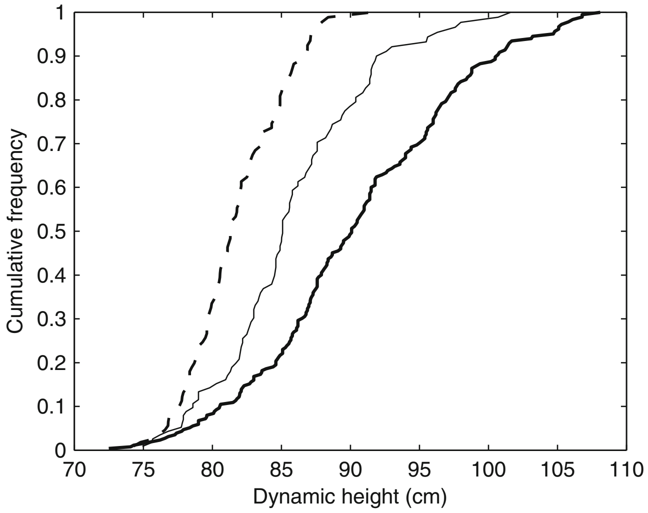

Fig. 4.50 Cumulative distribution functions (CDFs) of the dynamic heights across which the eggs of anchovy (*dashed line*), Pacific sardine (*solid line*), and jack mackerel (*thick*, *solid line*) were observed during April 1998–2004. Kolmogorov–Smirnov tests indicate that all empirical CDFs were significantly different from each other (From Asch and Checkley [32])

less than 10 % of the length of the CalCOFI time series at the time of publication, and is almost certainly not sufficient to characterize the variability in egg distributions including extreme events. Cumulative frequency distributions indicated that anchovy, sardine, and jack mackerel eggs were disproportionately located in discrete ranges of dynamic heights, 78–86 cm, 79–88 cm, and 84–99 cm, respectively.[30] During most years, the distribution of sardine eggs with respect to dynamic height peaked at intermediate dynamic heights between the maximums for anchovy and jack mackerel eggs. This fits the traditional model that anchovy are found nearer to shore than sardine, jack mackerel are generally found further offshore, and the general species-specific distributions of eggs in relation to dynamic height were different (Fig. 4.50). However, Asch and Checkley [32] noted exceptions to this pattern in 2000, 2002, and 2003 (and see Sect. 4.2.2.2).

The proxy effect of dynamic height on the distribution of small pelagic fish eggs was well illustrated by Asch and Checkley's [32] models. They first presented single variable Generalized Linear Models (GLMs), and found that dynamic height had the strongest effect on the distribution of eggs. Then they modeled all of the potential explanatory variables in a combined step-wise model along with dynamic height. They found that "The influence of dynamic height on sardine egg distribution could be completely accounted for by other oceanic variables in the stepwise GLM, causing dynamic height to become non-significant when added last to this model" [32]. Furthermore, "In models of all species, temperature, salinity, chlorophyll, and their interactions collectively accounted for 80–95 % of the dynamic height effect" [32]. If we have measurements of both proxy variables and of variables that are directly related to mechanisms determining spawning habitat (as we do from CalCOFI), it is preferable to use the variables most closely related to mechanism. However, in the absence of such measurements, Asch and Checkley's [32] work demonstrates that dynamic height is a very useful proxy variable. Considerable effort has gone into research on small pelagic fish habitat, and how the environment affects the habitat, but the relationship between habitat and recruitment is still elusive.

4.2.2.4 The Recruitment Bottleneck

The recruitment of small pelagic fishes is highly variable, and the effect of this variability on populations is affected by the lifespan, such that longer lived fishes can tolerate higher recruitment variability and still persist. Smith [515] reported that recruitment of anchovy varies 30-fold, recruitment of sardine varies 60-fold, and recruitment of hake varies 100-fold. This high variability in recruitment contrasts with recruitment of Dover sole (*Microstomus pacificus*) which varies less than 10-fold ([85] cited in [515]). A consequence of this high variability is that the frequency distribution of recruitments is far from normal, and the calculation of mean recruitment over a time series is generally not representative. The distribution of annual recruitments is dominated by years with recruitment far less than the mean (about 25 % or a quarter), and years with recruitment far greater than the mean (about 200 % or double). The default recruitment for any given year is essentially recruitment failure. Relatively fewer years produce extremely good recruitments, and these allow the population to persist as the cohorts from strong recruitment years grow through the age classes [515].

Hjort [214, 215] firmly established the paradigm that year class strength in fish is established by early life history mortality. Lasker expanded on this idea by proposing the "stable ocean hypothesis" [288, 290, 291, 293]. He considered that turbulent mixing conditions would lead to a poor year class of anchovy. The mechanism envisioned was that periods of low wind were necessary for density stratification in the water column to form. Dense aggregations of prey would develop, associated with density interfaces created by stratification. Anchovy larvae would be able to meet their bioenergetic demands for growth by exploiting these prey aggregations. Faster growing larvae would be in better condition, and suffer less mortality from predation, so a greater number of larvae would survive to recruitment. Laboratory work showed that anchovy and mackerel larvae

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[30] Asch and Checkley (2013) reported that "Spring observations of dynamic height in the southern CCE ranged between 68 and 108 cm. Reflecting the equatorward flow along the California coast, low dynamic heights (75–80 cm) were usually observed nearshore, while high dynamic heights (95–105 cm) occurred offshore" [32].

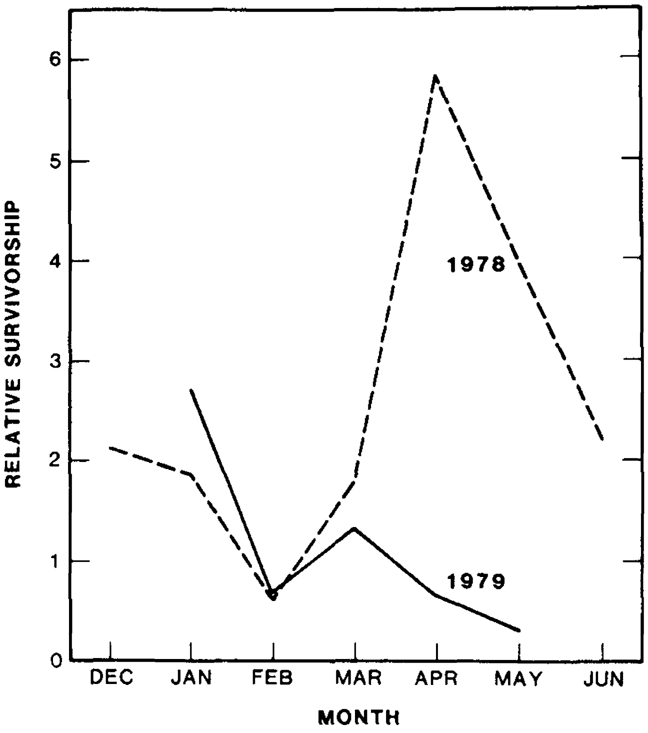

Fig. 4.51 Relative survivorship is the ratio of the fraction anchovy juvenile's birthdates to the fraction of annual larval production per 30 day. To enable comparison between years the relative survivorship for 1978 has been scaled by the ratio of recruitment (2.0) and the ratio of annual larval production (0.98) between the 2 years (From Methot [390])

were susceptible to starvation-induced changes in condition in the sea [548, 549]. The lab results supported the idea of food-limited growth and survival of young fish larvae in the sea. However, subsequent reviews of the literature [304, 364] and studies by Peterman et al. [446, 447] on anchovy found little support for an early critical period controlling recruitment.

Methot [390] added a twist to the recruitment puzzle when he compared monthly juvenile anchovy survivorship with the distribution of their birth dates. He examined the juvenile anchovy abundance collected in eleven CalCOFI surveys between December 1977 and May 1979, and the distribution of birth dates of juvenile anchovy collected in nearshore trawl samples along the Southern California Bight [390]. He found that survival differed markedly between the 2 years and that there was a strong seasonal pattern in larval mortality. He calculated the distribution of juvenile birth dates, corrected for mortality, and the larval production over the season. By taking the ratio of the monthly birth date frequency to the monthly larval production, he obtained an index of larval survival relative to other months in the season (Fig. 4.51) [390]. This showed that relative monthly survivorship was moderate in January and February of both years, but that survivorship differed widely by the end of the season. Integrated from January to May, the abundance of anchovy larvae was 1.2 times higher in 1979 than in 1978 [205]. However, relative survivorship was high in April-May in 1978, but very low in April-May 1979. The 1978 year class was very strong, contributing 65 % of the California commercial catch the following season, whereas the 1979 year class was weaker, contributing only 35 % of the catch in the following season [390]. There were also spatial differences in survivorship. Juvenile anchovy distribution was contracted both spatially and temporally in 1978 relative to 1979, and the juveniles were found both further south and further offshore[31] in 1979 [205]. Methot speculated that the low survivorship of anchovy larvae late in the season of 1979 was due to stronger offshore transport associated with stronger wind-driven coastal upwelling in 1979, that prevented anchovy reaching nearshore juvenile nursery areas [390]. However Methot admitted that "it is simplistic to assume that only one factor is involved in recruitment and that the effect of this factor is linear" [390].

From an early date, there were suggestions that the numbers of surviving anchovy or sardine larvae were not correlated with recruitment, but the early studies did not draw statistically-based conclusions [7,390,512]. Hewitt and Methot [205] were unable to detect any significant difference in the mortality of larval anchovy in 1978 and 1979 based on length distributions, despite observations that seasonal survivorship was very different in the 2 years. As one of their conclusions, Hewitt and Methot (1982) wrote that "… there is reason to doubt that larval surveys alone are sufficient to consistently predict recruitment" [205].

Peterman et al. [447] performed an interesting test to determine the recruitment bottleneck for anchovy. They used 13 years of CalCOFI data (between 1965–1985) to test for correlations between the numbers of anchovy egg and larval stages and the numbers of recruits (estimated from a VPA), defined as 1-year old anchovy. Their hypothesis was that the number of recruits is correlated with the numbers of the life history stage that determines recruitment. The stage most highly correlated with the numbers of recruits, if it were unique, would constitute the "recruitment bottleneck." They found no correlation between abundance of early life stages of anchovy and anchovy recruits [447]. More importantly, there was no correlation evident between the age-1 recruits and the numbers of pre-recruits [447]. This was contrary to expectation, because their earlier work showed that 65 % of the variation in mortality of first-feeding anchovy larvae could be explained by a wind index of turbulent mixing

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[31] The mean differences in distance offshore for four cruises between January to May were only 30–60 km [205]. For comparison, the width of wind-driven upwelling off central California ranges from 15–50 km, so small cross-shelf distances can make a substantial difference in environment in some areas.

[446]. This initial study appeared to support the stable ocean hypothesis. However, from their subsequent study on the correlations between life history stages, they concluded that their results did not support the hypotheses of either Hjort or Lasker.

Peterman did find significant correlations between the numbers of eggs and the number of yolk sac larvae, as well as between yolk sac larvae and pre-recruits. However neither eggs nor yolk sac larvae were correlated with age-1 recruits [447]. They calculated instantaneous mortality rates from the abundance estimates of each life stage and concluded that mortality in the time between pre-recruits and age-1 recruits was higher than for any other life stage. Only 3.4 % of 19-day old pre-recruits were estimated to survive to become age-1 recruits [446]. Pre-recruits also had the most variable survival rate. It was almost 3 times more variable than survival from the egg to larval stage. Peterman et al. [447] reported that the variability in survival of pre-recruits destroyed any correlation between early life history stages and age-1 recruits. From these results the critical period or recruitment bottleneck for anchovy appears to be the pre-recruit stage between about day 19 and 1 year, as opposed to the early larval stage that lasts less than about 2 weeks (or 20 % of the duration of all larval stages ([230] cited by [447].).

Notwithstanding Peterman's results, it is entirely possible that there is no "recruitment bottleneck" for small pelagic fishes. For example, Bailey et al. [35] provided evidence that a critical period, or the life stage at which recruitment failure is determined, can occur at any pre-recruitment stage in walleye pollack. If this were the case for small pelagic fish, then all life history stages younger than recruits would need to be monitored to understand the drivers for recruitment variability [515]. Another possibility is that the progeny of only a small portion of the spawning stock might determine recruitment ([199, 200] cited in [515]). These aspects of recruitment await further investigation.

4.3 Seasonal-Scale Variability (1 Month–1 Year)

4.3.1 Sardine Migration

Sardine seasonally migrate along the production gradient (Sect. 2.5.4) from the Pacific coast of Mexico into southern Canada (but see Sect. 4.1.3.3). The migration was originally detected from tagging studies. Sardines tagged off southern California in the spring (February-March) were captured off British Columbia in the early summer (July) ([121,255] cited by [320]). At the same time, sardine tagged between Punta Eugenia and Punta Colonet, Baja California were recaptured off southern and central California, but did not reach the Pacific northwest ([121,255] cited by [320]). Sardines tagged off British Columbia in July and August were subsequently recovered off California, but not off Mexico, in the following December and January (see [195] and previous reports by same author, cited by [320]). This suggested the existence of distinct northern and southern sardine "stocks" on the Pacific coast, excluding the Gulf of California, that have approximately synchronous timing of seasonal migrations. These two "stocks" have different southern and northern limits to their distributions [320].

The understanding of migration is complicated by the limited understanding of stock discrimination. Smith [516] reviewed the evidence for discrimination of sardine stocks in the northeast Pacific. Summarizing the current state of knowledge, Smith (2005) wrote "The sardines … of the northeast Pacific have been referred to as three subpopulations based on tagging [120], size-at-age [158], isolated spawning centers [361], blood groups [569], vertebral column count [587], estimated natural mortality rate [252, 411], or bimodal seasons of recruitment [90]". He concluded that there was limited evidence of heterogeneity in size at age, spawning season, spawning centers, time of recruitment, blood type, and number of vertebrae. The isolated spawning centers are in the Gulf of California, in the inshore region of the southern part of the Baja California Peninsula, and offshore of southern and central California [516]. Based on these lines of evidence, Smith [516] considered that it would be precautionary to manage sardine as if there were separate stocks, despite the fact that neither genetic analyses nor other characters listed above provide a clear separation of stocks.

In most years, the northern "stock" of sardine spawn off southern California and on the central California coast as far north as San Francisco during spring (March/ April). After spawning, the larger mature fish move northwards and are generally found closer to shore, where they can exploit the higher production that develops on the shelf in the summer [320]. This classic pattern of the seasonal spawning and subsequent migration of sardine along the west coast of North America is illustrated by results from the 2008 NOAA coast-wide survey. This survey covered the entire US west coast from Mexico to Canada in both April/ May and then again in July/ August 2008 (Fig. 4.48) [366]. Sardine spawned offshore from southern and central California in April, as far north as San Francisco. Surface pelagic trawls caught adult sardine on the spawning grounds, but virtually no sardine (actually one fish) were caught north of San Francisco (Fig. 4.48). By July/ August the sardine had moved north and the surface trawls caught adult fish mainly close to shore, to the north of Cape Mendocino. No significant numbers of sardine eggs were found in these northern waters, indicating that the sardine had moved out of their actual spawning habitat.

The proportion of sardine migrating between southern California and the Pacific northwest can vary widely from year to year, and this variation may be related to year class strength [325]. Based on four surveys, Lo et al. [325] found that almost all of the sardine larger than 210 mm migrate to the Pacific northwest, but only 42–44 % of the smaller fish migrate. This means that years like 2003, with successful recruitment producing a strong year class, will be followed by a year in which a much smaller proportion of the population migrates, because the new recruits are too small [325].

Recent modeling of the spawning habitat suggests that northward expansion of favorable spawning habitat controls the arrival of the adults off Oregon [599]. It seems unlikely that expansion of potential spawning habitat could be the entire reason, because sardine seldom spawn north of San Francisco although they have migrated as far north as the inlets of Vancouver Island in summer since the mid-1990s. The assumption is that potential spawning habitat coincides with the potential habitat for the adult sardine, and so the spawning habitat model of Zwolinski et al. [599] can be used to model the northward seasonal expansion of the potential adult sardine habitat.

A south-north gradient of increasing chlorophyll concentrations occurs between the tip of Baja California and the Canadian–US border from the coast to 100 km offshore. This gradient is evident in all seasons, but is intensified in the summer (May–September) when chlorophyll levels are 0.5–1 $\mathrm{mg\,m^{-3}}$ off southern California and further south compared to $> 3\,\mathrm{mg\,m^{-3}}$ north of 45°N (approximately Newport, Oregon) [209, 301] (Fig. 2.31). It is generally accepted that the sardine move northward to exploit higher production in these areas [121, 254, 255, 317], although adult sardine are likely eating more small zooplankton than phytoplankton. The details regarding what initiates the migration are still not well known.

4.3.2 Hake Migration

Pacific hake (*Merluccius productus*), like sardine, migrate seasonally along the North American west coast to feed in more productive northern waters in the summer and to spawn in more southern waters during the late winter months [4]. Hake begin their seasonal migration in spring and early summer after spawning between January and March at depths of 100–200 m. After spending the summer further north they move offshore and southward to return to their spawning grounds off southern and central California ([36] cited by [4]). Larger fish tend to migrate further north than the smaller fish ([54] cited by [4]). The migration extends as far as the north of Vancouver Island, and the northern limit is thought to be affected by climate ([57] cited by [4]). Angostini et al. [4] considered that "the [seasonal] hake migration is motivated first and foremost by a search for food and is therefore primarily governed by factors related to food availability". Euphausiids are a primary prey for hake, and in summer large hake aggregations occur over the shelf break from Oregon to northern Vancouver Island where euphausiids also occur [4].

The relationship between hake distribution and temperature is weak [4]. The adults are found in temperatures ranging from 3.5 to 17.5 °C. In contrast, the distribution of hake appears to be related to northward current flow, perhaps because stronger northward flow aids the northward migration. Hake are found in a relatively narrow range of current velocities, mainly associated with the northward flow of the California Undercurrent [4]. Angostini et al. [4] concluded that hake distributions were associated with subsurface poleward flow and not with a specific temperature range. Years with stronger than normal poleward flow result in more small hake arriving at Vancouver Island, supporting the idea that northward flow aids migration ([141, 510] cited by [4]). A second possible advantage for hake associated with the edge of the Undercurrent is that it places the hake at the shelf edge where concentrations of euphausiids often occur [4]. Hake may have evolved to time their migration to the seasonal intensification of the Undercurrent, thereby permitting them to swim north while expending less energy, and at the same time positioning them at the shelf edge with higher densities of prey to fuel their migration [4].

4.4 Weather Scale Variability (Less than 1 Month)

Many studies have attempted to relate recruitment success in clupeoids to environmental and ecological factors. No single factor explains the observed variability in clupeoid recruitment but the role of water column stability is considered to be critical for survival of the early larval stages. Lasker's original idea [289] now referred to as the "stable ocean" hypothesis, suggested that survival of first-feeding anchovy larvae and subsequent recruitment would be improved when food of a suitable size and concentration aggregated in layers, associated with a stable water column, in the absence of intense upwelling advecting the larvae into possibly unfavorable food environments. However, evidence for the correlation of stability with larval survival is variable and has seldom been shown to agree with theoretical expectations [91, 127, 446]. The survival of newly hatched larvae is most likely determined by a combination of physical and biological characteristics, rather than by feeding conditions alone [409]. Furthermore, sardine recruitment appears to be determined by the mortality experienced by post-larvae to juvenile (age 0) fish [575], rather than by the first feeding stage (Sect. 4.2.2.4).

Table 4.1 Summary of the predicted effects of stability on larval fish recruitment at both large (order 1° latitude) and fine (order m in vertical) scales

Stability	Scale	Forcing	Result	Category	Effect
Low	Broad	Mixing	Nutrient entrainment enhances phytoplankton growth	Physical	Positive
Low	Fine	Storms or intense upwelling	Disperses layers of prey	Physical	Negative
Low	Fine	Storms or intense upwelling	Interferes with prey capture	Behavioral	Negative
High	Broad	Intense stratification	Prevents nutrient entrainment	Physical	Negative
High	Fine	Stratification	Permits layers of prey to form	Behavioral	Positive
High	Fine	Stratification	Reduces predator-prey encounter rates	Behavioral	Negative

From McClatchie et al. [373]

Stability exerts an effect at a range of scales by altering the prey environment experienced by larval clupeoids as they lose their yolk sacs and begin feeding. In the case of anchovies, the prey are often dinoflagellates [288], whereas first feeding sardine consume copepod nauplii [576]. First feeding larvae must encounter prey of suitable size at sufficient densities to meet their metabolic requirements for growth [288]. Aggregation of the prey in layers provides a sufficiently concentrated food source for the larvae to be able to meet their metabolic requirements for growth and to grow rapidly enough to minimize predation mortality (See Chap. 5). Some species of early stage larval fish can swim well enough to locate the layers of prey and to successfully capture food particles if the stability conditions are favorable [352]. Although there is little swimming speed data for sardine larvae, it is thought that postflexion larval stages are likely to be able to move into food layers [307]. Earlier work suggested that planktivores could be well-nourished either when turbulence levels were low enough to permit patchiness to develop or when turbulence levels were high enough to enhance the encounter rates between predators and prey. Mullin [410] speculated that intermediate levels of turbulence were likely to be the least advantageous for larval predators. Subsequent studies built on the earlier concepts to provide a more nuanced view.

Water column stability is important to food availability at both large and small scales. Low stability at large horizontal scales (order 1° latitude [235]) permits mixing necessary to entrain nutrients required for growth of phytoplankton, possibly enhancing the prey environment. Low stability at small scales (meters in the vertical) whether due to intense upwelling or to storm events, disperses fine-scale food layers, producing a poor food environment for clupeoids [146, 289]. Low stability also interferes with the striking behavior of the visually feeding fish larvae, reducing feeding efficiency [352]. High stability at large scales can have a detrimental effect on the prey environment by providing a cap to nutrient transfer across the thermocline [129]. High stability at small scales enables accumulation of thin layers of zooplankton and phytoplankton prey to develop [385], but reduces the encounter rate between predators and prey, according to individual-based foraging models where relative velocities of predator and prey, due to both mixing and swimming, affect encounter rates [181, 353, 409]. Physical and behavioral factors work in contrary directions at both large and small scales (Table 4.1). These theoretical considerations suggest that at both large and small scales, larval clupeoids should survive best at mid-levels of stability, rather than at the extremes of high or low stability. This has recently been demonstrated in modeling and experimental studies [352], and in the ocean [41, 127, 572].

Owen [434] found that patchiness was greater during the day than at night, which is consistent with expected convective overturn [410]. Larval fish are visual feeders so greater patchiness in the daytime may help them achieve their required ration [288, 289, 296, 410]. However, as Mullin [410] pointed out, there is tremendous variability in the relationship between the concentration of zooplankton and their food, and in many cases there is no relationship between the vertical abundance or biochemical composition of phytoplankton and vertical distribution of the zooplankton feeding on them, or the depth at which zooplankton feed most intensively. The same variability pertains to larval fish, and so one cannot simply say that patchiness explains the apparent insufficiency of average food concentrations to sustain growth and reproduction of zooplankters or ichthyoplankton (see references in [410], p. 23).

Insights for Fisheries from Experimental and Predation Studies

5

Abstract

Experimental work was an important part of CalCOFI at the Southwest Fisheries Science Center in the 1970s and 1980s, but has now taken a less prominent role. These experimental studies were broadly focused on the two principal factors affecting the survival of the early life history stages of small pelagic fish, notably starvation and predation. The experimental studies relevant to CalCOFI spanned bioenergetics, growth, reproduction, feeding, behavior, cannibalism, and predation. Work in the laboratory and in the field complimented each other to effectively advance understanding of the early life history of the northern anchovy (*Engraulis mordax*) which was a key species of interest at that time.

Keywords

Invertebrate predation on ichthyoplankton • Vertebrate predation on ichthyoplankton • Bioenergetic studies on ichthyoplankton and zooplankton • Cannibalism by fish

> The abundant euphausiid in the California Current, *Euphausia pacifica*, may be an important predator of fish larvae. Laboratory experiments showed that . . . the percent capture of fish larvae by euphausiids was lower than usual when older, more active anchovy larvae were offered . . . The euphausiids were 60 % successful in capturing [newly hatched and 2-day-old] larvae. Successful capture dropped to 17 % when the larvae were 3 days old and to 11 % for 4-day-old larvae, all fed to the euphausiids at the same low density.
>
> (Gail Theilacker and Reuben Lasker [552])

> . . . the upper 30 cm of the ocean is the area which should be examined for further elucidation of this [copepod - anchovy larvae] predator-prey relationship
>
> (Kurt Lillelund and Reuben Lasker [308])

Although CalCOFI is generally thought of as a field program, there used to be an important experimental component to the program. The experimental studies spanned predation, bioenergetics, growth, reproduction, behavior, cannibalism, and sensitivity to ultraviolet radiation. This work was primarily conducted at the National Marine Fisheries Service Southwest Fisheries Science Center, mainly during the 1970s and 1980s, and was largely focused on anchovy.

Part of the impetus for this work was the early recognition that yolk sac fish larvae experienced huge mortality, even before using up the food supply in their yolk sac [7]. This suggested that predation was one of the most important causes of mortality on the early life history stages of pelagic fish [308]. The recognition of the importance of experimental work to understanding predation mortality on ichthyoplankton was expressed in Hunter's reviews [228, 229], followed by Alvariño's review of field studies [24] and then by Bailey and Houde's more broadly focused work [37].

5.1 The Framework for Predation and Feeding Studies

Both Reuben Lasker and Michael Mullin asked what contribution food web studies actually make to fisheries. They wanted to quantify how plankton production processes in the ocean support the production of fisheries [288, 410]. Lasker's approach built upon a breakthrough at the SWFSC[1] in 1969–1970 that permitted artificially-induced

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[1] Which at that time was still called the Fishery-Oceanography Center

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spawning of anchovy in the laboratory. The availability of artificially-induced anchovy eggs and larvae [306], and the larval rearing techniques described by Lasker et al. [295], led to a fruitful avenue of research at the SWFSC, where hypotheses addressing mortality and growth of the young anchovy larvae could be experimentally tested, and the results related to observations made in the ocean.

Artificial spawning was achieved using an artificial photoperiod of 4 h light and 20 h of darkness at 15 °C combined with an injection of human chorionic gonadotropin, followed by a second injection of a suspension of either salmon or carp pituitary 2 days later [306]. Artificially-induced spawning produced a reliable, all year long, supply of anchovy larvae, which permitted laboratory experiments to be undertaken on first feeding anchovy larvae in the laboratory.

Lasker used bioenergetic methods to try to test whether the average primary production off southern California could have been sufficient to support the biomass of sardine at their peak abundance (approximately 3.2 million t) in the early 1930s [294]. He estimated the monthly respiration and ingestion rates for the sardine population, the areal extent of the population, and applied a trophic conversion efficiency of 10 % to show that zooplankton production was only about half that needed to support the sardine population. He acknowledged that primary production might not be the best index of food available for the sardine, and that there were large uncertainties in the estimates of primary and secondary production, and uncertainty concerning the biomass of sardines [294]. He concluded that either the estimates of primary production available in 1988 underestimated the actual primary production, or that the sardine needed to exploit patchily distributed prey concentrations. A third possibility that Lasker [294] did not consider is that insufficient production off southern California compelled the larger sardine to migrate northward along the California coast on a seasonal basis in order to sustain the population by utilizing the more productive waters further north. In these calculations, Lasker [294] considered the high production on the central California coast only as a possible unmeasured source of nutrients injected into the SCB by mesoscale squirts and jets feeding intrusions into the more southern waters [294], rather than as a reservoir of higher production that could be exploited by a migrating population.

Lasker and Zweifel [296] reviewed the literature on feeding of anchovy larvae, including Lasker's earlier work in the laboratory and at sea. They came to the conclusion that not only did anchovy need a certain concentration of particles to stimulate feeding and gut-filling, but that the particles ingested needed to be of adequate size and quality. Anchovy larvae appear to need particles of 40–50 microns diameter at a concentration of 30–50 particles ml^{-1} for survival and growth [296]. They reported other studies demonstrating that anchovy larvae ignored particles smaller than 20 microns diameter. First feeding anchovy larvae require a critical density (50 particles ml^{-1}) of small (40–50 micron diameter) particles, and cannot survive on large (80–90 µm) particles alone [296]. In contrast to the first feeding larvae, Hunter ([227] cited in [296]) found that anchovy larvae of 6 mm length (approximately 9 days old) could not survive on small particles alone. Capture and ingestion of a larger particle of about 80 µm provided a better food packet even though the larvae handle the large particles less efficiently than smaller particles. These experimental results showed that particle size must be taken into account for any analysis of the food environment of the larvae [296]. Lasker and Zweifel [296] modeled the behavior of feeding anchovy larvae in simulated particle fields. They found that the proportion of large to small particles (e.g. nauplii to dinoflagellates) in particle mixtures had more effect on whether larval anchovy could achieve their daily ration than simply the density of large particles.

In addition to size, the type of particle is important because the food quality, or the nutritional and caloric intake, must be sufficient to meet metabolic requirements. For example, anchovy can be raised on the rotifer, *Brachionis plicatilis,* or the dinoflagellate, *Gymnodinium splendens* but the larvae died on a diet of veliger larvae. The larvae also could not survive on a diet of the dinoflagellates *Prorocentrum* or *Gonyaulax polyedra* ([503] cited in [296]). *Gonyaulax* is easily captured and handled by the larvae, but there is something about its nutritional quality that is inadequate for survival. Building on their laboratory and modeling work, Lasker and Zweifel [296] asked whether sufficient concentrations of the right kinds of particle for survival of anchovy larvae anchovy were common in the spawning season off both California and Peru. Based on a few examples they determined that it is necessary to determine both the horizontal and vertical particle distributions and densities, and their nutritional content to predict whether recruitment would be successful or not. Lasker and Zweifel [296] considered that anchovy larvae can survive in conditions that do not permit adequate growth.

Prey concentration and dispersion, prey size and prey quality all affect the growth and condition of both anchovy and sardine larvae, but the effects of food do not act alone to determine recruitment. Experimental work described below showed that predation on both well-fed and starving larvae was also likely to be a key determinant of larval mortality. The “loopholes hypothesis”put forward by Bakun and Broad [42] suggested that years of successful recruitment were caused by temporal gaps in the predation pressure on the early life history stages of sardine. Agostini et al. [3] showed that sardine recruitment was negatively correlated with mean annual zooplankton volumes off southern California, an observation that she suggested was consistent with the loopholes hypothesis. However in this paper she was still working with zooplankton displacement volume and only inferred that the volume of the samples expressed the effect of invertebrate predator abundance more than the effect of the abundance of prey. She did not actually measure either the density of predators or count the numbers of naupliar prey in the samples. A test of the loopholes hypothesis requires more detailed analysis before the relationship between sardine recruitment, zooplankton predators and zooplankton prey can be explicitly addressed.

5.2 Invertebrate Predation

In his review of the effects of predation on the early life history stages of cod and other fishes, Hunter [229] initially made a strong case for the impacts of predation on the eggs and pre-feeding stages of fish larvae, but then seemed reticent about how important these effects actually are in the field. He used experimental data on the feeding rates of predators on fish larvae done in small containers to infer that many species of copepods (especially the large calanoid *Euchaeta* and cyclopoid copepods), as well as euphausiids and hyperiid amphipods prey effectively on high densities of fish larvae. But he then went on to say that because copepods are much more abundant than fish larvae (which are generally relatively rare), and because rates of predation by copepod predators (but not euphausiids) are depressed by high densities of alternate copepod prey, predation rates on larvae in the ocean are not likely to be high [229].

Hunter [229] argued from the experimental results, that chaetognaths like *Sagitta* preferentially eat copepods rather than larval fish, which contrasts with Alvariño's conclusion [21] (Sect. 5.2.4). He [229] considered that hyperid amphipods are the only significant crustacean predators of larval fish in the ocean (which we now know is incorrect, Sect. 5.2.1). These amphipods are most common in inshore waters. Hunter [229] pointed out that gelatinous zooplankton can bloom extremely rapidly, have high, size-dependent ingestion rates on larval fish, and that ctenophores such as *Pleurobrachia*, siphonophores and many species of medusae, in both adult and juvenile life stages, are potentially voracious predators of larval fish (Sect. 5.2.3). But he went on to point out that it is often the case, with some notable exceptions, that blooms of gelatinous predators and the spawning locations and times for fish often do not coincide, and so the impact of these potential predators is reduced.

Blooms of gelatinous predators tend to be more persistent in inshore waters compared to offshore, and Hunter [229] concluded that the impact of the gelatinous predators is greatest in the inshore, and when the blooms of gelatinous predators coincide temporally with spatially restricted fish spawning. This is the case for herring and blooms of the jellyfish *Aurelia* in Kiel fjord, or for cod larvae in the Baltic where spawning coincides with blooms of the ctenophore *Pleurobrachia*. Hunter also points out that larvae that concentrate in the neuston can be very vulnerable to siphonophores [229]. In Californian waters in May, Bieri [64] found that jack mackerel eggs were the most important and common (48 %) prey in the guts of *Velella* (Sect. 5.2.3). However, Hunter [229] concluded that blooms of siphonophores are intermittent rather than widespread in the California Current System (see Figs. 5.1 and 5.2). Larval market squid are also known to consume fish larvae, and experiments suggest that they may prefer fish larvae to crustaceans [234], but there is little information about these potential predators.

In summary, Hunter's review [229] tells us that invertebrate predation on ichthyoplankton is highly selective, is influenced by the abundance and type of alternative prey at least for some predators, and is more important in nearshore waters where predators like hyperid amphipods and gelatinous plankton are more abundant. Predation impact is limited by the spatial and temporal co-occurrence of predators with their potential prey. We still know little about the feeding rates or functional responses of many potentially important invertebrate predators feeding on ichthyoplankton. These conclusions, drawn from a review [229] written almost 30 years prior to this book, are still relevant but there is little agreement about the significance of predation as a cause of mortality of the early life history stages of small pelagic fish.

5.2.1 Krill Predation

A strength of the CalCOFI work in experimental fisheries oceanography was the close linkage between the results of both the bioenergetic and predation experimental studies, and the data provided by the field surveys. Experimental work and field surveys leveraged off each other in the sense that observations at sea generated questions that were tested in experiments, and the experiments provided results that were used in calculations scaled up using the survey results. For example, experiments on the feeding rates of euphausiids preying on fish larvae [552] were combined with field data on krill abundances and distribution (e.g. [79], but actually unpublished at the time) to estimate the potential mortality of anchovy larvae caused by co-occurring *Euphausia pacifica*. Theilacker and Lasker [552] then used the results of bioenergetic studies on the temperature dependence of krill growth, moulting and respiration [286,287] to estimate the ration that *E.pacifica* would need to meet their metabolic needs when feeding on anchovy larvae. They achieved a rather surprising correspondence between the numbers of anchovies that were eaten by the krill in experiments (Fig. 5.3), with the predicted number of larvae that they would need to eat in the field at the temperature where the krill were collected, in order to meet their daily ration (Table 5.1). I say the result is

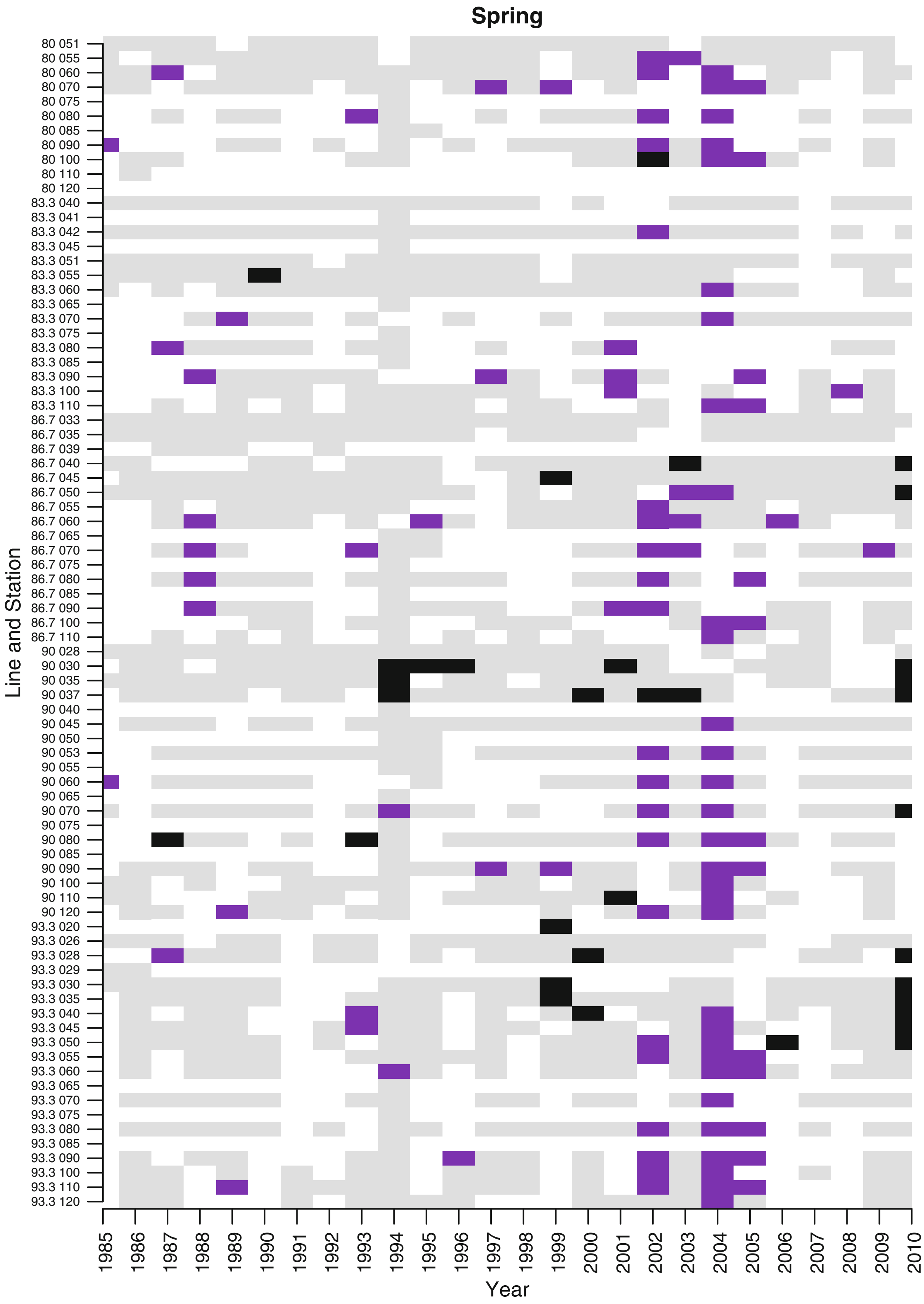

Fig. 5.1 Hovmöller plot showing dominance by either medusae or the chondrophore *Velella* in manta net samples from spring CalCOFI cruises (March–May) over 25 years. *White areas* on the plot show times and locations where there were no samples taken (Graph courtesy of Ed Weber, SWFSC)

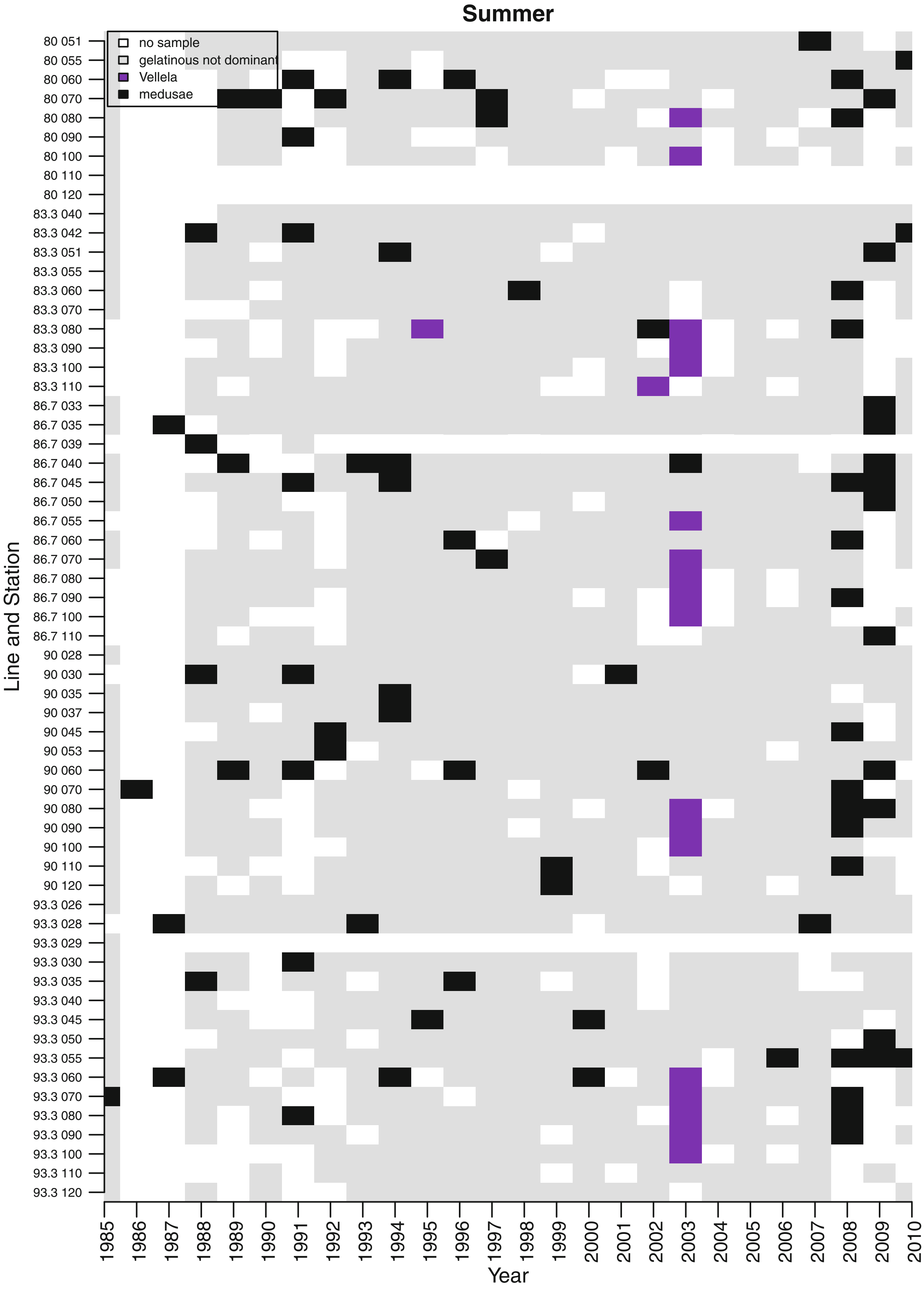

Fig. 5.2 Hovmöller plot showing dominance by either medusae or the chondrophore *Velella* in manta net samples from summer (June–August) CalCOFI cruises over 25 years. *White areas* on the plot show times and locations where there were no samples taken (Graph courtesy of Ed Weber, SWFSC)

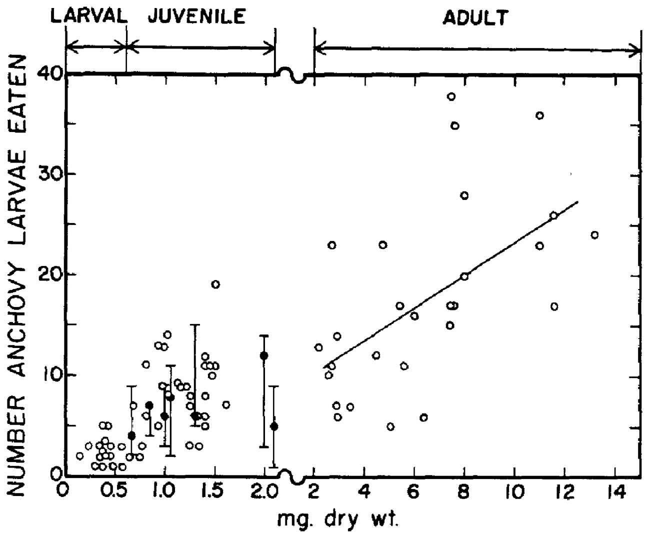

Fig. 5.3 Predation rate (anchovy larvae krill^{-1} d^{-1}) of larval, juvenile, and adult *Euphausia pacifica* based on laboratory experiments in containers with a volume of 3.5 l. Note that the *filled circles* are medians of individual measurements, and *vertical bars* show the range. *Solid line* is a least squares fit (From Theilacker and Lasker [552])

Table 5.1 Number of anchovy larvae needed per day by the krill *E.pacifica* to satisfy their daily carbon requirements at 17 °C compared to the daily consumption of anchovy by krill in the laboratory experiments

		Anchovy larvae eaten	
E.pacifica	Anchovy larvae required d^{-1}	Median	Maximum
Larval	1–2	2	5
Juvenile	5–8	7	19
Adult	11–45	17	38

From Theilacker and Lasker [552]

surprising because krill may exhibit low feeding rates in small containers of the size used in these experiments (3.5 l) compared to rates obtained in larger containers (50–200 l) [365, 451].

Another important result of these studies was their finding that although krill could prey effectively on young yolk sac anchovy larvae, their ability to capture the fish larvae declined quickly as the larvae aged. Later studies showed that this was generally true for ichthyoplankton predators, and appeared to be due to the fact that older larvae were more proficient swimmers with well-developed escape responses to predators [37]. The increased predator-prey encounter rate that resulted from more activity in the fish larvae, and which should increase predation success in the absence of other factors, is more than offset by their increased ability to escape capture. For *E.pacifica* preying on anchovy larvae in the laboratory experiments, capture success dropped from 60 % for 1–2 day old yolk sac larvae to 17 % success rate on 3-day old larvae, and then to only 11 % on 4-day old larvae.

Theilacker and Lasker [552] made a "back of the envelope calculation" of potential larval mortality due to krill in the discussion section of their paper using the years 1953, 1954 and part of 1955 for which they had density data for both anchovy larvae and *E.pacifica* in the same area (within and offshore of the Southern California Bight). Making several assumptions about the vertical distribution of krill and anchovy larvae, and the timing of predator and prey overlap during krill diel vertical migration, they used the laboratory estimates of krill feeding rates and the densities of predators and prey to estimate the numbers of anchovy larvae that would be consumed by krill. They concluded that krill may exert heavy predation pressure on the anchovy larvae, and could influence the degree of patchiness of the fish larvae (but see Sect. 5.3). While their preliminary calculation undoubtedly contains an unknown degree of bias, the application of their results raises an interesting hypothesis that still has not been fully tested almost 40 years after the publication of their paper.

While that is true, Theilacker and her colleagues followed up on their laboratory results by developing sensitive methods to detect predation by krill on fish larvae in the ocean. To do this they developed an immunoassay method to detect larval anchovy egg yolk in the guts of the krill *Euphausia pacifica* [551]. This work required feeding yolk sac anchovy larvae to krill in the laboratory, preparation of the antigen and antisera, followed by the assay [551]. The assay needed to be very sensitive because sample size was small and sensitivity to the anchovy yolk could be low [551]. The goal was to develop a method that could be used in large-scale field surveys to provide information on predation mortality, which along with starvation was considered to be an important determinant of recruitment success [229, 549].

Theilacker [550] applied the immunoassay in a field test to determine the predation rate of krill on anchovy larvae. To do this she took field density estimates of adult krill and larvae, adjusted them to the proportion of krill found in the depth range where anchovy occur, weighted the larval predation rates to reflect their lower feeding rates relative to adults, and applied a temperature dependent gut passage time. The assay could determine the presence or absence of anchovy yolk in the krill gut, but could not be used to determine how many anchovy had been eaten. Positive assay results combine the results of one or more consumed anchovy eggs or larvae, whereas negative results are obtained from krill guts that have not consumed eggs or larvae more recently than the digestion time, which was about 4 h [550]. Theilacker [550] used a Poisson distribution fit to the frequency of negative assays in the samples to estimate the mean number of eggs or larvae consumed per digestion interval. By combining this with the estimated period when krill and anchovy larvae overlapped in their depth distribution (about 10 h per day) she was able to estimate the daily predation rate of the krill on the anchovy, given the known abundance of both predators and prey from net tows [550].

This work showed that credible krill predation rates on anchovy could be obtained from the field. Subsequent application of the method showed that 47–78 % of the natural mortality of eggs and young larvae of anchovy off southern California could be explained by euphausiid predation [553]. Theilacker et al. [550] estimated that krill ate about 2.8 % of the anchovy population per day in the inshore area and 1.7 % per day in the offshore area. Krill predation rates were about 0.1–2 anchovy krill^{-1} d^{-1} which was reasonable given the laboratory functional response curves and the likely presence of alternate prey in the ocean [550]. While these rates would differ spatially and temporally, predation by krill was clearly an important source of anchovy mortality in the ocean, and there were indications that predation rates differed between inshore and offshore. Inshore predation rates by euphausiids were about three times higher than predation rates on anchovy eggs and larvae in offshore waters [550], which was consistent with Hunter's [229] conclusion that predation was more important near shore.

Theilacker and Lasker's paper [552] was prescient in two other ways that occupied other researchers in subsequent years. First, their experiments suggested that krill, or at least *E.pacifica*, did not alter their predation rate on larval fish as a function of the availability of other palatable alternate prey. This characteristic was different from predatory copepods feeding on larval anchovy [308]. Second, they presented results that effectively constituted a functional feeding response (i.e. the relationship between ingestion rate and prey concentration) (Fig. 5.4), although they did not call it a functional response, nor did they fit a model curve to describe a functional response. The data show a saturation threshold for feeding at high prey concentrations (greater than about 20 larvae L^{-1}, Fig. 5.4), which is the kind of information that is vital for individual based models. It is worth noting that anchovy larvae probably are never found at such high concentrations in the ocean, so the functional response of this species of krill feeding on very young anchovy is essentially non-saturating.

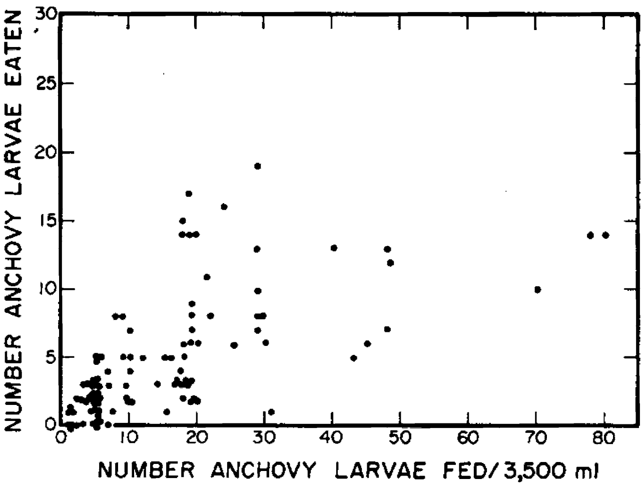

Fig. 5.4 Relationship between ingestion of yolk sac anchovy larvae by *Euphausia pacifica* and the concentration of anchovy larvae based on laboratory experiments (From Theilacker and Lasker [552])

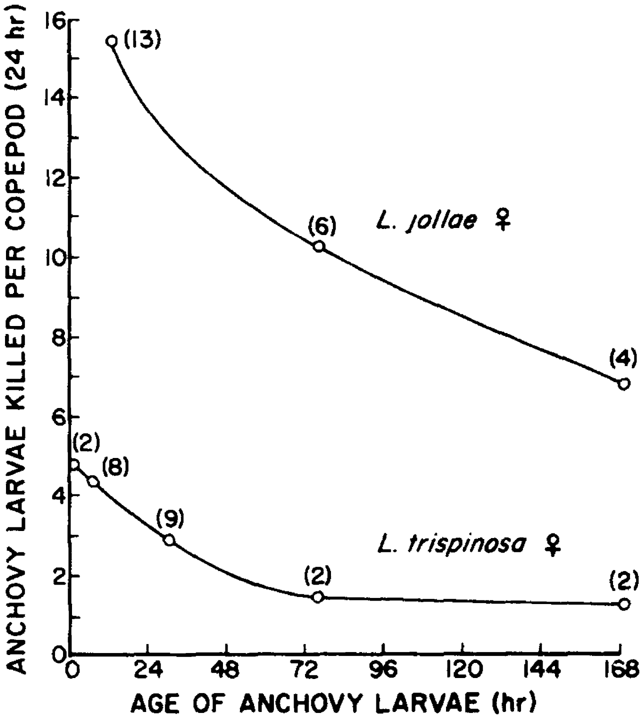

Fig. 5.5 Predation rates by two species of the copepod genus *Labidocera* on anchovy larvae of different ages. *Open circles* represent the mean of the number of experiments shown in *brackets* (From Lillelund and Lasker [308])

5.2.2 Copepod Predation

One of the earliest CalCOFI studies of predation on anchovy larvae focused on the copepods of the genera *Labidocera* and *Pontellopsis* [308], because they were readily available in the Southern California Bight. Lillelund and Lasker [308] found that quite a range of copepods could capture and eat anchovy larvae, or injure and kill them by biting their delicate cuticle. These genera included *Acartia*, *Euchirella*, *Labidocera*, *Pleuromamma*, *Euchaeta*, *Aetideus*, and *Candacia* (the species are given in Lillelund and Lasker [308]). As is the case for krill, the ability of *Labidocera* to kill or capture and eat anchovy larvae falls off rapidly with age of the larvae. The copepods could capture or kill only half as many 7 day-old larvae compared to the number of 1 day-old larvae that they captured or killed (Fig. 5.5). It is interesting to note that, in contrast to both *Euphausia pacifica* and both species of *Labidocera*, the copepod *Pontellopsis occidentalis* was able

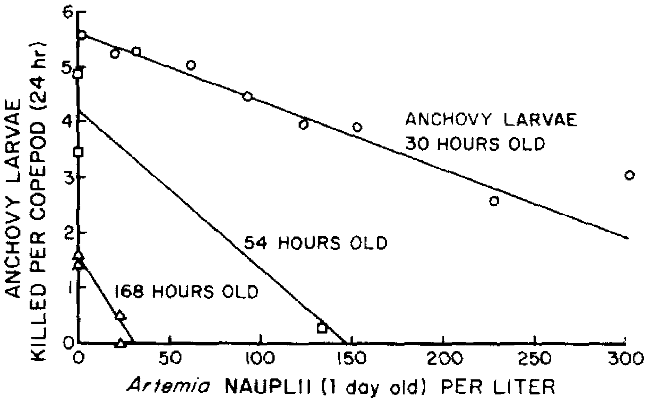

Fig. 5.6 Feeding rate of the copepod *Labidocera trispinosa* on anchovy larvae depressed by the presence of alternate prey (*Artemia* nauplii) (From Lillelund and Lasker [308])

to kill and capture 3.5 day-old (84 h) larvae as easily as yolk sac larvae [308].

Some species of copepods within the same genus were more voracious than others. *L. jollae* killed three to four times as many anchovy as *L. trispinosa* [308] (Fig. 5.5). However, despite the ability of these copepods to kill large numbers of anchovy larvae (up to 16 larvae per day), respiration experiments showed that *Labidocera* could meet their daily caloric ration by consuming as few as 1–4 larvae [308]. As mentioned previously, *Pontellopsis* predation did not show the rapid decrease in larval kill rate as a function of larval age (Fig. 5.5), suggesting that it is a more voracious larval predator than *Labidocera*.

In contrast to Theilacker and Lasker's results with krill [552], predation by *Labidocera trispinosa* on anchovy larvae was depressed by the presence of alternate prey (*Artemia* nauplii) [308] (Fig. 5.6). This response was also strongly affected by the age of the anchovy larvae. Alternate prey depressed feeding on older anchovy larvae more than it affected feeding on younger larvae (Fig. 5.6). This suggests that the alternate prey were preferentially selected as the anchovy larvae became harder to capture, due to their increased larval swimming ability and escape responses.

Lillelund and Lasker [308] presented some limited data that show both predatory *Labidocera* and anchovy larvae tend to be disproportionally abundant in the upper 10 m of the water column. They used data from Ahlstrom [6] to show that "50 % or more of anchovy larvae up to 3 weeks old are above 10 m in depth". For anchovy less than 1 week old, the larvae were distributed even closer to the surface (above 3.5 m depth in the day and above 2 m at night, [308] attributed to [6]). Lillelund and Lasker [308] cite Longhurst et al. [333] to show that *Labidocera trispinosa* was mainly in the upper 10 m of the water column, and that large numbers of *Labidocera* and anchovy larvae were collected in the upper 30 cm. They speculated that the neuston should be investigated more closely to elucidate the predator-prey relationships, but 40 years later there is still little predation-related research focused on the neuston assemblage.

5.2.3 Gelatinous Predators

In a recent unpublished study, McClatchie et al. examined manta net samples collected at CalCOFI stations over the last 25 years off southern California and non-quantitatively recorded whether medusae or the chondrophore *Velella* were dominant in the samples, as indicated by the volume of individuals in the sample jars. We were not able to count or identify gelatinous plankton in these samples yet, and so we cannot quantitatively equate dominance of medusae in the samples to high densities. Nevertheless we can infer the relative abundance of small medusae and *Velella* to determine if they only occur at certain seasons, years and areas off southern California. *Velella* appear to show higher variability than siphonophores, medusae, ctenophores, and even salps. They occasionally form massive blooms and these were evident in the 2003 and 2005 spring surveys off southern California (Fig. 5.7a). During these years, approximately 40–60 % of the stations sampled yielded nueston tows that were dominated by *Velella*. Salps also seem to be prone to outbursts. In 1985, 2010 and 2012[2] more than 20 % of stations sampled showed neuston samples dominated by salps (Fig. 5.7a).

This qualitative analysis of CalCOFI samples can be used to determine how common medusae and *Velella* are off southern California. We found that small medusae were common in the neuston at many locations between Point Conception and San Diego in samples collected between 1985 and 2010 in the summer months (i.e. June–August). Medusae were found both inshore and offshore (Fig. 5.2). We found little evidence that medusae were especially common in any particular year. On the one hand, *Velella*, which is a small chondrophore with a gas bladder was unusually common in the summer of 2003 (Fig. 5.2). There was also an outburst of *Velella* in the spring of both 2002 and 2004. When the spring and summer seasons are considered together, the years 2002, 2003, 2004 and to a lesser extent 2005 were unique in the 25-year period from 1985–2010 in showing high numbers of *Velella* across almost the entire core CalCOFI domain (Figs. 5.2 and 5.1). *Velella* were more common in the spring than the summer and are prone to outbursts or blooms, but we do not understand the mechanism leading to blooms of this predator. On the other hand, medusae were much less common in the spring compared to the summer (compare Figs. 5.2 and 5.1). We conclude from this qualitative analysis that medusae are more consistently abundant in the surface

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[2] The most recent data are not presented here.

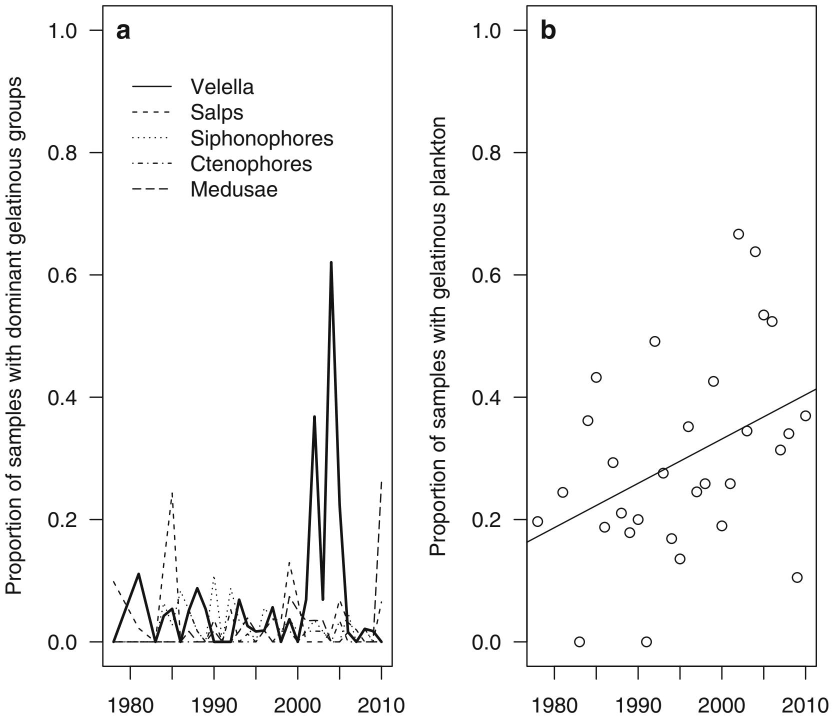

Fig. 5.7 A qualitative analysis of gelatinous zooplankton samples from manta net tows off southern California during spring time (March–May), showing (**a**) occasional massive outbursts of the chondrophore *Velella*, and (**b**) an increase in the proportion of manta net samples containing gelatinous zooplankton

waters off southern California than are *Velella*, except when there are blooms of *Velella*, but that medusae are primarily a summer rather than a spring phenomenon. Blooms of *Velella* in the SCB in spring-time would be expected to have a very significant predatory impact on the mortality of small pelagic fish eggs, based on the observation by Bieri [64] who found guts of *Velella* to be packed with mackerel eggs.

The most common siphonophores off California and Baja California are *Muggiaea atlantica*, *Chelophyes appendiculata* and *Eudoxoides spiralis* [22]. Of these, *Chelophyes appendiculata* is the most abundant, and Alvariño [22] found them to be more common off Punta Eugenia and San Diego than off Monterey based on samples from a 1969 CalCOFI cruise. These species are known to be active predators of fish larvae, but the impact of siphonophore predation and its interannual variability is poorly studied.

The CalCOFI neuston data show an increase, over the last 30 years, in the proportion of spring samples from off southern California that contain gelatinous plankton. The proportion with gelatinous plankton doubled from 20 to 40 % in thirty years (Fig. 5.7b). The preliminary analyses presented here suggest that further, more quantitative analysis of these trends is strongly warranted.

5.2.4 Chaetognath Predation

Much information on the field distribution of invertebrate predators of ichthyoplankton, particularly chaetognaths and siphonophores, is found in the descriptive work of Angeles Alvariño [21–23]. Alvariño [21] considered that the important predators on larger (as opposed to smaller) anchovy larvae are chaetognaths, siphonophores, chondrophores (which include *Velella*), medusae and ctenophores. Most of these predators do not generally prey on fish eggs, although *Velella* is certainly an exception [64, 65]. They are also difficult to study in the laboratory, and so most available information about these predators comes from field studies [21].

Sixteen to eighteen species of chaetognaths were identified by Alvariño [21], between CalCOFI lines 60–137 (Fig. 1.5) from monthly cruises in 1954, 1956, and 1958. Among these *Sagitta euneritica* (maximum size 15.5 mm), *S. bierii* (maximum size 15 mm), and *S. enflata* (maximum size 25–30 mm) were the most abundant. Alvariño [21] considered that the larger chaetognath, *Sagitta enflata* has the greater predatory potential. Chaetognaths, like ichthyoplankton can be very patchy. For example, 36 % of *Sagitta decipiens* collected by Alvariño [21] in monthly samples over 3 years were collected at a single station.

Alvariño [21] compared the abundance of different plankton groups with the abundance of anchovy. Her non-quantitative analysis was inconclusive, but she made an interesting observation that high densities of anchovy tended to occur in association with high densities of both euphausiids and copepods, which are both predators of anchovy larvae (Sect. 5.2.1) and prey for adult anchovy. She also noted that anchovy were scarce in waters dominated by gelatinous zooplankton such as salps, doliolids and pyrosomes [21].

5.3 Vertebrate Predation and Cannibalism

Most of the studies reviewed by Hunter [229] on predation of eggs and larvae by fishes were done on North Atlantic species. These studies indicate that herring (*Clupea harrengus*), Atlantic mackerel (*Scomber scombrus*), and anchovy (*Engraulis encrasicholus*) are voracious predators of ichthyoplankton, but that other potential predators such as sprat (*Sprattus sprattus*), whiting (*Merlangus merlangus*), haddock (*Melanogrammus aeglefinus*), dab (*Limanda limanda*) or the grey gurnard (*Eutrigla gurnardus*) actually consume few fish eggs and larvae.

Among the species occurring in the California Current System, Pacific mackerel is known to be a strong predator of larval fish [231]. Studies off Peru also indicate that Pacific mackerel are ichthyoplankton predators, even when they are only juveniles as small as 3.7 mm [313].

Northern anchovy (*Engraulis mordax*) are known to consume fish eggs, including their own, as are other species of anchovy [232, 334]. Hunter and Kimbrell [232] provide evidence that an anchovy school passing through a patch of eggs may reduce the density of eggs by as much as 50 %. Based on several assumptions they [232] estimated that as much as 30 % of the mortality of anchovy eggs could be caused by the adults filter feeding on their own eggs. The patchiness of eggs, filter feeding selectivity and feeding behavior were considered important factors. Observations of anchovy behavior in a tank indicate that schools may cease searching and focus on concentrations of eggs to filter feed. The combination of laboratory experiments on feeding rates [423] and gut evacuation rates with observations on behavior and field sampling [232], indicate that cannibalism is an important density-dependent source of mortality on the early life history stages of anchovy. However, cannibalism is still an unquantified effect on anchovy mortality and recruitment.

Butler and Pickett [95] quantified the responses of sardine and anchovy larvae to attack by adult anchovies under experimental conditions in order to assess their vulnerability to predation. When the responses of sardine and anchovy larvae to attack were compared, the sardine larvae were found to respond less to attack than anchovy larvae of the same size (Fig. 5.8a). Although escape responses in sardine and anchovy larvae develop at the same rate, the different response to predation by larvae of the same size is a result of different size at hatching and different growth rates in the two species. When response to attack is compared on the basis of age, there is less difference between the responses of the two species (Fig. 5.8b) [95]. As might be expected, younger larvae were less responsive to predatory attack than were older larvae that have better developed coordination and perception [95]. Nevertheless, very few small larvae escaped attacks by adult anchovy. Only 3 % of small (8 mm) sardine larvae and 6 % of small anchovy larvae escaped attack (Fig. 5.9). Thirteen percent of 20 mm sardine larvae escaped attack, but fully 73 % of 22 mm anchovy larvae escaped (Fig. 5.9), illustrating that sardine larvae are much more vulnerable to anchovy predation overall [95].

Larval vulnerability depends on both response to the predator and the rate of successful avoidance of the attacking predator. Very young larvae are harder for a visual predator to see and they respond less frequently to the approach of predators, so their survival depends upon not being seen. Older larvae are more pigmented and therefore more easily seen, but they have better developed musculature and lateral lines so they can more readily avoid an attacking

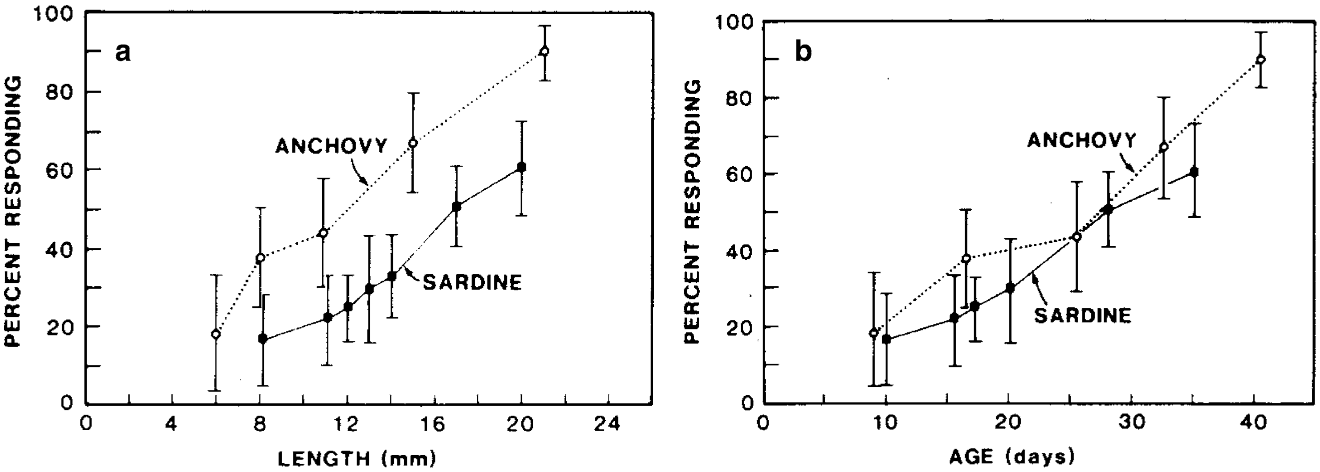

Fig. 5.8 **(a)** Percentage of sardine larvae and anchovy larvae responding to attack by adult anchovy as a function of larval size (means with 95 % confidence intervals). **(b)** Percentage of sardine larvae and anchovy larvae responding to attack by adult anchovy as a function of larval age (From Butler and Pickett [95])

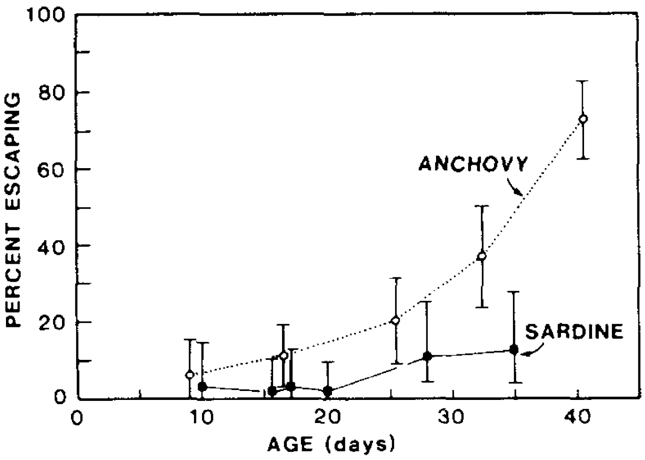

Fig. 5.9 Percentage of sardine larvae and anchovy larvae escaping attack by adult anchovy as a function of larval age (mean and 95 % confidence intervals) (From Butler and Pickett [95])

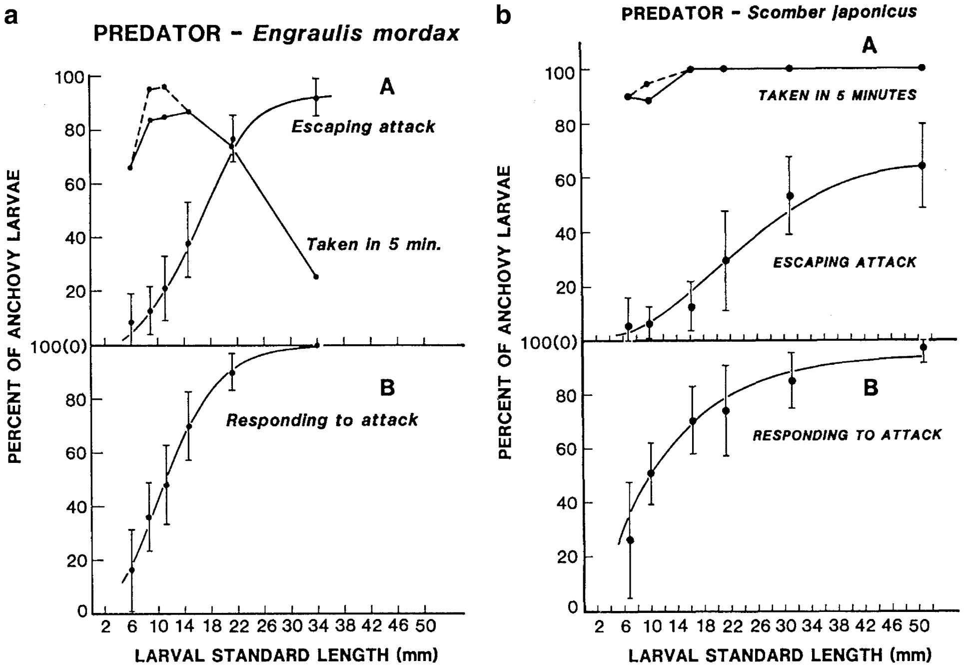

Fig. 5.10 (**a**) A, Percentage of anchovy larvae escaping attack by adult anchovy; bars are 2 × SE and line is Weibull curve fit. B, Percentage of anchovy larvae that responded to the attack of an adult anchovy. (**b**) Same as in (a) except that the predator is Pacific mackerel (From Folkvord and Hunter [172])

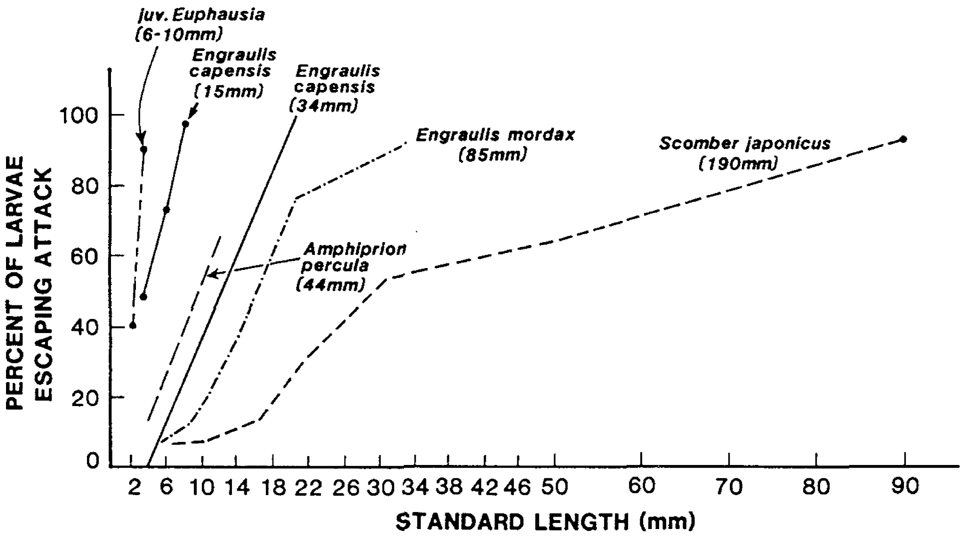

Fig. 5.11 Percentage of larval and juvenile anchovies escaping attacks of various predators as a function of length. Data for *Engraulis capensis* feeding on larval *E. capensis* are from Brownell [87]; juvenile *Euphausia* fed *E. mordax* from Theilacker and Lasker [552]; *Amphiprion percula* fed *E. mordax* from Webb [578]; and others are from Folkvord and Hunter [172]. Numbers indicate length (mm) of the various predators (From Folkvord and Hunter [172])

predator [172]. Vulnerability to different predators varies widely. While young anchovy larvae do not differ much in the proportion responding to either anchovy or mackerel predators, a much lower percentage of larvae escape an attacking Pacific mackerel (Fig. 5.10b) compared to the number that escape an attacking anchovy (Fig. 5.10a) [172]. This is likely because the mackerel attack at much faster speed [172].

While larval escape ability increases with larval size, the overall vulnerability to predators is still largely a function of predator size. This can be illustrated by defining the predator field as the range of prey sizes over which the larval escape rate is 100 %, and comparing different predators. Folkvord and Hunter [172] used this method with data from their own experiments and data from the literature to show that the krill *Euphausia pacifica* of 6–10 mm size can only prey on yolk-sac-sized anchovy larvae (Fig. 5.11). Adult anchovy predators larger than 85 mm can prey on anchovy eggs and larvae up to about 40 mm in length. In contrast, Pacific mackerel of about 190 mm length can prey on a much wider size range of anchovy larvae, juveniles, and adults, up to a maximum size of about 120 mm (Fig. 5.11) [172]. This insightful analysis by Folkvord and Hunter [172] showed that krill are comparatively inefficient predators of small anchovy larvae (but see Sect. 5.2.1), while anchovy are more effective cannibals of their own eggs, larvae and juveniles, and Pacific mackerel are flexible and effective predators on all life stages of anchovy.

6 Fisheries Stock Assessment, Environmental Variability, and CalCOFI

Abstract

Stock assessments of commercially important fishes are conducted knowing that environmentally-driven variability in population dynamics is an important factor in the fluctuations of stock sizes. The ways in which this variability can be incorporated into assessments are controversial and there are few assessments that explicitly incorporate environmental factors in any way. Long-term databases have been increasingly mined in the last 20 years to develop indices or indicators that summarize environmental variability. Even when environmental time series are not used, the fishery-independent time series from ichthyoplankton surveys have proven invaluable to estimate spawning stock biomass trends for stock assessments. Univariate or multivariate indices are used in management frameworks either to assess performance of a fishery or to provide thresholds for management action. The Pacific sardine is one of the few assessments with an environmental control rule to provide a threshold for management action. I discuss the development of this indicator and its use in management. I use the sardine example to highlight some problems that can arise when environmental indices are reassessed. I also discuss the development of new and potentially more robust indicators.

Keywords

California Cooperative Oceanic Fisheries Investigations and stock assessment • Ichthyoplankton time series • Indices of spawning fish stock biomass • Environmental index for sardine • Fishery-independent indices of fish biomass • Fishery-dependent indices of fish biomass

> Designing a good ichthyoplankton survey that stratifies sampling, both geographically and by depth, over a defined sample frame is usually quite tractable. We argue that there is no better stage in the life history to obtain an unbiased sample of abundance, which can then be used to back-calculate the size of the spawning population that produced the plankton samples.
>
> (Stephen Ralston and Bruce R. MacFarlane [457])

> An important turning point, from the standpoint of the Fishery Division research efforts in the CalCOFI program, occurred when we became convinced that there was little or no recruitment signal in the abundances of life stages of fish larvae commonly taken in the surveys.
>
> (John R. Hunter 2011)

> Effectively sampling juveniles is something that has eluded us since the last days of Reuben Lasker. The Holy Grail was to elucidate those factors that controlled larval survival through metamorphosis with the expectation that we predict recruitment. The big assumption was that juvenile mortality was constant and we could skip over that part of the life history. When Rick Methot showed that the temporal distribution of juvenile birth dates did not line up with time of peak spawning we knew we had a problem, and Reuben's grand notion of validating Hjort's hypothesis began to unravel.
>
> (Roger Hewitt 2012)

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6.1 The Value of CalCOFI Data for Understanding Fluctuations in Fish Biomass

While the CalCOFI program originated from the need to provide information to manage the sardine fishery, there have been repeated calls to show how the CalCOFI program continues to be relevant to understanding variability in fish stocks and recruitment. The next section outlines the cases where CalCOFI survey data were used in support of both fishery-independent and fishery-dependent methods for estimating spawning stock biomass or total biomass of commercially important fish populations, or where CalCOFI data were used to increase the accuracy of assessments. As explained earlier, CalCOFI serves more than the assessment community, but part of its funding is still justified by its relevance to currently exploited species. Part of the importance of the CalCOFI survey is that it is truly multi-species, going well beyond just the commercially important species. As such it is an important resource for ecosystem based management.

6.1.1 Fishery-Independent Methods

6.1.1.1 Ichthyoplankton Time Series and Spawning Stock Biomass

The Daily Egg Production Method (DEPM), which was preceded by the Annual Egg Production Method [487], is perhaps the best known application of ichthyoplankton survey data to stock assessment. The DEPM was described by Lasker [292], and subsequently refined by Lo et al. [319, 322, 323]. In the California Current System, ichthyoplankton surveys provided data for DEPM or Daily Larval Production Method (DLPM) estimates of spawning stock biomass for several important commercial species including anchovy (by DEPM) [167, 253, 292], sardine (by DEPM) [322], rockfish (*Sebastes* spp. by DLPM) [455], hake (by DLPM) [326] and Pacific mackerel (by DLPM) [321]. The method is currently only formally incorporated into the assessment for sardine. Sardine Total Egg Production (TEP) is also used as one of the time series in the sardine stock assessment [211].

Smith and Richardson [522] were early advocates of the advantages of using fish eggs and larvae to estimate the biomass of small pelagic fish, and they presented examples from sardine, anchovy and Pacific mackerel surveys to support their case. They argued that early life history stages of fish with pelagic eggs and larvae are restricted to upper depth layers of the ocean, and are vulnerable to capture by plankton nets. The plankton gear required for sampling can be deployed from a variety of vessels and data can be obtained for additional species at less cost than by sampling the adults [522]. Furthermore, the zooplankton collected with the ichthyoplankton by the nets provides information on both the invertebrate predators and the prey of the larval fishes, and can easily be combined with oceanographic sampling of physical and chemical variables that help to characterize the environment of the communities. The samples provide information on the biodiversity of the community, and can be used to determine where spawning adults will be concentrated and vulnerable to capture by a fishery. The spatial extent of spawning also provides information that may help to define the range of stocks which is essential information for management.

The disadvantages of using ichthyoplankton surveys are also considerable, and overcoming these disadvantages has occupied a generation of scientists at the NOAA's Southwest Fisheries Science Center. In the 1970s the taxonomy of early life history stages was well known for only a few of the species [522]. More than 30 years of studies on the distribution and abundance of ichthyoplankton in the California Current System (work which is still continuing to be refined today) has completely changed that situation [5, 10–12, 14, 15, 279, 397–402]. The culmination of the ichthyoplankton taxonomic work is provided in a 1,505 page monograph on the early stages of fishes in the California Current region edited by Geoff Moser [394] (now available online). Smith and Richardson also point out that high standards of data collection and processing are essential to obtain reliable estimates of egg and larval abundance. This is the reason that several technical manuals were written to provide extensive detail on every aspect of ichthyoplankton surveys, from planning, to data collection at sea, to the processing of samples in the laboratory [281, 292, 522]. Refinements and improvements to all aspects of ichthyoplankton (and sometimes zooplankton) survey and processing methods were the subject of numerous technical reports and primary publications [11, 203, 322, 323, 426, 517, 519, 520], some of which are described in detail elsewhere in this book. Last but not least important, Smith and Richardson [522] pointed out that the highly patchy distributions of ichthyoplankton pose considerable problems for sampling, analysis and the use of these data in management [319, 513].

Moser et al. [402] stated that "[a]lthough CalCOFI surveys were designed to encompass the wide-spread open-ocean spawning of Pacific sardine, it is a surprising fact that trends in larval abundance of nearshore species in CalCOFI collections usually track changes in abundance of adults quite well, even when a species is greatly undersampled due to the offshore emphasis of the CalCOFI sampling pattern" [403]. Precision can be a problem when the distribution of spawning adult fish is very patchy such as is the case for small pelagic fish like sardine, anchovy and Pacific mackerel [457]. Adaptive sampling has been used to address problems of precision arising from contagious spawning [319].

Contagion does not appear to be such a problem for spawning rockfishes [457]. Ralston and MacFarlane [457] considered that ichthyoplankton surveys are good at minimizing bias because the eggs and pre-flexion larvae are dispersed in the water column and are vulnerable to plankton nets, so that when ichthyoplankton surveys are properly stratified an unbiased abundance sample can be obtained and used to back calculate the spawning stock biomass. This is less true for post-flexion larvae that have strong net avoidance capability [323] and may be more abundant in the neuston layer (which is however sampled by the manta nets on the CalCOFI surveys).

The CalCOFI ichthyoplankton time series have been used in stock assessments of two rockfish, the cowcod (*Sebastes levis*) [93] and bocaccio (*Sebastes paucispinis*) [251,457], as well as in some of the Pacific or chub mackerel assessments [318]. Egg and larval survey data from CalCOFI have also been used to estimate spawning stock biomass even when not explicitly incorporated into an assessment. For example, CalCOFI data were used to estimate spawning area as a proxy for spawning stock biomass of sardine [514], and to estimate spawning stock biomass of sardine from presence-absence data [354].

6.1.1.2 Larval Time Series for Monitoring Population Fluctuations: The California Halibut

The California halibut, *Paralichthys californicus,* has supported commercial and recreational fisheries for about 100 years and catches have varied in approximately 20-year cycles until the 1970s when the fisheries declined [408]. Moser and Watson [408] used CalCOFI survey data and data from the Marine Review Committee ichthyoplankton studies at San Onofre to show that the catch cycles reflected trends in availability rather than catch rate, and to show the value of the ichthyoplankton time series for monitoring California halibut abundance. California halibut spawn mainly between Bahía Magdalena (approximately 24.6°N), Baja California, and Point Conception (34.45°N), with a spawning center in Bahía Sebastian Vizcaino (approximately 28.25°N). Eighty-five percent of the larvae are found over the continental shelf (depth < 200 m), indicating predominantly coastal distribution [408]. The larvae concentrate in the upper 30 m of the water column, more large larvae are found in the neuston, and disproportionately more small larvae move downward at night [408]. Peak spawning differs by geographic group. North of Bahía del Rosario (29.87°N) in Baja California more larvae are found in February to March, whereas south of this latitude the peak larval abundance is in June-September [408].

Moser and Watson [408] showed a strong positive correlation between the trends for annual southern California commercial landings of California halibut and the annual mean abundance of the larvae off southern California between 1958 and 1981 (Fig. 6.1). The correlation was even better when the annual mean abundance of the larvae was estimated from all CalCOFI stations, rather than just the stations off southern California. Unfortunately the correlation was reversed for the earlier years (1951–1958) when the abundance of larvae was low. The authors attributed the lack of correlation during that period to inadequate taxonomic identification of *Paralichthys californicus*, but they were unable to prove or disprove that possibility.

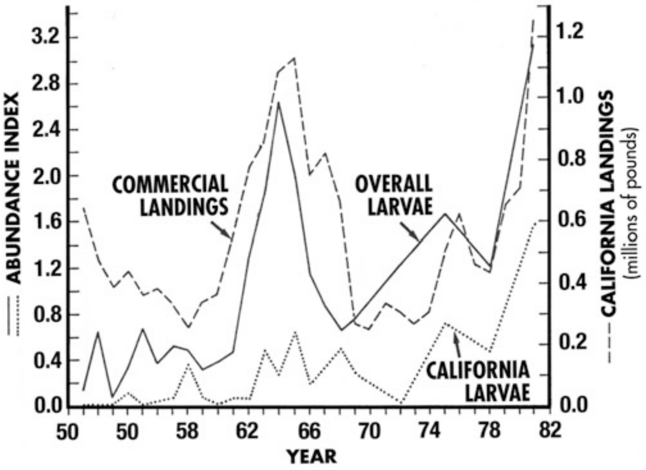

Fig. 6.1 Annual abundance index for California halibut, *Paralichthys californicus*, from all CalCOFI stations 1951–1981 and from California stations compared to commercial landings in California (From Moser and Watson [408])

6.1.1.3 CalCOFI Ichthyoplankton Data as an Unbiased Time Series of Relative Spawner Abundance: The Bocaccio Example

The suite of 59 exploited and unexploited *Sebastes* spp. (rockfishes) includes 15 species that have been assessed [457]. Assessments for all of these species depend upon reliable historical time series of relative abundance from fishery-dependent and fishery-independent sources to establish the stock trajectory [457]. Most rockfish, including cowcod and bocaccio, are found over rough ground, ill-suited to trawling, which renders trawl-based abundance series either biased or imprecise. Further, fishery-independent sampling methods such as trawling or hook and line surveys that harm adults are prohibited in some rockfish conservation areas such as the Cowcod Conservation Area, leaving these critical areas devoid of monitoring [166]. The alternative to trawl-based time series is to use ichthyoplankton time series to develop larval indices of relative abundance [457], or to calculate spawning stock biomass from the daily egg production method (DEPM) [455].

Sebastes spp. are well suited to DEPM because they are viviparous which means that the larvae can easily be

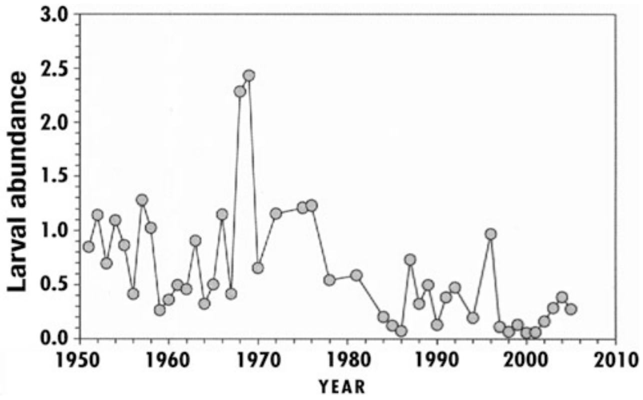

Fig. 6.2 Relative abundance index of bocaccio in the Southern California Bight based on the averaged year effects from a GLM modeling larval densities on spatial location, year, month and day-night (From Ralston and MacFarlane [457])

aged from their otoliths during their first 2 weeks of life [457]. Bocaccio larvae can readily be identified through all larval stages [397, 402] and have been sorted from southern California CalCOFI bongo net tows made since 1950 [457]. Larval bocaccio abundances estimated from the CalCOFI ichthyoplankton time series are also surprisingly precise, with CVs of 10–12 % based on jackknife resampling [457].

The legacy of incorporating the fishery-independent CalCOFI time series of bocaccio larvae into assessments is long, beginning with a NMFS SWFSC administrative report by Jacobson et al. [251], then further developed by Ralston and Ianelli [456] in a stock assessment symposium, and by MacCall in a Pacific Fishery Management Council paper [341], ultimately published in the peer-reviewed literature by Ralston and MacFarlane [457]. Ralston and MacFarlane [457] used bocaccio larvae counts from oblique bongo net tows from 1951–2005 for CalCOFI lines 80–93 and stations inshore of station 60 to create a Generalized Linear Model (GLM) with main effects for location, year, month and day-night to estimate a time series of relative larval abundance [457]. Year effects from the model, averaged over all spatial locations showed "a long-term decline in abundance of bocaccio larvae within the study area" [457] (Fig. 6.2).

The bocaccio assessment model fits eleven fishery-dependent and fishery-independent time series to the data, estimating a total of 98 parameters [456]. The CalCOFI-derived relative larval abundance time series is only one of the eleven. The time series were listed by Ralston and Ianelli [456] as (1) the trawl fishery length composition data, (2) trawl fishery surface age composition data, (3) trawl fishery break-and-burn age composition data, (4) hook-and-line fishery length-frequency data, (5) set net fishery length-frequency data, (6) recreational fishery length-frequency data, (7) a recreational fishing effort series, (8) the triennial trawl survey time series of catch rate, (9) triennial [groundfish] survey length compositions, (10) the pelagic juvenile rockfish survey, and (11) the CalCOFI larval abundance survey (assumed proportional to spawning biomass). The model solves for the mortality coefficient necessary to provide an exact match to the fishery landings [456].

There were concerns over the usefulness of several of the time series in the bocaccio assessment model, and to deal with these concerns the time series were classified into primary, secondary and tertiary groups [456]. "The primary data types were used in the estimation of growth, year-class strength, and population trend. The secondary data were used only to estimate selectivity patterns for the different gear types and the tertiary data were effectively omitted from the analysis except to highlight their deficiencies" [456]. It is notable that the CalCOFI larval time series were classified as primary data that did not suffer from deficiencies hampering the other time series [456].

6.1.1.4 Using CalCOFI Data to Extend Time Series, Standardize Indices and Tune Assessment Models: The Case of Cowcod

Adult cowcod are found over rocky ground generally deeper than 100 m that is not well suited to trawling [93]. The CalCOFI larval time series for cowcod was used to develop an "extended time series of catch and abundance data" to derive standardized abundance indices, and to "tune the stock assessment models to presence-absence indices with binomial distributions, low expected values, and zero values" [93].

Cowcod are one of the few rockfish whose larvae are readily identifiable, which is an important criterion for the development of a larval index. Furthermore the Southern California Bight is the center of distribution for cowcod as well as the best sampled CalCOFI region, so the cowcod larval time series is well sampled. Cowcod larvae off southern California are mostly found between January and May with a peak in March [394], although some larvae are present over the wider period from November to August [93, 400]. The larvae spend about 100 days in the plankton before settling.

Butler et al. [93] fit a logistic Generalized Linear Model of cowcod larval presence-absence to years, months and a categorical variable for inshore locations, in order to derive a standardized index of larval abundance [93], essentially following the methods of Mangel and Smith and Smith [354, 514]. The logistic larval index was combined with two other indices of recent abundance (the Poisson CPUE index from logbooks and the proportion of positive tows from bottom trawls) in order to tune the cowcod assessment model [93]. The logistic model provided an index of the probability of positive tows for cowcod larvae. The "probability of a positive tow in CalCOFI [. . .] indices is almost proportional to abundance when positive tows are rare [354]. At higher levels the probability of a positive tow is a nonlinear function

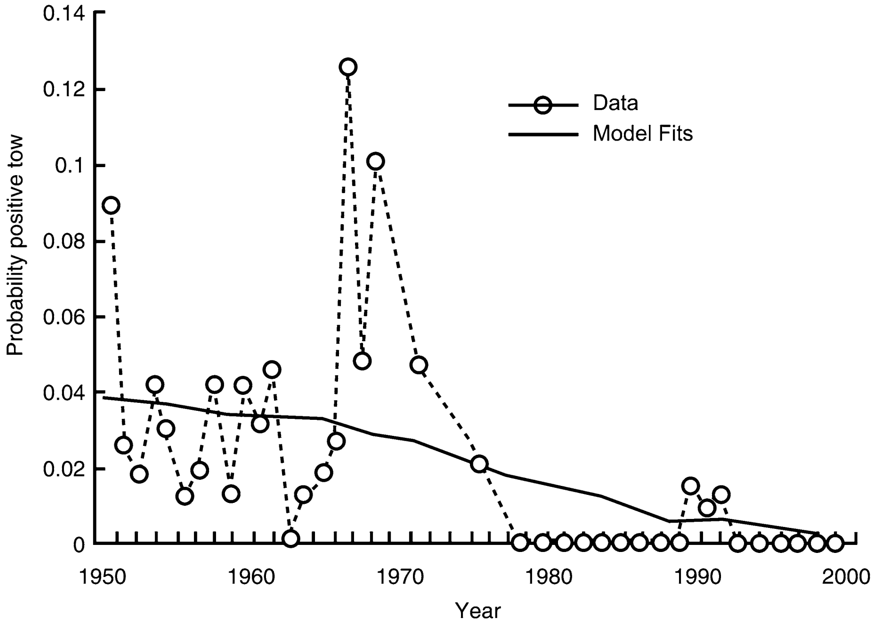

Fig. 6.3 Index for cowcod fishable stock abundance derived from a logistic GLM predicting probability of presence of cowcod larvae from CalCOFI samples. 'Data' are from the GLM model results for larval presence, and 'Model Fits' are predicted values from the assessment model (From Butler et al. [93])

of larval abundance" [93]. The CalCOFI presence-absence data were used as an index of fish-able stock abundance when modeling abundance (Fig. 6.3) [93]. In this context, the CalCOFI time series provided data that complemented and confirmed the downward trend in cowcod abundance that was observed in other time series (from recreational CPUE, trawl data, and the assessment model) [93].

6.1.1.5 Pacific Mackerel Larvae as an Index of Spawning Stock Size

Use of the time series of Pacific mackerel from CalCOFI surveys in the mackerel stock assessment was summarized by Weber and McClatchie [581]. Lo et al. [318, 321] created a time series of daily larval production by using water temperature, larval abundance and larval size to estimate the development rates and mortality rates of the larvae [581]. The time series of larval production was initially incorporated into the assessment as an index of spawning stock size [142], but was later removed over concerns that the modern CalCOFI sampling pattern does not sample the full range of the Pacific mackerel stock [123]. Subsequent investigation of this problem using a statistical model of Pacific mackerel spawning habitat [581] showed that it would be necessary to broaden the sampling into Mexican waters (as was done in the early years of CalCOFI), or to obtain data from Mexican surveys, in order to develop a representative relative index of spawning stock biomass of Pacific mackerel from the ichthyoplankton time series. If this was done, Lo et al. [318] concluded that "the long time series of Pacific mackerel larval density, preferably the daily Pacific mackerel larval production, followed by the bias-corrected larval density, is a cost-effective fishery-independent population index obtained yearly and is beneficial to . . . a better understanding of [Pacific mackerel] dynamics" [318].

6.1.1.6 Pacific Hake Larval Production Time Series for Stock Assessment

Pacific hake (*Merluccius productus*), also called Pacific whiting, are abundant over the shelf and slope from 25–50°N in the California Current System [217]. Lo [326] provided estimates of hake larval production from 1951–2006 using CalCOFI data from lines 93.3 to 60 (off San Diego to San Francisco). This area encompasses the major spawning ground for hake (Fig. 6.4), and is considered to be a favorable area for survival of larval hake [217]. In keeping with the many refinements that Nancy Lo has made to ichthyoplankton-based assessment methods, Lo [326] identified some of the potential problems with using the larval production estimates for assessment purposes, and proposed future studies to address some of the issues. Hake larvae are extremely patchy, more so than most other pelagic species. The patches can be large and dense ([219] cited in [326]), and persist longer at the depth of maximal larval abundance than in the mixed layer ([94] cited in [326]). Extreme patchiness could bias the net sample density estimates for larval abundance. Lo also noted that the mesh extrusion factor to correct for larval escapement through the meshes of the plankton net was based on jack mackerel data, and she recommended that experiments be conducted to verify the extrusion correction for hake [326]. She further suggested that temperature dependent growth curves for hake yolk sac larvae should be obtained experimentally, as was done for anchovy, to obtain a better estimate for the calculation of larval production [326]. While the escapement correction and the temperature dependent larval growth can be easily improved, the patchiness issue is less tractable [219].

Lo [326] argued that hake larval production could be used in the stock assessment because the data are collected at nominal extra cost as part of the CalCOFI surveys, the area

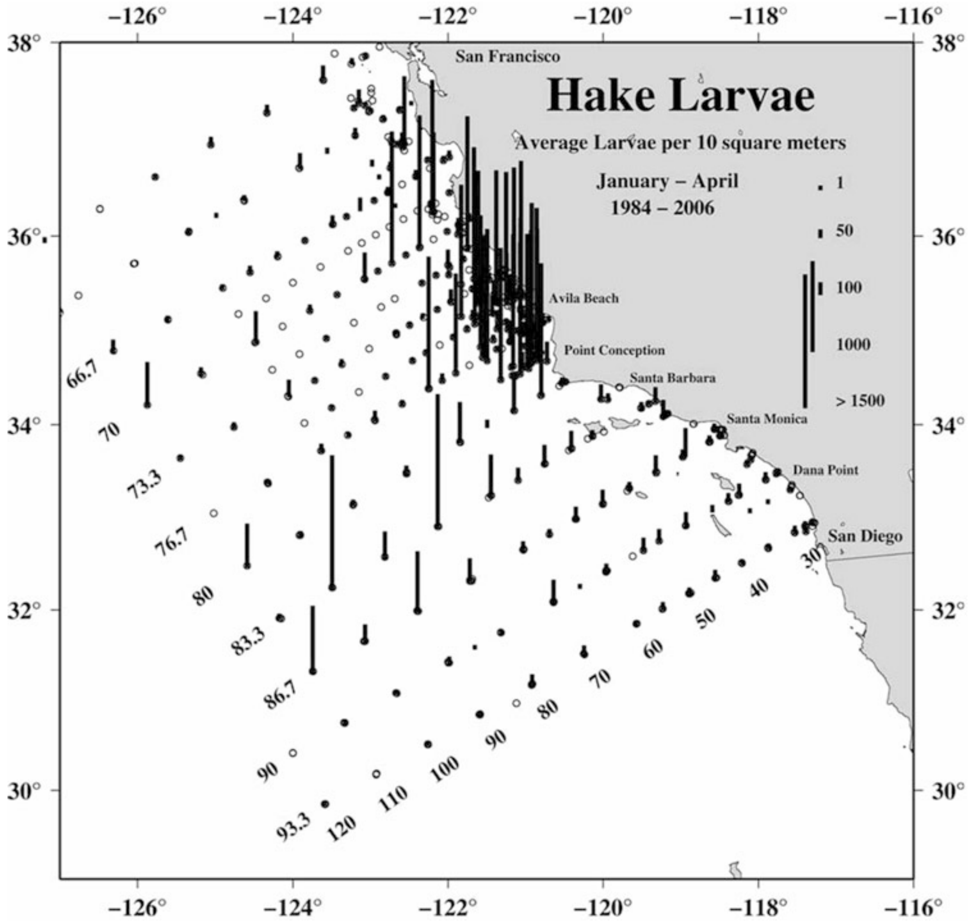

Fig. 6.4 Pacific hake (*Merluccius productus*) larval densities from January–April 1984, 1985, 1987, 1988, 1991, 1994, 2003–2006. Some irregular stations in the northern area were non-CalCOFI stations (From Lo [326])

sampled includes offshore areas where hake spawn in some years (although most spawning is nearshore), and the larval time series is consistent with the acoustic-trawl time series (showing a simple correlation of 0.76, significant at the 5 % level[1]) [326]. Until recently (2012 and 2013), the acoustic-trawl survey for hake was not conducted every year (and prior to 2007 it was triennial), whereas the CalCOFI surveys are conducted four times per year. Two, and occasionally three, of these surveys are during the hake spawning season.

6.1.1.7 Recruitment of Pacific Hake in Relation to Environmental Variability

Like the sardine, hake undergo a seasonal migration to the northern part of their range in the summer to feed, returning to central, southern and Baja California in the winter to spawn [217]. There is some limited spawning in the north in summer, at least in some years. Spawning occurs at depth (100–500 m) in the late winter and early spring (January to March), and eggs and larvae are found beneath the mixed layer [6, 34, 483]. Hake show marked variability in recruitment. Adjacent year classes can differ by ten to thirty times [217]. For comparison, subsequent year classes of anchovy can vary by a factor of three [217]. It is interesting to note that a decade after Hollowed and Bailey's [217] paper, Smith [515] reported up to ten times higher variability in recruitment for hake and anchovy, but he did not limit himself to adjacent year classes, which could explain the difference (see Sect. 4.2.2.4).

Studies partitioning density-dependent from density-independent factors in the hake recruitment time series showed that the large variability in recruitment is driven by environmental (i.e. density-independent) factors ([582] cited by [217]). Hollowed and Bailey [217] found that both winter and spring wind-driven upwelling, and the location of the larvae during the upwelling season, were important in explaining why certain years seem to provide better conditions for successful hake recruitment. They used a comparison of the annual abundance of large larvae and juveniles with the annual number of recruits to determine that the critical life history period for hake recruitment is the late larval or early juvenile stage. For the most part, strong year classes (1967, 1970, 1973, 1977 and 1980) that sustained the fishery were characterized by higher percent occurrence of larvae, higher CPUE from

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[1] Inspection of the time series of hake biomass from the acoustic survey and hake larval production in Fig. 14 of Lo [326] suggests less coherence than the simple correlation coefficient.

fishery-independent mid-water trawl surveys, and higher recruitment [217].

Hollowed and Bailey [217] built on the findings by Bailey [34] who found that spring upwelling in March was critical for larval hake survival. What they discovered was that it is the combination of spring upwelling in March (supporting greater production), with winter upwelling in January and February that is critical. Strong winter upwelling has a negative effect on hake recruitment because the larvae are transported offshore, out of the higher production areas favorable to rapid growth of the young larvae. In contrast, weak winter upwelling permits the young larvae to remain nearer shore, and southward advection transports them into the Southern California Bight. In the Bight the larvae are more protected from offshore transport and they can benefit from enhanced production supported by spring upwelling in March [217]. However, upwelling in the Southern California Bight is weak, so other mechanisms are more likely than upwelling to drive the production that hake exploit (see Sect. 2.6.2.1). Rapid growth, fueled by abundant food provided by enhanced spring-time production, would provide a refuge from predation because the larvae grow quickly under productive conditions. An additional refinement to this idea was added by Bakun [39] who pointed out that both the speed and the volume of Ekman transport need to be considered.[2] The speed of Ekman transport is low in the winter, medium in the spring and highest in the summer, so offshore advection occurs most rapidly in the summer. Late winter spawning minimize loss to less productive offshore areas during the low-speed advection period in the winter (January–February) and sets up the larvae to utilize springtime (March) production.

6.1.1.8 The Environmental Component of the Sardine Harvest Control Rule

One way to incorporate environmental variability into stock assessments is to create some sort of index, based on one or more variables, which has associated trigger points or thresholds that if exceeded will initiate some management decision. There are few stock assessments where the effects of environmental variability on a stock are either expressly incorporated into an assessment model or used in a decision rule to set a harvest guideline [491, 492]. The sardine harvest policy is unusual because a proxy for environmental variability, 3-year average surface temperature at the Scripps Institution of Oceanography pier (SIO pier) in La Jolla, California, USA, has been used as one parameter in the formula for a decision rule-based harvest guideline [212, 435].

An MSY control rule, according to U.S. federal regulations, is "a harvest strategy which, if implemented, would be expected to result in a long-term average catch approximating [Maximum Sustainable Yield (MSY)]" [436]. MSY stock size is taken to be the long-term average size of the stock or spawning stock biomass that would be achieved using an MSY control rule with constant fishing mortality [436]. All actively managed stocks have MSY control rules, as well as definitions of overfishing and over-fished stocks [436]. MSY control rules provide fisheries managers with a tool for adjusting fishery exploitation levels. In the context of coastal pelagic species (CPS) (sardine, anchovy, mackerels and market squid) the emphasis is on biomass rather than catch because CPS are important forage species in the ecosystem. The approach is conservative so as to achieve a stock biomass at least as large as the MSY stock size [436]. Based on 2010 and 2011 revisions to the CPS Fishery Management Plan (FMP), Optimal Yield for a CPS harvest is "defined to be the level of harvest, which is less than or equal to Allowable Biological Catch (ABC) estimated using an MSY control rule ... and used by the Council to manage the stock" [436].

The Allowable Biological Catch, ABC, is "a prudent harvest level calculated based on an MSY control rule" [436]. ABC can be less than the Optimal Yield if needed to prevent overfishing. ABC differs depending on the choice of the probability of overfishing (P^*) [28] under Amendment 13 of the CPS FMP [436]. P^*represents the level of risk of overfishing that the Pacific Fishery Management Council (PFMC) is willing to accept and its maximum value is set to 0.5, or a 50 % risk level. In practice, ABC is calculated at 4 levels of $P^* = 0.45, 0.40, 0.30$ and 0.20, giving $ABC_{\{0.45\}}$, $ABC_{\{0.40\}}$, $ABC_{\{0.30\}}$ and $ABC_{\{0.20\}}$ = 163,140, 155,810, 141,325 and 126,073 t respectively in the November 2011 sardine assessment [211].

The MSY control rule is a proxy for F_{MSY} (i.e. the fishing mortality rate that achieves equilibrium Maximum Sustainable Yield), and for sardine, it is presently constrained to range between 5 % and 15 % of total biomass. The Scripps pier temperature index plays an important role in the sustainable management of sardine, specifically in the calculation of the F_{MSY} proxy used in the harvest guideline, the Allowable Biological Catch and the Overfishing Level. The SIO pier temperature time series provides an environmental proxy that helps to determine the fishing mortality rate that maximizes catch biomass in the long-term (F_{MSY}). The SIO pier temperature index values observed from 1981 through 2008 have been consistently higher than the temperature threshold that would trigger the decision rule to reduce the exploitation fraction and consequently the F_{MSY} exploitation fraction has been 15 %. Essentially this means that the environmental parameter had no effect on the harvest guideline under conditions pertaining up to 2012, nor has it ever been used to reduce catches since its implementation in 2000, but if SIO pier temperature index values drop this could lead to a management decision to reduce the exploitation fraction.

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[2] Speed of Ekman transport = Volume of Ekman transport / Mixed layer depth [39].

The MSY control rule for sardine follows the general guideline for CPS: $HG_{yr+1} = (BIOMASS_{yr} - CUTOFF) * FRACTION * DISTRIBUTION$ where HG_{yr+1}(t) is the total USA (California, Oregon, and Washington) harvest guideline in the year following the assessment, $BIOMASS_{yr}$ (t) is the estimated stock biomass (ages 1+) from the assessment model, *CUTOFF* (150,000 t) is the lowest level of estimated biomass at which harvest is allowed, *FRACTION* is an environment-based percentage of biomass above the *CUTOFF* that can be harvested by the fisheries, and *DISTRIBUTION* is the percentage of $BIOMASS_{yr}$ in U.S. waters, assumed to be 87 %. A maximum allowable catch (*MAXCAT*) is set at 200,000 t [435]. *CUTOFF* provides a buffer for the spawning stock in the event of overfishing from which the stock could rebuild. *MAXCAT* protects the stock against over-exploitation if there is a biomass calculation error, and also potentially reduces year-to-year variability in catch levels, and is designed to reduce over-capitalization of the fishery during periods of high biomass [436].

Given this F_{MSY} and the productivity of the sardine stock have been shown to increase when relatively warm-ocean conditions persist [250], the following formula has been used to determine an appropriate (sustainable) *FRACTION* value: $F_{MSY} = 0.248649805(T^2) - 8.190043975(T) + 67.4558326$ where $T(°\mathrm{C})$ is the running average sea-surface temperature at the SIO pier during the three preceding seasons (July–June). The formula predicts a steep drop in F_{MSY} with small changes in temperature but the function is U-shaped and so could theoretically result in either an increase or decrease in F_{MSY} as a function of temperature. *FRACTION* is constrained to between 5–15 % unless the control rule for sardine is revised. These constraints are policy bounds based on social, biological and economic criteria [436].

F_{MSY}, calculated from the Scripps Pier temperature, is also used to calculate the Over-Fishing Level, $OFL = BIOMASS * F_{MSY} * DISTRIBUTION$ and the Allowable Biological Catch, $ABC = OFL * BUFFER$. The only difference between *ABC* and *OFL* is the *BUFFER* parameter which is supposed to take into account uncertainty in the biomass estimate. Overfishing is deemed to occur when catches exceed the ABC. Overfishing is approached whenever fishing mortality or exploitation are likely to exceed the ABC level within 2 years, whether stocks are at a high or a low level [436]. The PFMC must take action to prevent overfishing if forecasts suggest that exploitation is approaching the overfishing level.

The Scripps Pier Temperature Index Re-evaluation

The Scripps pier index was re-evaluated [369], and as a result, the index was removed from the harvest guideline. McClatchie et al.'s [369] argument was based on two main points. First, the Scripps pier temperatures are warmer than the offshore spawning area for sardine and the difference in temperatures is increasing. This means that the temperature at the SIO pier is no longer representative of the temperature on the sardine spawning grounds [369] (Fig. 6.5). Second, the originally proposed linear temperature-recruit relationship was no longer significant when the regression was updated with more recent data [369] (Fig. 6.6). Both the SR anomalies and the R/S anomalies were linearly related to 3-year SIO pier temperature in the early years, in agreement with Jacobson and MacCall [250] (Fig. 6.6c, e), but the relationship broke down when more recent data from 1991 to 2008 were added (Fig. 6.6d, f).

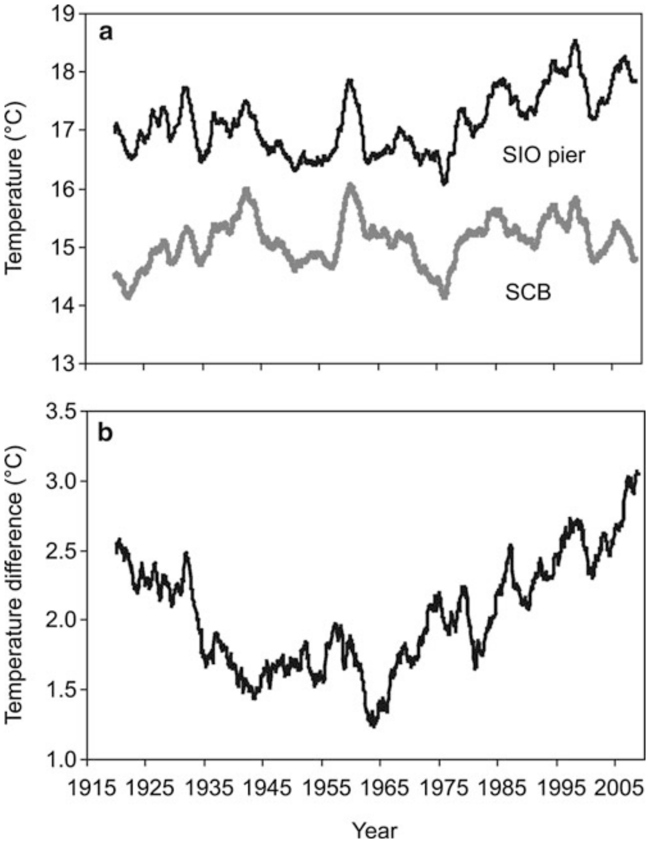

Fig. 6.5 (**a**) Comparison of the 3-year average SIO pier surface temperature with the 3-year average 10 m depth reconstructed temperatures from the 2×2° grid squares in the offshore sardine spawning area of the SCB (**b**) Difference between the two time series calculated as SIO pier temperature – offshore SCB temperature (From McClatchie et al. [369])

Lindegren and Checkley [309] refit the sardine temperature-recruit relationship using a GAM, as in the original work [250]. However, they only modeled the modern data (1981–2010), omitting the years 1935–1963 because the assessment method was different at that time. Another important difference was that while the original model [250] fitted a linear relationship between temperature and recruitment, Lindegren and Checkley [309] fitted a non-linear temperature-recruit relationship (Fig. 6.7). They

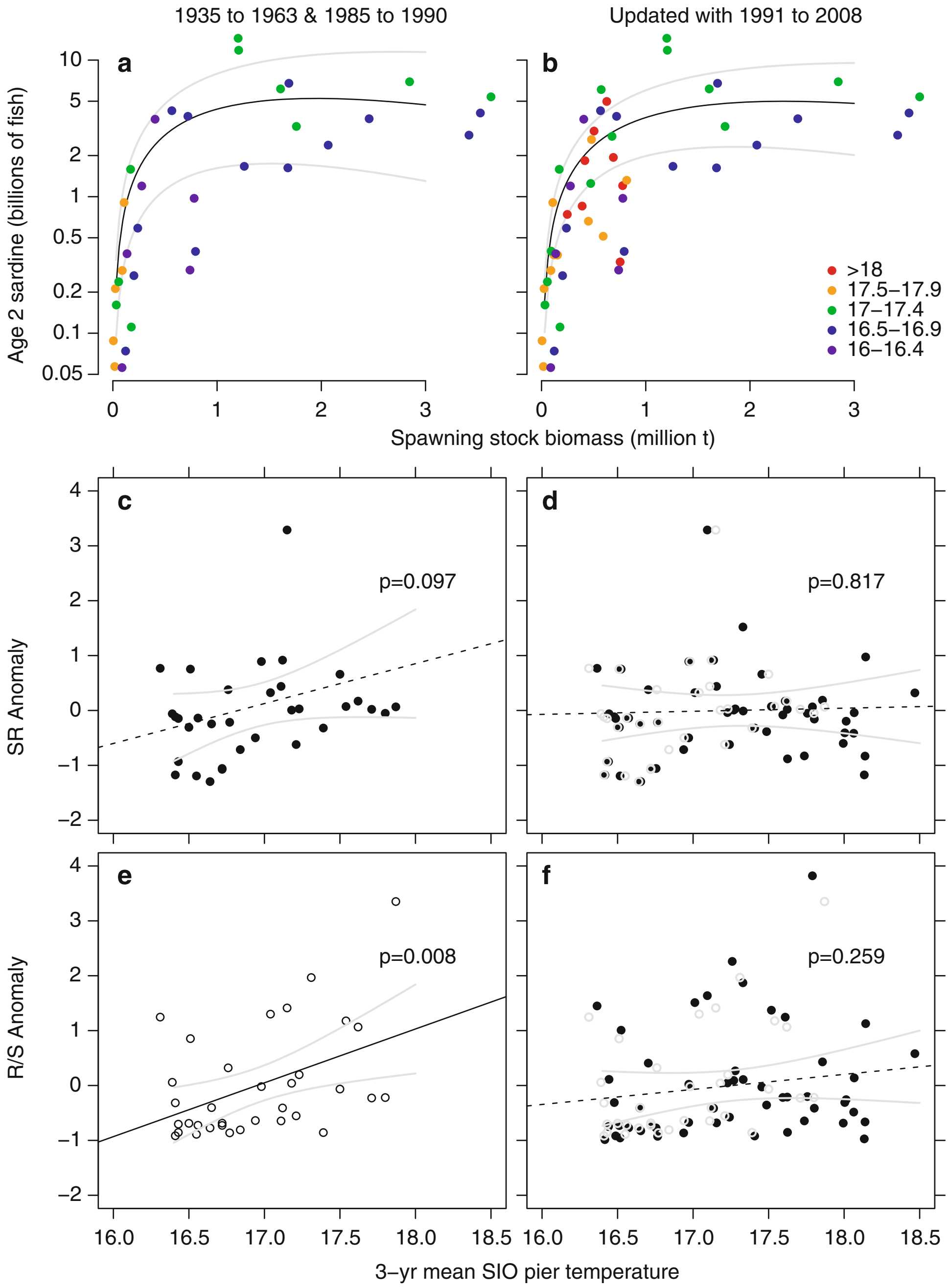

Fig. 6.6 (**a**) Spawning stock biomass-recruit (age-2 sardine) relationship using data from Jacobson and MacCall [250] Table 1 (Erratum) for years 1935–63 and 1985–90. *Black line* is a fitted Ricker curve and *gray lines* are 95 % confidence intervals. Data points are color-coded by SIO pier temperature (°C). (**b**) Same as (**a**) updated with data (1991–2008) from Hill et al. [212]. (**c**) Stock-recruit (*SR*) anomaly calculated from (**a**) in relation to SIO pier temperature for years 1935–1963 and 1985–1990. *p* is the probability that the slope of the linear regression is not different from zero. *Grey lines* are the 95 % confidence intervals (**d**) SR anomaly calculated from (**b**) in relation to updated SIO pier temperature, updated with recent years (1991–2008). (**e**) Recruitment success (R/S) anomaly based on numbers of age-2 sardine in relation to the 3-year mean SIO pier surface temperature using data from Jacobson and MacCall [250] (1935–1963, 1985–1990). (**f**) Same as (**e**), but updated with recent years (1991–2008). *Grey circles* are the data from (**e**)

concluded that the temperature-recruit relationship was still valid for use in the harvest guideline, but that the mean annual temperature from the 66-station CalCOFI pattern should replace the 3 or 5-year mean of Scripps Pier temperature in the model [309].

Regional Variability and the Likely Spatial Distribution of Recruitment

Work in progress at the time of writing suggests the location where sardine recruit may be further offshore and further south than previously expected. Surface drifters deployed off the Channel Islands in September 2012 in collaboration with Scripps Institution of Oceanography provide information on potential advection of sardine larvae (Fig. 6.8). These drift patterns were collected during late summer–winter (September to January) and so they are not directly relevant to recruitment of spring spawning sardine. However, the drift patterns compare well with our results from advection of sardine eggs and larvae by hydrodynamic models which indicate that sardine larvae spawned off southern and central California in springtime are advected far offshore and then southward over their first 5 months of life (Fig. 6.9). Both these results indicate that sardine recruitment is likely occurring offshore in Mexican waters, unless the larvae and

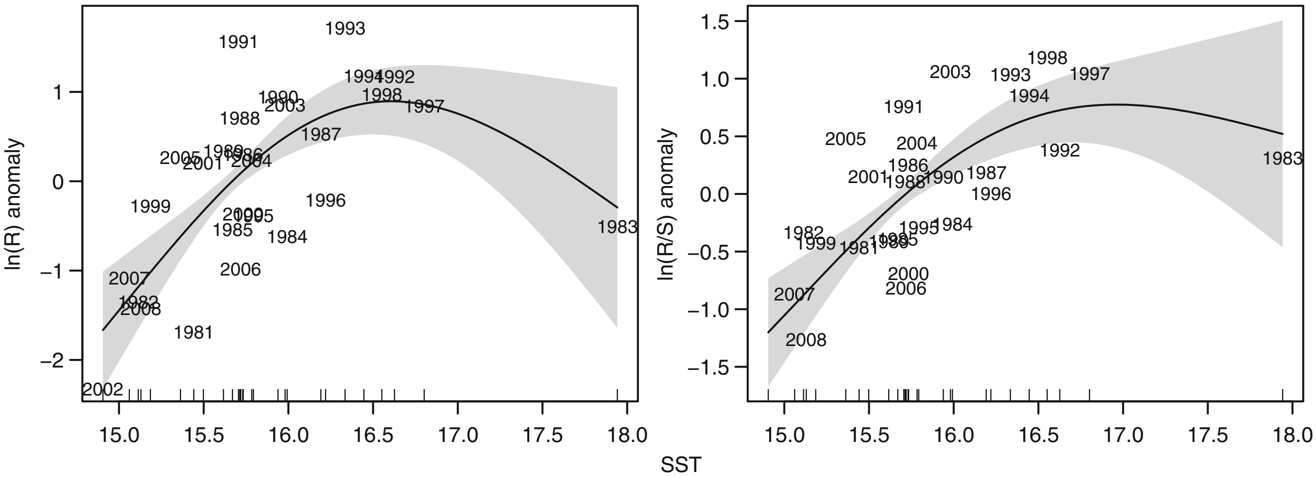

Fig. 6.7 (*Left*) Relationship between sardine recruitment (Age 2+ fish) and temperature derived from averaged annual temperatures between 5 and 15 m depths for all stations along CalCOFI lines 76.7–93.3. (*Right*) Relationship between sardine recruitment success and temperature. Upper and lower confidence intervals for the model fit are shown in *gray* (From Lindegren and Checkley [309])

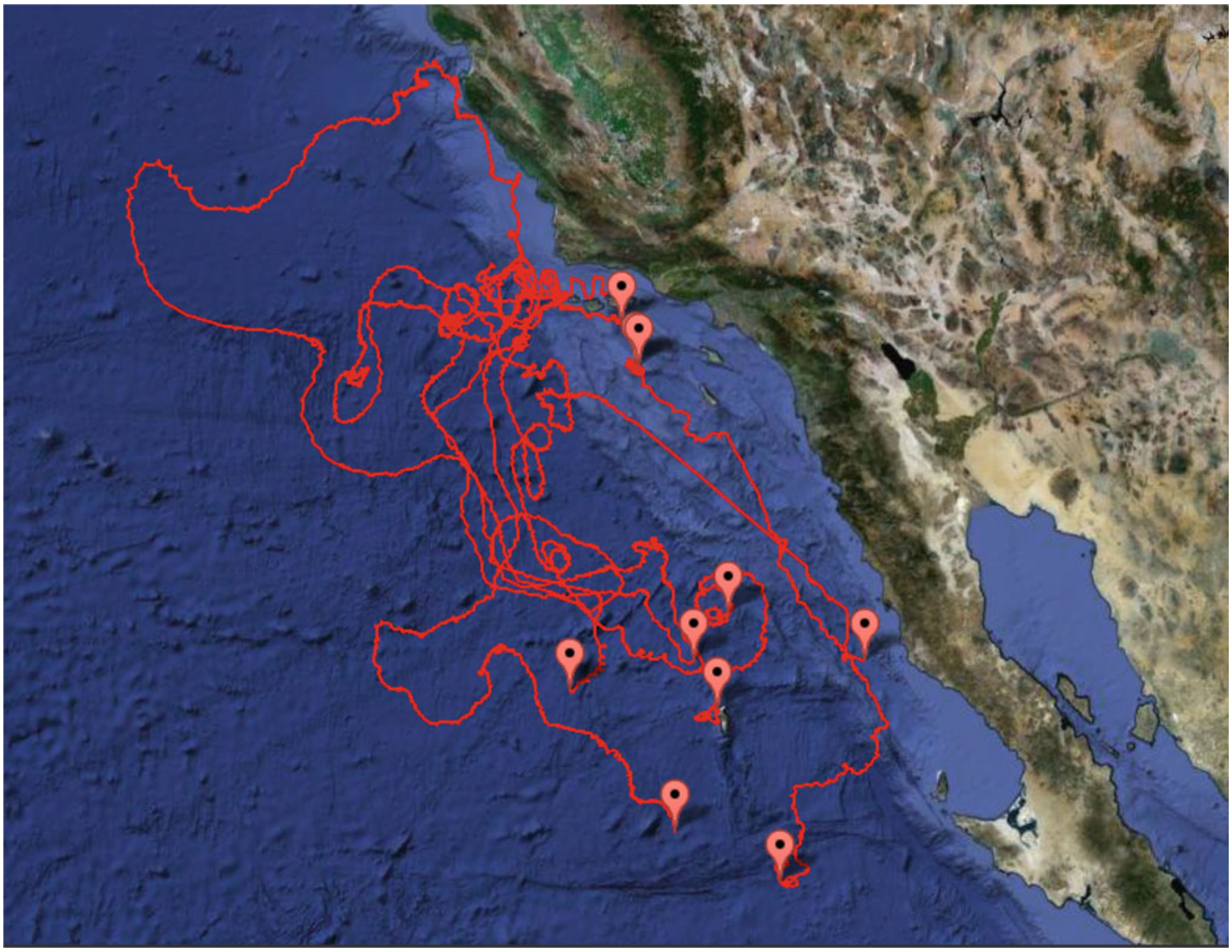

Fig. 6.8 Tracks as of January 17, 2013 of drifters deployed off the Channel Islands by NOAA Fisheries during September 2012. *Markers* indicate last recorded position of each drifter (Courtesy of Luca Centurioni, Scripps Institution of Oceanography)

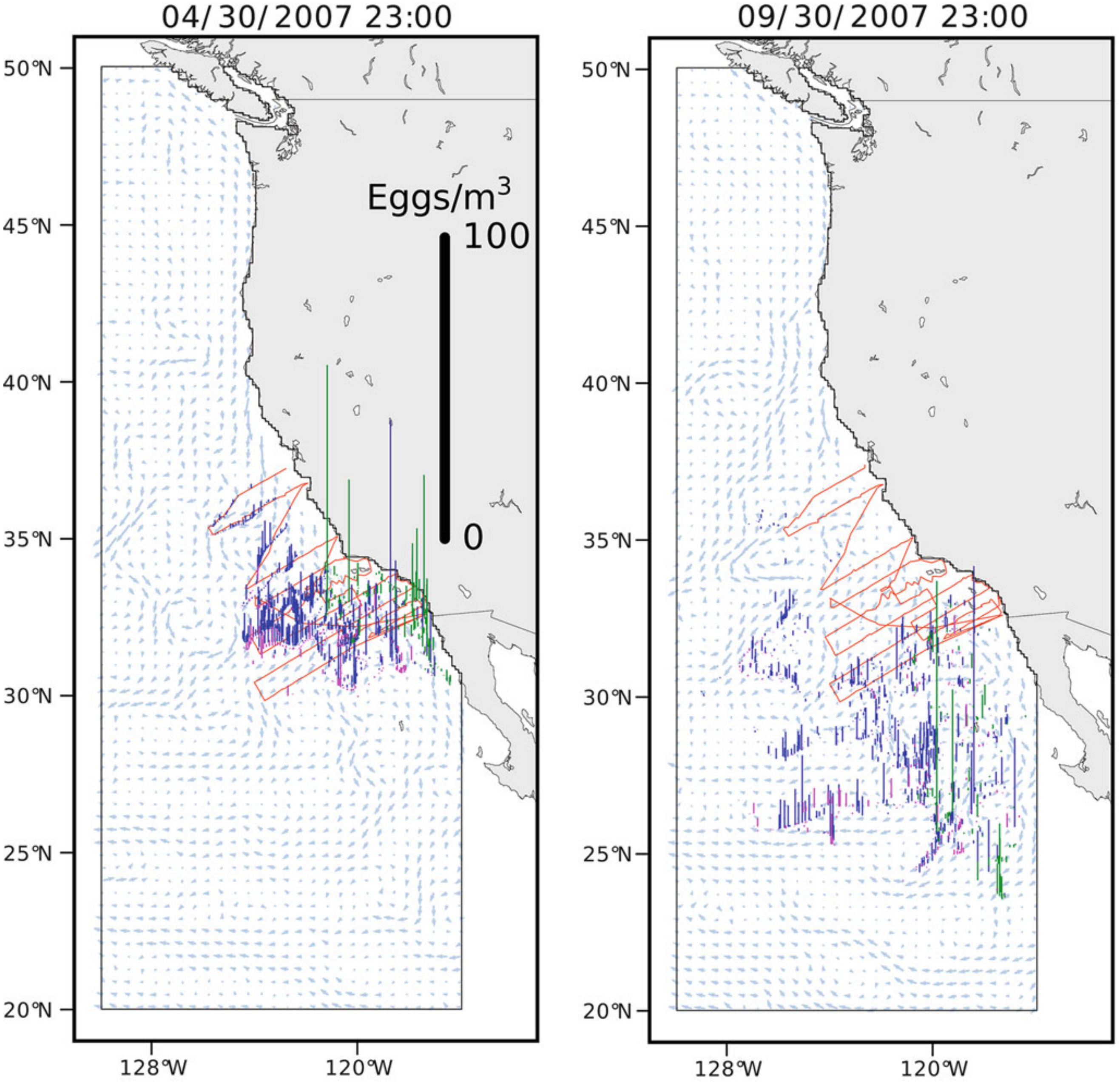

Fig. 6.9 Example showing advection of small pelagic fish eggs by a high resolution Regional Ocean Modeling system (ROMS) model of the California Current System. *Vertical bars* indicate the density of sardine eggs (*blue*), jack mackerel eggs (*pink*) and anchovy eggs (*green*) collected using the Continuous Underway Fish Egg Sampler (CUFES) along the cruise track (marked in *red*) during the spring CalCOFI/ Coastal Pelagic Species cruise of April 2007. *Left panel* is a snapshot of egg positions during the cruise on April 30, 2007. *Right panel* is a snapshot of the positions of young juvenile fishes 5 months later, assuming development of diel vertical migration but no active horizontal swimming. *Light blue arrows* show mean current vectors in the upper 50 m at this time step (Courtesy of Ed Weber, NOAA Fisheries SWFSC, and Yi Chao, Remote Sensing Solutions Inc)

very young juvenile sardine actively swim against the current to recruit somewhere else. These results do not support the concept that sardine are recruiting nearshore in the Southern California Bight.

Sardine range widely along the American west coast, with a large stock in the Sea of Cortez and a seasonally migrating population thought to comprise a northern and southern stock on the Pacific coast (Sect. 4.3.1). The northern stock in particular covers a wide latitudinal range. It is seldom considered that it may be inappropriate to apply a single environmental index when the stocks occupy such different environments, and when age classes experience very different environmental variability, since the immature fish do not take part in seasonal migrations. Galindo-Cortes et al. [175] examined three regions based on the fisheries landings: Magdalena Bay (southwest Baja California), Ensenada near the Mexican-U.S. border, and North Pacific which includes the San Pedro, Monterey, Oregon, Washington and British Columbia fisheries [175]. They selected sea surface temperature (SST) plus three indices to represent the effects of the environment on sardine recruitment: the Southern Oscillation Index (SOI), Multivariate ENSO Index (MEI), and an Upwelling Index (UI). In all three regions SST was correlated with both SOI and MEI. SOI and MEI were also correlated (by definition of MEI). In the North Pacific region, the SST and UI were also correlated [175]. Galindo-Cortes et al. [175] applied a principal components analysis to these data and found that the first principal component representing SST and the ENSO indices accounted for 62–67 % of the variance in recruitment for the three regions, while the second principal component which was determined only by the upwelling index accounted for 20–24 % of the variance (Fig. 6.10).

Rather than using GAMS like Jacobson and MacCall [250] and Lindegren and Checkley [309], Galindo-Cortes et al. [175] used least likelihood and AIC to select the most appropriate stock-recruitment model (either a Ricker model, a Beverton-Holt model, or a density-independent model), and then refit the stock-recruitment models by adding an environmental term to create stock-recruitment-environment models. For the Magdalena Bay and Ensenada fisheries, they found that a Beverton-Holt model of stock-recruitment provided the best fit when an environmental term was included. They tested only the Beverton-Holt model for the North Pacific regions.[3] All of the stock-recruitment-environment models show large residuals. Despite the variability, an interesting result is that both the sign and the variable in the environmental term of the stock-recruitment-environment models differed by region. For the Magdalena Bay fishery, sardine recruitment was negatively related to the upwelling index,[4] but for the Ensenada fishery, sardine recruitment was positively related to the upwelling index. In contrast to these two Pacific coast Baja California fisheries, recruitment in the North Pacific sardine fisheries was not related to upwelling, and instead was positively related to SST and the ENSO indices [175]. This suggests that the environmental variables to be incorporated in a sardine stock-recruit-environment relationship may differ with region. Unfortunately the authors explanations of the mechanisms underpinning these relationships are not very convincing.

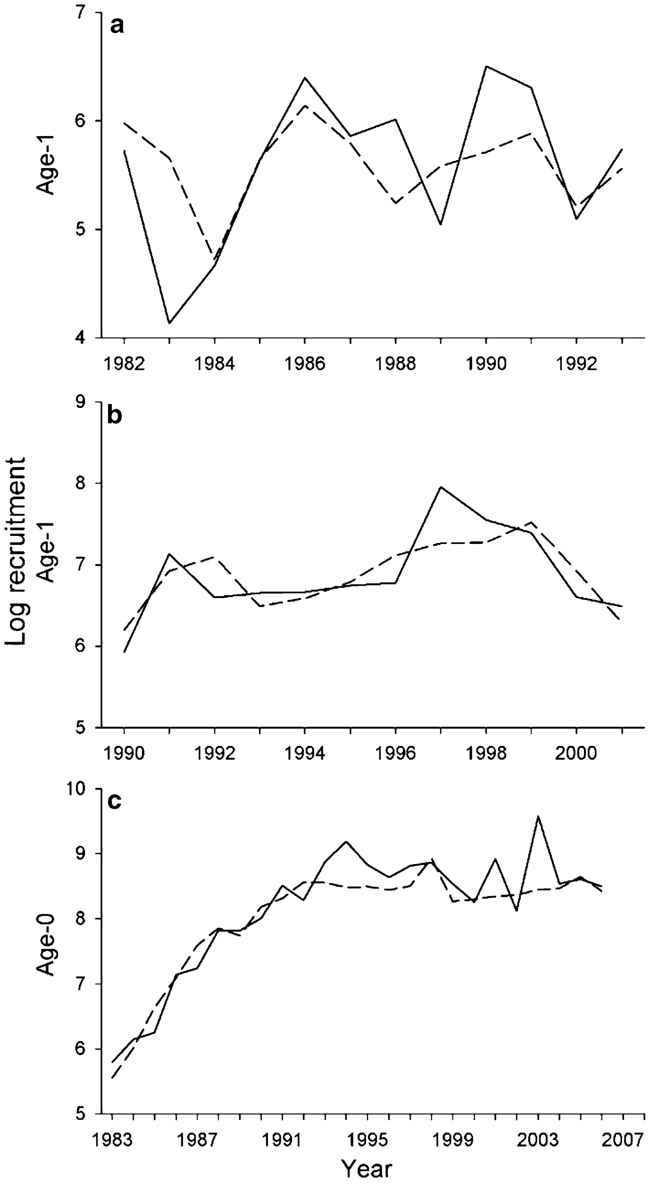

Fig. 6.10 Comparison of log-transformed sardine recruitment (*solid line*) and best stock-recruitment-environment model prediction (*dashed line*) shown in (**a**) Magdalena Bay, (**b**) Ensenada and (**c**) North Pacific fisheries (From Galindo-Cortes et al. (2010) [175])

An Alternative Approach: Curl-driven Upwelling Index for Sardine Surplus Production

An alternative to modeling the effect of environment on sardine recruitment is to model the effect of environment on surplus production. While there are several papers on the temperature index for sardine recruitment (Sect. 6.1.1.8) the wind stress curl index for sardine surplus production [482] has been much less discussed (see Sect. 2.6.2.1). Rykaczewski and Checkley [482] calculated annual sardine

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[3] “[The 2011 U.S. sardine assessment [211]] explored models fit with Ricker and Beverton-Holt stock-recruit (S-R) functions. Models based on the Ricker function were ultimately more stable and improved the trend in recruitment deviations. Jacobson and MacCall [250] found that Pacific sardines were best modeled using Ricker assumptions, and past assessments . . . included a modified Ricker S-R function” [211].

[4] There seems to be an inconsistency in the Discussion of Galindo-Cortes et al. [175] where they explain the potential positive effects of upwelling and subsequent production on sardine recruitment but the environmental parameter pertaining to upwelling in the best stock-recruit-environment model for Magdalena Bay is negative in their Table 6.

surplus production per unit biomass (ASP) from 1983–2004 using: $ASP_t = (b_{0,t} + \delta C_{0,t}) + (b_{1+,t} - b_{1+,t-1} + \delta C_{1+,t})$ where b and c are the biomass and catch of fish less than 1 year old (age 0) or greater than 1 year old (age 1+) at time, t, and δ is a correction factor accounting for the proportion of fish that would have added to the biomass had they not been harvested by the fishery [482]. Annual surplus production is a measure of the net growth of the population which is largely due to recruitment of young fish. ASP was normalized to biomass by dividing by the biomass of age 1+ sardine. The linear trend in ASP was removed prior to comparing with the environmental time series (Fig. 2.52) to compensate for density-dependent recruitment that produces declining numbers of recruits per spawner in an expanding fish population [482]. These authors also used previously published estimates of ASP available for the period 1948–1962 (but no data are available to estimate ASP from 1963 to 1981).

The effect of environmental forcing was incorporated into the annual surplus production by modifying a Fox surplus production model to include an environmental parameter [482]:

$$ASP_t = rB_t\left(1 - \frac{ln\left[B_t\right]}{ln\left[K\right]}\right)$$

where r is the intrinsic rate of increase, B_t is the biomass of age 1+ fish, and K is a constant equal to B_{max} or the carrying capacity of the population. The environmental parameter was incorporated assuming that the effect of environment modifies the population carrying capacity through modifying the term K in the model: $K = B_{max}\left(E_t + \alpha\right)$where $E_t$is the environmental time series and α is a scaling parameter [482]. As discussed in Sect. 2.6.2.1, several 3-month seasonal time series were calculated as standardized anomalies (i.e. by subtracting the series mean and dividing by the series standard deviation), and the best fit determined.

6.1.2 Fishery-Dependent Methods Incorporating CalCOFI Data

6.1.2.1 Pelagic Fish Spotters

Fishers targeting pelagic resources routinely use aerial fish spotters to search for both large pelagic fishes such as bluefin tuna (*Thunnus thynnus*), albacore (*Thunnus alalunga*), yellowfin tuna (*Thunnus albacares*) and swordfish (*Xiphias gladius*), and small pelagic fish such as sardine, anchovy, chub or Pacific mackerel, Pacific bonito (*Sarda chiliensis*), and jack mackerel [324, 531]. From 1963–1990 the National Marine Fisheries Service contracted spotter pilots to keep logs of estimated tonnages of fish schools in 10 × 10 min block areas from northern Baja California to San Francisco. Four to five pilots flew a total of 3,000 h per year [531]. Effort was counted as the number of times the flight path entered a block, termed a block area flight (BAF) and tonnages of fish (T) were estimated by eye [531]. There are considerable diurnal differences in observations by species with anchovy, sardine, chub mackerel and jack mackerel commonly seen at night, while Pacific bonito and bluefin tuna were more often observed during the day [531]. The data from these observations are quite different from those derived from a scientifically designed aerial survey which is a fishery-independent survey method. Interpretation of spotter data are affected by a wide range of factors including imprecise biomass estimates, differences between fish spotters, patchiness, lack of survey design, environmental variables, and regional, seasonal and time of day differences [324]. Nevertheless, indices of relative abundance for pelagic fish, especially anchovy, were developed based on estimated tonnages per block area flights (T/BAF) [529–531]. The original T/BAF was subsequently scaled to permit comparisons of the index between species, and further modified to estimate abundance trends in species-specific core distribution areas [531]. Lo et al. [531] used temperature and mixed layer depth data from CalCOFI surveys in extended delta-lognormal models of spotter data to determine whether addition of environmental data could improve a new index of relative abundance for anchovy.[5] They found that the environmental data were important in interpreting the fish spotter data, especially when conditions were anomalous, as in El Niño years. Lo et al. [531] correlated their modeled index with the stock synthesis estimate of anchovy biomass and concluded that when environmental data were included the correlation with the "true" biomass was greater than for earlier, less complex T/BAF indices (attributed to [529, 530] by [324]). They concluded that environmental data from CalCOFI surveys could be used to improve the precision of relative abundance indices derived from spotter pilot observations [324].

6.1.3 Summary of Use of CalCOFI Data in Stock Assessments

The best known successful application of CalCOFI ichthyoplankton data to stock assessment is the Daily Egg Production Method (DEPM) which is the method currently used to estimate the spawning stock biomass of sardine.[6] The

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[5] The test including environmental data used only a subset of the total dataset comprised of 3,700 flights out of a total of 16,000 flights conducted between 1963–1990. Years with no CalCOFI data were omitted from the test [324].

[6] Total biomass, as opposed to spawning stock biomass, of sardine is estimated using DEPM, acoustic and aerial survey results in combination with an assessment model [211].

DEPM was originally developed to assess anchovy spawning stock biomass, and a daily larval production method was shown to have potential use in the assessment of hake (Sect. 6.1.1.6), rockfish and Pacific mackerel. I reviewed the cases where relative indices of spawning stock biomass developed from CalCOFI ichthyoplankton larval time series were used in assessments (bocaccio, cowcod and Pacific mackerel) (Sects. 6.1.1.3, 6.1.1.4 and 6.1.1.5). The method was successful for the two rockfish species, but had limited utility for the more widely distributed Pacific mackerel. So there are three cases (sardine, bocaccio, cowcod) where CalCOFI surveys provide fishery independent data used in current assessments, one case (Pacific mackerel) where the data have been used but are no longer considered directly useful for the assessment, and one case (anchovy) where the data were used for assessment, but the assessment is no longer being done.

It has also been shown that the time series of California halibut from CalCOFI has the potential to track trends in the population (Sect. 6.1.1.2). The utility of larval time series as indices in stock assessment is sometimes limited by the spatial domain of CalCOFI sampling. This was found to be the case for Pacific mackerel. For nearshore, rocky-reef fishes such as cabezon and sheephead and *Paralabrax spp.* (kelp and sand bass) Moser et al. [403] recommended that the larval index could be improved as a proxy of adult abundance by re-establishing CalCOFI stations off central California. Northward extension of the winter and spring CalCOFI surveys to San Francisco for DEPM measurements now gives information from the central coast (Fig. 1.6). Adding the SCCOOS stations to the CalCOFI sampling pattern now provides information that was lacking on the inshore species in the Southern California Bight (Fig. 1.4).

CalCOFI temperature data have also been used to improve a fishery-dependent method (pelagic fish spotters) for estimating a time series of relative abundance, but this method is not currently directly used in any assessment (Sect. 6.1.2.1). Temperature data used in sardine harvest control rule were originally taken from the Scripps Institution of Oceanography Pier which is much closer to shore than the 66-pattern CalCOFI stations. However, a recent revision of the environmental control rule reinstates the environmental parameter using offshore temperature data from the CalCOFI survey (Sects. 6.1.1.8 and 6.1.1.8).

7 The New CalCOFI and Fisheries

Abstract

The future of CalCOFI includes new roles to play and the incorporation of new types of information derived from ocean observing systems. An important role is contributions to Ecosystem Based Management (EBM). The involvement of CalCOFI in the historical development of ecosystem science helps to inform the role that CalCOFI can play in the development of an Integrated Ecosystem Assessment (IEA) for the California Current System. I first define the terms for EBM, IEA and Coastal Marine Spatial Planning, before discussing how CalCOFI can contribute to Ecosystem Based Management. The development of indicators for the state of the ecosystem can be approached in many ways, but CalCOFI offers a unique opportunity to develop fishery-independent indicators for the California Current System, both because of the length and quality of the time series, and because of the remarkable taxonomic resolution of the ichthyoplankton database. The ichthyoplankton assemblage data provide information about spatial and temporal variability in the system that can be combined with indices based on physical oceanography. The new indices will provide much more specific information about the state of the system than do uni-variate indicators based on temperature, or large-scale climate indices related to ENSO, PDO, or NPGO. Ocean observing systems in the California Current incorporating gliders, moorings, and satellites in combination with high-resolution models will play an increasing role in CalCOFI in the future.

Keywords

California Cooperative Oceanic Fisheries Investigations and Ecosystem Based Management • California Cooperative Oceanic Fisheries Investigations and Integrated Ecosystem Assessment • Ocean Observing Systems and California Cooperative Oceanic Fisheries Investigations

> There is an extraordinary amount of controversy, and not a little confusion, in contemporary debate over "ecosystem management" with regard to virtually all of its aspects – political, scientific, legal, and administrative. Indeed, abundant disagreement is manifest not only over what the specific goals, institutional format, and procedures of ecosystem management should be in practice but even in discourse over the definition of the term itself.
>
> (Harry Scheiber [490])

> We do not need to ever have a full and complete understanding of ecosystem processes. However, we do need an investment in the data required to elucidate the magnitude of ecosystem processes. We do need to expand multispecies, trophodynamic, biophysical, and ecosystem modeling and monitoring, and we do need an explicit recognition that ecosystem processes can have significant effect on fish stocks, ultimately to the point of being formally addressed.
>
> (Jason S. Link [312])

> Indicators are imperative for assessing the status of large marine ecosystems in a fisheries management context.
>
> (Jason Link [311])

> Philosophically, I'm not ready for fish.
>
> (Peter Franks, LTER annual meeting, SIO, 2012)

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7.1 Ecosystem Based Management

7.1.1 The Role of CalCOFI in the Historical Development of Ecosystem Science

In his review of the ecosystem idea Scheiber [490] described the maintenance of biodiversity in complex systems as a "core idea" that has been advanced in most theoetical and administrative formulations of Ecosystem Management (EM). He suggested that a complementary objective was to involve the full list of "stakeholders" or "interest groups", including governmental or corporate groups, interested citizens and environmental groups [490]. The maintenance of biodiversity is not universally held to be a core function of ecosystem management. Attempts to describe what ecosystem management is came to the conclusion that there is "a great variety of interpretations of EM [189] … [and that it is] "a new and slippery concept that contending interests in resource exploitation and management (and also scholars in natural science, public policy and law) were busy trying to capture on their own various terms and for their divergent purposes" (attributed to [190] by [490]).

Scheiber argued that historical trends in fisheries science influenced approaches to ecosystem science, and that programs in California following World War II, including CalCOFI, were fundamental to the development of ecosystem approaches. He highlighted three historical developments that fostered ecosystem science in fisheries research. The first development came out of European fisheries science in the 1890s when a group of scientists began to focus on fish habitats and the effect of the environment on fish population dynamics. These developments were driven by the recognition and subsequent concern that depletion of fisheries could occur as a result of technological advances in industrial fishing. A new understanding of population fluctuations was necessary to inform management regimes [490]. From the 1890s to the 1930s, Norwegian, Danish, English, Scottish and German scientists including Johan Hjort, Johannes Schmidt, Fridtjof Nansen, Michael Graham, and Alistair Hardy laid the foundations for an understanding of the relationships between the physical environment, plankton production and fish recruitment. World War I curtailed both fishing and funding for fisheries science, allowing the European fish stocks to recover from exploitation, but leaving a lasting legacy of low levels of funding due to economic pressures in the interwar period of 1919–1939, compounded by the Great Depression of the 1930s.

In this period, fishery science moved away from the environmental approach, and led by scientists on the West Coast of the US and Canada, took up a "harvest-yield" approach to research [490]. Focusing initially on catch per unit effort and year class strength, this approach led to the development of the estimation of maximum sustainable yield. The focus shifted to a species-based approach, with emphasis exclusively on single species, and the calculation of reference points that could be used in management in the absence of information on how the environment affected population dynamics [490]. Scheiber asserts that the scientists who carried out the harvest-yield analysis, and particularly those who carried out the important assessments of the International Halibut Commission in the 1930s, remained interested and informed about the environmental approach, but lacked the technology, ships and funding to carry out the more demanding environmentally focused surveys.

The collapse of the sardine fishery off California in the post-war years provided the impetus for the second historical development influencing ecosystem science in fisheries. The CalCOFI program, along with the Pacific Oceanic Fisheries Investigations (POFI) program run the the Bureau of Commercial Fisheries in Hawaii, was initiated with a level of funding, ships, and new technology[1] that was unprecedented for any nation since before World War I [490]. An important distinguishing feature of the program, espoused clearly by Roger Revelle who was a key figure in the organization of the project, was that it would embody the ecosystem approach derived from the European tradition, rather than relying upon harvest data alone and a narrow single-species focus. The program was to take a holistic approach to the ocean environment of a large part of the eastern Pacific [490]. It is worth repeating Scheiber's [490] quote of Revelle who said:

> In attacking a problem of such magnitude, all possible scientific tools and methods will have to be employed. It will be necessary first to describe as completely as possible the existing oceanographic and biological situations; second to establish empirical statistical correlations between the various environmental and biological factors; and third, and most important, to make analyses where possible of the processes in the sea, that is the cause and effect relationships which affect sardine production … The sardines cannot be treated as isolated organisms living in a vacuum. The investigation must be an integrated one in which proper weight is given not only to the currents and other aspects of the physical environment but also to the entire organic assemblage including the plants and animals which form the food chain of the sardines, their competitors for the food supply, and the predators, including man …

It is clear from this that the larger vision of an ecosystem approach was fundamental to the CalCOFI program from the outset. The scale of the CalCOFI program in terms of area covered, intensity of sampling and the range of measurements taken was unprecedented. More conventional harvest-yield studies continued at the California state fisheries agencies, but these also received extra funding to broaden the basic science studies undertaken [490]. From the outset the CalCOFI program focused on the dynamics of change in the

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[1] Including bathythermographs and sonar recently developed during Word War II.

ecosystem. The long-term database provided by the CalCOFI program now provides a unique resource for the study of climate change. Within about a dozen years of its inception, there was no other area of the world's ocean, except perhaps the seas of Norway, that was as well studied as the California Current System [490]. The CalCOFI program is an example of Large Marine Ecosystem Research initiated four decades before the concept became widely used. Even before the 1970s, research was conducted under CalCOFI that meets the scientific criteria for ecosystem science underpinning ecosystem management ([117] cited in [490]). These criteria include "a focus on sustainability and on the dynamic character of ecosystems, a recognition of the importance of appropriate spatial boundaries, and an awareness of uncertainty and adaptation" [117]. CalCOFI research also gave attention to inter-species competition for food supply which is particularly relevant for multispecies management [490].

The third significant historical development of ecosystem science that Scheiber describes is the California Coastal Zone concept, initiated in the mid-1960s [490]. Scheiber [490] maintains that the CalCOFI scientists kept themselves somewhat apart from the rough and tumble of management, preferring to let the scientific data speak for themselves. The connection between the ecosystem science conducted by the CalCOFI program and the application of those scientific results to management remained diffuse. Following two key meetings in 1964 and 1965, a study was published that reflected the multidisciplinary and integrative approach to ocean and coastal issues. Milner Schaefer, a leading figure in Pacific tuna research, along with Roger Revelle and Wilbert Chapman insisted that "specialists in political science, law, sociology, economics and public administration be brought into the process of study and policy formulation" [490]. They took the view that the social, organizational and institutional aspects of the integrated social and ecological system had to be addressed, if an adequate analysis of the ecosystem was to be achieved [490]. Ultimately this shift led to the formation of the California Coastal Commission in 1972, by which California established a model for "a systems approach to coastal and marine policy" [490]. Interestingly Schaefer [490] points out that "consensus agreements among interest groups and /or scientific or other policy advisors do not reflexively produce acceptable law or policy, any more than the mere accumulation of massive quantities of scientific data in and of itself provides adequate guidance for policy" [490].

7.1.2 Defining EBM, IEA, and CMSP

Before discussing the role that CalCOFI can serve in Ecosystem Based Management (EBM), Integrated Ecosystem Assessments (IEAs), and Coastal and Marine Spatial Planning (CMSP), I will present the definitions of the terms, since the definitions and distinctions between the terms are often not apparent. I have made liberal use of quotation in this section to avoid modifying the definitions by attempting to paraphrase them. These definitions of EBM, IEA and CMSP are quoted from [29].

In terms of their functional relationship,

> EBM is the unifying principle and way of doing business by which NOAA implements its strategic goals and objectives to enhance the sustainability of valued ecosystem services and the overall health, resilience and productivity of our nations coasts and oceans. IEAs and CMSP are, respectively, an analytical tool and a public planning process that, along with other relevant NOAA scientific and resource management capabilities, can inform and advance EBM across NOAA's broad stewardship mandates. [29]

The broad framework of Ecosystem Based Management (EBM) is defined as:

> … an integrated approach to management that considers the entire ecosystem, including humans. The goal of ecosystem-based management is to maintain an ecosystem in a healthy, productive and resilient condition so that it can provide the services humans want and need. Ecosystem-based management differs from current approaches that usually focus on a single species, sector, activity or concern; it considers cumulative impacts of different sectors. Specifically, ecosystem-based management:
>
> - emphasizes the protection of ecosystem structure, functioning and key processes;
> - is place-based in focusing on a specific ecosystem and the range of activities affecting it;
> - explicitly accounts for the interconnectedness within systems, recognizing the importance of interactions between many target species or key services and other non-target species;
> - acknowledges interconnectedness among systems, such as between air, land and sea; and
> - integrates ecological, social, economic, and institutional perspectives, recognizing their strong interdependences. [384]

Within the broad framework of EBM, Integrated Ecosystem Assessments (IEAs) provide a process for working with stakeholders and managers to provide robust decision-support information and to identify priority management issues. The process involves evaluating benefits and risks to social and ecological sectors (i.e. tradeoffs), and evaluating alternative management scenarios (management strategy evaluation). If performance is monitored and evaluated, IEAs provide the basis for adaptive management [29].

> NOAA defines IEAs as a synthesis and quantitative analysis of information on relevant physical, chemical, ecological and human processes in relation to specified ecosystem management objectives … IEAs integrate diverse ecosystem data, including socio-economic information, to analyze ecosystem and community status relative to a defined issue and then predict future status based on forecasts of natural ecosystem variability coupled with evaluation of alternate management strategies. [29]

IEAs are an "analytical engine" for EBM

> bring[ing] scientific and technological rigor to resource management decisions by incorporating diverse sources of data into

> ecosystem models that evaluate trade-offs among management decisions related to competing objectives. [29]

Coastal and Marine Spatial Planning, on the other hand, is focused more on the optimal application of multiple uses to a region:

> Coastal and marine spatial planning is a comprehensive, adaptive, integrated, ecosystem-based, and transparent spatial planning process, based on sound science, for analyzing current and anticipated uses of ocean, coastal, and Great Lakes areas. Coastal and marine spatial planning identifies areas most suitable for various types or classes of activities in order to reduce conflicts among uses, reduce environmental impacts, facilitate compatible uses, and preserve critical ecosystem services to meet economic, environmental, security, and social objectives. In practical terms, CMSP provides a public policy process for society to better determine how the ocean, coasts, and Great Lakes are sustainably used and protected - now and for future generations. [29]
>
> CMSP provides regional planners and stakeholders with a science-based, transparent means of matching emerging human uses to appropriate ocean and coastal areas in ways that minimize conflicts and impacts, while ensuring sustainable benefits . . . [from] ecosystem services.” [29]

7.2 CalCOFI and Integrated Ecosystem Assessment

An important component of IEAs involves “. . . analyz[ing] ecosystem and community status relative to a defined issue and then [to] predict future status based on forecasts of natural ecosystem variability”. Doing this involves “synthesis and quantitative analysis of information on relevant physical, chemical, ecological and human processes in relation to specified ecosystem management objectives”. Among the many data and analyses required for IEAs, CalCOFI can provide physical, chemical and ecological time series to develop quantitative indicators or indices. Despite the enormous literature derived from the CalCOFI program, the research to develop indicators to characterize resilience, to quantify changes in biodiversity, to formulate combined physical-biological indices, all of which can be used to detect changes in the ecosystem over time, has only just begun. It is also unclear at this stage, what the best indicators might be, from the many that could be developed. Furthermore, we do not yet know how well relatively simple indices or indicators will work in terms of characterizing “ecosystem and community status” which is sometimes loosely referred to as the “health” of the ecosystem. It is also uncertain to what degree such indices will facilitate “predict[ing] future status based on forecasts of natural ecosystem variability”.

Link [312] presented a long list of questions (61 in total) that need to be considered in the implementation of ecosystem-based approaches into fisheries management. He then suggested that not all questions need be addressed and that a “triage” approach be adopted where the magnitude and relative importance of processes in an ecosystem are documented by answering selected key questions, and the answers to these questions could be used to modify fisheries management advice in a quantitative way [312].

He argues that it is necessary to minimize complexity when discussing Ecosystem Approaches to Management (EAM), and that scientific advice can be heuristic, tactical or strategic. He characterizes heuristic advice as background information of the kind that comes from answering the short (triage) version of his long list of questions. This kind of advice alone is not sufficient to determine control rules, decision rules, or reference points for management decisions. Strategic management advice pertains to the bounds on the entire ecosystem and this sort of advice, which is currently not widely used, can be applied to set limits on large scale secular trends that would affect multiple aspects of the system. An example provided by Link [312] is an El Niño event that affects the bounds of overall system productivity and might require quantitative changes in total system removals or aggregate (e.g. guild, trophic level or species group) biomass allocations. Tactical advice covers the more familiar recommendations based on reference points and control rules (such as the Scripps pier temperature index used in sardine management). This kind of advice is short-term, binding, and often pertains to a single species. Link [312] argues that tactical advice should be broadened to include more information (not just using temperature, for example) where it is applied to single species, and that it should be applied to multispecies and aggregate groups as well.

Link [310] argued that fishery management in an ecosystem context will require increased monitoring, among other things. Link [310] lists a series of “emergent properties” that could serves as proxies for management decision criteria. These include a number of metrics that can be calculated using the CalCOFI ichthyoplankton database including systems analysis metrics such as resilience, persistence, resistance, and stability. The ichthyoplankton database can further be used to calculate community metrics such as diversity indices, species richness, evenness, dominance, overlap indices and interaction indices. Recent re-processing of CalCOFI net samples will also make zooplankton size spectra available, which Link [310] listed as an community metric that should be monitored. The caveat here is that these metrics are not currently available from all of the components of the ecosystem, from phytoplankton to whales, and likely never will be. Nevertheless, CalCOFI provides long time series for the ichthyoplankton and zooplankton components of the system that can be used in Integrated Ecosystem Assessments. I give some examples of CalCOFI-based indices for the California Current Integrated Ecosystem Assessment in the next section.

7.2.1 Developing Indices or Indicators

Indices are metrics that provide quantitative or semi-quantitative summaries of the underlying complex interaction between often poorly understood components of an ecosystem. The assumption is made that these summaries hold useful information that can be used for management decisions, thereby avoiding becoming lost in the interactions of a complex ecosystem [472]. Indices are more attractive when there is a requirement for stakeholder involvement, because their interpretation is easier than the output of dynamic ecosystem models [472].

Indices or "indicators" were originally used to measure how well a fishery was doing [210]. Rochet and Trenkel [472] refer to this as an "audit function", where the index can be used in a management strategy evaluation.[2] Typical indices used in this capacity are the biomass of a stock, or estimates of mortality [210]. More recently, indices have been used to trigger management action [470], which Rochet and Trenkel [472] refer to as a "control function". The search for useful indices has become increasingly common in fisheries oceanography in the last 20 years. Available datasets, both long-term (such as CalCOFI and the SAHFOS[3] series) as well as shorter time series, have been increasingly mined in the search for indices. Many different indices have been proposed and there is increasing recognition that different indices would be necessary for different operational frameworks for decision making. The most developed frameworks include the Australian Ecologically Sustainable Development Reporting Framework which has ecological, human and economic components [116], or the frameworks proposed by FAO[4] [157,472]. Exactly how indices are incorporated into stock assessments is still a point of discussion [216].

Developing indices and selecting the most appropriate combinations of indices is fraught with difficulties. Lavaniegos and Ohman [298] made an important point when they stated that "it is apparent that characterizing physical climate variables alone is inadequate for understanding and forecasting trajectories of plankton ecosystems". Their point is also relevant to fish. They argued that temporal trends in populations are influenced by non-linear dynamics between and within species rather than linear tracking of climatic forcing [220, 224], except where the generation time of an organism approximates the dominant period of environmental forcing [221]. This suggests that caution is warranted when balancing parsimony with mechanism. The simplest approach, e.g. using temperature or other single physical variable as an environmental index for population fluctuations, while parsimonious, will generally be inadequate to represent the underlying mechanisms. Interestingly, in the case of sardines, the realized generation time (approximately 4–8 years) does approximate the dominant period for ENSO forcing (4–7 years), so in this case ENSO-related climate variables may prove useful as a component of a new environmental index.

7.2.1.1 Variability of Stock-Recruitment-Environment Relationships

There is now considerable evidence that relationships between stock, recruitment and environment may prove to be ephemeral. In most cases where statistical relationships have been found between environmental variables and either the biomass of commercially exploited fishes or some index of recruitment, the relationships were not robust when further data were added to the original dataset [412]. The observation that stock-recruitment-environment relationships generally fail has not prevented a burgeoning literature presenting newly discovered relationships. One emergent generalization from Myers review [412] is that stock-recruitment-environment relationships tend to be more robust at the margins of a species geographical range. This is presumably because the physiological tolerances of species are approached and so the impact of climate change on environment have greater effect. However, environmental factors such as temperature exert an effect both directly (through physiological tolerances, for example) and indirectly through the foodweb by their effects on prey and predators affecting sensitive life-history stages [266].

Interaction between environmental effects and the impacts of fishing on biomass or recruitment are affected by geographical location and the biogeographic range of species. As mentioned above, environmental indices may correlate better with stock and recruitment at the margins of species range, and so the effects of environment alone could induce population collapse [55]. In contrast, in the center of the species range, the effects of environment may be less, and the relative impact of fishing may be greater than the effect of environmental conditions on biomass or recruitment. As a result it may be difficult to develop environmental indices using data over an entire species range. The explanatory power of indices can be high and well-correlated with shifts in species abundance in one region within the species range, but have low explanatory power in another part of the range.

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[2] "[Management Strategy Evaluation] (MSE) involves assessing the consequences of a range of management options and laying bare the trade-offs in performance across a range of management objectives. Key steps in the approach involve turning broad objectives into specific and quantifiable performance indicators, identifying and incorporating key uncertainties in the evaluation, and communicating the results effectively to client groups and decision-makers" [509]. MSE specifically seeks to identify the consequences of alternative decision options by explicity addressing uncertainty and trade-offs [509].

[3] Sir Alister Hardy Foundation for Ocean Science operates the Continuous Plankton Recorder in the north Sea and North Atlantic.

[4] Food and Agriculture Organization of the United Nations.

This was shown by Beaugrand and Kirby [55] where their plankton index was correlated with the decline of Atlantic cod in the North Sea, but had low explanatory power for fluctuations of Atlantic cod biomass off Iceland.

The effect of geographical range and regional differences on the explanatory power of environmental indices is complicated by the evidence that populations and communities are modifying their geographical ranges with climate change. Developing indices necessarily requires time series, but if the distributional ranges of species are shifting latitudinally with climate change, the movement in the margins of the range will tend to obscure the relationship between environmental indices and biomass or recruitment by increasing the variability of the relationship.

A further complication is that correlations between environmental variables and either biomass or recruitment may not be consistently significant, or even in consistent in sign, over different time scales. Sliding correlation analyses of relationships between temperature, plankton indices and the biomass and recruitment of Atlantic cod showed that relationships can be (1) consistent over time, (2) may strengthen over time, or (3) may change sign over time from positive to negative correlations [266].

These three considerations; that stock-recruit-environment relationships are strongest at the margins of a species biogeographic range, that the ranges of populations shift with climate change, and that correlations may be inconsistent over time, indicate that stock-recruit-environment relationships are both spatially and temporally dynamic. Recent studies show that the search for stock-recruit-environment relationships that apply over the full spatial domain of a fish species using long time series of indices independent of the spatio-temporal variability may be doomed to temporary success at best.

There is some evidence that the most consistent predictor variables are likely to be those that exert both direct effects on physiological tolerances and that affect food web processes such as energy allocation, predator-prey interactions and benthic-pelagic coupling [55, 266]. Kirby and Beaugrand [266] used partial correlation and path analysis to reveal consistent correlative relationships with the relative abundance of *Calanus finmarchicus* (an important prey item for larval Atlantic cod), and the biomass and recruitment of cod. They interpreted these non-linear correlations as trophic amplification of the effects of temperature through the food web. The observation that the correlations are greatest with a time lag was used to infer that the amplification was acting on sensitive life history stages, namely the larval phase of development. There is also a distinct possibility that the most consistent predictor variables in stock-recruit-environment relationships will be different between species.

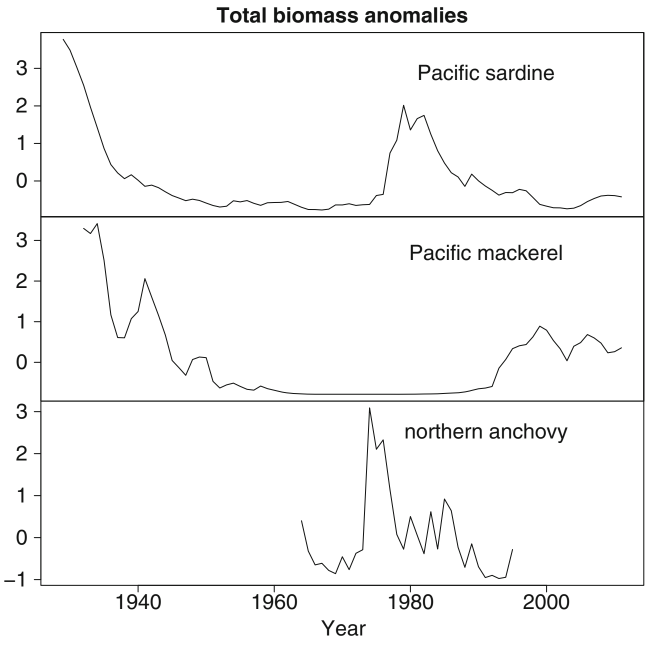


Fig. 7.1 Total biomass anomalies of three small pelagic fish species, Pacific sardine (*Sardinops sagax*), Pacific mackerel (*Scomber japonicus*), and northern anchovy (*Engraulis mordax*) are the best estimates provided by a member of the SWFSC stock assessment team (Paul Crone) in June 2012. Each series was standardized as anomalies by subtracting the series mean and dividing by the series standard deviation. Units are standard deviations

7.2.1.2 Utility of Fishery-Dependent Versus Fishery-Independent Time Series

Long time series are fundamental to detecting changes in the ecosystem over time, both in terms of secular trends and shorter time scale fluctuations. In some cases, such as for time series of total biomass of commercial fish species, it is necessary to merge estimates derived from different methods (e.g. VPA, DEPM, acoustics, assessment model) into a consensus time series. In the case of CalCOFI, standardized time series exist for an extraordinary range of both commercial and unexploited species, and these can be manipulated in various ways to provide information on the current state of the ecosystem in the context of variability and trends over the past 60+ years. Time series trends of zooplankton displacement volume, copepods, thaliaceans, euphausiids, ichthyoplankton, and sardine were discussed earlier (see Sects. 4.1.3.3 and 4.1.3.3).

Figure 7.1 shows a time series for biomass anomalies of coastal pelagic species. The commercial catch time series for sardine, Pacific mackerel, anchovy, jack mackerel, and market squid (Fig. 7.2) were not considered informative enough to be included as an index in the Calfornia Current IEA, mainly because there are so many factors that influence commercial catches, apart from environmental factors.

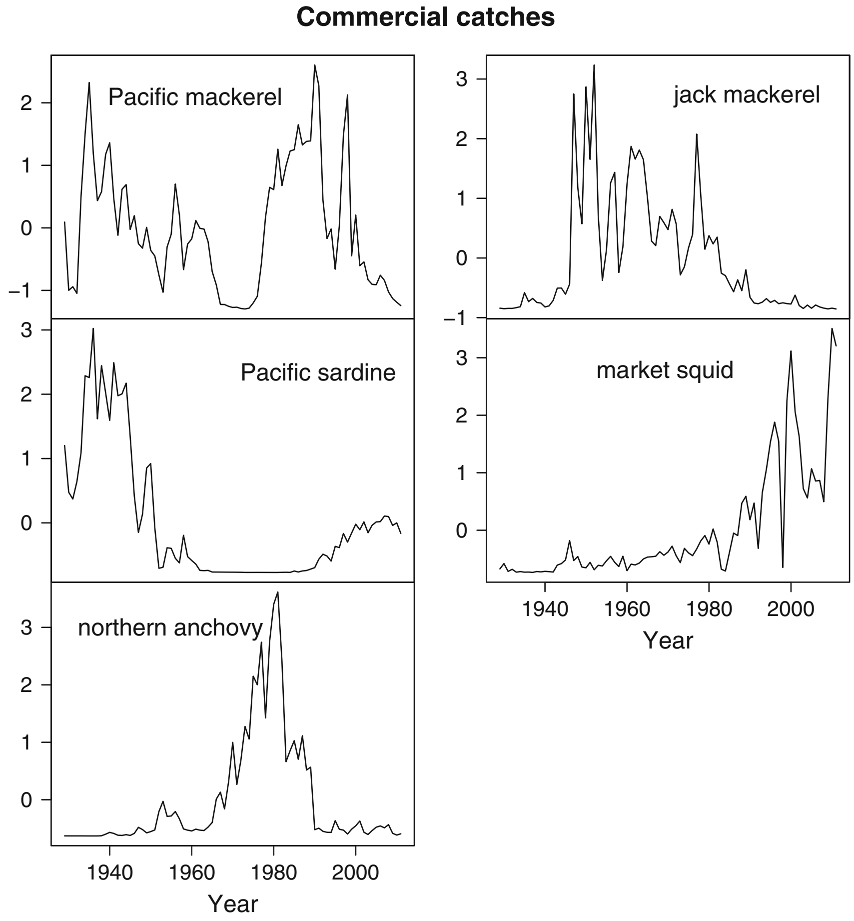


Fig. 7.2 Total commercial catch anomalies of five coastal pelagic species, Pacific mackerel (*Scomber japonicus*), Pacific sardine (*Sardinops sagax*), and northern anchovy (*Engraulis mordax*), jack mackerel (*Trachurus symmetricus*) and market squid (*Doryteuthis opalescens*) provided by a member of the SWFSC stock assessment team (Paul Crone) in June 2012. Pacific mackerel, sardine, and anchovy include landings from Mexico and the Pacific Northwest U.S., while jack mackerel and market squid catches are from California only, reflecting the distribution ranges of these fisheries. Each series was standardized as anomalies by subtracting the series mean and dividing by the series standard deviation. Units are standard deviations

However, biomass time-series from the stock assessments were useful as indices in the IEA, despite the very different lengths of the time series for individual species (Fig. 7.1). At present, Pacific sardine and Pacific mackerel are assessed species, but jack mackerel, anchovy, and jack mackerel are only classed as monitored species. There are no current formal annual biomass estimates for monitored species. The point is that fishery-independent time series are more likely to be accepted as useful input to the process of developing indices for an IEA than are unstandardized fishery-dependent time series. Next I consider a few of the fishery-independent time series from CalCOFI that were being considered in 2012 for inclusion as indices in the first IEA of the California Current System.

7.2.1.3 Fishery-Independent Time Series from CalCOFI

CalCOFI provides a species-rich database from which to construct informative indices. However, spatial variability is very high, and large temporal fluctuations in the time series of individual species should be interpreted with caution. It is also necessary to take care with consistency of sampling, if bias is to be avoided. Time series of individual species may be less informative than time series of carefully grouped assemblages of species known to be associated with certain oceanographic conditions. I present one case here by way of example.

Oceanic Mesopelagic Ichthyoplankton and Forage Fish as Indicators

To provide an integrated measure of large-scale responses to environmental variability, we aggregated the mesopelagic fishes into cool- and warm-water groups following Hsieh et al. [220]. These groups are likely to reflect general trends in the ecosystem better than time series for individual species, some of which are relatively data poor. Results from previous studies revealed that the larvae of oceanic ichthyoplankton assemblages fluctuate with climatic variability more than either coastal-oceanic or coastal species [224, 270, 275, 401, 407, 521, 557]. Consequently, assemblages of oceanic mesopelagic ichthyoplankton are likely candidates to develop indices related to climate variability (see Sect. 4.1.3.3 for a fuller explanation of why this should be the case). Oceanic mesopelagic species found off southern California can be broadly categorized as warm-water associated or cool-water associated (Table 7.1).

All data are from the core CalCOFI sampling area (lines 76.7–93.3, stations 28.0–120.0; Fig. 7.3) for years when the

Table 7.1 Mesopelagic and coastal pelagic species from CalCOFI surveys categorized as warm- or cool-water associated off southern California

Genus species	Common name	Subcategory
Bathylagus pacificus	Slender blacksmelt	Cool-water
Leuroglossus stilbius	California smoothtongue	Cool-water
Lipolagus ochotensis	Eared blacksmelt	Cool-water
Protomyctophum crockeri	California flashlightfish	Cool-water
Stenobrachius leucopsarus	Northern lampfish	Cool-water
Tarletonbeania crenularis	Blue lanternfish	Cool-water
Vinciguerria spp.	Lightfishes	Warm-water
Triphoturus mexicanus	Mexican lampfish	Warm-water
Symbolophorus californiensis	Bigfin lanternfish	Warm-water
Bathylagoides wesethi	Snubnose blacksmelt	Warm-water
Ceratoscopelus townsend	Fangtooth lanternfish	Warm-water
Diogenichthys atlanticus	Longfin lanternfish	Warm-water
Diogenichthys laternatus	Diogenes lanternfish	Warm-water
Sebastes jordani	Shortbelly rockfish	Not categorized
Sardinops sagax	Pacific sardine	Not categorized
Merluccius productus	Pacific hake	Not categorized
Engraulis mordax	Northern anchovy	Not categorized
Citharichthys sordidus	Pacific Sanddab	Not categorized

All species were captured as larvae and enumerated in units of mean larvae $10m^{-2}$ captured in the CalCOFI core area on quarterly cruises and summed over all four quarters for a year

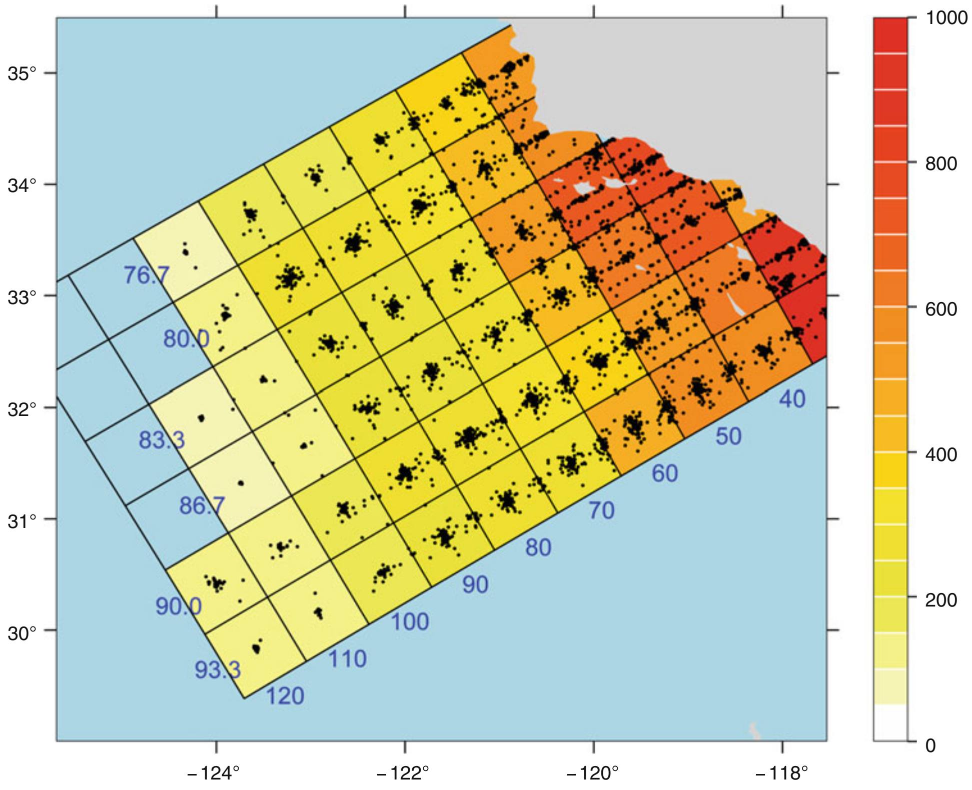


Fig. 7.3 Grid pattern of 3.3-line by 10 station cells in the core CalCOFI sampling area (CalCOFI lines 76.7–93.3). *Color key* indicates the actual number of sorted oblique tow samples collected within each cell for the period 1951–2010. *Black dots* indicate the actual sample locations (Courtesy of Ed Weber, NOAA Fisheries SWFSC)

core area was sampled during each quarter of the year. Mean larval abundances (larvae10 m^{-2}) were estimated for each 3.3-line by 10-station cell in the core area for each quarter, and then cells were summed over the year. Means across the entire time series were then calculated using the delta-lognormal distribution [444]. This procedure standardized the data given unequal sampling effort during some cruises, many zero catches, and seasonal but variable patterns of spawning for the fishes analyzed. Under the current IEA framework, an indicator is considered to have changed in the short-term if there are obvious increasing or decreasing trends over the last 5 years. An indicator is considered to be

Fig. 7.4 Time series of sardine and anchovy larvae from oblique net tows on CalCOFI cruises off southern California (see Fig. 7.3). *Dotted horizontal line* shows the delta log-normal long-term mean and the *solid horizontal lines* show ± one standard deviation above the long-term mean. The *arrow* indicates the trend in the long-term mean (horizontal is stable). A *dot* indicates that the 5-year mean is within one standard deviation of the long-term mean. Positive or negative signs indicate that the 5-year mean is either above or below one standard deviation of the long-term mean

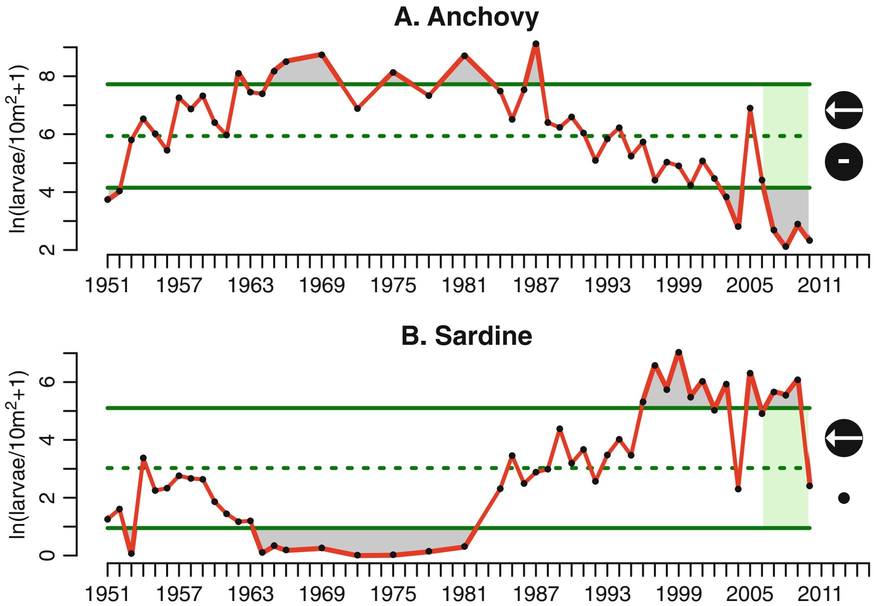
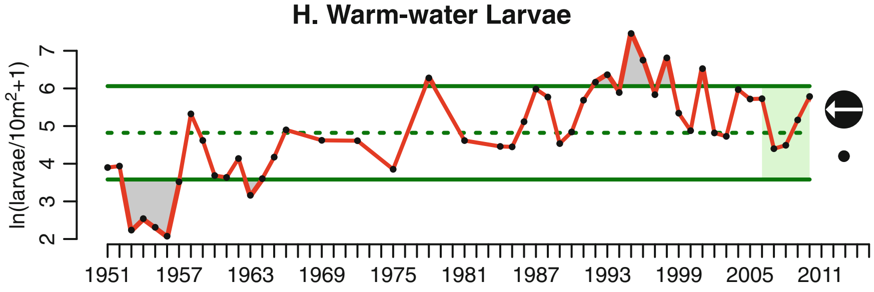


Fig. 7.5 Time series of warm-water associated mesopelagic fish larvae (species listed in Table 7.1) from oblique net tows on CalCOFI cruises off southern California. Data and symbols are as for Fig. 7.4



above or below long-term norms if the mean of the last 5 years of the time series differs from the mean of the full time series by more than one standard deviation.

Anchovy larval abundance has generally decreased over the last 30 years (Fig. 7.4). The decline in anchovy larvae followed a long-term increase over the previous 30 years (1950–1970s) (Fig. 7.4). Sardine larvae show an entirely different trend to anchovy, and it has been argued that abundance peaks of these species alternate at decadal time scales [101, 315, 496]. Such long-term changes hint at a low-frequency out of phase fluctuations in abundance, but the generality of the observed species alternation cannot be definitively assessed with the relatively short 65-year CalCOFI time series [367] (see Sect. 4.1.3.3). Sardine larvae in the 1980s and 1990s increased from the collapse of the stock in the 1950s. Although there has been a minor decline in sardine larval abundance since 2000, it has generally remained above the mean of the last 60 years (Fig. 7.4). There are other interpretations of the trends in sardine abundance [597] that differ from this interpretation based on the trends of larval abundance. It is important to note that trends in ichthyoplankton abundance should not be interpreted as equivalent to trends in adult abundance without careful validation (see Sect. 6.1).

Warm-water associated oceanic mesopelagic larval fish assemblages show strong, episodic fluctuations about a mean value that has been relatively stable over the past 60 years, but with some evidence of declines in larval abundance over the last 20 years (Fig. 7.5) (see [225, 270, 275]). Cool-water associated larvae appear to show a decline over a longer time scale than do the warm-water associated larvae (Fig. 7.6). Cross-correlation of the two mesopelagic assemblage time series[5] shows periods of alternating positive and negative correlations (Fig. 7.7). The warm-water mesopelagic species are on the northern margin of their range when present off southern California. Consequently, a reasonable explanation for the reversing pattern of correlations in Fig. 7.7 is sequential overlap or separation of the cool-water and warm-water assemblages. The cool-water mesopelagic assemblage is more generally resident off southern California, and the warm water mesopelagic assemblage may be periodically advected northward with intrusions of warmer Equatorial Pacific Water or North Pacific Central Water. This should

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[5] Both time series were first scaled as standardized anomalies and then first-differenced to create stationary series prior to calculating the cross-correlation.

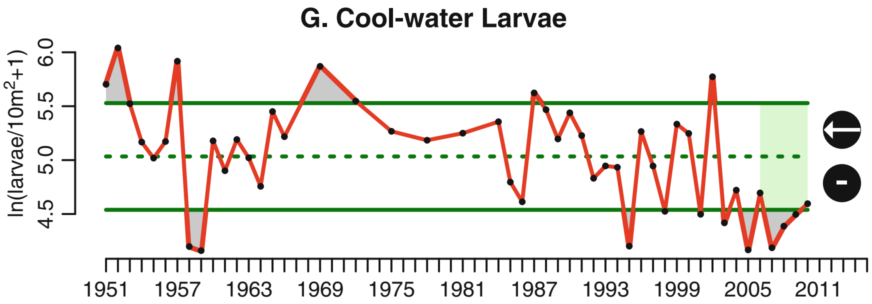

Fig. 7.6 Time series of cool-water associated mesopelagic fish larvae (species listed in Table 7.1) from oblique net tows on CalCOFI cruises off southern California. Data and symbols are as for Fig. 7.4

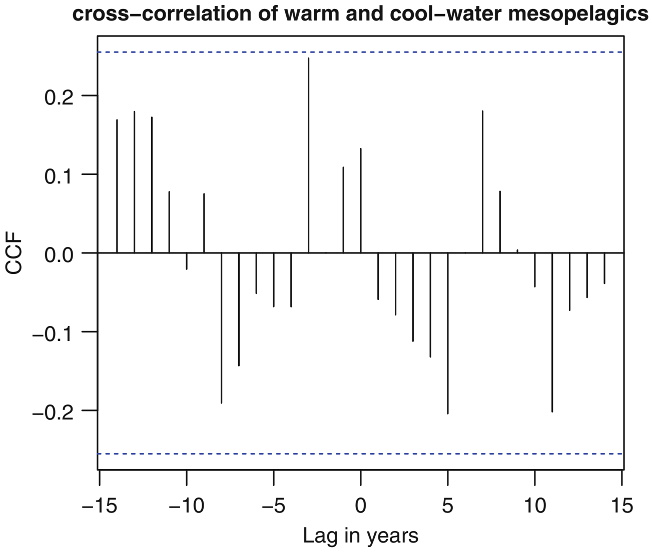

Fig. 7.7 Cross-correlation of warm-water and cool-water associated mesopelagic larvae from Fig. 7.5

be verifiable by examining the spatial patterns of the larval assemblages in relation to water mass properties.

Even in the absence of a deeper analysis, the temporal pattern of these climate-related ichthyoplankton assemblages provides insight into changes in the state of the ecosystem off southern California. This is a key function for indicators in the IEA, and illustrates the value of the species-rich CalCOFI database for such developing indicators.

7.3 Perspective

The CalCOFI program will be strengthened as its relevance and utility to climate change studies and ecosystem management increases. Its value to the scientific community is greatly enhanced when potential users can access quality-controlled and error-checked data directly through the Internet. Despite this, data were often retained by research groups, rather than made available to the broader scientific community. While there are many reasons for retaining data within research groups, NOAA has a clear policy commitment to making all tax-payer funded data available to the public. If the data cannot be downloaded from the Internet, they are available from the relevant supervisory staff within NOAA. If the data cannot be obtained from the supervisory staff, a simple email request to a NOAA Freedom of Information Act liaison will initiate formal procedures to release the data, but this should be an option of last resort. There are more restrictions for data collected by university researchers associated with CalCOFI, and some data may only be made available through collaborations. If all of the data collected by CalCOFI were made fully available, the value of the program would be further increased. It is only recently that the full richness of the CalCOFI species-specific ichthyoplankton data have been made fully available on the Internet. The process of making data available is not yet complete for all taxonomic categories collected on CalCOFI cruises (phytoplankton, zooplankton, micronekton, nekton, seabirds and mammals). In contrast, the oceanographic data collected on CalCOFI cruises has been widely available for many years.

Early work using the CalCOFI data often focused on a species group, or in some cases even a single species. As the taxonomic resolution of the databases increased, it became possible to examine the variability and trends of complex assemblages, and the relevance of CalCOFI to ecosystem management increased. It was also quite common for analyses to be limited to the sub-discipline of the researchers, but truly multidisciplinary studies using CalCOFI survey data are increasing in number. The richness of CalCOFI will not be fully exploited until taxonomists, fisheries scientists, assessment scientists, engineers, biological oceanographers, physical oceanographers, and modelers work together in various combinations on multidisciplinary problems. CalCOFI is essentially a work in progress, building on a rich history, contributing to new problems, and providing a basis for new collaborations. The history of CalCOFI is built upon the work of many people from different disciplines who have contributed in many different ways over the years. The final chapter brings together accounts and perspectives by some of these people. Each of their stories adds a more personal touch to the science.

Perspectives on CalCOFI

8

Abstract

CalCOFI has a legacy in the people who collect the samples, analyze the data, and interpret the results. There are many colorful characters in the history of CalCOFI. In this chapter, I gather some of their stories as recollections and photographs. While there are many others who are not included here, the present contributions add depth to the CalCOFI story by exposing a more personal dimension. This chapter contains biographical accounts from George Hemingway, John McGowan, Carl Boyd, Roger Hewitt, Dave Griffith, Ron Dotson, James Wilkinson, John Butler, Geoff Moser, Bill Watson, Andrew Thompson, Paul, Smith, Tony Koslow, Gail Theilacker, John Hunter, Nancy Lo, Steve Bograd, Ralf Goericke, Bertha Lavaniegos, Dan Rudnick, Amanda Netburn, Noelle Bowlin, and Rebecca Asch.

Keywords

California Cooperative Oceanic Fisheries Investigations history • Personal perspectives of California Cooperative Oceanic Fisheries Investigations

8.1 George T. Hemingway: From Naples to La Jolla: 1952–1999[1]

In 1954 I returned to the United States after 2 years living in Portici, the ancient port of Pompeii and Herculaneum on the Bay of Naples. During that time, at 12 and 13 years old, I used to hang around the Stazione Zoologica *Anton Dohrn* on the Naples waterfront and at the digs at Ercolano. I had several trips with the Stazione and with the Scouts to the pristine and species-rich waters of Ischia and Capri. It seemed appropriate then, that a year after arriving back on US soil I was invited by my biology teacher at Mission Bay High School in San Diego to submit an application for an NSF Summer Scholar program at Scripps. I was accepted into the program for the summers of 1956 and 1957.

Wheeler North managed the program out of the old T Building east of the Research Support Shops. I was assigned to work for Carl Hubbs and his wife-assistant, Laura. One of Carl's projects was the Temperature data collection along the coast of Baja California. Volunteer families, living in coves and beach communities, from Rosarito to Guerrero Negro, took daily mercury-in-glass temperature readings in the adjacent surf. Al Stover and Art Flechsig were Carl's techs, and one or the other was the driver for our 3-week sojourns into Baja California. The road south from Tijuana was paved to Guerrero Negro, but the side roads were often two-rut, dirt roads, that wound along, following the contours of canyon heads and arroyos. We would stop along the coast at private homes by the water, to collect our data sheets. We left behind new underwear and socks, and for one lady, hot-cross buns or cinnamon rolls were always in demand. We were always fed and watered and welcomed. Al and Art knew all of these families personally. These were my first experiences with the collecting of time-series data, and thinking about how they provided a different scale and quality of information from point-in-time data. These were also my first experiences trying to make Neapolitan Italian work to communicate in Mexican Spanish: my hosts were very appreciative and patient indeed! My shore-side work station was in the cellar

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[1] George Hemingway was involved with CalCOFI for 33 years during his work at Scripps Institution of Oceanography in La Jolla, California until his retirement in 1999.

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Fig. 8.1 George Hemingway in 1969 examining the broken end of a bongo net lanyard (Photo by Elizabeth Venrick)

Fig. 8.2 George Hemingway in retirement, aged 71 years (Photo provided by George Hemingway)

of the old aquarium. A special treat those two summers was spending a part of each lunch hour singing ballads and chanteys with Sam Hinton, then director of the aquarium.

Little did I know that 9 years later, after college and Army artillery service, I would sign on with Dick Mead, up in T-21, for what would become a 33 year career at Scripps, collecting multivariate time series oceanographic data, in the company of the most skilled and disciplined technical teams in the world. The BCF (later NOAA-SWFCS) biologists, and sometimes the CDFG biologists, accompanied us on the CalCOFI Cruises. At the beginning it was eight or so each year, and we served one-on, one-off. Our funding was part DOD and part State of California, for the most part, as "thermocline studies" were still matters of interest to the Navy.

Our primary work platforms in those days were the R/V *Alexander Agassiz* and the NOAA Ship *David Starr Jordan*, and later, R/V *New Horizon*. Other ships I served on were R/V *Ellen B. Scripps*, R/V *Oconostota*, B/I *Alejandro de Humboldt*, R/V *Paolina T*, USCGC *Pontchartrain*, B/I *Alejandro Alzate*, NOAA Ship *McArthur*, R/V *Argo*, and R/V *Horizon*.

From time to time we carried Mexican scientists from Departamento de Pesca and from the universities and graduate schools of Baja California and Baja California Sur. About 1970, Dick Mead and Dick Schwartzlose asked me to take on five students per semester in a course called "Practical Oceanography". I was appointed a part-time lecturer at SDSU, and took on my first classes of students. They were required to prepare seminars, one per student per week, to present to the others. I didn't let them off the hook just because they were going to sea: they collected all their material for their seminars before sailing, and presented their talks at sea as well as on land.

It was on one of those survey cruises in the Gulf of California that Mexican academicians from Ensenada attended my classes, and then went to Dick Schwartzlose to ask him to lend me to them for a year or two. My wife, Jean, new baby Gillian, and two dogs departed August of 1973 to spend some life-changing years in Ensenada where I was appointed *Catedratico en Biología* at the Marine sciences school of the Autonomous University of Baja California. Newly arrived geologist Tim Baumgartner lived for a time in an apartment of our house on the south edge of Ensenada. He is still a professor at CICESE, the graduate school across the highway from the UABC north campus. Tim's research was crucial to our understanding of long-term natural variation in sardine populations off the coast of the Californias. He later played a critical role in re-establishing the biological-oceanographic survey cruises along the Mexican part of the California Current region that CalCOFI had relinquished.

When I returned to La Jolla in 1975, the experiences, enhanced language skills, and friends I had gained while working in Mexico, led to much increased interactions between

CalCOFI and the Ensenada marine scientists. This was paralleled, in some cases preceded by, the work of Paul Smith, John Hunter, Nancy Lo, Angeles Alvariño and Geoff Moser with the scientists in La Paz, Baja California Sur, and by Reuben Lasker and Dick Schwartzlose's friendships with Jorge Carranza, Saul Alvarez and Daniel Lluch. Ed Brinton and Tom Hayward gave guest lectures in Ensenada and other Mexican labs from time to time. Many of those friendships survive to this day, as I was reminded in November of 2010 at the 16th Biennial Oceanographic Congress of Mexico held at Ensenada.

These relationships led to us receiving a $360,000 International Cooperative Assistance grant from the Office of Sea Grant for Mexican-UCSD collaboration, as well as a series of grants from the Tinker Foundation, in support of Latin American graduate students at SIO in pursuit of Master's and Doctoral degrees, in the realm of a half million dollars. During that era Mexican marine scientists were encouraged to attend and present papers at CalCOFI conferences while Mexican student attendance was aided by the travel scholarships that we originated. Countless Mexican scientists, students, and academicians have participated on CalCOFI cruises.

Our principal SIO vessel in support of CalCOFI cruises when I came aboard was the R/V *Alexander Agassiz*. A recycled Army inshore freighter cum floating machine shop, She served the University of California from 1962 until 1976. She was to be replaced by the State of California vessel R/V *New Horizon*. The sale of the *Agassiz* in 1976 left us no University ship for the 1977 CalCOFI cruises. Dick Schwartzlose was very good friends with Dr. Jorge Carranza Fraser, Director General of the Department of Fisheries in the Secretariat of Fisheries of Mexico (SEPESCA). Dick approached Jorge about possibly "renting" a SEPESCA research vessel for the year. Dick made the arrangements and sent me down to Mexico City to take care of the formalities. Since CalCOFI did not have the juridical nature to sign a contract with the Mexican Government (GOM), the contract had to be negotiated with the Office of the President of the University of California. A signing ceremony took place at SEPESCA with Lic. Fernando Rafful Miguel, signing the agreement, and Dr. Carranza and the PESCA staff witnessing. I brought the half-executed documents back from Mexico City and delivered them into the hands of the UCSD Business Office. There they languished while lawyers and business people and translators scrutinized the papers. Weeks went by. A month and more. Time was wasting and we needed to get the ship to Nimitz Marine Facility for modifications, upgrades, and outfitting. I expressed my frustration with Dick. He counseled patience. More time passed and finally I called the Office of the President and got to a friendly ear who knew something about ship movements and timing of planning and logistics. He said he'd call the UCSD Business Office. I got a call very quickly from them advising me to keep my nose out of their business. I told Dick and said, "I have a mind to retrieve the papers and take them myself to the Office of the President. Dick amusedly said words to the effect, "go for it". I called Oakland and made an appointment for 2 days later. Next day I flew to Oakland and spent the night in a nearby hotel and at 7:30 am I announced myself to the secretary of the Vice President for Business Affairs. The secretary took the papers to the assistant to the VP. In a few moments the VP came out, thanked me for the "special delivery" and said he would send the executed documents to San Diego when they had been reviewed. I said that I would prefer to stay and wait for them. He objected. I said I'll stay and I sat down. About 1:00 a secretary brought me a half a sandwich left over from the staff lunch and said, "I don't think you'll get them today." I said "I'll wait." She went back inside and I heard slightly elevated voices. She came back outside and smiled at me. At about 3:30 she brought me some coffee. At 4:30 she left for the day. At about 5:15 the VC came out and said, "Here are the fully executed documents. There is a car and driver waiting down stairs. He will take you to the airport. We have a reservation for you on the 6:30 flight. Don't ever do anything like this again!" I thanked the VC and acknowledged my presumption, bowed out and left, papers in hand, flew back to San Diego and called Dick, and said, "Dick, we have a ship."

The SEPESCA vessel, B/I *Alejandro de Humboldt*, completed six cruises for CalCOFI between December 1977 and August 1978, before going into dry dock at National Marine in San Diego for a leaking main shaft. A variable pitch propeller technician came from Norway and a seal specialist from Germany came to oversee the repairs. The ship missed the final, scheduled cruise of the year due to this difficulty.

I had the unequaled pleasure of serving as the ship's *Patron* for that entire year, dealing with purchase and installation of new electronics and satellite navigation system, new mattresses, an upgrade to the galley, new flooring on the main deck passageway, provisioning for sea, union crewmen, crusty immigration personnel, and the transportation of SEPESCA scientists and crew from Mazatlan to San Diego and back again. Many friends were made. Jorge Carranza and Joe Reid celebrated the completion of the work with a dinner and party at my home, the two competing with songs and tunes on guitar and organ, while Mexican scientists "grazed" in my garden on freshly plucked *jalapeños.*

Garth Murphy was the first CalCOFI Coordinator (1959–1965); he was paid by the MRC, he was followed by J.L. Baxter (1966) paid by CDFG, P. M. Roedel (1967–1968) paid by CDFG, J.L. Baxter (1969) paid by CDFG, and Marston Sargent (1970–1973) paid by the MRC. Herb Frye of CDFG was the last CalCOFI Coordinator under the Marine Research Committee (1974–1978). But change was in the wind for CalCOFI:

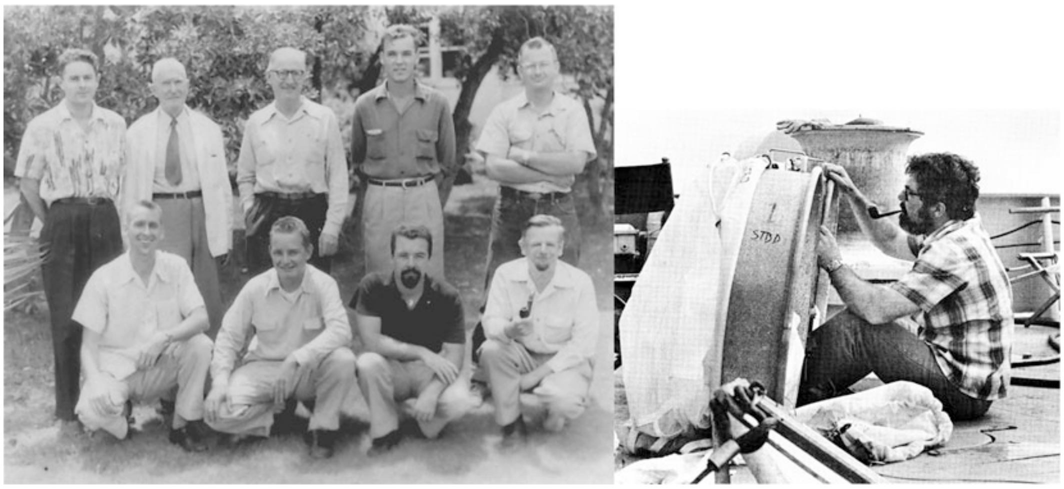

Fig. 8.3 (*Left*) July 9, 1953. Standing, *left* to *right*: C. Hand, W. Cob, M. Johnson, D. Arthur, L. Bevn. *Front*, *left* to *right*: R. Bieri, R. Menzie, J. McGowan, J. Hegepeth. (*Right*) John McGowan as a young man working on a bongo net at sea (Photos provided by John McGowan)

> With the passage of the Fishery Conservation and Management Act of 1976, the United States established a conservation zone between 3 miles and 200 miles off the coast within which the United States has management authority over fishery resources excepting tuna. The original utility to the fishing industry of the Marine Research Committee, that of forestalling management of the resources, was somewhat removed. Therefore, at the request of the California fishing industry, at the end of 1978, the Marine Research Committee was dissolved by an act of the California Legislature; however, by mutual agreement, the University of California, the National Marine Fisheries Service and the California Department of Fish and Game are continuing the California Cooperative Oceanic Fisheries Investigations as a viable cooperative research unit, beginning in 1979.
>
> (John Radovich, CalCOFI Reports 23, 1982).

I was appointed Coordinator (1979–1982) following the sunset of the MRC. Until 1993, the coordinator slot rotated each 3 years among the three agencies: SWFSC-NMFS, CDFG, and SIO. John Grant (CDFG served from 1983–1986; Gail Theilacker (NMFS 1987–1990); Patty Wolf (CDFG 1990–1992). I then served continuously from 1993 to 1999, when I retired permanently. Thirty three years with the best people on earth![2] What a run!

8.2 John A. McGowan: CalCOFI: A Personal Account[3]

I came to Scripps Institution, as a beginning graduate student and research assistant in the Fall of 1952. I already had an interest in plankton so I was assigned to Professor Martin Johnson's laboratory. He was one of the authors of "The Oceans" [544], a planktologist and connected to the nascent CalCOFI program. As an artless young graduate student, I got the impression that the entire CalCOFI program was divided into something akin to collaborative task groups. The groups were: The Bureau of Commercial Fisheries; California Depart of Fish and Game; Scripps Institution of Oceanography; Stanford University's Hopkins Marine Station and the California Academy of Sciences. The determination of the spatial and temporal patterns of sardine (and other fish) spawning and larval abundance was the job of the old Bureau of Commercial Fisheries (now National Marine Fisheries Service, NMFS), while the state Department of Fish and Game collected catch statistics and monitored the distribution of adult fish. Hopkins Marine Station had a modest water column sampling program in Monterey Bay. I was uncertain of the role of the California Academy of Sciences except that they supported an important (and often ignored) study of the gut contents of the adult sardine and arranged our annual meetings. The Scripps role appeared to me to be one of the largest: it was to determine the circulation and chemistry of the system as well as the ecology of its zooplankton.

Since in those early days, the sardine population covered several hundred thousand square nautical miles, it was no small task to study its habitat. It meant, essentially, a study of the physics and biogeochemistry of the entire California Current. The work at Scripps (SIO) was subdivided into the Data Collection and Processing Group (DCPG) and the Marine Life Research Group (MLRG), two strongly coordinated and overlapping entities under the administrative heading of Prof. John Isaacs. It was the job of the DCPC to collect and process all of the physical/ chemical data and to prepare cruise reports. That group was (and still is) a hard-working, sea-going bunch of experi-

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[2] From a 1980s SIO bumper sticker.

[3] John McGowan was a research biologist and professor of oceanography in the Marine Life Research Group at Scripps Institution of Oceanography at the University of California, San Diego from 1960 until his retirement.

enced technicians and their cruise reports are a treasure trove of information. The MLRG was, in the early days, pretty much devoted to analyzing large plankton samples. The NMFS plankton program was designed to determine the spatial/ temporal distribution of fish eggs and larvae. The net tows, of about 300 m^3 water each, taken for that purpose, could not avoid sampling the meso-zooplankton which co-occurred with the fish eggs and larvae. Since these, together, were the community within which the sardine population dynamics played out, analyzing zooplankton was an important task. Although West Coast intertidal algae, invertebrates and shore fishes were well known by the early 1950s, there were very few studies of the flora and fauna of the much larger, pelagic realm of the main body of the California Current. Martin Johnson decided that the pelagic, planktonic species content of this domain and their temporal/ spatial patterns was necessary factual background for any understanding of food web "trophodynamics" and "yield" of energy available to the sardine. Prof. Johnson, as chairman of PhD committees, parceled out the study of species patterns of the zooplankton of the California Current to no less than seven graduate students, so that all major plankton taxa were represented. Since I was a late-comer to the plankton group, I was assigned the numerically insignificant pelagic mollusks for analysis [375]. Since this category included larval squid, I was eventually redeemed, from my study of the inconsequential, when much later, squid became, somehow, “more important".

As the species distribution maps accumulated, a general pattern began to emerge. Not surprisingly, it appeared that most holoplanktonic species had much larger spatial ranges outside of the California Current. Very few local endemics were found in any of the taxa. Further, there were obvious north-south and east-west abundance gradients and a great deal of agreement among those species as to the space/ time patterns. In almost endless conversations and debates among us students, the consensus was reached that temporal changes in biomass and species abundance structure were strongly influenced by advective input of waters and their fauna, from the north, west and south. These provinces all had their own species assemblages. These disparate faunas, all of which had different environmental histories, were mixed together, especially in the Southern California Bight. Thus this area, the chief spawning zone of the sardine, is what plant ecologists call an ecotone, a broad mixing or transition zone between “different but adjacent sectors of landscape”. These are, in our case, the Sub-Arctic, Central Gyre and Equatorial species provinces whose water mass structure differs strongly. It appeared to us, then, that the state of this system was very strongly influenced by physical advection, immigration-emigration, as well by the internal dynamics of the more orthodox ecosystem model of density-dependent regulation within the system, through trophic level energy flow.

An important aspect of our version was that there is a diminished role for feedback loops regulating the state of the system, and therefore, a dubious role for either top down or bottom up regulation. We thought of it, at the time, as sort of a sidewise density-independent regulation. The sardine and anchovy and other harvested fish appear to be highly adaptable species that have managed to colonize such complex zones. The studies of species time/ space patterns in the California Current System led us to two more important results: the determination of basin wide community/ ecosystem biogeography (recurrent group patterns) [156] and strong evidence that temporal changes in biomass within the California Current System were strongly associated with the external forcing by climatic variability and change. The great El Niño of 1957–1958 was a profound perturbation to the plankton community structure (including fish and squid larvae) [376, 378, 382] as were other such variations and even long-term climatic trends [475]. There were large responses but rapid recoveries in species abundance patterns and species dominance structure. We were able quantify these effects because of our biogeographic monitoring before during and after these events. The role of climate in regulating the state of the system became quite clear.

8.3 Carl Boyd: Life on the CREST[4]

Dr. Norris Rakestraw, a remarkable man as a chemist, teacher, and human being played a major role in my career in oceanography and in my participation both as a collector and a grateful user of CalCOFI data. Dr. Rakestraw, sometime in the spring of 1955, sent letters to aquatic scientists in the US asking for help in finding students to work for summer employment on ships at Scripps Institution of Oceanography. He offered a small amount of money and an opportunity for neophytes to experience life in oceanography. I was finishing up a B.Sc in Zoology at Indiana University and was looking forward to my routine summer job in the construction business. Going to sea seemed like a good alternative to the pick and shovel life, and I asked Dr. David Frey to offer my name to Dr. Rakestraw. Life in Biology at Indiana University at that time was a hot bed of molecular genetics; Jim Watson had graduated from IU a couple of years earlier, and his work with Crick at Cambridge was exploding the field of genetics. I had taken more courses in genetics and biochemistry than in ecology, and would have enjoyed pursuing molecular genetics as a career. But I had never seen the Pacific Ocean,

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[4] Carl Boyd was a professor in the Oceanography Department at Dalhousie University in Halifax, Nova Scotia, Canada prior to his retirement.

Fig. 8.4 (*Left*) Carl Boyd at sea on a CalCOFI cruise April 20, 1960 (Photograph from a San Francisco Chronicle article) and (*right*) under better weather conditions, also in 1960 (Photos provided by Carl Boyd)

and Jacques Cousteau and Rachael Carson and coral reefs sounded wonderful to a boy from the prairies of Kansas and Oklahoma.

In early June 1955 I got on a Grayhound bus in Indianapolis, rode several days and nights through the southwest to San Diego, and ended up at a small inexpensive hotel in La Jolla (yes, they existed then), and that night had my first view of the Pacific from the La Jolla Cove, looking out at the lights that I was to later learn were shining from the Scripps pier. Dr. Rakestraw drove me down to Point Loma and gave me the details of how the job worked. I was to be billeted on whatever research ship was at the dock in Point Loma, was to cook my own meals in the ship's galley (food in the freezer), and find any bunk that was available. The work was to go to sea on the monthly CalCOFI cruises as an assistant to a Scripps employee. When other programs needed technical help, I would be assigned to those cruises. On the return of the ships to Point Loma I was to work up on the hill with the Point Loma data analysis group, analyzing the data that we had collected. I was too naïve to be stunned, but I certainly wondered what I had gotten myself in for. The fringe benefits were considerable – when I wasn't at sea I had all of San Diego and La Jolla available to me. The three or four of us summer employees learned that we could check out a car from the lab, and head out to see much of the life and nightlife of San Diego. Security problems at Point Loma didn't exist. I could board any Navy ship in the harbor, could come and go at my leisure through the Point Loma gates, and enjoy un-restrained access to all of Point Loma and San Diego.

It wasn't all roses. My first cruise was on the RV CREST, a Yard Mine Sweeper that had been given by the US Navy to Scripps to be used as a research vessel. She was 136 feet long, made of wood and bronze so that her magnetic signal was minimal, she was designed to sweep mines in harbors and near shore approaches, and was never designed to go to sea. Her twin screw diesel power system and her careful speed control made her ideal for sweeping mines as well as for nearshore oceanographic work. Conversion to oceanography involved the installation of a hydrographic winch and a BT winch. Otherwise she was pure US wartime Navy. My first cruise was to run the CalCOFI lines north of Point Conception, around the Farallon Islands, probably around north of Line 70. The routine of the CalCOFI lines, and other cruises that followed, became standard: typically there was a shallow bottle cast with a Nansen bottle, a plankton tow with a 1 m net, mesh #3, down to 140 m at a speed of about 2 knots designed to keep a 45° wire angle, and a BT cast. Water samples were taken for salinity and phosphate, and we tossed in several drift bottles. At certain stations we did the full bottle cast with 15 reversing, protected thermometers down to maybe 1,000 m, and at some stations we towed an electrode assembly called a GEEK, or geomagnetic electro kinetograph designed to measure the direction and magnitude of surface currents. Plankton samples were washed into liter bottles, pickled with formalin, and marked with a location and date and log number. My initials are on a lot of the plankton labels in those CalCOFI bottles. Unknowingly, all these data came to be of fundamental interest to me when I set about studying the distribution and behavior of the pelagic crab *Pleuroncodes planipes*. The CREST behaved well in the usual seas off California, and I eventually got used to the motion of normal swell, but the CREST and I were very much out of our element in storms and high seas, and I failed completely in a storm off the Farallons. My bunk in the focsul was the perfect place to test a novitiate. The CREST rolled 45° side to side, tossed and turned, lifted and dropped and went sideways, the crash of dishes in the galley was absolutely frightening. There was nothing to do except to wedge myself in my bunk and try to sleep. In the middle of the second night the engine crew warned us that the wooden deck was opening up, allowing seawater to spill down the walls of the engine room where the electrical panels were starting to get wet. In those few hours I realized that oceanography was not for me, and that maybe I could go back to Indiana University and enroll in the dental program. With this thought and discomfort I went to sleep, to awaken to a ship that rolled gently, that moved along nicely, there was sunlight when I went up on deck, and overhead I saw the underside of the Golden Gate Bridge. My thoughts of disaster at sea had not been far off; the surge of the storm waves on the ship's rudder had caused the steering cable to part, with the probable consequence of the ship having real trouble. The engine crew had spliced the cable back together with some flimsy device, and the captain had set course for repairs in San Francisco. We entered the harbor in blue skies and calm water, tied up near the ferry landing at the Embarcadero, and I felt like I had gone to heaven. All of San Francisco was there as I stepped off the gangplank. I had a few days of wandering about the city, doing the jazz clubs, taking the ferry over to Oakland, taking it all in. It was wonderful – my first exploration of many foreign ports, and there has been none better. The storm off the Farallons had quieted, we headed back to finish our lines, my sealegs were repaired and my appetite was rediscovered. I recall sitting on the bow of the CREST as we went through the Channel Islands, eating a baloney and onion sandwich that I thought was absolutely delicious. Maybe I could do oceanography after all.

I met and spoke to Dr. Carl Hubbs when I returned to La Jolla and questioned him about applying for graduate school at Scripps. He looked at my background of courses and suggested that I go back to Indiana to take a Masters degree; his reasoning was that Scripps offered no courses in the basics of anything – lots of advanced courses, but teaching basics was not a strength of Scripps. I needed to get additional courses in biochemistry, physiology, biology of algae, etc. because there was no way to get that information at Scripps. UCSD was still a deserted marine corps base up on the cliffs above Scripps. Dr. Hubbs had given me excellent advice, I enjoyed the work for the Masters degree, and I was pleased to be accepted for graduate work at Scripps. I was accepted to work with Dr. Martin Johnson, who was collecting data on the distribution phylosome larvae *Panulirus interruptus* in the CalCOFI samples. He was exploring the age-old question of how do planktonic larvae of near-shore benthic organisms manage to return to the shores of their birth to reconstitute the parent population, and he was coupling the phylosome occurrences with data on ocean currents that were being accumulated at that time via geostrophic measurements and GEEK measurements that I knew well. As part of my research assistantship I sorted the samples for these thin, transparent, invisible larvae that were ideally built to drift in the ocean and to not be seen in a dish of miscellaneous zooplankton. Dish after dish were examined under the microscope, and occasionally a phylosome larva was seen and removed for DJ, as we called him. The effort, however, gave me an excellent opportunity to become familiar with the names and types of zooplankton in these bottles, and I had access to the world's experts who were also fellow students, Ed Brinton, Leo Berner and John McGowan who could identify these new animals and tell me something of their biology.

The people who did most of the sorting of the CalCOFI samples were technicians working with Dr. Johnson. Marnie Knight, Dr. Johnson's head technician, held our cohort of zooplankton specialists together with a wisdom and grace that guided me though the ups and downs of being a graduate student in a remarkable research institution. Marnie sorted phylosomes, ran the office, mothered and scolded and supported all of us in degrees according to our needs. Gail Theilacker worked beside Marnie as a sorter and helped maintain the attitude of good fun, all the while competently picking out the phylosomes. Gail eventually left our lab to work with Reuben Lasker up on the hill, to develop techniques for rearing fish larvae that are standard lab practice today. One bottle I sorted from a station off Magdalena Bay of Baja California had an extraordinary number of a strange zoea larvae – that one bottle near CalCOFI Station 143.40 had an estimate of larvae of 42,000/1,000 m^3, almost a pure culture. I knew nothing of decapod larvae, but Ed Brinton in the lab next door thought maybe they were zoea of *Pleuroncodes planipes*, a crab that was unusual in that it was bright red and swam at the surface in deep water, a pelagic crab. There was nothing in the literature about these larvae, and I was off to my first publication, a classical presentation of the five stages of the larvae, with drawings, mouthparts, all that. Drawing them under the tutorage of Dr. Johnson was a bit of a shock. He thought my beautiful first drawings were terrible and sent me back to the microscope to see more detail and back to the drafting table to produce drawings with cleaner lines. Two papers of careful, classical drawings resulted [74, 76]. Again, I was earning my spurs but didn't know it. The year 1957 was an El Niño year, but we really didn't appreciate the nature or the importance of those now well-studied events. John Radovitch wrote a paper that was sub-titled something like "1957—the year of warm water and southern fishes" [453], and in December of 1957 the beaches of La Jolla were covered with adult *Pleuroncodes* that had drifted up from their usual waters off Baja California and had been blown ashore on the Scripps beach. *Pleuroncodes* resembles a small and lighter version of the Atlantic lobster; it is about 3 in. long, is bright red, and has long legs covered with bristles that allow the animal to settle through the water as if on an umbrella. Newspapers headlined their stories with "Reds are invading California Beaches". (This was in the worst of the Cold War, McCarthy was deluding everyone, and Reds were on the beaches as well as under the beds). But I was the resident expert on *Pleuroncodes*, and I got my picture in the San Francisco Times holding a handful of these small crabs. Nobody, including me, knew anything about these strange beasts: my thesis topic was presented to me there on the beach.

My primary resource was, of course, the CalCOFI plankton samples that had been collected off Baja California for several years with enough frequency for me to build a credible story about sites of abundance, probable growth rates and general life history from larval development up to adulthood. I did the usual thing of going through hundreds of the CalCOFI bottles, pulling out Red Crabs, counting and measuring them, plotting the data, and building the story. But I had my fill of working on pickled plankton, and found a new and unexpected opportunity to study a member of the community of pelagic crustaceans, not just as specimens pickled in formalin, but as living organisms. The CalCOFI samples gave me the essential information concerning where *Pleuroncodes* lived, how they were distributed by local ocean currents, and information about how the populations were transported up the California coast, well beyond their usual home waters off Baja California. But I enjoyed most of all keeping *Pleuroncodes* alive in the newly constructed aquarium laboratory just down the steps from my office. Marine zooplankton are notoriously difficult to keep alive in the laboratory, and hence we infer concepts such as how these animals eat, what they eat, and how long they live only by making observations on the dead specimens. By coupling the information from the CalCOFI samples with my tendency to work on live animals, I was able to pose some of these questions to live, named and numbered individual *Pleuroncodes*. Some of the crabs that had washed up on the beach had eggs attached that hatched out as larvae; I was able to achieve the unusual success of raising the larvae of *Pleuroncodes* from adult to Stage One larvae to adult, a process that required careful gardening of live animals for over a year. The aquarium facilities allowed me to keep larvae, juveniles, and adults alive in a controlled setting that was remarkable, and gave me the opportunity to determine growth rates of live animals, observe their method(s) of feeding, measure feeding rates, molting, and a host of other life functions that can only be implied for most marine zooplankton [75].

I realize now that I was riding a crest, this time from the thrill of research going well in a remarkable setting. The underlying goal of Martin Johnson's lab was to link the occurrence of various species of zooplankers to "water masses" as defined by Sverdrup. Ed Brinton did brilliant work on euphausiids, Bill Clarke on deep-sea mysids, and Leo Berner on salps and doliolids, and later Abe Fleminger brought a solid knowledge of copepods to the group of experts. John McGowan developed an interesting relationship by noting the occurrence of a peculiar pelagic worm *Peobious* in a water mass off the northwest US. Bill Fager assembled these several studies into a statistically robust analysis that described various communities of zooplankton in the Pacific and associated these clusters of species with specific water masses. The work of this collective demonstrated that distinct communities of zooplankton existed that were defined spatially (and presumably genetically) by the geographic limits of these distinct large bodies of water. The sum of the work is a marvelous package – an understanding of how distinct assemblages of plankton can exist in a seemingly unbounded ocean. The group in Martin Johnson's lab was able to achieve its understanding of the relationship between species of zooplankton and continuity of the surrounding water mass because of the collections of animals available to the scientists. These samples and the associated data, largely from the CalCOFI program, have been the basis of a rich body of information about the California Current and the oceans in general. They constitute a long time-series, extending back to the 1950s, and have already been mined for information about decadal changes in this current, with inferences of global warming. They represent a remarkable tool for future studies.

8.4 Roger Hewitt: "We're Always Where They Want to Be"[5]

I came to the SWFSC in the early 1970s to work with Paul Smith on the use of sonar to map epi-pelagic fish schools, and later with Reuben Lasker on the development of the Daily

Fig. 8.5 Roger Hewitt on bridge of NOAA Ship David Starr Jordan circa mid-1970s (Photo provided by Roger Hewitt)

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[5] Roger Hewitt is the Assistant Director for Ships and Infrastructure at NOAA Fisheries Southwest Fisheries Science Center in La Jolla, California.

Egg Production Method–both eventually became assessment tools. I also analyzed the CalCOFI larval data set to look for patterns of mortality and spatial dispersion as part of my thesis at SIO. In between, I switched gears and worked as the relief mate on the David Starr Jordan. I think this may make me unique in CalCOFI history as someone who helped collect the data, analyze the data and drove the boat.

At the time, our ability to get good fixes outside of radar range of land was limited, and we dead-reckoned (i.e. extrapolated our position using direction and speed) for several hours or even days as we progressed out to the seaward extent of a long line of CalCOFI stations and then returned on the next line to make landfall – sometimes several miles from where we expected. We also maintained a log on the bridge that indicated the desired station position and the actual position. Once we had a good fix, being a contentious navigator I distributed the error between our actual position and the dead-reckoned one among the station locations and changed the log to reflect what I thought was our best estimate of where we actually were at each station. That is, until the first mate caught on to what I was doing, severely chastised me, and informed me that "we're always where they want to be". Thereafter the desired position and the actual position were identical.

8.5 David A. Griffith: Life on the David Starr Jordan, January, 1990 as Best Remembered[6]

I had just been hired as a full time employee of the Southwest Fisheries Science Center in La Jolla, California as of December 18, 1989. My first duty was to learn the ways of conducting a scientific cruise aboard the NOAA Ship David Starr Jordan under the watchful eye of Billy Flerx. I hadn't a clue what I was in for. The ship was to depart from the Nimitz Marine Facility in Point Loma on the fourth day of January, 1990 and head for the offshore waters of the great Northwest. Destination, Coos Bay, Oregon. To make a very long story short, the cruise sucked. We hit bad weather every time we turned around. By the time that we reached Coos Bay, our boilers were done for and the ship was freezing. Since the ship was essentially a floating icebox, they put us up in hotels in Coos Bay. Several days later, boilers fixed and we're ready to go. Unfortunately the weather was not so cooperative. We were able to make it out several times during that time period to get some of the work done, but it seemed like something was always going wrong. During the entire cruise, we went through seven turbo chargers. Not a good sign. So, here is my significant story.... We had finally been able to leave port, whether it was Coos Bay or Newport I can't remember, but we got on station and the weather turned very, very bad. If I remember correctly, and that's a stretch, we hove to for a few days with winds well over 60 knots and the seas were more than fifteen feet. By that point we all had more than enough and the decision was made to head back into Newport. By the time that we reached the entrance to Newport, the surf was so high that it was almost breaking across the entrance channel. So we sat at the entrance and scratched our combined heads. I can still remember the scene, everyone on board was either on the bridge or standing out on the wings to watch the spectacle. On that cruise, the captain was Tom Meyer, the first mate was Wayne Ellis and Mark Hulsbeck was the XO. Unfortunately for Mark, he was on watch so it was his responsibility to bring the ship in safely. We actually sat at the entrance and counted the swells with the hope that every seventh swell actually is the largest. Most of the time that is actually true. After a very large swell passed by (I think it actually was the seventh) Mark made the decision to go for it and pointed the ship directly down the center of the channel. As the Jordan began to gain speed (as best the Jordan could), we felt the stern start to lift just as we entered the channel. Not only did the stern begin to lift but the ship started quickly picking up speed as well. It might have actually been an exciting entrance if the swell didn't push the Jordan's stern to starboard resulting in a radical turn to port. At this point Mark was frantically spinning the helm in hopes of bringing the ship back around to our original course rather than one directly towards the northern jetty. As I looked at the bow out of the bridge windows I could see the jetty passing from starboard to port as the swell continued to carry us down the channel sideways. During this entire operation you could have heard the veritable pin drop as everyone was transfixed on what they were seeing evolve in front of them. But finally the silence was broken as Mark threw his arms into the air and proclaimed, "That's it! I've got no more steerage!" Well those weren't exactly the most comforting words that I wanted to hear at that time. Fortunately my eyes fell on Wayne Ellis standing amidst everyone with his arms crossed in his standard jump suit, expression calm and his voice low when he simply said, "Don't worry, she'll come around". I figured that 25 years experience on the Jordan definitely has some credibility. So for a few more harrowing seconds we all held our collective breaths and then Wayne's words came true. Without doing a thing, the swell passed underneath the hull and the Jordan snapped back around on course as if nothing had ever happened. Newport sure looked good that day even though I think it was snowing. I think I might have had a beer when I got into town. Since that

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[6] Dave Griffith is a supervisory research fishery biologist and the leader of the Ship Operations group of the Fisheries Resources Division at NOAA Fisheries Southwest Fisheries Science Center in La Jolla, California.

Fig. 8.6 NOAA Ship David Starr Jordan was retired in 2010 after long service as NOAA Fisheries main platform for the CalCOFI surveys (Photo provided by Dave Griffith)

was my first cruise with NOAA, I figured that it could only get better from there. I must have been right because I'm still here.

8.6 Ronald C. Dotson: Forty Years of Change: Observations of CalCOFI Procedures and Equipment 1970–2010[7]

I started working for the Bureau of Commercial Fisheries, the predecessor to the National Marine Fisheries Service, in February of 1970 at the La Jolla laboratory. I joined the albacore group made up of Mike Laurs, Ron Lynn, Ken Bliss and Robert Nishimoto and although the group's primary responsibilities were studying albacore tuna, we were also part of the coastal fisheries program at the lab and hence closely involved with the CalCOFI program as well. Personnel in the lab were freely utilized by the numerous loosely organized disciplines within the lab at that time.

Sam McClatchie had asked me for my input on the changes observed in the CalCOFI sea-going program over the span of my career. Thinking long and hard on this, which I no longer do much now that I've retired, I decided that although there were numerous, and sometimes important sociological changes over the past 40 years, the technological advances that have come about totally overshadow these for importance and impact on the program.

The sea-going station sampling program for CalCOFI is made up of both biological and oceanographic parts. In the early 70s, the biological sampling components were an oblique tow with a 1-m ring net, replaced by the Bongo net design in the early to mid 70s, and a towed neuston net to sample the surface air/water interface which was also replaced by the manta net in the late 70s to early 80s. Nets were already synthetic fiber rather than the silk nets of much earlier studies and mesh sizes were the present day 505 μm mesh. The oceanographic component was a Nansen bottle cast to 500 m, depth permitting, with 20 bottles outfitted with reversing thermometers placed at "standard" depth increments and tripped using weighted messengers that slid down the wire. From this bottle temperature at depth was obtained by readings of the reversing thermometers and water samples were taken for determination of salinity, oxygen, and nutrients. My recollection is that these bottles held 0.7 l of water, so sampling carefully was critical. Salinity was determined by running the water samples through a salinometer, oxygen determined using titration and a modified Winkler methodology, and nutrients were run on an auto-analyzer. All data was hand written onto data sheets throughout the duration of the cruise. A CTD cast was also taken with the temperature-conductivity and the depth data traced on a paper trace and also recorded on a magnetic tape.

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[7] Ron Dotson is now retired from NOAA and previously worked as a seagoing research fishery biologist in the Ship Operations group of the Fisheries Resources Division of the NOAA Fisheries Southwest Fisheries Science Center in La Jolla, California.

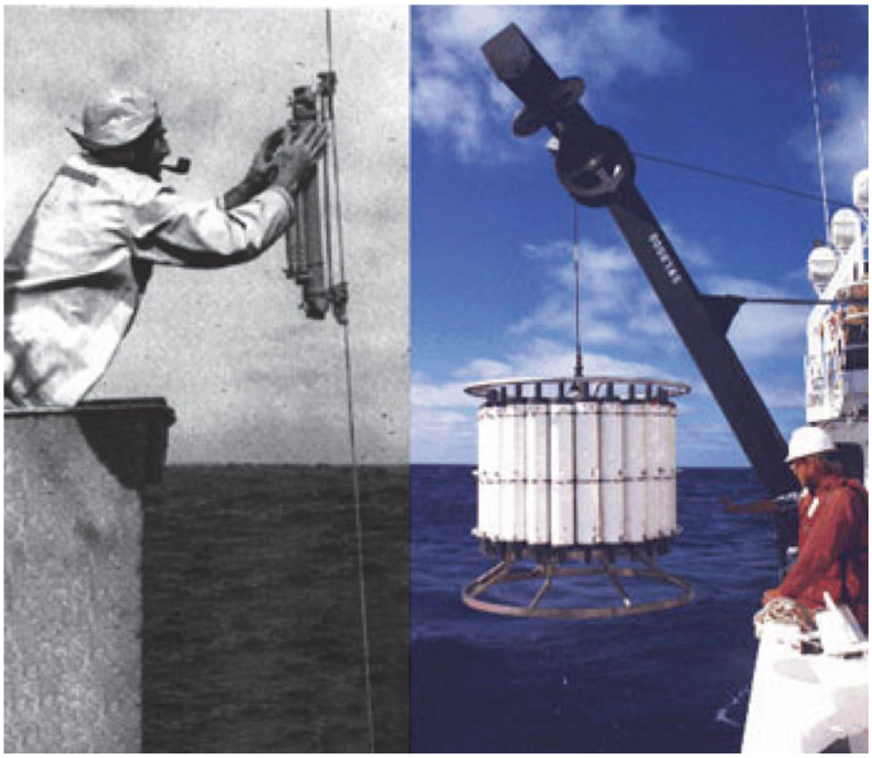

Fig. 8.7 Collecting hydrographic data on CalCOFI cruises evolved from Nansen bottles strung on a wire and activated with messengers (*left*) to the modern CTD-rosette package shown with Ron Dotson in attendance (*right*) (Credit: CalCOFI photo library and James Wilkinson)

Sensors on CTDs were in their infancy at this time and often prone to giving erroneous data. Bottle values of temperature and salinity were hand plotted on the CTD traces after the cruise and used to calibrate the CTD data, while bottle values that looked like outliers could be compared to the CTD trace for possible anomalous conditions in the subsurface structure. Oceanographers were very slow to accept CTD data as accurate and most oceanographic calculations were done using bottle data for decades after the advent of the CTD. In the early 1970s, there were no electronic hand calculators, a "computer" took up an entire large room at the University of California and all computer calculations performed on the data were done post-cruise after the data had been punched up on punch cards and submitted to the University to be run through programs.

Compare the above scenario to the CalCOFI sampling programs of today. A CTD that used to only give you conductivity and temperature versus depth first had oxygen sensors added (the first ones were very poor), then chlorophyll sensors, transmissometers and other functions followed through the 90s and into the twenty-first century. Sensors not only became more accurate and reliable, but smaller in size as well. Separate bottle casts were discontinued in favor of Niskin bottles on the CTD frame, with a capacity to collect 10 l of water, or more, at each sampled depth allowing for studies requiring large quantities of water, such as trace metals. Computers began going to sea as soon as the first desktop models became available and were soon an integral part of CTD operations, replacing the old magnetic tapes and paper traces with digital output. Labs are now filled with desktop and laptop computers and flat screens at every desk. Satellite imagery, beginning in the early nineties, became available for viewing surface chlorophyll and temperature data, making possible some pre-planning of cruise strategy prior to going to sea based on observed oceanographic conditions. At the present time, these data can be updated daily while at sea and used to modify sampling if needed. In addition, moored buoys in the equatorial Pacific monitor El Niño or La Ni na conditions which provide advance warning of anticipated conditions in the California Current. Biological sampling still depends on an oblique Bongo tow and a surface neuston tow, with the addition of a vertical Pairovet or CalVET net used for fish egg sampling and since the late 90s, a Continuous Underway Fish Egg Sampler (CUFES) that continually collects fish eggs and invertebrates throughout the course of the cruise. At present, these biological samples must still be sorted and identified by hand using skilled technicians.

Technology has also impacted the running of the research ships as well. Navigation has gone from celestial navigation techniques, supplemented with Loran-A in the early 70s, to Loran-C, then Omega navigation (lasted briefly) and then on to GPS navigation which now allows the ship to be placed accurately to within meters of a given location, rather than miles. Communications have changed from Morse code and single side band radio to satellite radio and phone communications that can be accessed by anybody on the ship.

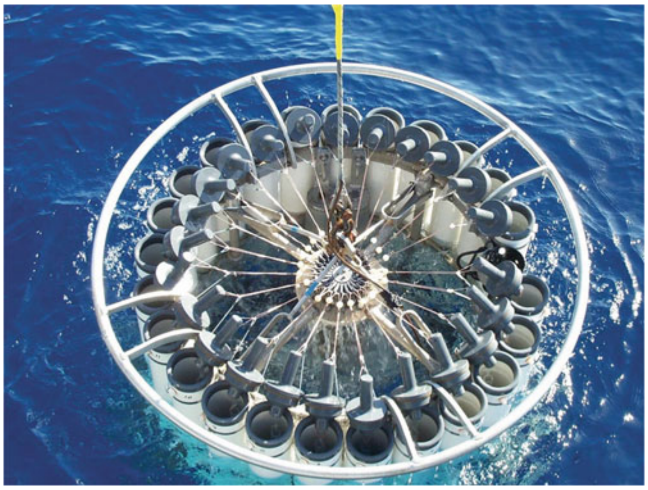

Fig. 8.8 Scripps Institution of Oceanography CTD-rosette being deployed on CalCOFI survey showing open array of niskin bottles (Credit: CalCOFI photo library)

As technology continues to advance past experience indicates that ocean research programs will continue to keep adopting and inventing new techniques to sample and monitor the world's oceans. This will serve to further advance our understanding of the world's oceans and how they work.

8.7 James Wilkinson: The Development of Near Real-Time Data Delivery from CalCOFI Surveys[8]

I joined the CalCOFI group full-time as part of the Marine Life Research Group at SIO in 1990. Although my degree was in Biological Oceanography, the main reason I was hired was due to my skills with computers and electronics. IBM-compatible personal computers were becoming standard equipment for acquiring and processing data at sea. CalCOFI was ready to transition from hanging bottles to collecting continuous, real-time-viewable electronic data and targeted seawater samples using a CTD-rosette. I became the primary CTD technician because of its computer interface requirement and the electronics involved. It took 3 years to fully transition to the CTD because the Seabird system was new and everyone was learning, particularly me. We required 100 % (or at least 98 %) confidence the system replacing bottle samples would work every station, every cruise. It was also important the data generated by the new instrument compare favorably with the 40 year CalCOFI bottle data time-series. Meanwhile, while ironing out the bugs of the CTD, I was developing software to improve our ability to key-enter and process data at sea. That process continues to this day.

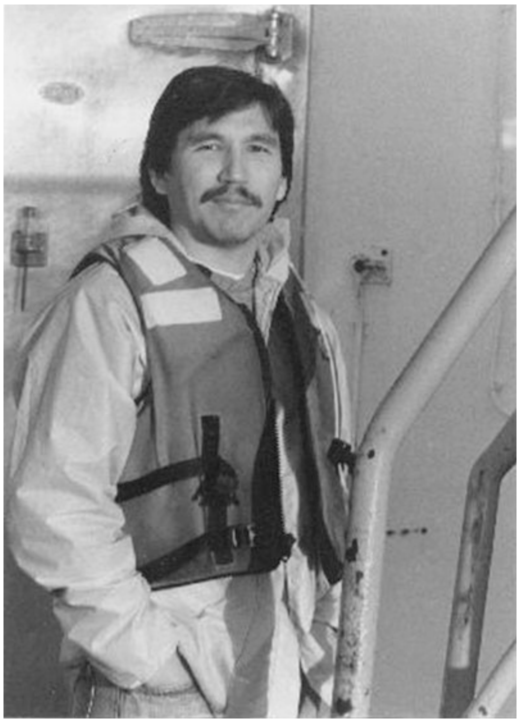

Fig. 8.9 Jim Wilkinson at sea (Credit: CalCOFI photo library)

The transition from hanging bottles to CTD was possible because of the micro-computer and it was my good fortune to join the group as the work evolved from analog to digital. When I started, all the data collected were handwritten on forms then key-entered into spreadsheets. Key-entry was a tedious process as well as checking for mistakes in the transcribed data. Over the last 20 years, the two computers have grown into a complex computer network where data are collected, exchanged and integrated onto a server. All analyses done at-sea on seawater samples are computerized. Data from the CTD sensors can be compared to analytical samples during the analyses. This capability improves our ability to detect problems with the CTD, analytical equipment, reagents, and sample collecting or analytical techniques.

I remember a time when we were happy to carry preliminary data printouts and floppy discs off the ship at the end of a cruise. Now, with the internet available at sea, the demand for real-time or near real-time data has become an expectation. For quite some time, the CalCOFI final data were not available for at least a year after a cruise was completed. Additional shore-based sample analyses, data

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[8] Jim Wilkinson is a programmer-analyst supervisor in the Integrated Oceanography Division of Scripps Institution of Oceanography in La Jolla, California.

processing, quality-control, publishing, printing and mailing of CalCOFI Data Reports took a year or longer. Now, it's possible to make preliminary data globally available near real-time, uploaded from the ship to our calcofi.org website or emailed. Highest-resolution, processed CTD data are available online immediately after the cruise. Final bottle sample data are electronically published within a few months of a cruise.

The scope and technical aspects of the CalCOFI program are broadening as we try to understand the complexities of the California Current and near-shore ecosystems. The quantity of data collected grows exponentially each year and, fortunately, digital storage media is keeping pace. As the data volume grows, the size of computers shrink, with handhelds and tablet computers taking the place of desktop workstations. Data collection and entry can be done wirelessly and integrated data products are available faster and faster every cruise. I started with CalCOFI before the internet became a public entity, when google was a number with a 100 zeros, and I am witness to how it has impacted the distribution of information. We are the "Google-generation" – if we have a question, it can be answered in an instant with a click of a mouse. This expectation carries over to our work as we continue to make our high-quality oceanographic observations available as soon as humanly and technologically possible. Data, which once took a year or longer to make available at the library, are now available globally in minutes with a click of a mouse.

8.8 John L. Butler: A Critical Decision in the History of CalCOFI[9]

A critical decision was made at the beginning of CalCOFI by Dr. Elbert Ahlstrom. While the initial goal of the program was a sardine survey, Ahlie, as he was known world-wide, insisted that all fish eggs and larvae should be sorted from the plankton tows, and that all species should be identified. It would be many years before that goal was achieved, but the fruits of that labor are borne today in time series of larval abundances for both exploited and unexploited species of fish. The Ontogeny and Systematics of Fishes, dedicated to Ahlie and published by the American Society of Ichthyologists and Herpetologists, is a tribute to his foresight and contributions.

8.9 Geoff Moser: Building the Multi-species Time Series for the Fish Eggs and Larvae Collected on CalCOFI Surveys[10]

In the fall of 1961, when I arrived for graduate study at the University of Southern California, my advisor, Jay Savage, hired me to work in his NSF study of the deepwater fish communities of the basins off Southern California. This entailed one or two cruises each month aboard the Velero IV, sampling the basins with a 10-m Isaacs-Kidd Midwater Trawl and working up the catches. Each of our trawls had a 1-m plankton net at the codend, ensuring that all life stages of the ichthyofauna were sampled. In identifying the catches I noticed that the California smoothtongue, *Leuroglossus stilbius*, a deep-sea smelt, was particularly abundant. Because all of its life stages were present, and year classes were evident, I thought it had potential for my dissertation research and submitted a research proposal to Jay. He thought it had promise but said we should drive down to La Jolla to the Bureau of Commercial Fisheries lab on the SIO campus and check with Dr. Ahlstrom to get his opinion. Dr. Ahlstrom was the Laboratory Director and the foremost expert on ichthyoplankton taxonomy and ecology. Jay knew "Ahlie" from the years when the fledgling CalCOFI laboratory was housed in Jordan Hall on the Stanford campus. The meeting with Ahlie took place in his office in the wooden building, formally the SIO Director's home, across from the public aquarium. After looking over the proposal Ahlie said he liked it but that he already had a manuscript that covered the major aspects of the study. I guess my disappointment was obvious because he offered me a job the following summer working on the CalCOFI fish egg and larval collections. Following the meeting I had a chance to meet some of Jay's friends from Stanford days. Reuben Lasker came down from his lab on the hill to meet Jay and his new student. I remember how warm and friendly he was and how genuinely interested he was in my graduate work. I could not have imagined how important his support would be to the CalCOFI program when he became Chief of the Fisheries Resources Division of the future Southwest Fisheries Science Center.

What Ahlie had in mind for me that summer was to learn to identify the fish larvae in recent CalCOFI survey samples, with special attention to the rockfish larvae, a group that had not been identified beyond genus. My instructors that summer were David Kramer and Lois Hunter who, under Ahlie's tutelage, were identifying larval fish species in the CalCOFI

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[9] John Butler was a supervisory research fishery biologist in the Fisheries Resources Division at NOAA Fisheries Southwest Fisheries Science Center in La Jolla, California until his retirement in 2012.

[10] At the time of his retirement in 2002 Geoff Moser was the leader of the Ichthyoplankton laboratory in the Fisheries Resources Division at NOAA Fisheries Southwest Fisheries Science Center in La Jolla, California.

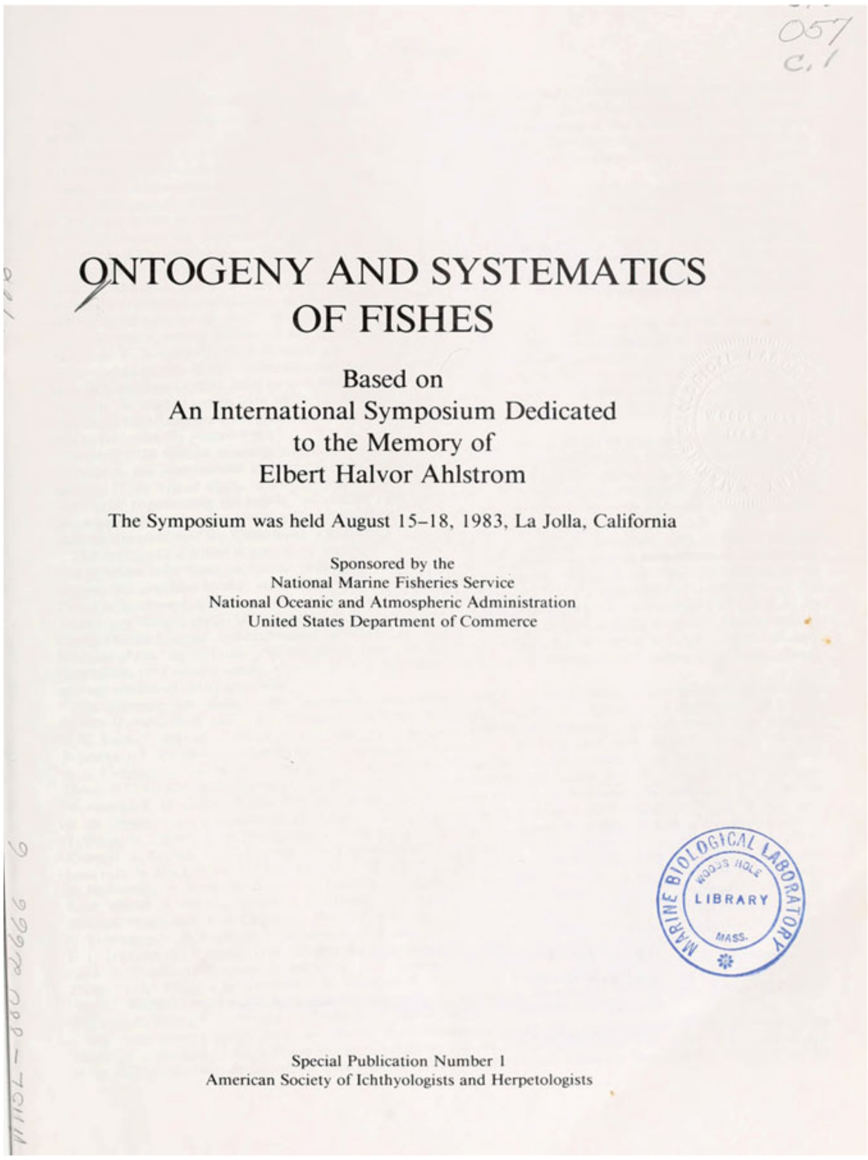

Fig. 8.10 Title page of Ontogeny and Systematics of Fishes, dedicated to Dr. Elbert Ahlstrom and published by the American Society of Ichthyologists and Herpetologists

ONTOGENY AND SYSTEMATICS
OF FISHES

Based on
An International Symposium Dedicated
to the Memory of
Elbert Halvor Ahlstrom

The Symposium was held August 15–18, 1983, La Jolla, California

Sponsored by the
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
United States Department of Commerce

Special Publication Number 1
American Society of Ichthyologists and Herpetologists

samples. By the end of the summer I could recognize most of the taxa Ahlie had identified in CalCOFI samples and, together with Ahlie, had identified larvae of bocaccio, an important rockfish trawl species, down to its earliest stages. Ahlie was pleased with my progress and offered me a job for the following summer. Even more exciting was his offer to let me make collecting trips on the lab's research vessel, the Black Douglas, when it was in port between CalCOFI quarterly cruises. Rockfish are viviparous and the larvae of the most advanced broods have pigment and morphological features that can be used to tie them to the earliest plankton-caught specimens. We hoped that the number of identifiable rockfish larvae could be increased by collecting advanced pregnant females of many species on trips to the outer banks (e. g., Tanner, Cortes, 43-Fathom, 60-mile banks) off Southern California. At the same time I would be able to augment collections of reproductive tracts and endocrine tissues for my dissertation research on the reproductive biology of bocaccio and other rockfish species. Those cruises on the Black Douglas worked out well and by the summer of 1964 I had enough material to progress with my research.

During the summer of 1964 Ahlie offered me a research position at the lab which was about to move up the hill to the new laboratory building overlooking the cliffs. One important job was to gather all the identified fish egg and larval samples from their various locations and organize them into a cohesive collection in the new laboratory building. At that time the plankton sorting lab was at Point Loma where the samples were "volumed" and fish eggs and larvae separated from the invertebrate zooplankton. Sardine and anchovy eggs and larvae were separated and the lengths of the larvae were recorded. When sorting was completed

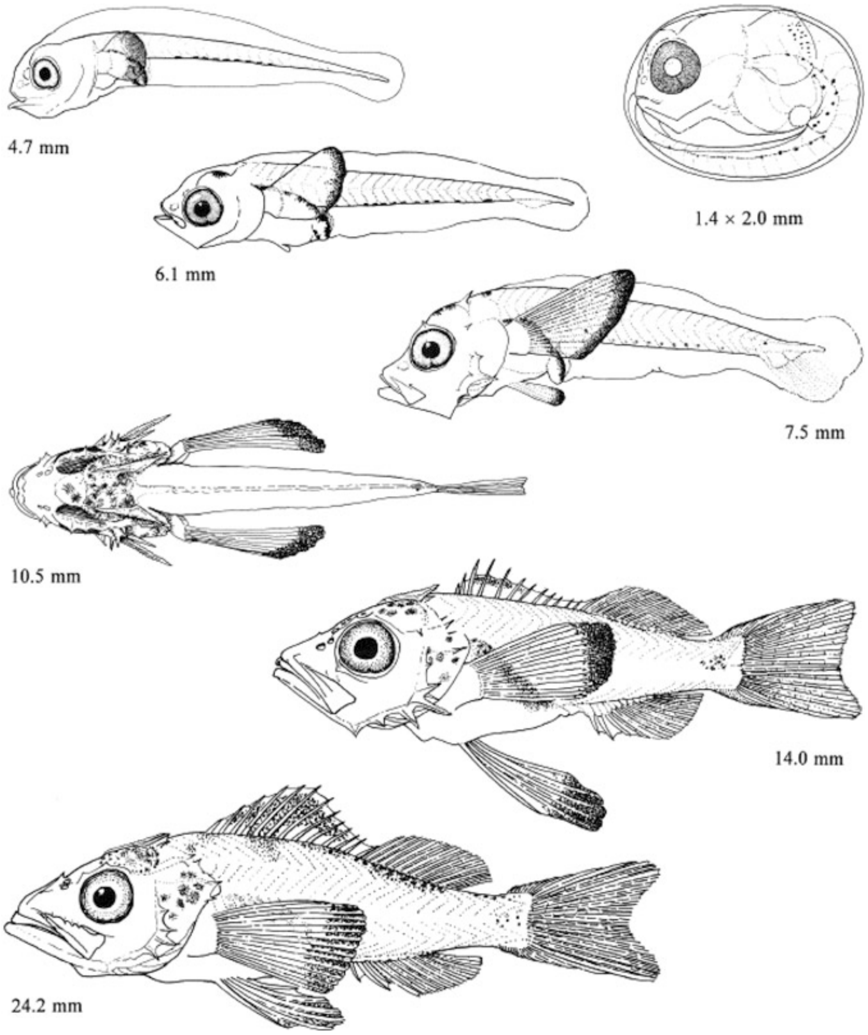

Fig. 8.11 Larval stages and egg of the bocaccio, *Sebastes paucispinis*(family Scorpaenidae) (From Moser [394])

each station was represented by a group of 2-dram vials containing: sardine eggs, sardine larvae, anchovy eggs, anchovy larvae, "OFE" (other fish eggs), and "OFL" (other fish larvae). Identification of the many OFL species was done at the La Jolla Laboratory by Ahlie, David Kramer, Lois Hunter, and Robert Counts. When finally brought together, catalogued, and carefully curated these collections proved to be a critical resource in the further development of the CalCOFI ichthyoplankton time series.

Soon after moving to the new laboratory Ahlie was awarded the laboratory's Senior Scientist position and Alan Longhurst became the new laboratory director. Free from administrative duties, Ahlie turned his attention to identifying and analyzing the ichthyoplankton samples from the newly established Eastropac program, a multi-vessel biological-oceanographic survey of the eastern tropical Pacific. Once again, as he had done with CalCOFI, Ahlie pioneered the ichthyoplankton investigations of a major oceanic region, doing the fundamental research on species identification and ecological analyses and publishing the founding papers for future investigators to follow. Also, during 1971–1977, Ahlie presented a series of six courses on the basic aspects of ichthyoplankton surveys, with CalCOFI as the model program (Fig. 8.12[11]). These courses, attended by scientists from U. S. and international fisheries laboratories and universities, were important in conveying CalCOFI concepts and techniques to organizers of ichthyoplankton surveys

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[11] **1975 SWFSC instructional staff:** Elbert Ahlstrom, Geoffrey Moser, Elaine Sandknop Acuna, John Butler, Elizabeth Stevens, Barbara Sumida McCall. **Course attendees:** Joseph Abordo (Fisheries Research Unit, Tema, Ghana), Jose Alvarez (Marine and Fresh Water Science Center, Mexico City, Mexico), Angeles Alvarino (SWFSC, La Jolla, CA), David Ambrose (Moss Landing Marine Laboratories, Moss Landing, CA), David K. Arthur (Scripps Institution of Oceanography, La Jolla,CA), Marek Baranowski (Marine Plankton Laboratory, Szczecin, Poland), Arnold Berqueno (Dept. of Marine Science, Hermosillo, Mexico), Cindy de Gorgue (Middle Atlantic Coast Fisheries Center, Highlands, NJ), Leanard Ejsymont (Marine Plankton Laboratory, Szczecin, Poland), Stefan Grimm (Sea Fisheries Institute, Gdynia, Poland), Dennis Gruber (SWFSC, La Jolla, CA), Jerry Hardy (Chesapeake Biological Laboratory, Solomons, MD), Daniel Jimenez (National Fisheries Institute, Mexico City, Mexico), Betty Louw (South African Museum, Cape Town, South Africa), Gede Merta (Marine Fisheries Research Institute, Jakarta, Indonesia), Ellen Moxley (SWFSC, La Jolla, CA),

Fig. 8.12 The Ahlstrom Ichthyoplankton Class (1975) (see footnote for attendees) (Photo provided by Geoff Moser)

around the world. The central theme of these month-long courses was the identification of fish eggs and larvae from plankton survey samples. A morning lecture on a major group of larval fishes was followed by morning and afternoon laboratory sessions on that group of fishes. Ahlie's multi-species approach provided an array of ontogenetic characters useful in establishing phylogenetic relationships among fish taxa and was a vital building block for present-day concepts of ecosystem resource management.

After Ahlie's death in 1979, his close colleagues organized a symposium to honor his memory and his monumental contributions to fisheries science. Scientists from 9 countries presented 86 papers on the development and phylogenetic relationships of fishes. The symposium volume, popularly known as the "Ahlstrom Volume," has been an essential resource for anyone studying the early life histories of fishes [405].

Throughout the 1980s and 1990s the primary mission of our Ichthyoplankton Ecology group, was to build an integrated multi-species time series for the fish eggs and larvae collected on CalCOFI surveys. This involved working up the large backlog of unidentified survey samples and updating the identifications in light of the advances in our ability to identify previously unknown species. During this period the list of identifiable larval fish species was more than doubled compared with previous decades. Comparison of original data sheets with archival specimen collections permitted us to verify and update the identifications and numerical data for the entire time series. This task was accomplished by a dedicated staff that included William Watson, Elaine Sandknop Acuña, David Ambrose, Morgan Busby, John Butler, Sharon Charter, Susan D'Vincent, Amelia Gomes, Barbara Sumida McCall, and Elizabeth Stevens. The laboratory's experimental aquarium proved to be an important asset in our effort to increase the number of identifiable larvae in CalCOFI samples. We collected fish eggs from nearshore areas, brought them back to the laboratory, and reared them through successive larval stages on a diet of cultured rotifers and live plankton. The developmental series obtained from these cultures were particularly important in establishing the larval characters of a number of coastal species (e. g., species of croakers of the family Sciaenidae and sea basses of the genus *Paralabrax*). Larvae obtained from pregnant rockfish females proved to be difficult to rear but we were able to bring some species through to mid-larval stages and John Butler and I reared a complete developmental series of the calico rockfish, *Sebastes dallii*.

Our efforts in building the CalCOFI ichthyoplankton time series were closely coordinated with Richard Charter, the CalCOFI data manager, who was responsible for developing the computer database for the time series. The data for each annual survey was published in a NOAA Technical Memorandum, co-authored with Richard Charter. Other documentation of the time series included CalCOFI Atlases 31, 32, 34, and 35 [398–401], also co-authored with Richard Charter. These atlases summarized the distribution and abundance

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Abdelaziz Moumen (O. N. P., Safi, Morroco), Henry Orr (SWFSC, La Jolla, CA), Edwin Osada (Moss Landing Marine Laboratories, Moss Landing, CA), Michael O'Toole (Sea Fisheries Branch – Cape Town, South Africa), David Potter (Northeast Fisheries Center, Woods Hole, MS), David Rice (Biological Sciences Dept., California State University, Hayward, CA), Pedro Rubies (Institute of Fisheries Investigations, Barcelona, Spain), John Wyatt (Fisheries Ecology Research Project, University of the West Indies, Jamaica, West Indies).

of each larval fish taxon analyzed by our group. A major accomplishment of our group was the production of a multi-authored identification guide to the early life stages of the fish species of the CalCOFI region, published as CalCOFI Atlas 33 [394]. I served as editor of the guide and Bill Watson, as sole author or as co-author with other members of our group, contributed half of the chapters of the guide. Systematic and ecological analyses of the time series were published by our staff in CalCOFI Reports and in numerous other scientific journals. When I retired in 2002, William Watson became leader of the Ichthyoplankton Ecology group. Under his leadership the CalCOFI multi-species time series of fish eggs and larvae continues to be a fundamental fisheries-independent resource for population assessments and ecological investigations of the fishes of the California Current region.

8.10 Bill Watson: Taxonomic Resolution and the Mother of All CalCOFI Atlases[12]

Before coming to Southwest Fisheries Science Center in 1989, I worked at a consulting company for several years, mainly on nearshore ichthyoplankton and adult fishes in the Southern California Bight. During those years I made many visits to SWFSC to consult with larval lab personnel on identifications of fish larvae, and to take advantage of their insights into the ecology of coastal fishes, which they developed in large part through analyses of the ichthyoplankton collected on CalCOFI cruises, supplemented with other work directed more specifically at shorefish species. The CalCOFI survey actually isn't bad at sampling many taxa of the distinctive nearshore ichthyoplankton assemblage, even though the basic station pattern has an offshore bias better suited to the coastal pelagic species for which the program was designed. In fact, as noted by Moser et al. [403], larval abundances of many nearshore fish taxa in CalCOFI collections track adult abundances pretty well, which suggests that CalCOFI ichthyoplankton data might be useful in the management of some nearshore fishes.

Soon after I came to SWFSC the larval lab began a major project preparing a descriptive atlas of the early life history stages of fishes of the California Current region, which was published in 1996 as CalCOFI Atlas 33 [394]. The primary sources of specimens for that undertaking were the ichthyoplankton reference specimen collection and the ichthyoplankton sample archive, assembled under the direction of Geoff Moser. The sample archive consists predominantly of CalCOFI collections including early sardine surveys dating back to 1938, but also includes collections from other areas such as Eastropac and other surveys of the eastern tropical and central Pacific, the Gulf of California, and the coastal zone of southern California. These collections were such a rich source of material that Geoff's original plan for Atlas 33 to be a 3-year project covering the 250 most abundant larval fish taxa ultimately expanded to a 6-year project covering more than 500 taxa.

Taxonomic resolution gradually improved over the years in the SWFSC ichthyoplankton program, but during preparation of CalCOFI Atlas 33 substantial advances were made. As a result, a number of taxa previously identifiable only to genus or above have been identified to species since 1996. Fortunately, because the sample archive has been regularly curated to maintain it in good condition, it was possible to begin reanalyzing the earlier collections to bring identifications up to current standards, with the ultimate goal of taxonomic uniformity throughout the entire 60+ year-long ichthyoplankton data base.

In the latter 1990s, during an informal discussion of FRD research plans, John Hunter suggested that since ichthyoplankton seems to work well in tracking changes of spawning stock biomass in a number of fishes, maybe "larval" market squid in CalCOFI samples could provide a useful index to abundance changes in adults of that species. So, in 1997 we began sorting and identifying paralarval cephalopods from the CalCOFI plankton samples. Preliminary analysis of results suggested that paralarval abundance does track adult market squid abundance, and in 2002 we undertook a project to extend the paralarval abundance time series back in time. We did this by reanalyzing CalCOFI Manta (surface) plankton samples archived in the SIO Pelagic Invertebrates Collection which, like the ichthyoplankton sample archive, is an invaluable resource that is cataloged, curated, and available to support these kinds of retrospective analyses. Analysis of the longer paralarval market squid time series confirmed that trends in their abundance track reasonably well with trends in commercial fishery catches, and cephalopods are now permanently added to the larval lab species list.

8.11 Andrew Thompson: Visions for the Future of the SWFSC Ichthyoplankton Ecology Group

The Ichthyoplankton Ecology group at the SWFSC has provided an unparalleled contribution to our understanding of the early life history of fishes in the California Current region and around the world [see Geoff Moser's vignette in this chapter]. The seeds of these accomplishments were sown through the far-ranging visions of Drs. Elbert Ahlstrom and Geoff Moser, who provided a research plan that would be implemented at a decadal time scale, and who guided it over

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[12] Bill Watson is a supervisory fishery biologist leading the Ichthyoplankton group of the Fisheries Resources Division at NOAA Fisheries Southwest Fisheries Science Center in La Jolla, California.

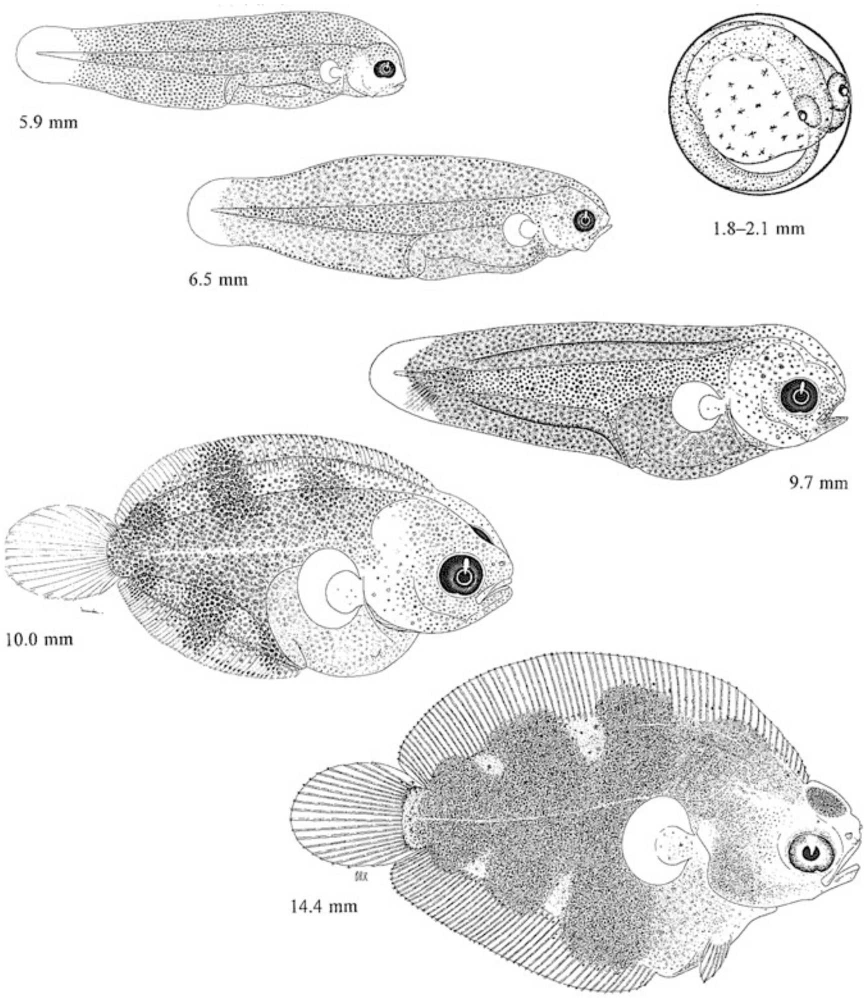

Fig. 8.13 The egg and larval stages of curlfin turbot, *Pleuronichthys decurrens* (family Pleuronectidae) (Image from Moser [394])

the years. As the 60th anniversary of the CalCOFI program passes we, the current members of the ichthyoplankton group,[13] are humbled by the past accomplishments of the lab and excited to carry on its legacy. Here we wish to reflect on our role in the CalCOFI program and lay down some of our thoughts about potential avenues for future ichthyoplankton research in the California Current ecosystem. We will see how well our ideas are borne out 50 years from now!

The overriding objective of CalCOFI ichthyoplankton research is to augment understanding of processes that affect fish population and ecosystem dynamics. We envision that the ichthyoplankton lab will continue to contribute to this mission by conducting research in three dynamic categories: (1) identifying fish larvae and eggs; (2) optimizing sampling strategies; and (3) utilizing ichthyoplankton data in novel analyses. Historically, research in the ichthyoplankton lab focused primarily on the first category. Indeed, the core skills of our group have been morphology-based identification of fish eggs and larvae, and thorough understanding of the life history and ecology of the myriad fishes, primarily in the eastern Pacific and especially in the California Current region. Augmenting our capacity to identify fish eggs and larvae, and better understanding the life history characteristics of each species, will continue to be major foci of our group. This knowledge is critical for the continued success of CalCOFI because, for example, it guides optimal implementation of survey designs. Over the years there have been several modifications to the CalCOFI sampling regime and further changes will undoubtedly occur in the future. Deep insight into the ecology of species is critical for predicting how populations will respond to environmental variability, and thus how to best document population and ecosystem dynamics. As such, optimizing sampling design and analysis is contingent upon having thorough knowledge of the species being studied.

Although our past research in the first category focused mostly on morphological identification, in the future we anticipate including new technologies to more efficiently identify fish eggs and larvae. An example of a tool that we

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[13] Andrew Thompson, William Watson, Noelle Bowlin, Sharon Charter, and Elaine Acuna.

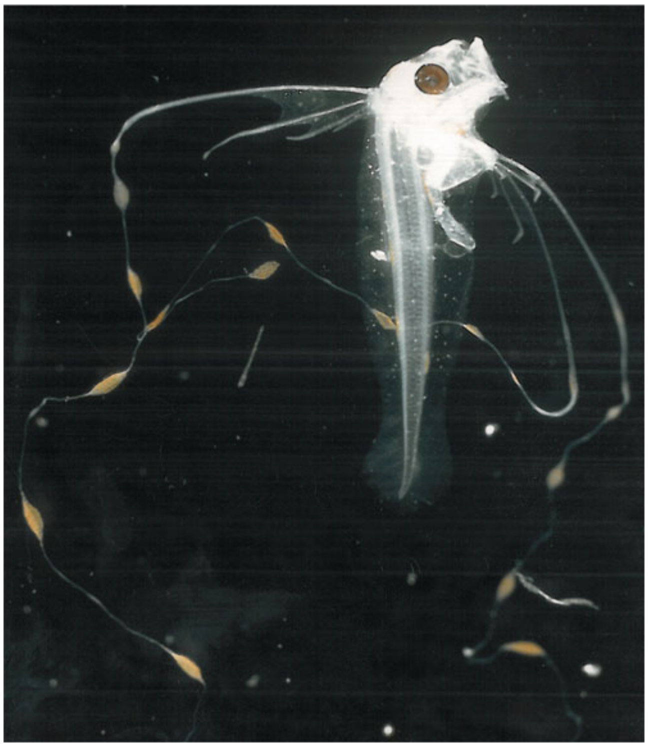

Fig. 8.14 Scalloped ribbonfish, *Zu cristatus* (Photo provided by Andrew Thompson)

increasingly are using is genetic identification. Genetic techniques have become more accessible over the past decade, both in cost and ease of use. In cooperation with the genetics labs at the SWFSC and at SIO, we are using genetic probes and sequencing to identify morphologically indistinguishable fish eggs and larval rockfishes, respectively. Results are providing exciting new insights into patterns of distribution and abundance of many fishes in the California Current. For example, our rockfish work shows that the assemblage off southern California is currently made up primarily of small species that are not targeted by fisheries. Further, through genetic identifications we are finding that some of the previously unidentified larvae actually have morphological characters that can be used to reliably distinguish species. Thus we anticipate revisiting older CalCOFI samples to create time-series of larval abundances for species that were previously identifiable only to genus. Our goal is to stay abreast of technological developments to help us obtain more informative data from the ichthyoplankton samples.

Our second focus is to optimize sampling designs (i.e., where and when samples are collected) to provide the most comprehensive view of the ecosystem. At the inception of the CalCOFI program samples were collected monthly from the southern tip of Baja California to northern California. It is unlikely that such a sampling scheme will return, but there are ways to provide a more comprehensive view of the ecosystem now and in the future. One way is to collaborate more closely with other groups that are studying the California Current System (CCS). One of the founding tenets of the CalCOFI program was the necessity of sampling the CCS from multiple perspectives to obtain an integrated view of the ecosystem. At present, several research groups autonomously conduct ichthyoplankton surveys off the west coasts of Baja California, California, Oregon, Washington and Canada. It would be of great value to work closely with these groups to once again track ichthyoplankton dynamics at a scale covering most of the biogeographic range of many of the sampled species. This is particularly important in a realm of climate change, as species' distributions may shift away from the current sample frame.

Another way to augment sampling efficacy is to coordinate with groups using different tools to sample the CCS. For example, systematic surveys have been conducted in the Southern California Bight using remotely operated vehicles (ROV) and acoustic techniques. Direct integration of ichthyoplankton, acoustic and ROV sampling should provide a more complete view of the ecosystem than a survey relying on any individual technique. A template for such a sampling strategy was carried out in 2005 when ichthyoplankton, ROV and acoustic data were collected in and around the Cowcod Conservation Area (CCA) in order to characterize the rockfish assemblage in this marine reserve. Initial results suggest that each survey technique provides a slightly different view of the assemblage and that our best understanding of the distribution and abundance of rockfishes is found when results of each technique are examined in concert.

Finally, another important factor for optimizing ichthyoplankton survey design is the statistical analysis used to analyze the resulting data. For example, targeted sampling that augments CalCOFI collections to ask specific questions should to be linked *a priori* to a statistically-sound sampling design. Staying abreast of the sampling design literature will be a priority of the ichthyoplankton group. Increased collaboration and sampling in a statistically optimal way should lead to optimal utility of ichthyoplankton data in the future.

A key focus of our work will be integration of CalCOFI ichthyoplankton data into analyses focused on better understanding species and ecosystem dynamics in the CCS. In the past, CalCOFI ichthyoplankton data have been used for analyses such as comparing dynamics of fished and unfished species, evaluation of assemblage responses to environmental forcing, and as a source of fishery-independent data for stock assessment. In addition to continuing these types of analyses, we provide three examples of how we think CalCOFI ichthyoplankton data can be used to address emerging questions. First, a natural fit for CalCOFI ichthyoplankton data is in Integrated Ecosystem Assessment (IEA). At present, the rapidly developing science of IEA is generating predictions regarding the effects of factors such as fishing pressure on the dynamics of both fished species and those trophically linked to the focal species. These analyses currently are mostly theoretical, and there is a real need for actual data to validate model predictions. CalCOFI ichthyoplankton samples provide systematic information on species at many trophic levels that are targets of varying degrees of fishing pressure, and that have very different life histories. Thus, CalCOFI ichthyoplankton provides one of the best data sources for true ecosystem assessment. Second, we anticipate that a novel application for ichthyoplankton data will be the assessment of marine reserve efficacy. Over the past decade, tens of spatially-static marine protected areas (MPA) were implemented in the Southern California Bight. One of the main justifications for the use of spatial management is that spillover of larvae and adults will eventually augment regional fishery production. Although MPAs are designed to affect fisheries at a regional scale, MPA monitoring typically focuses exclusively on local scales where surveys within a reserve are compared with nearby areas outside the reserve. Because CalCOFI ichthyoplankton sampling encompasses the entire Southern California Bight it may be better-suited than traditional, small-scale MPA monitoring to address regional impacts of reserves. In addition, targeted ichthyoplankton sampling can be used to identify sources of larval production to better discern if the reserves really protect essential fish habitat. Third, there should be an increased use of ichthyoplankton data in stock assessment. We are currently using genetic sequencing to develop a time-series for rockfish larvae in the CalCOFI samples. Once this effort is complete, we will generate the only time-series of relative rockfish abundances from the whole SCB. This time-series will include samples taken within rockfish conservation areas (e.g., the 14,750 km^2 CCA) that for more than a decade have not been sampled with traditional, fishery-independent sampling methods such as trawling or hook and line surveys to avoid harming the adult stocks. These data could be used in future rockfish stock assessments. In addition, CalCOFI ichthyoplankton data are available for many many other fishes (e.g., Pacific sanddab and northern anchovies) for which formal stock assessment will likely be conducted in the future and should provide valuable fishery-independent time series for these analyses.

IEA, MPA, and stock assessment analyses are just three examples of potential uses for CalCOFI ichthyoplankton data; as new types of analysis and questions emerge our knowledge of species' life history and ecology can help guide sampling strategies to best address these issues. Much of Dr. Ahlstrom's vision of describing the early life history stages of California Current fishes has been realized. However, we have just scratched the surface in exploring the knowledge that CalCOFI ichthyoplankton data can bring to our understanding of the CCS and the dynamics of fish stocks. We live in a world where environmental conditions are changing at a rate unprecedented in the past 5,000 years. The CalCOFI ichthyoplankton data make us uniquely poised to contextualize current ecological changes relative to past variation and to thus elucidate the relative effects of the environment and management on fish populations and ecosystem dynamics. We are enthused to carry on the legacy of the SWFSC ichthyoplankton ecology group in the new century.

8.12 Paul E. Smith: Pattern and Process in Recruitment to Schooling Pelagic Populations[14]

Despite the technical advances in fisheries oceanography and accumulating time series of physical and biological features of the environment, "the recruitment process is still not well understood and fluctuations in year-class abundance remain a major source of uncertainty in managing marine fisheries" [262]. This is particularly true of the sardine. The scale of the recruitment process and the physical and biological oceanographic factors controlling individual growth and survival are as yet barely studied.

While the hazards of the 'first feeding' stage remain important, it is probably advisable to regard several points in the early life history as 'critical'. It seems unlikely that the successful stage determining the recruitment rate is the same stage, within or among species, under all conditions.

The studies of basin scale correlations with population recruitment have advanced the study of California Current recruitment, but the failure to distinguish the local driving forces may well explain the neither negative nor positive correlation among the pelagic spawning species on a year by year basis. The intense spatial pattern required for high fertilization rates observed for these pelagic spawners is the apparent source of much sampling variability. Because of the continued CalCOFI surveys, the temporal and spatial scales of the "spawners' habitat" is well known [44] but that of the "survivors' habitat" [331] is not.

Spatial scales of the "spawners' habitat" are established by the behavior of the spawning females attracting coteries of males to fertilize the eggs in the open sea. There is no information on this for hake, but sardine and anchovy exhibit dusk deviations in sample estimates of sex ratio in collections of actively spawning females affiliated with about four times as many males. At other times of day the sex ratio approximates 50:50. In the course of a week, each mature female spawns about once and the males may be active on alternate nights. If we consider on other grounds [511] that the school is 10s to 100s m in diameter and schools underlie less than 1 % of the sea surface [518], there must be tens of thousands of spawning sites active each night in the populations of schooling pelagic spawners.

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[14] Paul Smith was a supervisory research fishery biologist in the Fisheries Resources Division at NOAA Fisheries Southwest Fisheries Science Center in La Jolla, California prior to his retirement.

Fig. 8.15 *Left*: Paul Smith and Dimitry Abramenkoff in 1985 deploying a net. *Right*: Paul Smith in 1969 with a rig to compare retention of anchovy and sardine eggs collected using 505 µm nylon mesh (type 3 net) and 333 µm nylon mesh (type 2 net) [305]. A previous test in 1966 using the same frame compared the retention of anchovy and sardine eggs in a standard CalCOFI silk net with nominal mesh dimension of 550 µm (1 m mouth diameter, type 1 net) with a nylon net of 333 µm mesh (0.5 m mouth diameter, type 2 net). After 1969 the type 3 net replaced the type 1 net on CalCOFI surveys (Photographs courtesy of Nancy Lo, NOAA Fisheries SWFSC) (Photos provided by Paul Smith)

There are 'key' transitions to consider in the progress from a spawning population to the eventual recruitment to that population. Examples are fertilization, hatching, first feeding, school formation and development of omnivory. In open sea habitats of anchovy and sardine, the time scales of fertilization are minutes and the spatial scale of interest is meters. The spawning bout of a single female may only last minutes per week over less than a third of the year. The space of a single egg, a nominal millimeter in size, must be washed in the sperm of several males with proximity to that egg of microns. As hatching approaches, each egg becomes visible to predators from centimeters away with motion inside the egg creating a possible enhancement to predation. Upon hatching, the tiny larva is encumbered by a yolk sac, which must supply the energy required for elaborations of pigments for eyesight, neural implementation and anatomical formations. The result is a voracious predator successfully striking over millimeter range at motile microorganisms several times per minute in the first days of planktonic life. Within a week, this surviving predator exhibits the ability to evade oncoming meter-scale plankton samplers, approaching at a meter per second with a day-night difference in vulnerability. This flight of predators begins the schooling habit for defense in a month and persists as obligate carnivores for about a third of a year, finally recruiting to their omnivorous populations as 50 mm filtering juveniles. Most anchovies become fecund at that point and most sardines undergo an additional season of growth before doing so.

The very structure in time and space that enables these life events requires massive sampling effort to quantify from microns to thousands of square kilometers. Yet the description of recruitment requires this, and the analysis of causes of quantitative change in these transitions requires much more.

Another approach is needed to interpret the recruitment process. Each recruit contains a time history of growth rate and an estimate of the spawning time in its otoliths. Before investing in the direct estimation of survival and growth rates of pre-recruits at sea, there should be a thorough analysis of the otoliths as the recruits enter the fishery. A small sample of otoliths could be analyzed annually to determine the season of maximum growth rate at monthly intervals and the estimation of date of birth. With this information, and the basic evaluation of the spawning process provided by the annual biomass estimates, a sampling strategy could be devised for direct estimation of survival and the location of the survivors' habitat. The timing of the maximum growth rate for the cohort, would allow the selection of the appropriate sampling devices, and the design of the analytical and process oriented cruises for the age group of interest. Continued development of meso- and micro-scale techniques by analysis of satellite detected features of the environment, acoustic displays of plankton and fish aggregations, and the robotic glider instrumentation exploring the depth dimension of the survivors' habitat would expand our capability for managing ecosystem level fisheries.

To summarize, the oceanographic and biological pursuits of CalCOFI have provided time series of larval indices on which general levels of spawning biomass are based. The later larvae have provided crucial information on the time history of species diversity in the eastern boundary biome. The egg production method has introduced the absolute quantitative and instantaneous estimates of spawning biomass for use in calibration of more efficient methods on selected species. With these methods in hand it is now time to begin the approach to describing formation of recruit stages in the life history of local sardine and anchovy populations.

8.13 J. Anthony Koslow: CalCOFI and the Impact of El Niño in the California Current[15]

Today, El Niño is widely known as a pan-Pacific phenomenon and a driver of the physical and biological oceanography in the California Current. To an oceanographer, this paradigm is as fully integrated into his conceptual background as the theory of evolution. However, when the CalCOFI program got underway, El Niño was an obscure phenomenon known only from the coast of Peru. In the absence of systematic observation programs, major perturbations to the ocean may occur without anyone taking much notice, except anecdotally. Thus it was that although Scripps and other oceanographic institutions had been established along the west coast since the late nineteenth and early twentieth century, the significance of the El Niño phenomenon remained unappreciated until the advent of CalCOFI.

In the winter of 1957–1958, after CalCOFI had been underway for almost a decade, there was one of the largest El Niño events of the century. Highly unusual meteorological and oceanographic conditions were reported across the Pacific. A special CalCOFI symposium was held in June 1958 to examine 'The Changing Pacific Ocean in 1957 and 1958.' As John Isaacs, Director of the Marine Life Research Group, responsible for

CalCOFI-related research at Scripps, stated in his introductory remarks:

> By the fall of 1957, the coral ring of Canton Island, in the memory of man ever bleak and dry, was lush with the seedlings of countless tropical trees and vines. . . . Elsewhere about the Pacific it also was common knowledge that the year had been one of extraordinary climatic events. Hawaii had its first recorded typhoon; the seabird-killing El Niño visited the Peruvian Coast; the ice went out of Point Barrow at the earliest time in history; and on the Pacific's Western rim, the tropical rainy season lingered six weeks beyond its appointed term [241].

Off California, sea surface temperatures were about 3 °C warmer than usual, the fall rains in 1957 were the heaviest in 21 years, and there were record landings of warm-water game fishes [241].

Warren Wooster, who had recently returned from Peru and who would go on from CalCOFI and Scripps to lead the UN Intergovernmental Oceanographic Commission (IOC), found the Pacific ICES (or PICES), and direct the Institute of Marine Studies at the University of Washington, introduced the hypothesis that the oceanography off Peru and California might be linked:

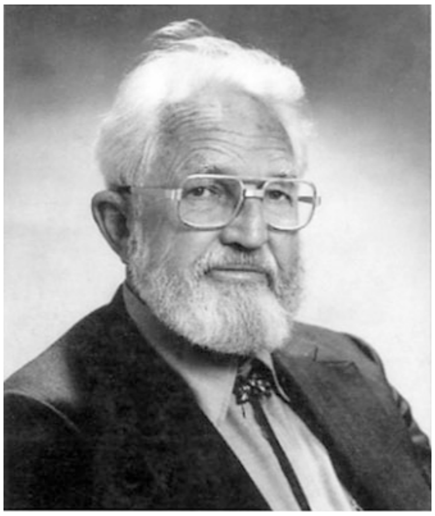

Fig. 8.16 John Isaacs (Photo provided by Tony Koslow)

> One of the most celebrated of oceanic disturbances is that known as El Niño, an occurrence of the first half of the year which is reported at irregular intervals from the coast of Northern Peru.... Similarities between this phenomenon and conditions observed off the California Coast and in other coastal upwelling zones suggest that the underlying causes of the observed abnormalities are the same. Unfortunately it is not easy to discuss the Peruvian Niño in quantitative terms. The lack of a long record of systematic observations throughout the year makes it difficult to determine satisfactory averages with which to compare observations believed to be abnormal.

The symposium proved exceptionally fruitful for Jerome Namias, then Chief of Extended Forecast Division of the U.S. Weather Bureau. Listening to the presentations and discussions led him to advance the hypothesis that links between ocean and atmosphere drive climate phenomena such as El Niño: that the ocean through its heat capacity provides the so-called 'memory' for low-frequency variability, while rapid communication through the atmosphere enables teleconnections to link phenomena on ocean basin scales [471]. Namias would develop this hypothesis for much of the rest of his career: As he stated in his presentation:

> Of course, this is the sketchiest type of hypothesis and it is only the delightful informality of this meeting that encourages me to suggest it. But the history of meteorology and perhaps oceanography indicates that such imaginative excursions are probably initially required for progress.

Namias would soon move to Scripps, where he and others developed the theory to understand how oceanic and atmospheric conditions across the Pacific basin set up the El Niño-Southern Oscillation (ENSO).

Remarkably, however, more than 20 years were to pass before an understanding would emerge how ENSO influenced

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[15] Tony Koslow is the Director of the Scripps CalCOFI program at the Scripps Institution of Oceanography.

Fig. 8.17 (*Left*) Gail Theilacker using Warburg manometry to measure respiratory rates of groups of sardine eggs, June 1968. (*Right*) Portrait of Gail Theilacker, 1975 (Photo provided by Gail Theiacker)

the biological productivity of the California Current. How this happened tells a great deal about the role of serendipity, communication and interdisciplinary collaboration in oceanography – and the fundamental importance of time series.

In the late 1970s, two Scripps graduate students were working, unbeknownst to each other, on two aspects of ENSO forcing on the California Current: even then, Scripps was sufficiently large that students did not necessarily know what those in other disciplines were working on. Dudley Chelton, a physical oceanography student, was examining time series of sea level along the west coast as a measure of the strength of the California Current and its advection. Patricio Bernal, a biological oceanography student, was examining the CalCOFI time series of zooplankton displacement volume. Patricio could see large fluctuations in zooplankton displacement volume, a measure of zooplankton biomass, that were obviously related to ENSO: anomalously low zooplankton volumes over the entire California Current during El Niño periods, in particular the 1957–1958 event, and anomalously high volumes during the contrasting La Niña periods of relatively cool conditions off the coast of California. However, he was struggling to understand the mechanism underlying these changes in biological productivity. Was it due to changes in upwelling conditions through the ENSO cycle or was it differences in the advection of cool productive water from higher latitudes? Then Patricio attended a seminar by Dudley Chelton on advection in the California Current. Dudley's figures showing time series of sea level along the coast of California perfectly mirrored his own time series for zooplankton volumes. The two students soon set to bringing together the physical and biological time series, collaborating on the classic paper that first demonstrated how ENSO drove a coherent response in biological productivity over the extent of the California Current [108].

The concept that the climate forcing and the ecology of the ocean were linked on very large scale spatial scales, a commonplace today, was then quite novel and proved enormously influential. I was a graduate student at Scripps with Chelton and Bernal. In 1980 I graduated and moved to Dalhousie University in Halifax, Canada, where I found similar large-scale coherence in the recruitment to cod, haddock, mackerel and herring stocks across the northwestern Atlantic that was linked to large-scale atmospheric and oceanographic patterns in the North Atlantic [272, 274]. Warren Wooster moved to the University of Washington in 1976, where he collaborated for many years with scientists in academia and at NMFS on studies of northeast Pacific climate influence on the region's fisheries and ecosystems [173, 218].

8.14 Gail Theilacker: Experimental Approaches to Answering Fishery-Oceanographic Questions[16]

CalCOFI touched my life for many years. Even before joining forces with Reuben Lasker in 1959 at the Bureau of Commercial Fisheries (BCF), I was associated with a grand group of scientists gathered together by Martin W. Johnson at SIO to describe the abundance and distribution of plankton in the California Current. The group's sharing of their expertise and knowledge about specific invertebrates had an impact on the direction of my research in later years, in particular, on euphausiid predation of larval fish (Ed Brinton, Annie Townsend and Angeles Alvarino) and on copepod culture (Abe Fleminger), and Marnie Knight, Pooh Venrick and John McGowan always were eager to inspire.

Understanding everything we could about the early life of fishes was key during my tenure at BCF with Rueben Lasker. At that time, the paradigm was that the strength of a year-class of fishes was determined during the larval stage. So our first task was to identify and understand the causes of larval fish mortality, and we concentrated on assessing starvation of

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[16] Gail Theilacker was a research fishery biologist in the Fisheries Resources Division at NOAA Fisheries Southwest Fisheries Science Center in La Jolla, California prior to her move to what is now called the Alaska Fisheries Science Center.

fish larvae and predation on fish larvae. But to do this, first, we needed to learn how to raise fish in captivity.

Initially we collected the fish eggs at sea. I loved the 'sea' time – going to out on the small SIO "T" boat. I grew up fishing off Southern California, and nothing beats being out on at sea, in the sun, searching for fish, even very small fish. We looked for slicks where the fish eggs appeared to concentrate. In the early days, we collected sardine eggs, and later on, anchovy eggs in addition to mackerel and several flat fishes.

It was extremely time consuming and tedious sorting individual eggs, one by one, into rearing tanks at the aquarium at SIO, and later, at the new National Marine Fisheries Service aquarium. Our early experimental work was done on eggs and yolk sac larvae because we couldn't find a small, suitable food for first-feeding larvae. It took years to find nutritious foods that were 'easy' to culture in large quantities and that yielded adequate larval growth rates, similar to growth rates of fish on natural foods. We had many failures. First we experimented with copepods because the young stages of copepods are the natural larval fish prey. Abe Fleminger helped and later Reuben sent for Howard Feder, an invertebrate zoologist, to join us. 'Howie' successfully spawned several molluscs. Their spawn and young stages were eaten by the fish larvae, but in the end, growth rates were slow, probably because the molluscs began to secrete their indigestible shells.

After many unsuccessful trials, our final diet for small-mouth, first-feeding larval anchovy was a naked, single cell dinoflagellate (about 51 micron diameter) followed by several life stages of a rotifer invertebrate (isolated from the Salton Sea) for older larvae. The rotifer was fed a high quality, easily cultured algal diet, so each bite the fish took was high in calories, and contained good fats! These foods were supplied worldwide by the La Jolla Laboratory to academic and mariculture institutions. Just a couple years ago, almost 40 years since publishing the rotifer mass-culture paper with Mike McMaster, I visited a sablefish rearing facility on Vancouver Island. When the farm manager saw my name as I signed in – he gave me a long stare, and said "not THE Gail Theilacker?" Talk about a moment of glory! Scientists still are mass culturing rotifers for raising fish.

Concurrently, while assessing growth of fishes on various diets, I noted that rearing container size affected their growth rates. This study led to the development of an optimal container size and configuration for subsequent studies.

It is the earliest struggles that are dearest to my heart. In the early '60s, while we were struggling to figure out how to raise the fish, Reuben and I concentrated our experimental work on physiological studies of eggs and early, yolk sac larvae – determining their energy requirements. Key in these studies was measuring the temperature-specific rate that yolk was utilized, estimating oxygen consumption in eggs and larvae and determining whether there were salinity stresses.

To estimate the effect of temperature on fish incubation time, development and growth, we borrowed a long, aluminum block from Dr. ZoBell, at SIO that he used for bacteriological studies. The block was cooled at one end and heated at the other and had rows of holes drilled into it for holding large test tubes. About 10 tubes per row gave us many replicates at the relevant constant temperatures. I measured the daily decrease in egg and larval yolk volume and increase in size larvae kept in the tubes. This was fairly direct study and easily done, and at a later date, this information was used to create growth models.

But we also needed information on respiration, and it was these studies that were a challenge. We called upon many at SIO to help, from glass blowers to engineers, to create a Cartesian reference diver apparatus (originally designed by P.F. Scholander, SIO) to measure respiration of individual sardine eggs and larvae. We learned to make tiny glass capsules to hold a single egg (1.7 mm diameter) and an even smaller 'diver'. The diver, cut from a plastic capillary tube and plugged with paraffin at one end, was inserted into the capsule using a hog's eyelash (Martin Johnson's idea). Then the capsule was attached with tubing to a mercury-filled manometer. The whole setup was in a constant temperature bath. Creating suction with the manometer expanded the air trapped inside the diver and formed a bubble, floating the diver. In theory, as the fish egg utilized oxygen from the seawater, oxygen from the air bubble would dissolve into the seawater, forming an equilibrium, and the diver would fall. I manipulated the manometer to keep the diver at a constant height, and the difference in millimeters of mercury in the manometer was equated to oxygen uptake. It all sounds fairly straight forward.

But there were so many places where plans went amiss. I often would lose the diver – a slight sneeze, a draft and poof, the diver's gone; when maneuvering it into the capsule via the hog's eyelash, it would flick off the lash. And often, when I would finally get the diver into the capsule, the bubble would stick to the side of the capsule. The most exasperating diver interludes were when an egg hatched into an active larva with a wagging tail that constantly misplaced my diver. I know it is hard to visualize this when looking at the respiration figure in our publication, but each dot, representing 'an active larva', also represents much frustration on my part.

After learning how to raise fish in the aquarium, we could begin addressing the paradigm question – is starvation a significant cause of larval fish mortality? I developed several techniques to assess starvation in the laboratory, and later, in the field. In the laboratory, manipulating the diets and including periods of starvation yielded fish growing at different rates and in various stages of vigor. Studies on these fish were used to calibrate the various techniques.

Histology was the first approach I used for assessing starvation; other studies included taking many body measurements of the larvae and measuring the height of the midgut cells. All of these analyses were good indicators of starvation, but the histological study was the most robust.

I based the histological assessment of nutritional state on distinct histological changes that occurred in tissues (brain, digestive tract, liver and musculature) when fish are deprived of food. The extent of the changes was scored for 11 histological characteristics, and I classified the larvae into four categories – healthy, recovering from starvation, starving and dying – depending on the laboratory feeding conditions. After the analysis was proven robust in the laboratory, I took it to sea, sampling larval jack mackerel at two contrasting sites, and found that young larvae living offshore were starving while those living near shore, around islands were healthy. This was the first study to show that starvation of fish larvae does occur and that the young stages of jack mackerel are vulnerable.

After finding that young larvae are starving in the field, Roger Hewitt, Nancy Lo and I sampled a mackerel-spawning site at a group of CalCOFI stations off the coast of California for 4 days to try to estimate the predation mortality. We compared the starvation mortality, determined by histology, with the total mortality and partitioned that portion of mortality due to predation. Predation appeared to be the dominant cause of mortality for the youngest larvae, but decreased as larvae fed and developed motility.

Trying to understand, describe and quantify predation on eggs and larvae was difficult. We knew fish and invertebrates captured and ate eggs and larvae; Alvarino found chaetognaths with larval fish in their guts and Brinton had seen euphausiids grasping larval fish. Subsequently, Reuben and I conducted predation experiments in the laboratory by offering anchovy larvae to euphausiids and determining the number of larvae that various stages of euphausiids ate daily. Yolk sac anchovy larvae were most vulnerable.

But transferring this information to the field was problematic – how can you identify the soft, digested remains of fish larvae in a predator's gut?

I took a leap into the field of immunology, hypothesizing that if I could develop an antibody to anchovy yolk protein, there would be a means to detect the yolk in the gut of a euphausiid. Since Reuben and I had found that yolk sac larvae that were most vulnerable, there should be yolk protein along with muscle protein in the predator's guts. A college student, Amy Kimball, was working with me that summer (she's currently a medical doctor at John Hopkins) and James Trimmer, SIO, joined us. We were good students, and with Trimmer's expertise in immunological techniques, we succeeded in developing antisera to anchovy yolk protein. This involved using rabbits to produce the antiserum. We injected the rabbits with purified anchovy yolk several times over 6 months; and the final bleed was taken 10 months after the first injection. For us, the days we had to inject or bleed the rabbits were distressing; we didn't want to hurt our rabbits. We befriended them, often bringing carrot treats, and found that happy rabbits produce high-titre antibodies!

The immunoassay we used detected nannogram quantities of yolk, and we were capable of identifying 75 % of the laboratory-fed euphausiids. With these favorable results, I took the study to the field, assessing euphausiid predation on larval anchovy at two contrasting sites off California. Results from this early study showed differences in mortality of anchovy between inshore and offshore sites could be accounted for by differences in rates of euphausiid predation.

Later, with Nancy Lo and Annie Townsend (SIO), we quantified predation by euphausiids on the early stages of anchovy off California at CalCOFI stations between Point Conception and San Diego. We determined that between 47 and 78 % of the natural mortality of anchovy eggs and yolk sac larvae could be explained by euphausiid predation.

Finally, we had some robust experimental techniques that could be used to understand the processes that affect recruitment of young fish to a fish stock.

Other critical problems also were addressed using experimental techniques. For example, abundance estimates of anchovy larvae caught at sea were adjusted for growth using laboratory growth rates based on live length. Sea-caught larvae are captured in a net and then preserved in a fixative. A significant bias existed because the conversion from live length to net-collected and preserved length was unknown.

I ran a series of experiments to identify the causes of changes in length and other morphometric measurements of larval anchovy as a function of capture technique and preservation fluid. Models developed using this data predict live size, and thus age, of sea-collected anchovy to yield valid abundance estimates.

I was CalCOFI Coordinator in 1988 and 1989, during CalCOFI's 40th Anniversary. During my tenure, I negotiated nonprofit status from IRS, raised funds for graduate students, established the Lasker Memorial Fund for student scholarships and organized the annual conferences. My major legacy to CalCOFI was achieving increased professional visibility for CalCOFI Reports. As managing editor of the Reports, I elevated the status of the journal by setting up an Editorial Board and requiring peer reviews, gaining acceptance for the Journal in Aquatic Sciences and Fisheries Abstracts and the International Scientific Information System, Current Contents. Heretofore articles appearing in the journal were inaccessible to retrieval indexing and because the review system was inadequate, publications in the journal were not considered peer reviewed.

Fig. 8.18 *Left*: John Hunter in 2003. *Right*: John Hunter at sea with friends and colleagues. Beverley Macewicz was standing next to John Hunter (Photographs courtesy of Nancy Lo, NOAA Fisheries SWFSC)

8.15 John R. Hunter: Improving the Fishery Information from CalCOFI[17]

A theme that keeps returning to my mind as I think about those years (1980–2003, the last 23 years of my career) would be a narrative on our struggle to improve the fishery information that can be derived from CalCOFI while sustaining the time series and related survey program (Paul Smith worked on this problem long before I became active in CalCOFI.)

I believe we were successful in a number of ways; developing a fundamental understanding of issues affecting accuracy and precision of sampling ichthyoplankton, the creation of new methods for estimating biomass from eggs and larvae, developing more precise larval abundance indices, providing basic information on larval ecology and behavior, and adult spawning behavior and exploring the long-term dynamics of exploited and unexploited species in the time series. We were less successful when it came to overcoming the imprecision and geographic and temporal biases of what by 1980 had become a quarterly survey [largely] limited to the Southern California Bight [and waters further offshore].

An important turning point, from the standpoint of the Fishery Division research efforts in the CalCOFI program, occurred when we became convinced that there was little or no recruitment signal in the abundances of life stages of fish larvae commonly taken in the surveys. We felt that new advances depended upon quantitative sampling of the late larval and juvenile stages. We began work on identifying how we might sample quantitatively the later life stages of anchovy where recruitment processes might be more clearly defined. After developing a new net (MIK [Modified Isaacs Kidd]) [see Sect. 3.1.3.2], and preliminary sampling, it became clear, owing to patchiness and lower abundances of such life stages, that the costs of quantitative surveys for these life stages was incompatible with the standard CalCOFI survey plan and an independent prerecruit survey for pelagic fishes was required. Such a survey was beyond our resources at the time. Our first priority over the years was always continuation of the CalCOFI time series with all its imperfections, over surveys with a more specialized fishery objective. Our faith in the inherent value of such long-term ecosystem time series, always trumped more specialized fishery surveys or experiments. When resources were short, and they often were, CalCOFI surveys always got the nod. This resulted in the ending of Reuben Laskers's field experiments on recruitment, as well as any hope for a prerecruit survey.

Around 1980, we began to shift our attention from research on understanding recruitment processes to improving methods for using eggs and larvae as a measure of biomass and reproductive effort. As we increased our focus on using eggs and larvae as measures of adult abundance, we struggled with two issues common to any plankton surveys used to monitor adult fish abundance: (1) one could not be certain that changes in abundance of eggs, or larvae, were not a result of geographic shifts in spawning rather that changes stock size because the CalCOFI pattern did not sample the full geographic range of most spawning stocks; and (2) indices of stock abundance based on eggs and larvae taken in standard CalCOFI tows are imprecise, and may not track abundance with sufficient precision to be routinely used in fishery assessment models.

The obvious answer to such uncertainties is to increase the sampling of ichthyoplankton in time and space, either by increasing the coverage of the surveys, conducting independent surveys, or improving the precision of existing surveys and models. We worked on all these fronts over the next 20 years.

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[17] John Hunter was Director of the Fisheries Resources Division of the NOAA Fisheries Southwest Fisheries Science Center in La Jolla, California from 1998 to 2003, prior to his retirement.

Fig. 8.19 CalCOFI Conference photo (Idyllwild, California, 1983) showing (*left* to *right*): Elizabeth Venrick, Paul Smith, Nancy Lo and Gail Theilacker (Photo courtesy of Gail Theilacker)

8.16 Nancy Chyan-huei Lo: Perspectives, Experiences and Stories of CalCOFI[18]

As a statistician, I treasure sound datasets, e.g. design-based data sets, because they are likely to produce unbiased estimates and when sample sizes are large, the estimates will be highly precise. For sea surveys, both spatial and temporal aspects are important. One such sound dataset is derived from the CalCOFI surveys, from 1949 to the present. Prior to 1985, the coverage of CalCOFI in most years was from San Francisco to Baja California through the whole year. The ichthyoplankton net-tows were 1-m ring net from 1951 to 1975, and bongo net tows from 1978 to present. In 1985, a new vertical net (California Vertical tow: CalVET) was designed and used to collect fish eggs with 0.05m^2 surface area, mesh size of 0.15 mm, to reach down to 70m depth and to minimize volume of water filtered per unit depth [519]. Since 1949, the eggs and larvae of hundreds of species have been collected together with oceanographic variables, zooplankton and phytoplankton, and nutrients. CalCOFI is undoubtedly the best biological and oceanographic time series in the world.

One of the purposes of CalCOFI survey was to find out why sardine were declining in the late 1940s. As 490 ichthyoplankton species have been identified (as of 2010), the data sets are ideal for the ecosystem studies [398–400]. During the very first CalCOFI survey conducted in 1949, when hake larvae were caught [it became apparent] that hake spawn in the CalCOFI area. One newspaper article reported on "the unusual abundance of hake larvae" 2 months after the first cruise of the CalCOFI program in 1949. Until the CalCOFI surveys, no one suspected that hake spawn off California in January–April as most of the hake fishery takes place in the Northwest area [141]. This discovery led to the understanding of the north-south movement of hake off the west coast of American continent: adult hake move to the northwest to feed in late spring after spawning off California during winter and spring.

Experiences of Using CalCOFI Data

Based on the CalCOFI database, time series for many species were constructed: anchovy egg production from 1961 to 1991 [253], recently updated anchovy egg production time series from 1981 to 2009 [167], daily larval production of hake from 1951 to 2006 [326], daily larval production of Pacific mackerel from 1951 to 2009 [318], egg density of Pacific mackerel from 1986 to 2009, bocaccio (*Sebastes paucispinis*), [457], cowcod [93], and others. Two time series of anchovy egg production were used in the stock assessment [253]. The time series of Pacific mackerel was used in the stock assessment in 2007, but was excluded in the last two stock assessment due to frequent occurrence of zero values [318]. The larval production of hake from 1951 to 2006 was not used in the stock assessment as spawning biomass index due to the high coefficient of variation. However the time series was used to derive estimates of virgin spawning biomass based on average larval production index between 1951 and 1965 [202].

One of the reasons for the high fluctuation of both Pacific mackerel and hake ichthyoplankton time series was due to the high patchiness of larvae. The high among-year fluctuation of time series prevents the time series from being included in the stock assessment process. In our experience, egg and larval time series with either a low degree of patchiness, or a large sample size even when patchiness is high, are likely to be useful and to be included in the stock assessments. This explains why egg and larval time series for anchovy and sardine have been used in assessments, in contrast to those for Pacific mackerel and hake. Regardless of whether the egg and larval time series were used in the stock assessments, those time series provided a general trend of the spawning biomass of the species even though the current CalCOFI survey area was a fraction of the original survey area. The time series of both Pacific mackerel and hake were useful indices for the high and low points of the adult populations.

The hake ichthyoplankton time series is also related to environmental variability. For example, the decrease of hake larval production coincided with the increase of sea temperature since the 1980s. The spawning center of hake is believed to move to the north during warm years and to the south during colder years in area between CalCOFI line 60.0 and 136.7 based on data collected in 1951–1984.

In addition to the high patchiness of larvae, the zero values in some years of Pacific mackerel and the high among year variation of Pacific mackerel and hake were also due to the

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[18] Until her retirement in 2011 Nancy Lo was a Supervisory mathematical statistician and leader of the Small Pelagic Fisheries group in the Fisheries Resources Division at NOAA Fisheries Southwest Fisheries Science Center in La Jolla, California.

coarseness of the grid, i.e. small sample size. This is also true for other species, in particular for surveys after 1984. Of course, timing may not be optimum for Pacific mackerel, because the quarterly spring CalCOFI cruise typically is a little early, and the summer cruise is too late. Pacific mackerel larvae are very patchy and have a more inshore distribution and hence their distribution is a poor fit to the CalCOFI sample pattern. Any species-specific survey tailored to the timing of spawning, geographic distribution, larval patchiness, and net avoidance would certainly produce a better index. Such surveys would be much more costly and time consuming. However, a CalCOFI index for a non-target species is nearly free. Thus there are trade-offs using CalCOFI survey data for any species collected during the survey relative to a species-specific survey.

From the outset, the goal of CalCOFI was to understand and study the physics, chemistry, and biology of the ecosystem of which sardine is a part. CalCOFI has become a model of other regions of the world. For example, TaiCOFI (Taiwan Cooperative Oceanic Fisheries Investigations) [314], revised from a survey started in 1970, is now run by the Taiwan Fisheries Research Institute since 2003 modeled on the CalCOFI survey and sampling the area around Taiwan with 62 stations in four quarterly surveys to monitor the coastal environment and offshore fishing grounds in Taiwan.

Perspectives for the Future

I would like to revive the survey designs prior to 1981 from Baja California to north of San Francisco (CalCOFI line 157–40) and all months, which requires funding, ship time and manpower. We can even expand the surveys north to British Columbia and call it BC to BC CalCOFI. Wider sampling is important for trans-boundary species, like sardine, Pacific mackerel, and hake. Thus collaboration between CalCOFI and IMECOCAL is important and worth pursuing, in particular the data exchange between CalCOFI and IMECOCAL. The BC to BC survey concept was initiated in 2003 by John Hunter to include five paired lines at Monterey, Bodega Bay, Arcata, Newport and the Columbia River. Related proposals suggest an additional five lines transect lines off British Columbia, Canada.

8.17 Steven Bograd: "It is Difficult to Overstate the Importance of CalCOFI"[19]

I came to Scripps to begin my CalCOFI Post-Doctoral Fellowship in 1998, the year of a very strong El Niño event and a lot of rain in San Diego (relatively speaking). The following 2.5 years that I spent at SIO were among the best in my career. In addition to being immersed in a vibrant academic environment and having the opportunity to contribute to a world-class program, I was fortunate to be mentored by a fantastic group of scientists. Teri Chereskin was my immediate advisor and mentor, and my principal research with Teri involved the analysis of ADCP data that had been collected for many years on the CalCOFI cruises. Mike Mullin and Tom Hayward at SIO took a strong interest in my development as a young scientist, and I also began a very fruitful collaboration with Ron Lynn at NOAA Southwest Fisheries Science Center. And there was always a veritable 'Who's Who' of world-class oceanographers available for discussion and enlightenment, including Dave Checkley, Ralf Goericke, Arnold Mantyla, John McGowan, Art Miller, Mark Ohman, Joe Reid, Dean Roemmich, Paul Smith, Pooh Venrick, and many others.

Fig. 8.20 Steven Bograd with Joe Reid, one of the pioneering physical oceanographers of CalCOFI (Photo provided by Steven Bograd)

My time at SIO was also very exciting from an oceanographic perspective. The El Niño had large impacts on the physics and biology of the southern California Current, and was quickly followed by a strong La Ni na event and a significant shift in the productivity of the ecosystem. Through Tom Hayward's leadership, CalCOFI was able to supplement the quarterly surveys with monthly surveys during this period, providing unprecedented sampling of the evolution of an ENSO event in the California Current. It is difficult to overstate the importance of CalCOFI in improving our understanding of how the California Current works – CalCOFI's longevity, flexibility, interdisciplinary sampling,

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[19] Steven Bograd is a supervisory oceanographer in the Environmental Research Division at NOAA Fisheries Southwest Fisheries Science Center in Monterey, California.

Fig. 8.21 At sea on SIO vessel Roger Revelle helping to deploy the CTD (Photo provided by Steven Bograd)

and inclusion of numerous ancillary observing programs over the years make it truly exceptional in the marine sciences.

In late 1999, Tom Hayward took an extended leave of absence to sail around the world (I don't think he ever came back), and I was asked to fill in as Acting Coordinator while he was gone. In this capacity, I helped to coordinate and supervise each of the quarterly CalCOFI cruises[20] (NH0001, DSJ0004, NH0007, NH0010) and to oversee the timely processing and distribution of the data. This was my first experience in any kind of managerial role, and I must say, it was by far the easiest. The CalCOFI team (Ed Renger, Sherry Cummings, Dennis Gruber, Fernando Ramirez, Jim Wilkinson, and Dave Wolgast), with decades of at-sea experience between them, ensured that everything went smoothly. There was very little I needed to do.

Following my move to the Pacific Fisheries Environmental Laboratory in Pacific Grove, CA, in January 2001, I have continued to collaborate with my CalCOFI and SIO colleagues. CalCOFI represents a lot of things to me: first-rate science, a brilliant history and tradition, and wonderful mentorship of young scientists. My career has benefited greatly from my association with CalCOFI, and I hope it continues to inspire future generations of marine scientists.

8.18 Ralf Goericke: The CalCOFI Funding Crisis of 2003[21]

About a year after I came to Scripps in 1993 I went on my first CalCOFI cruise and to my first CalCOFI conference. I quickly revised my not so positive, East Coast biased view of CalCOFI. I had found a great platform for my research and a great community of scientists and friends within the Marine Life Research Group. Throughout the following years either I or my post-docs or students went on many CalCOFI cruises. During this time Mike Mullin helped me a lot with advice, encouragement and resources. All this came to an end when Mike unexpectedly died in December of 2000. Pooh Venrick took over as Director of CalCOFI and MLRG. By this time I had not only realized that CalCOFI is a great research platform but that it was exciting and rewarding to study the CalCOFI data sets. When Tom Hayward retired in Nov 2001 I took over his position to supervise the SIO-CalCOFI seagoing group and work with the CalCOFI data. However, I was joining a ship in trouble. In the summer of 2001 the State of California decided to reduce funding to the University of California system dramatically. The UC system chose to implement these cuts by decreasing research funds made available to the individual universities. These were the funds that CalCOFI relied on, and indeed the director's office at Scripps decided to cut funding for CalCOFI as of the summer of 2003. The days when CalCOFI was funded by line-items in the state budget or even fees levied on fishermen, had long been gone. We, the Scripps CalCOFI community, reacted with disbelief – defunding CalCOFI had to be impossible,

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[20] The first two letters of the cruise code denote the vessel, where in this case NH was the SIO vessel New Horizon and DS was the NOAA vessel David Starr Jordan. The next two numbers indicate the year, where 00 denotes 2000, and the last two digits are the month label for the cruises, in this case January, April, July and October.

[21] Ralf Goericke is a Researcher in the Integrated Research Division of Scripps Institution of Oceanography in La Jolla California, California.

after all it had been going on for more that 50 years. Our group went into overdrive; we needed to overturn this decision. We had meetings and meetings where we told ourselves how important CalCOFI was and that this could not happen. We put together a CalCOFI white paper, drafting a new mission statement, outlining goals for the next 50 years, describing CalCOFI, explaining why it is so important to both Scripps and the larger scientific community and what it had achieved. In early 2002 we gave a presentation on CalCOFI to the SIO Academic Council. That spring we solicited letter of support for the continuation of CalCOFI from well respected scientists all over the world. But all this was in vain. What we did not know, or more likely, did not want to realize, was that the SIO administration had no other choice and that its decision to cut funding for CalCOFI was firm. SIO CalCOFI still had 'carry-forward funds' that would allow it to provide technician salaries for more than a year. The UC funds for CalCOFI were cut during FY 03/04 in half and in their entirety the next year. The SIO Director's office, however, never intended to abandon CalCOFI. Their plan was to find outside funds for SIO CalCOFI, an effort that was lead by Kathleen Ritzman, SIO's director of government relations. First she secured us funding from ONR that bridged a gap in the shiptime funding and secured technician salaries. Later she was able to insert a line item into the federal budget directing NOAA to fund CalCOFI – SIO CalCOFI had become a 'pork barrel' project. We did not mind; indeed, during this time it became clear that CalCOFI was becoming central to NOAA's emerging efforts to assess the state of the California Current ecosystem and manage its living resources in an ecosystem context. For example John Hunter's planning of the PACOOS predecessor ACCEO (Alliance for California Current Ecosystem Observations), occurred at the same time that SIO CalCOFI was struggling to secure new funding. We realized that NOAA was willing to fund CalCOFI because of its importance for NOAA's mission and today SIO CalCOFI is fully funded by NOAA fisheries. In retrospect I have to say that the process we went through was extremely beneficial for us and CalCOFI. Of course we did not achieve our objective, reinstate funding for SIO CalCOFI through the State of California, but through our struggles we reinvented CalCOFI in our minds and the minds of the Scripps and national communities. CalCOFI began to change quickly over the next few years. In 2004 nearshore stations were added to the CalCOFI grid that allows us to link offshore observations to the nearshore. The SIO CalCOFI community was able to obtain funding for a Long-Term-Ecological Research (LTER) project in 2004 which, at the time of this writing, is in its second 6-year phase. The California Current-LTER program augments CalCOFI sampling through additional measurements targeted at the biogeochemistry of the system and the population structure of the lower trophic levels, thus greatly expanding our view of the ecological system. The CCE-LTER process and modeling studies will hopefully lead to a mechanistic understanding of the phenomena that have been observed by CalCOFI scientists for the last 6 decades and most importantly, the community of scientists at Scripps that is involved in CalCOFI / CCE-LTER work has more than doubled. We now talk about the New CalCOFI and I wonder if these changes would have come about if we had not been so rudely awakened by the State budget cuts of 2003.

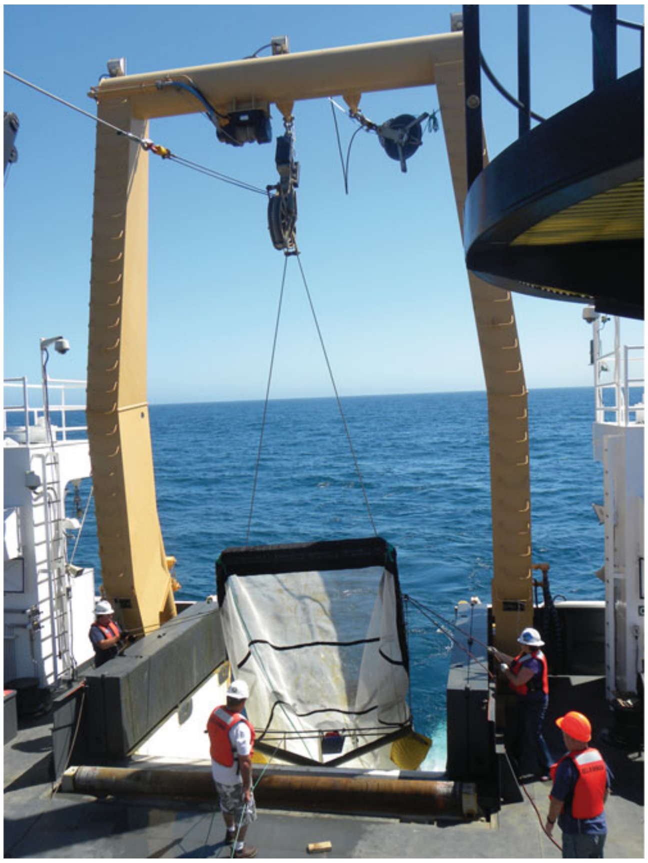

Fig. 8.22 MOHT deployment from NOAA ship Bell M. Shimada in October 2010 in the Southern California Bight (Photo by Sam McClatchie)

8.19 CalCOFI, Midwater Fishes, and the California Current Ecosystem

by J. Anthony Koslow[22]

I was a graduate student at Scripps from 1975 to 1979. My research focused on the feeding selectivity of northern anchovy schools and its influence on the zooplankton community. The anchovy was the dominant small pelagic planktivorous fish at

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[22] Tony Koslow is the Director of the Scripps CalCOFI program at the Scripps Institution of Oceanography.

the time and a major focus of the CalCOFI program. Looking back, however, it is surprising how little involved I was with CalCOFI, considering that Mike Mullin and John Isaacs were my chief mentors – both led the Scripps CalCOFI program at various times – and John Hunter and Paul Smith from the NMFS laboratory were also on my doctoral committee. Then in 2007, I returned Scripps to direct its CalCOFI program, following in the footsteps of my former mentors.

Prior to returning to Scripps, I worked for 17 years in Australia at the Commonwealth Scientific and Industrial Research Organization (CSIRO). My research there curiously paralleled many of the research directions at CalCOFI. I had led scientific teams to develop acoustic and egg surveys to assess some of Australia's new deepwater fisheries for the orange roughy and the local hake known as blue grenadier or hoki. I had also carried out research on the deepwater food chain that supported these fisheries and examined the impact of the orange roughy fishery on the fragile benthic seamount habitats on which they were fished. In my last 5 years at CSIRO, I initiated the first ocean observation program off Perth in Western Australia. This effort was largely run out of an 8 m (26 foot) shark cat, so I was pleased to trade it in for the opportunity to work with CalCOFI.

One of CalCOFI's great strengths is the way it has continued to evolve, adding new observations to its program, such as for seabirds and marine mammals, while maintaining its core physical, chemical, and biological measurements. During my time with CSIRO, I had used acoustics in combination with midwater trawling as a high-resolution quantitative tool to sample the water column. I had also come to appreciate that the midwater fauna – in particular the myctophids and other micronekton that comprise the deep scattering layer – were inextricably linked with epipelagic ecosystems. Much of this so-called mesopelagic micronekton feeds each night in near-surface waters, only inhabiting mesopelagic depths during the day as a means to avoid visual predators. There are at least a billion tonnes of these midwater fishes, more than ten times the global marine fish landings. This fauna is a major consumer of global plankton production and a key link to myriad higher predators, including various tunas and billfishes, squids, seabirds and marine mammals. However, this fauna was a critical gap in the CalCOFI program. Little was known about this fauna off southern California, not even its approximate biomass.

In coming to Scripps, I collaborated with David Demer, a leading acoustician at the NOAA Southwest Fisheries Science Center (SWFSC), in a proposal to the Gordon and Betty Moore Foundation to develop an acoustic/trawl observation program as a new component of the Scripps CalCOFI program. A Simrad multi-frequency acoustic system was purchased and installed on the RV New Horizon, the Scripps vessel that carried out two of the four annual CalCOFI cruises, along with a Motoda-Oozeki-Hu trawl, a frame trawl with 5 m^2 mouth opening that could be towed at 3 to 5 knots to sample the krill, midwater and juvenile fishes. Adding this component to CalCOFI should soon enable us to assess the role played by the midwater micronekton in linking the plankton and higher trophic levels in the California Current.

One of the great surprises in returning to Scripps to work with the CalCOFI program was the richness of its data and how much still remained to be explored. Despite the several generations of CalCOFI researchers who had preceded me, so much was still unknown! One of the data sets that I undertook to examine was the ichthyoplankton data for the abundance by taxon from the CalCOFI plankton tows. This was one of the finest of the CalCOFI data sets because of its taxonomic resolution, built up by several generations of larval fish scientists at the SWFSC from "Ahlie" Ahlstrom to Geoff Moser and Bill Watson. Using recurrent group analysis, a multivariate statistical method developed by Ed Fager at Scripps, Ahlstrom, Moser and Paul Smith at the SWFSC, along with Valerie Loeb, Mike Mullin and Dennis Gruber at Scripps, convincingly demonstrated considerable spatial and assemblage structure in the CalCOFI data [188, 328, 406, 407]. Thus, despite the advective nature of the California Current and the considerable mixing of water masses in the Southern California Bight, this analysis based on presence-absence data revealed considerable fidelity of ichthyoplankton assemblages with northerly (sub-Arctic/transition zone), southerly, coastal zone, and other affinities. More recently a Scripps graduate student, Zack Hsieh in George Sugihara's lab, and collaborating with a number of Scripps and SWFSC scientists, had begun to explore trends in the abundance and distribution of dominant taxa, leading to high-profile series of publications on the impacts of fishing and climate warming [222–225]. Because larval abundance reflects the abundance of the adult spawning stocks, these studies revealed interesting patterns in the diverse fish community of the California Current, both fished and unfished, and not only the ichthyoplankton.

However, multivariate analysis had not been used to examine temporal patterns in this diverse community of fishes. I decided to analyze the ichthyoplankton data using principal component analysis, which I had previously used effectively to uncover pattern in complex ecological data sets. Working in collaboration with Ralf Goericke, the Scripps CalCOFI coordinator, my post-doc, Ana Lara-Lopez, and Bill Watson, leader of the SWFSC ichthyoplankton lab, we found that the oscillations of the anchovy and sardine populations did not comprise the dominant pattern in the data set nor was the pattern most closely related to the regional trend in sea surface temperature. Instead, the dominant pattern involved dramatic and hitherto unknown changes in the abundance of about two dozen taxa of midwater fishes [275]. Oxygen concentrations in the oxygen minimum zone at midwater depths had varied by about ±20 % since the 1950s. The abundance of these midwater fish larvae, a proxy for the abundance of their spawning stocks, was highly correlated (r = 0.75) with these changes in oxygen concentration. In the last 20 years, the abundance of these midwater fishes had declined by more than 60 % in apparent response to declining oxygen levels. Our CalCOFI acoustic surveys showed that the deep scattering layer was concentrated in the marginally hypoxic waters just above the core of the oxygen minimum zone. Studies of the CalCOFI data by Steve Bograd, Sam McClatchie and various collaborators had shown that this layer had shoaled on average 41 m over the last 20 years [71, 370]. Presumably the deep scattering layer had similarly shoaled, rendering the midwater fishes that much more vulnerable to their visual predators.

Global climate change models predict that oxygen levels at mid-depths will decline by 20 to 40 % in the next century or so as increased stratification of the upper mixed layer significantly reduces ventilation of deeper waters. One of the greatest impacts of this growing hypoxia will be on the midwater fauna. Once again, the rich CalCOFI time series have provided insight into how the ocean is responding to changing environmental conditions. And the CalCOFI data set will continue to provide such insight, no doubt in ways we cannot yet foresee, as humanity enters a new era of climate change.

8.20 Bertha Lavaniegos: IMECOCAL: A Legitimate Child of CalCOFI

Some time ago there used to be meetings between Baja California research centers and Scripps Institution of Oceanography. In one of those meetings I met Prof. Edward Brinton when I was doing my Masters thesis. He taught me about euphausiids during innumerable visits to Scripps to check up on my taxonomic identifications of krill from the Gulf of California. Then was when I got to know Margaret Knight and Annie Townsend, the rest of the euphausiid team, and who kindly he helped me with splendid drawings and much patience. Ed dedicated hours to explain to me aspects of euphausiid biology and he always made sure that I got back to Ensenada with new papers to read. It was an extraordinary learning experience and I progressed greatly in my understanding of plankton and how the pelagic ecosystem works. I had no idea about the surprising diversity awaiting me in the California Current System (CCS). I began my Doctoral studies at CICESE in 1988 with Ed Brinton as my adviser, and I analyzed CalCOFI samples from the time when the waters off Baja California were sampled.

Some time later I worked with CalCOFI again, when the concept of "climate regimes" became popular. Atmospheric and hydrographic data in combination with biological time series revealed a regime shift in the winter of 1976–1977. There was much excitement generated by the reported decline of zooplankton off southern California [475]. Many question emerged concerning probable changes in species composition, a possible tropicalization of the ecosystem, and whether other region of the CCS were similarly affected. John Hunter, Tom Hayward, and Mike Mullin persuaded colleagues in Mexico to begin CalCOFI-type cruises off Baja California. They wanted to know how the "climate regime shift" looked in Baja California and also whether zooplankton was decreasing with sea surface warming in that region. They encouraged us to undertake cruises monitoring the oceanic ecosystem and to construct a picture of environmental changes and the movements of the sardine. Tim Baumgartner played a pivotal role firstly as a contact person between researchers and later as leader of the first proposals to get funds for the cruises.

The planning of the "Mexican CalCOFI" before it became the IMECOCAL program took some time due to the geographic dispersion of the interested researchers. We had many discussions and two important meetings, first in La Jolla between the CalCOFI group and Mexican researchers from CICESE, CICIMAR and UABC. Later we met in La Paz to define potential institutions to participate in the new program, including CRIP from Mazatlan, CIBNOR and UABCS from La Paz. We had then, and we continue to have, serious limitations with the research vessel. The only participating institution having a vessel capable of operating in the open sea along the largely uninhabited coast off Baja California is CICESE. The R/V Francisco de Ulloa (Fig. 8.23), although small and uncomfortable, has allowed the realization of more than 50 cruises. This has been exhausting work due to scarce economic resources and the absence of technicians dedicated to the program. Today many people want to use the IMECOCAL data and is clear that the effort has been worthwhile. As part of the scientific IMECOCAL committee, I have been involved in different activities related to zooplankton sampling, laboratory analysis and care of the pelagic invertebrate collection.

Simultaneously to my work with IMECOCAL, I collaborated with Mark Ohman on retrospective analysis of zooplankton off southern California. That region has the best CalCOFI sampling coverage and it was essential to know the zooplankton structure, and which taxa were behind the declining zooplankton biomass reported by Roemmich and McGowan [475]. I participated in a project directed by Mark to analyze the taxonomic composition of zooplankton as accurately as possible. Among the participants were Dave Checkley and Ginger Rebstock who tackled copepod diversity, while Ed Brinton and Annie Townsend did a great job with the euphausiids. I analyzed the rest of the taxa, with particular attention in gelatinous plankton. This represented a great challenge for me, because both a record of sizes was required and I needed to identify the dominant species of each functional group. Ed Brinton had commented that salps could be the reason of the decrease in biomass, and it was amazing how well the information fit his expectations [297].

Fig. 8.23 (*Left*) The IMECOCAL research vessel Francisco de Ulloa. (*Right*) Recovery of a bongo net (Photos provided by Bertha Lavaniegos)

Similar data series are now needed for the Baja California waters, and by now we have 15 years of monitoring with IMECOCAL. Information to species level is essential in order to describe the zooplankton community in that complex region adjacent to the tropics. The integration of data from IMECOCAL, CalCOFI, and other programs in northern sectors of the CCS has produced spectacular descriptions of the ecosystem status and regional features have been highlighted. However comparisons in species composition along the CCS have been so far limited. This is the next challenge for us.

8.21 Daniel L. Rudnick: The Potential of Autonomous Gliders to Contribute to the New CalCOFI[23]

I would classify myself not as a CalCOFI insider, but as an admirer. CalCOFI is certainly one of the most important long time series in oceanography, notable especially for its inclusion of so many physical, chemical, and biological variables. The impressive legacy of CalCOFI carries the burden of ensuring data quality over the decades. As technology advances, this creates a tension as the requirement for continuity resists the promise of new approaches.

My primary scientific interests involve the processes of the upper ocean. I have spent much of my career using new technology to achieve the best possible resolution of these processes. When I returned to SIO as an assistant professor in 1993, my start-up package included some money towards the purchase of a SeaSoar system [452]. SeaSoar is a towed undulating profiler that cycles from the surface to about 400 m in about 12 min at a tow speed of 8 knots, resulting in horizontal resolution of better than 3 km. The tow cable has several conductors, so all manner of instruments can be deployed on SeaSoar from CTD to bio-optical sensors. At the time, I thought about using SeaSoar to do the standard CalCOFI survey between lines 93 and 77 (see Fig. 1.4), which could be completed in 11 days at a speed of 8 knots. The 3-km horizontal resolution would have been a substantial improvement. However, the requirement for dedicated ship time, and especially the inability to collect water or tow nets made the idea unworkable. Still, I wondered what could be learned from sustained observation at fine horizontal resolution.

Autonomous underwater gliders offer the opportunity of sustained fine resolution observations of the coastal ocean [481]. As used in the California Current System, the underwater glider Spray (developed at Scripps Institution of Oceanography, [505]) dives between the surface and 500 m, completing a cycle in 3 h, during which time it moves 3 km in the horizontal. Spray occupies lines 350–550 km long, completing one transect in about 3 weeks. Measured variables include pressure, temperature, salinity, absolute velocity, chlorophyll fluorescence for phytoplankton, and acoustic backscatter for zooplankton. Data are transferred to shore at the surface when piloting commands may be received. Recoveries and deployments are done from small boats, with a typical mission lasting about 100 days.

Since 2006, operations have been carried out nearly continuously on lines 90, 80, and 66.7 (see Fig. 1.6). To date, the Southern California glider network has covered over 92,000 km in over 4,500 glider-days, creating a substantial database. As gliders are relatively new, there are some questions about their benefits and liabilities as observing platforms. Consider a comparison with CalCOFI ship stations on Line 90 since October 2006 (Fig. 8.24). Several differences in glider and ship sampling are apparent. First, Spray samples are so closely spaced (~3 km) that it is difficult to distinguish individual points in the figure, while ship station spacing is as large as 75 km offshore. Second, in order to increase temporal resolution in the inner 500 km Spray did not sample

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[23] Dan Rudnick is a Professor in the Climate Atmospheric Science and Physical Oceanography (CASPO) Division at Scripps Institution of Oceanography in La Jolla, California.

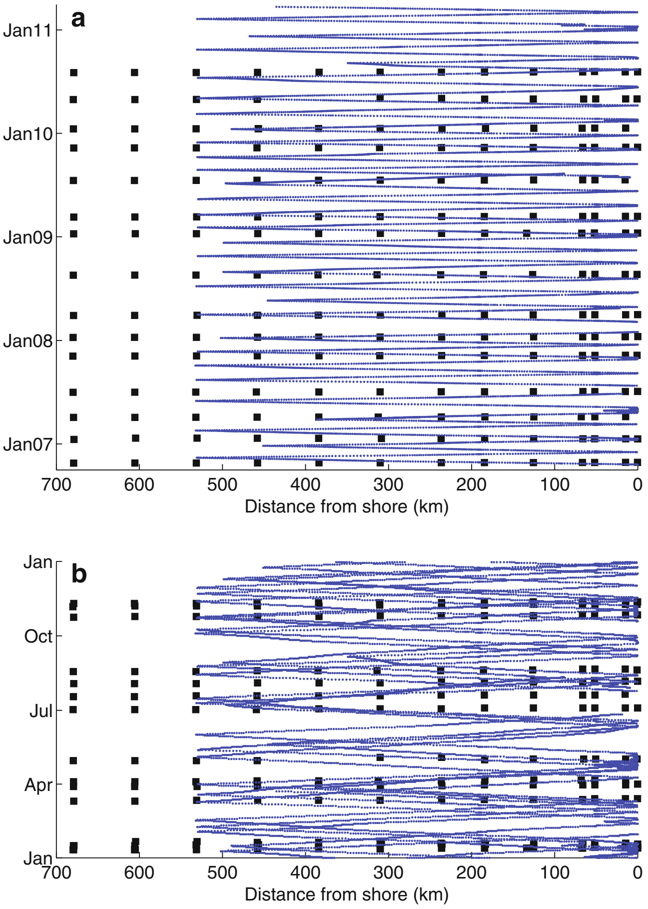

Fig. 8.24 Spray dives (*blue points*) and CalCOFI ship stations (*black squares*) along line 90. The *upper panel* has the time of each sample as a function of distance from shore. The *lower panel* has the month of the year against distance from shore to illustrate the sampling of the annual cycle (Graph by Dan Rudnick)

as far offshore as the ship. Third, Spray is relatively slow, manifest in the slope of the (blue) lines, while the more rapid ship (black squares) lines are nearly horizontal. Finally, even though Spray is slow, its continual presence provides about four times as many glider sections (every 3 weeks) as the ship does (every 3 months). Because a Spray is nearly always on the line, gliders are best for resolving the annual cycle (Fig. 8.24). There are observations throughout every season, even in this relatively short record. Spray does a profile every 3 h, so in a 3-month period there are about 720 Spray profiles while there are only 13 CalCOFI stations on Line 90. Thus Spray produces about 50 times more profiles along Line 90 than does CalCOFI. Even though no glider section is synoptic, glider monitoring is less aliased than a sequence of quarterly synoptic sections.

Scientific results are beginning to emerge from the Southern California glider network. Results from the first few deployments emphasized the co-location of fine scale physical and biological variables in such features as fronts and eddies [130]. Spray glider observations were used to track an effluent plume [558]. Glider observations were assimilated into a model of circulation in the Southern California Bight with the goal of quantifying the along-shore flow, producing a finding that cores of velocity propagate offshore as Rossby waves [560]. The El Niño of 2009–2010 was the first to be observed by gliders along the California coast. As gliders had a continuous presence, the rapid arrival of El Niño was found to be strongly influenced by an atmospheric teleconnection [559]. As the glider database grows, and as analyses probe deeper into the data, further results should emerge.

Continued development is focusing on adding sensors to Spray gliders. Dissolved oxygen sensors are now deployed to allow the continuous monitoring of hypoxic zones, and the estimation of acidification through established relationships [257]. Nitrate sensors are being tested with the goal of monitoring the distribution of this limiting nutrient. Passive acoustics are used to localize marine mammals through their vocalizations. As more sensors are made smaller and less demanding of power, it is easy to imagine their deployment on gliders.

Coastal observing systems of the future will incorporate gliders continuously occupying lines, consistent with the vision of the originators of CalCOFI. A network of such lines along the US coast is already being established. While the glider network will likely never replace ships, the most easily measured physical variables are already more efficiently measured autonomously. I look forward to the day when CalCOFI goals are addressed through a mix of observational platforms providing fine resolution data sustained over decades.

8.22 Amanda Netburn: Student Perspectives: What Going to Sea with CalCOFI Brought to My Thesis Research[24]

My first task as a new member of Dr. J. Anthony Koslow's lab was to lead the midwater sampling program on the Summer 2010 CalCOFI cruise on the R/V New Horizon. I had just finished my Masters degree with the Center for Marine Biodiversity and Conservation (CMBC) at SIO, and was preparing to start the PhD program in Biological Oceanography. A major draw to staying at SIO for my doctoral work was my love of spending time at sea. However, previous experiences at sea were quite different than CalCOFI research cruises. As a SCUBA Instructor and small boat captain in Hawaii, I had spent a lot of days on small (mostly "six-pack") boats. My previous experience conducting oceanographic research on a

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[24] Amanda Netburn is a graduate student in the Koslow lab at Scripps Institution of Oceanography in La Jolla, California.

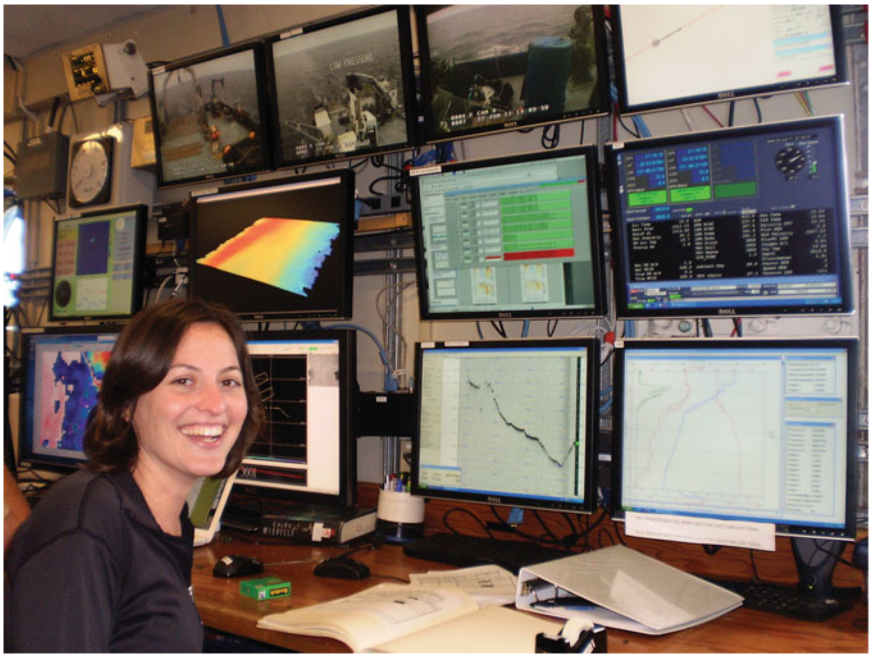

Fig. 8.25 Amanda Netburn as a Scripps graduate student on the Scripps vessel Melville, 2011 (Photo provided by Amanda Netburn)

multi-day trip was on a brigantine sailboat, the SSV Robert C. Seamans. Conducting oceanography off a brigantine was almost impossible. There was one small wet lab on the top floor, which was crowded when more than two people were present. Our entire equipment was a CTD and a small plankton net, which were each deployed twice a day (midday and nighttime). In the corner of the galley there were a couple of computers. I slept with all of my belongings at the foot of my berth. Since arriving at SIO, I had gone on a couple of day trips on the R/V Sproul, during which time I helped deploy a small Isaacs Kidd Midwater Trawl, an otter trawl, benthic sediment grabs, and a failed effort with a multi-corer. Each of these days at sea was busy, though we deployed just two or three instruments.

With this as my baseline, I was already astounded by the capacity of the CalCOFI program before we even loaded the ship. Several trucks were required to transport all of the equipment to the vessel, and when we arrived at MARFAC where the ship was berthed, a couple of vans were being bolted to the deck. I watched in awe as multiple plankton nets, two CTD rosettes, dozens of computers, hundreds of jars, jugs of chemicals, equipment to run the active and passive acoustics sampling, the nutrient analyzer, and countless other items were loaded onto the vessel and assembled. Looking out from a mess of wires and piles of boxes and gear, it appeared unimaginable that there would ever be enough time or deck space to deploy it all. Remarkably, over the next 48 h, the seemingly disheveled mess was organized into distinct stations. While other groups worked on setting up their at-sea lab space, I worked with members of my lab to put together the Matsuda-Oozeki-Hu Trawl (MOHT, see Sect. 3.1.3.3), which must be disassembled for washing and storage after each cruise. This was my first introduction to the trawl which I now know so well, and it took a good part of the day to put it all together and have it ready for deployment.

I continued to be astounded by the research cruise during the first few days at sea. The regularity of the CalCOFI cruises allows for the operations to go seamlessly. After all, the gear has always been out to sea just a few months earlier rather than sitting on a shelf for years as is often the case in oceanography, the staff know the gear well, and are quick to troubleshoot problems that arise. The scientists and technicians on board get into a rhythm, repeating the sequence of deployments at each of the 75 stations. The sheer number of gear deployments that occurs in a day is truly remarkable, and the quantity of data collected is quite impressive.

Not only impressive for sheer volume, the data are incredibly valuable to researchers and students such as myself. As I move forward with my dissertation research on the contribution of mid-trophic level fishes to the California Current Ecosystem food web and the role of deepwater hypoxic boundary layers in defining habitat for midwater organisms, I am enormously grateful for the 60 years of hard work and backbreaking science that has come before me, and that will allow me to place my work into a much larger context than is imaginable for most students. I now have several years of trawl and acoustic information on the composition and biomass of midwater assemblages in the Southern California Bight. Although midwater sampling is relatively recent, the ichthyoplankton time series and physical time series are invaluable for scaling current findings to long-term trends. In addition to this, of course, are data on the environmental variables as well as many of their prey and predators.

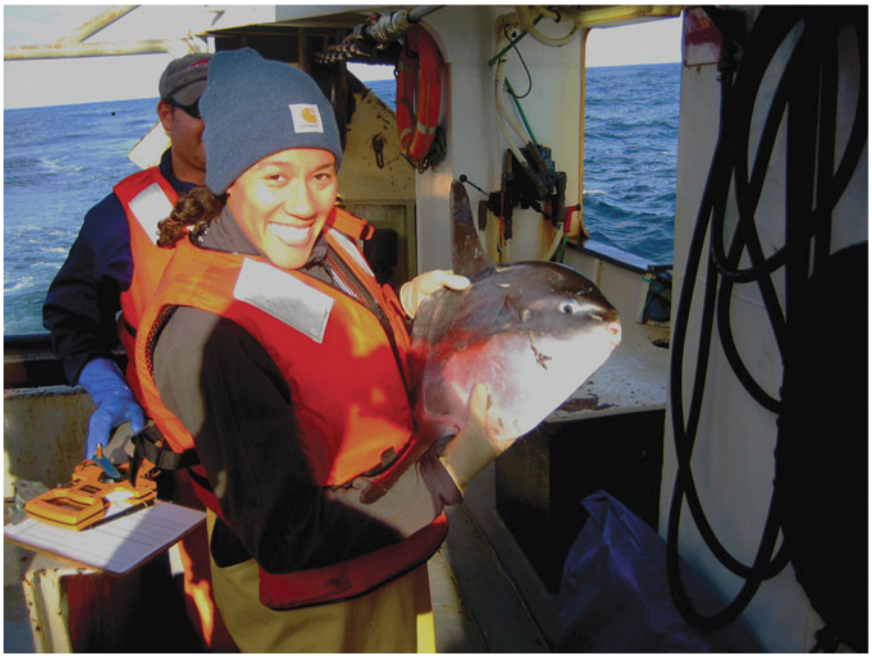

Fig. 8.26 Noelle Bowlin at sea holding an ocean sunfish (*Mola mola*) (Photo provided by Noelle Bowlin)

My previous work in sustainable seafood (consumer campaigns at the Blue Ocean Institute in New York, developing low impact aquaculture methods at Kona Blue Water Farms in Hawaii) followed by a Masters degree in biodiversity and conservation have guided me in a philosophy to always take an interdisciplinary and collaborative approach to solving problems in the ocean and effectively managing the resources. Working collaboratively with NOAA scientists, and applying my work towards management objectives demands an interdisciplinary approach to my research.

I really cannot think of a better way to have launched my doctoral work at SIO than through participation in CalCOFI. The program introduced me to a wide range of methods used to sample marine environments. I love being involved in a new aspect of CalCOFI – the MOHT sampling of the mesopelagic assemblages – while at the same time participating in CalCOFI which is a long-standing tradition at Scripps and NOAA's SWFSC. I look forward to many more CalCOFI cruises in the years to come, and to integrating our new trawl data with the program to increase our understanding of the California Current ecosystem.

8.23 Noelle Bowlin: Student Perspectives: From Technician to Graduate Student, to NOAA Scientist[25]

I joined the Ichthyoplankton Ecology group in late July 2002, a month after I finished my undergraduate work at UCSD. At that time I was planning to work for a year or so to pay down my student loans and to give myself time to search for a good terrestrial ecology graduate program on the east coast to study plant-insect interactions. Just before graduation, a classmate asked me if I needed a job because there was a position open in the lab where she worked part-time sorting ichthyoplankton. My inquiry about the job led to an interview with Rich Charter and Bill Watson during which I described my limited experience with sorting plankton samples in an ecology laboratory course at UCSD, my enthusiasm for science, and my need for employment. Shortly thereafter I started what I thought would be a 1–2 year contract as a sorter, which would be just the right amount of time before I left to study the evolution of plant structure and insect mouthpart morphology. I had no idea that this would be the door to my future career.

The environment in the Ichthyoplankton Ecology lab was wonderful because of the people I had the fortune of meeting and working with. Bill Watson was (and is currently) the leader of the group that included Dave Ambrose, Elaine Acuna, and Sharon Charter, with Sarah Zao and myself sorting the samples. Just a few months into my new job Rich Charter asked me if I'd like to go to sea on a CalCOFI cruise. I thought he meant in the future, but he meant 3 days from then because of the need to exchange personnel on the cruise that was out at that moment. Not knowing what to expect, I went out on my first cruise in November 2002. I was amazed with the amount of planning, coordination, skill, and effort it took to produce the jars of plankton that arrived at my desk to be sorted. After that, I was hooked. Prior to this position, as an undergraduate student, I was a single entity moving through the stream of academic life, by myself. At Southwest

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[25] Noelle Bowlin is a graduate student in the Hastings lab at Scripps Institution of Oceanography in La Jolla, California.

Fisheries working as a sorter and a sea-going technician, I felt part of a team that produced vital information used to manage California's fisheries.

As time went on, I realized that my interest in plants and insects had been replaced by a passion for ichthyoplankton and the role that research plays in fisheries management. I moved beyond sorting to learning the species identifications from Dave Ambrose and the rest of the Ichthyoplankton Ecology group. I became a member of the sea-going team led by Rich Charter and later by Dave Griffith, consistently participating in CalCOFI cruises, Sardine Surveys, and the California Current Ecosystem Surveys.

In early 2007, Bill Watson gave me the opportunity to help with a plastic debris and ichthyoplankton study. Being involved in the whole process from the research proposal to the final publication opened my eyes to the available possibilities: I was bitten by the science bug. In a conversation with Bill, I told him I wanted to work on additional projects with the same level of involvement, and that I had some questions of my own I wanted to explore. His response was that it was time to go to graduate school.

I started the Biological Oceanography PhD program at SIO in September 2009 as a member of Phil Hastings' lab. Working with Phil as my adviser is great not only because of his expertise as Marine Vertebrate Curator at SIO, or because of his extensive knowledge of fish ecology, but also because of the positive history between his lab (formerly led by Richard Rosenblatt) and the Ichthyoplankton Ecology lab at Southwest Fisheries. My dual status as a graduate student and Fisheries employee is hard to juggle at times, but I wouldn't give up either position. It is difficult to find the words to adequately express my deep appreciation and respect for the people I work with at Fisheries for teaching, inspiring, and encouraging me to pursue my passion and further my career. I feel as though I am standing on the shoulders of giants to reach my goals.

8.24 Rebecca Asch: Student Perspectives: Phenology in the California Current Ecosystem: CalCOFI and Beyond[26]

Climate change is one of the most daunting challenges facing humanity in the twenty-first century. As an ecologist, I am concerned about how climate change will impact species, communities, and ecosystems through warming oceans, increasing stratification, decreasing oxygen levels, ocean acidification, loss of sea ice, and destruction of coastal habitats due to sea level rise. To date, two main approaches have been used globally to detect changes in ecological communities and attribute those changes to warming trends. First, organisms may adapt to warming by moving to cooler regions, such as higher latitudes or deeper in the ocean. Second, organisms can alter the seasonal timing of activities that depend strongly on temperature. Meta-analyses examining these phenomena indicate that species are moving to higher latitudes at rates of 6.1–16.9 km per decade, while seasonal, biological cycles are occurring 2.3–5.1 days earlier each decade [113, 439, 440, 478]. The study of these seasonal, biological events and how they are affected by weather and climate is referred to as phenology. Unfortunately, the global meta-analyses examining phenological change have focused almost entirely on terrestrial organisms. In fact, the only exclusively marine species included in these meta-analyses is the subarctic copepod *Neocalanus plumchrus* [478], whose phenology was studied by [349]. This is disconcerting given that recent studies suggest that shifts in phenology may occur more rapidly in marine environments than terrestrial ecosystems [89]. In the context of the California Current Ecosystem (CCE), several pieces of evidence suggest that climate change induced shifts in phenology could have a large impact on ecosystem organization. For example, dramatic changes were observed across all trophic levels in the northern CCE when the seasonal onset of upwelling was delayed by ~2 months in 2005. In response to this anomalous event, chlorophyll in the surf-zone decreased by 50 % [49]; zooplankton biomass was reduced [350]; the seasonal timing of mussel and barnacle reproduction and recruitment was delayed [49]; fishes changed their geographic distribution so that offshore species were found closer shore and southerly species occurred farther north [84], and Cassin's auklet (*Ptychoramphus aleuticus*) abandoned breeding colonies en masse [545]. Many of these events resulted from mismatches between the timing of key events in the life history of species and the seasonal cycle of productivity in the CCE [128]. Many fish species have evolved to time their reproduction to coincide with seasonal peaks in phytoplankton and zooplankton biomass. If climate change alters seasonal patterns so that these events are no longer synchronized, little food may be available to larval fishes during a life stage when they are vulnerable to starvation. Poor survival of larvae can lead to recruitment failures and decreased catches of fished species. Given the profound effects that climate change induced shifts in phenology may have in the CCE, I have decided to dedicate much of my dissertation research to addressing this question.

While CalCOFI is the premier time series documenting changes in the biology and oceanography of the CCE, CalCOFI surveys weren't designed to monitor changes in phenology. Under most circumstances, phenological investigations require a time series that has at least a monthly resolution. Although monthly surveys were conducted by CalCOFI during the 1950s, quarterly surveys have been the

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[26] Rebecca Asch is a recent graduate from the Checkley lab at Scripps Institution of Oceanography in La Jolla, California.

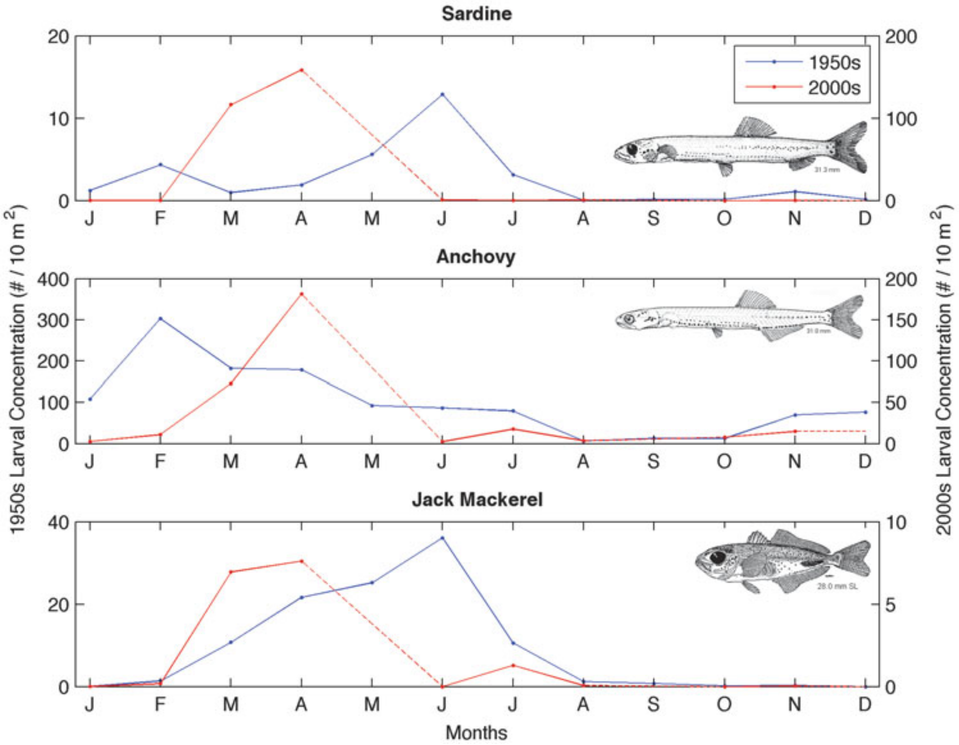

Fig. 8.27 Monthly concentration of larval sardine (*Sardinops sagax*), anchovy (*Engraulis mordax*), and jack mackerel (*Trachurus symmetricus*) caught with bongo nets during the 1950s and 2000s along CalCOFI lines 93.3-76.7. *Dotted lines* indicate months during which no samples were collected during the 2000s. In each subpanel, the scale of the left and right y-axes differ in order to emphasize changes in phenology rather than changes in larval abundance. Fish drawings were done by George Mattson, SWFSC, [363] and are also available on www.fishbase.org (Graph by Rebecca Asch)

standard since the 1980s. To overcome this challenge, I have come up with what I believe is a creative, but simple, solution. Due to logistical issues related to the availability of ship time, quarterly CalCOFI cruises do not always occur during the same month. Therefore, when CalCOFI data are averaged by decade, it is possible to construct a time series with some data available for each month. The one exception is the decade of the 2000s when there are gaps in which no surveys were conducted during May, September, and December. Using this approach, I have examined long-term phenological changes among the 43 most abundant species of larval fishes sampled in CalCOFI bongo net tows (Fig. 8.27). My initial results suggest that ~40 % of species are now spawning earlier than they were in the 1950s.

Moving beyond CalCOFI, there are many existing time series in the CCE that can be harnessed to gain an improved understanding of past and future changes in phenology. At the Scripps Pier, SST and sea surface salinity (SSS) have been measured on a daily basis since 1916. Similar, albeit shorter, time series measuring SST and SSS are available at other sites participating in the Shore Stations Program. Also, long-term changes in the timing of phytoplankton blooms could be elucidated by comparing current biweekly sampling of chlorophyll at the Scripps Pier with historical daily cell counts measured at the pier over a 20-year period beginning in 1918 [19]. Current and future changes in the seasonal cycles of physical oceanography and phytoplankton can be monitored via satellite remote sensing, buoys that form part of the Southern California Coastal Ocean Observing System (SCCOOS), and the gliders maintained by the CCE LTER program. There are also datasets available that would allow us to monitor the phenology of organisms in higher trophic levels. The Newport, Trinidad Head, and Monterey lines are surveyed more frequently (biweekly to bimonthly) than the sites in the standard CalCOFI grid in southern California. Data from these transects can be used to track variations in the phenology of mesozooplankton and ichthyoplankton in central California through Oregon. In southern California, several historical surveys of coastal ichthyoplankton that included weekly to bimonthly sampling could provide a baseline for examining fish phenology [299, 533, 570]. Another method that can be applied to study fish phenology is to use daily growth increments on otoliths to estimate the birth dates of fishes. Bio-acoustic moorings may provide an alternative, less time intensive approach to monitoring the phenology of organisms across a variety of size classes [258]. The phenology of seabirds has been well studied in the CCE. Egg laying dates and hatch dates of Cassin's auklet and common murre (*Uria aalge*) have been monitored since the 1970s at Southeast Farallon Island, Point Reyes Bird Observatory, and Triangle Island in British Columbia [2, 63, 493, 545]. Also, some marine mammal surveys record the start, end, and median dates of cetacean migrations [445]. If we integrated all of these time series, we would have the makings of a nascent marine phenology network that could be used to investigate the impact of climate change on marine organisms throughout the CCE. Such an effort would complement the California Phenology Project, a recently launched initiative to track the phenology of terrestrial ecosystems across the state.

When trying to develop a marine phenology network, it will be key to consider trade-offs between the spatial and temporal resolution of monitoring. For example, the utility of CalCOFI for investigating phenological changes could be increased if a few stations representative of broader oceanographic conditions were surveyed on a more frequent basis (weekly to monthly). This would provide a temporal context for the wider CalCOFI grid by revealing how oceanographic dynamics evolved between quarterly cruises. A small-scale effort to monitor phenology with CalCOFI methods at a limited number of stations may be feasible even though it would be too costly and labor prohibitive to routinely monitor the entire CalCOFI grid. A particular need for a CalCOFI-like program to monitor phenology in southern California stems from the fact that regional climate models predict different trends in phenology in the southern and northern CCE. Such models forecast delays in upwelling in the northern CCE, but not in the southern CCE [139, 525]. These results are also backed by empirical studies that show the onset of seasonal upwelling is occurring later in the northern CCE [70], while the timing of phytoplankton blooms is becoming earlier in the southern CCE [265]. These regional differences in phenology may be particularly stressful for species that feed in the northern CCE but migrate seasonally to spawning grounds in the southern CCE, i.e., sardine *(Sardinops sagax)*, Pacific hake *(Merluccius productus)*. Due to their migrations between habitats with contrasting trends in phenology, these fishes may be subject to increased mismatches with oceanic conditions in the future. Establishing a marine phenology network would provide a baseline to be able to better track such changes and provide additional information for fisheries management.

Glossary

Argo is a global array of temperature and salinity profiling floats that began in 2000. The goal stated on the Argo web pages (http://www.argo.ucsd.edu/) is to achieve "an array of 3000 floats [that] will provide 100,000 temperature/salinity (T/S) profiles and velocity measurements per year distributed over the global oceans at an average 3-degree spacing. Floats will cycle to 2000 m depth very 10 days, with 4–5 year lifetimes for individual instruments. All Argo data are publicly available in near real-time via the Global Data Assembly Centers".

Biomass "Biomass is defined as the amount of living material, but for practical and theoretical reasons, units have not been rigidly prescribed. Instead, 'biomass' has become a catch-all term with the operational definition, 'the amount of biological material that is of interest to the researcher.' The word is convenient and unlikely to be abandoned, but its meaning, at least within the field of planktonic ecology, is nebulous almost to the point of uselessness. Thus, any discussion of biomass should include a specific definition and should have a justification of the choice." (a direct quote from Cullen [124]).

CalCOFI station point interval = 4 nautical miles or 7.4 km (1 n. mi = 1.852 km). Therefore the distance between offshore station 100 and station 110 is 40 n. mi, between inshore 50 and 55 is 20 n. mi, and between nearshore station 28 and 30 is 8 n. mi.

Spacing between the transect lines and the distance between standard stations is (10 points) 40 n. mi or 74 km. Nearshore stations are half or less this spacing and the offshore stations are sometimes double this distance.

Core CalCOFI lines from south to north are lines 93.3, 90, 86.7, 83.3, 80, and 76.7. CalCOFI line 90 lies along 240° True off Dana Point, CA, and is the best studied line. Station 120 is 683 km offshore. Station 100 is 535 km offshore (see Fig. 1.4).

Ekman pumping is vertical motion in the water column caused by horizontal variations in surface wind stress. Ekman pumping can be expressed in terms of the change in sea surface elevation $\frac{dh}{dt} = -\frac{1}{\rho f} curl \overrightarrow{\tau}$, where $\overrightarrow{\tau}$ is the vector of the wind stress, ρ is density, f is the Coriolis parameter, h is sea-surface elevation and t is time ([107] attributed to [442]).

Production is a measure of concentration of biomass with units of Mass Volume^{-1}or Mass Area^{-1}.

Productivity is a rate with units of Mass Volume^{-1}Time^{-1} or Mass Area^{-1}Time^{-1}. Production and productivity differ in the time dimension and the terms are not equivalent. Productivity is a rate that can be used to express turnover. Production is not a rate.

The Southern California Bight (SCB) is the region from Point Conception to Ensenada, Mexico inshore of the Santa Rosa Ridge. CalCOFI stations with numbers 45 and lower lie within the SCB. CalCOFI stations with numbers 53 and higher lie to the west of the bathymetric ridge and so are outside the SCB.

Spiciness is a state variable $\pi_{(\theta,s)}$ that is most sensitive to isopycnal (i.e. constant density) thermohaline variations, and least sensitive to the density field. Its diapycnal gradient is related to the density gradient ratio, so it is sensitive to interleaving and double-diffusive mixing between overlying water masses of different density. It is conserved with respect to isentropic motion, meaning that it remains constant along surfaces of potential temperature (θ). $\pi_{(\theta,s)}$ is useful both for characterizing water masses and to indicate double-diffusive stability [168]. Spiciness is larger for warm, salty water.

Steric height maps or dynamic topography reflect the geostrophic flow at one surface relative to another. The steepness of the slope in dynamic topography is proportional to current speed and the distance between dynamic topography contours is inversely proportional to current speed. Tightly spaced contours reflect faster current speeds. Flows are along the contours with higher topography to the right in the Northern Hemisphere, and to the left in the Southern Hemisphere. The contrast between highs and lows in the oceanic gyres is on the order of 0.5–1.0 dynamic meters [546].

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Wind stress (τ) is the horizontal force of the wind on the surface of the water, or the vertical transfer of horizontal momentum. Surface wind stress is related to wind velocity by the "bulk formula":

$$(\tau_{wind_x}, \tau_{wind_y}) = \rho_{air} C_D u_{10}(u_a, v_a)$$

where $(\tau_{wind_x}, \tau_{wind_y})$ are the zonal and meridional components of stress, $C_D$is a bulk transfer coefficient for momentum (dimensionless), ρ_{air} is the density of air at the surface (kg m^{-3}) and $u_{10}(u_a, v_a)$ is the speed of the wind (m s^{-1}) at a height of 10 m in the x and y directions [362]. This equation is also written [534]:

$\tau = \rho_a C_D U_{10}^2$ where U_{10} is wind speed at 10 m. Units for τ are kg m^{-1}s^{-2} or Pa.

Wind mixing (u^{*^3}) is wind speed (m s^{-1}) cubed with units of m^{3}s^{-3} and is the rate at which turbulent energy is supplied to the ocean by the wind. This is related to the rate of mixing at the base of the mixed layer and the consequent transfer of nutrients across the pycnocline into the euphotic zone.

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