

==== California ====

Cooperative Oceanic
Fisheries Investigations

==== Reports ====

VOLUME 58

DECEMBER 2017

**CALIFORNIA
COOPERATIVE
OCEANIC
FISHERIES
INVESTIGATIONS**

Reports

VOLUME 58
JANUARY 1 TO DECEMBER 31, 2017

Cooperating Agencies:

CALIFORNIA DEPARTMENT OF FISH AND WILDLIFE
UNIVERSITY OF CALIFORNIA, SCRIPPS INSTITUTION OF OCEANOGRAPHY
NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION, NATIONAL MARINE FISHERIES SERVICE

CALCOFI COORDINATOR John N. Heine
EDITOR John N. Heine

This report is not copyrighted, except where otherwise indicated, and may be reproduced in other publications provided credit is given to California Cooperative Oceanic Fisheries Investigations and to the author(s). Inquiries concerning this report should be addressed to CalCOFI Coordinator, Scripps Institution of Oceanography, La Jolla, CA 92038-0218.

EDITORIAL BOARD

John N. Heine
Sam McClatchie

Printed and distributed December 2017, La Jolla, California
ISSN 0575-3317

CONTENTS

Scientific Contributions

State of the California Current 2016–2017: Still Anything but “Normal” in the North. <i>Brian K. Wells, Isaac D. Schroeder, Steven J. Bograd, Elliott L. Hazen, Michael G. Jacox, Andrew Leising, Nathan Mantua, Jarrod A. Santora, Jennifer Fisher, William T. Peterson, Eric Bjorkstedt, Roxanne R. Robertson, Francisco P. Chavez, Ralf Goericke, Raphael Kudela, Clarissa Anderson, Bertha E. Lavaniegos, Jose Gomez-Valdes, Richard D. Brodeur, Elizabeth A. Daly, Cheryl A. Morgan, Toby D. Auth, John C. Field, Keith Sakuma, Sam McClatchie, Andrew R. Thompson, Edward D. Weber, William Watson, Robert M. Suryan, Julia Parrish, Jane Dolliver, Stephanie Loreda, Jessica M. Porquez, Jeannette E. Zamon, Stephanie R. Schneider, Richard T. Golightly, Pete Warzybok, Russell Bradley, Jaime Jahncke, William Sydeman, Sharon R. Melin, John A. Hildebrand, Amanda J. Debich, and Bruce Thyre</i>	1
Are There Temporal or Spatial Gaps in Recent Estimates of Anchovy off California? <i>P. C. Davison, W. J. Sydeman, and J. A. Thayer</i>	56
California Anchovy Population Remains Low, 2012–16. <i>J. A. Thayer, A. D. Maccall, W. J. Sydeman, and P. C. Davison</i>	69
Trends in the Pacific Herring (<i>Clupea pallasii</i>) Metapopulation in the California Current Ecosystem. <i>Sarah Ann Thompson, William J. Sydeman, Julie A. Thayer, Anna Weinstein, Katherine L. Krieger, and Doug Hay</i>	77
Composition and Interannual Variability in Trace Element Profiles of Pacific Sardine Otoliths. <i>Barbara J. Javor and Emmanis Dorval</i>	95
Biological Indicator of 2014–15 Warming Conditions: Presence of the Mexican Lookdown (<i>Selene brevoortii</i>), Pacific Tripletail (<i>Lobotes pacificus</i>) and Cortez Bonefish (<i>Albula gilberti</i>) in the Temperate Eastern Pacific of Mexico. <i>Jorge A. Rosales-Casián</i>	105
Correcting for Bias in CalCOFI Ichthyoplankton Abundance Estimates Associated with the 1977 Transition from Ring to Bongo Net Sampling. <i>Andrew R. Thompson, Sam McClatchie, Edward D. Weber, William Watson and Cleridy E. Lennert-Cody</i>	113
Instructions to Authors	124
CalCOFI Basic Station Plan	inside back cover

SCIENTIFIC CONTRIBUTIONS

STATE OF THE CALIFORNIA CURRENT 2016-17: STILL ANYTHING BUT "NORMAL" IN THE NORTH

BRIAN K. WELLS*

Fisheries Ecology Division
Southwest Fisheries Science Center
National Marine Fisheries Service
NOAA
110 McAllister Way, Santa Cruz, CA 95060
brian.wells@noaa.gov

ISAAC D. SCHROEDER^{1,2},
STEVEN J. BOGRAD², ELLIOTT L. HAZEN²,
MICHAEL G. JACOX^{1,2}, ANDREW LEISING²,
AND NATHAN MANTUA³

¹University of California, Santa Cruz
Institute of Marine Sciences
100 McAllister Way, Santa Cruz, CA 95060

²Environmental Research Division
Southwest Fisheries Science Center
National Marine Fisheries Service
NOAA

99 Pacific Street, Suite 255A
Monterey, CA 93940

³Fisheries Ecology Division
Southwest Fisheries Science Center
National Marine Fisheries Service
NOAA

110 McAllister Way, Santa Cruz, CA 95064

JARROD A. SANTORA

Department of Applied Mathematics and Statistics
Center for Stock Assessment Research
University of California, Santa Cruz
1156 High Street, Santa Cruz, CA 95060

JENNIFER FISHER¹ AND
WILLIAM T. PETERSON²

¹Cooperative Institute for
Marine Resources Studies
Oregon State University
Hatfield Marine Science Center
2030 SE Marine Science Dr., Newport, OR 97365

²Fish Ecology Division
Northwest Fisheries Science Center
National Marine Fisheries Service
NOAA
Hatfield Marine Science Center
2030 SE Marine Science Dr., Newport, OR 97365

ERIC BJORKSTEDT¹ AND
ROXANNE R. ROBERTSON²

¹Fisheries Ecology Division
Southwest Fisheries Science Center
National Marine Fisheries Service
NOAA
110 McAllister Way, Santa Cruz, CA 95060

²Cooperative Institution for
Marine Ecosystems and Climate
Humboldt State University
1 Harpst Street, Arcata, CA 95521

³Ocean Sciences Department
University of California, Santa Cruz
1156 High Street, Santa Cruz, CA 95064

FRANCISCO P. CHAVEZ

Monterey Bay Aquarium Research Institute
7700 Sandholdt Rd., Moss Landing, CA 95039

RALF GOERICKE

Scripps Institution of Oceanography
University of California, San Diego
9500 Gilman Drive #0206, La Jolla, CA 92024

RAPHAEL KUDELA¹ AND
CLARISSA ANDERSON^{2,3}

¹Ocean Sciences Department
University of California, Santa Cruz
1156 High Street, Santa Cruz, CA 95064

²Institute of Marine Sciences
University of California, Santa Cruz
100 McAllister Way, Santa Cruz, CA 95060

³Southern California Coastal
Ocean Observing System
Scripps Institution of Oceanography
University of California, San Diego
8880 Biological Grade, La Jolla, CA 92037

BERTHA E. LAVANIEGOS AND
JOSE GOMEZ-VALDES

Oceanology Division
Centro de Investigación Científica y
Educación Superior de Ensenada
Carretera Ensenada-Tijuana No. 3918
Zona Playitas C.P. 22860 Ensenada
Baja California, Mexico

RICHARD D. BRODEUR¹,
ELIZABETH A. DALY²,
CHERYL A. MORGAN²,
AND TOBY D. AUTH³

¹Fish Ecology Division
Northwest Fisheries Science Center
National Marine Fisheries Service
NOAA

Hatfield Marine Science Center
2030 SE Marine Science Dr.
Newport, OR 97365

²Cooperative Institute for
Marine Resources Studies
Oregon State University
Hatfield Marine Science Center
2030 SE Marine Science Dr.
Newport, OR 97365

³Pacific States Marine Fisheries Commission
Hatfield Marine Science Center
2030 SE Marine Science Dr.
Newport, OR 97365

JOHN C. FIELD AND KEITH SAKUMA

Fisheries Ecology Division
Southwest Fisheries Science Center
National Marine Fisheries Service
NOAA
110 McAllister Way, Santa Cruz, CA 95060

SAM MCCLATCHIE,
ANDREW R. THOMPSON,
EDWARD D. WEBER, AND
WILLIAM WATSON

Fisheries Resources Division
Southwest Fisheries Science Center
National Marine Fisheries Service
NOAA
8901 La Jolla Shores Dr., La Jolla, CA 92037

ROBERT M. SURYAN^{1,2}.

JULIA PARRISH³,
JANE DOLLIVER¹, STEPHANIE LOREDO¹,
AND JESSICA M. PORQUEZ¹

¹Department of Fisheries and Wildlife
Oregon State University
Hatfield Marine Science Center
2030 SE Marine Science Dr.
Newport, OR 97365

²Auke Bay Laboratories
Alaska Fisheries Science Center
National Marine Fisheries Service
NOAA

17109 Pt. Lena Loop Rd., Juneau, AK 99801

³School of Aquatic and Fishery Sciences
University of Washington
1122 NE Boat Street, Seattle, WA 98195

JEANNETTE E. ZAMON

Point Adams Research Station
Northwest Fisheries Science Center
National Marine Fisheries Service
NOAA
520 Heceta Place, Hammond, OR 97121

STEPHANIE R. SCHNEIDER¹ AND
RICHARD T. GOLIGHTLY²

¹Vertebrate Ecology Laboratory
Moss Landing Marine Labs
8272 Moss Landing Road
Moss Landing, CA 95039

²Department of Wildlife
Humboldt State University
1 Harpst Street, Arcata, CA 95521

PETE WARZYBOK, RUSSELL BRADLEY,
AND JAIME JAHNCKE

Point Blue Conservation Science
3820 Cypress Dr., Suite 11
Petaluma, CA 94954

WILLIAM SYDEMAN

Farallon Institute for Advanced
Ecosystem Research
101 H Street, Petaluma, CA 94952

SHARON R. MELIN

Marine Mammal Laboratory
Alaska Fisheries Science Center
National Marine Fisheries Service
NOAA

7600 Sand Point Way NE
Seattle, WA 98115

JOHN A. HILDEBRAND,
AMANDA J. DEBICH, AND
BRUCE THAYRE

Marine Physical Laboratory
Scripps Institution of Oceanography
University of California, San Diego
9500 Gilman Drive, La Jolla, CA 92024

*Author groups are listed according to the order
of their contributions within

THE SHORT VERSION

From: Bill Peterson - NOAA Federal
<bill.peterson@noaa.gov>
Date: Mon, Apr 17, 2017 at 10:09 AM
Subject: Re: CalCOFI report 2016–17
To: Sam McClatchie - NOAA Federal
<sam.mcclatchie@noaa.gov>
Cc: Brian Wells brian.wells@noaa.gov ...

Brian, Sam, and Others:

The ocean off Oregon is anything but “normal.” Even though SST had cooled down a bit, we still have relatively warm/fresh water at depth as well as strong positive anomalies in copepod species richness and southern copepod biomass—all indicators that we still have a lot of “El Niño water” hanging around. And returns of adult spring Chinook past Bonneville Dam (Columbia River) are 10% of the ten-year average so far. Finally we are seeing small numbers of *Pseudo-nitzschia*. Nothing normal! The only good news is that *Euphausia pacifica* have returned.

Some years ago, we did a “warm in the north, cold in the south” (or was it the opposite title?).

Bill

ABSTRACT

This report examines the ecosystem state of the California Current System (CCS) from spring 2016–spring 2017. Basin-scale indices suggest conditions that would support average to below average coast-wide production across the CCS during this time period. Regional surveys in 2016 sampled anomalously warm surface and subsurface waters across the CCS. Chlorophyll concentrations were low across the CCS in 2016 and, concomitant with that, copepod communities had an anomalously high abundance of subtropical species. Early in 2017 conditions between northern, central, and southern CCS were dissimilar. Specifically, surface conditions north of Cape Mendocino remained anomalously warm, chlorophyll was very low, and subtropical copepods were anomalously abundant. Southern and central CCS surveys indicated that environmental conditions and chlorophyll were within normal ranges for the longer time series, supporting an argument that biophysical conditions/ecosystem states in the southern and central CCS were close to normal.

Epipelagic micronekton assemblages south of Cape Mendocino were generally close to longer-term average values, however the northern assemblages have not returned to a “normal” state following the 2014–15 large marine heatwave and 2016 El Niño. North of Cape Mendocino the epipelagic micronekton was largely composed of offshore and southern derived taxa. We hypothesize that

stronger-than-typical winter downwelling in 2017 and a reduced spawning biomass of forage taxa are contributors to the anomalous forage community observed in the north. Also of note, surveys indicate northern anchovy (*Engraulis mordax*) abundance was greater than average (for recent years) and nearer shore in northern regions. Finally, record-low juvenile coho and Chinook salmon catches in the 2017 northern CCS salmon survey suggest that out-migrating Columbia Basin salmon likely experienced unusually high early mortality at sea, and this is further supported by similarities between the 2017 forage assemblage and that observed during poor outmigration survival years in 2004, 2005, and 2015.

Generally, the reproductive success of seabirds in 2016 (the most current year available) was low in the north but near average in central California. At Yaquina Head off Oregon and Castle Rock off northern California some of the lowest reproductive success rates on record were documented. In addition to reduced abundance of prey, there was a northward shift of preferred seabird prey. Seabird diets in northern areas also corroborated observations of a northward shift in fish communities. Nest failure was attributed to a combination of bottom-up and top-down forces. At Castle Rock, most chicks died of starvation whereas, at Yaquina Head, most nests failed (95% of common murre, *Uria aagle*) due to disturbance by bald eagles (*Haliaeetus leucocephalus*) seeking alternative prey. Mean bird densities at sea for the 2017 surveys between Cape Flattery Washington and Newport Oregon were the lowest observed and may indicate continued poor reproductive performance of resident breeders in 2017. South of Cape Mendocino, where forage availability was typical, seabird reproductive success was also below average for most species in 2016, but did not approach failure rates observed in the north. Finally, in 2017, abundances of seabirds observed at-sea off southern California were anomalously high suggesting an improved foraging environment in that area.

Marine mammal condition and foraging behavior were also impacted by the increased abundance and shifting distribution of the northern anchovy population. Increases in the abundance of northern anchovy in the Southern California Bight coincided with improved condition of sea lion (*Zalophus californianus*) pups in 2016. Namely, lipid-rich northern anchovy occurred in great frequencies in the nursing female diet. Increases in northern anchovy nearshore in the central and northern CCS may have also contributed to a shoreward shift in distribution of humpback whales (*Megaptera novaeangliae*) in these regions. These shifts along with recovering humpback whale populations contributed to recent increases in human-whale interactions (e.g., fixed-gear entanglements).

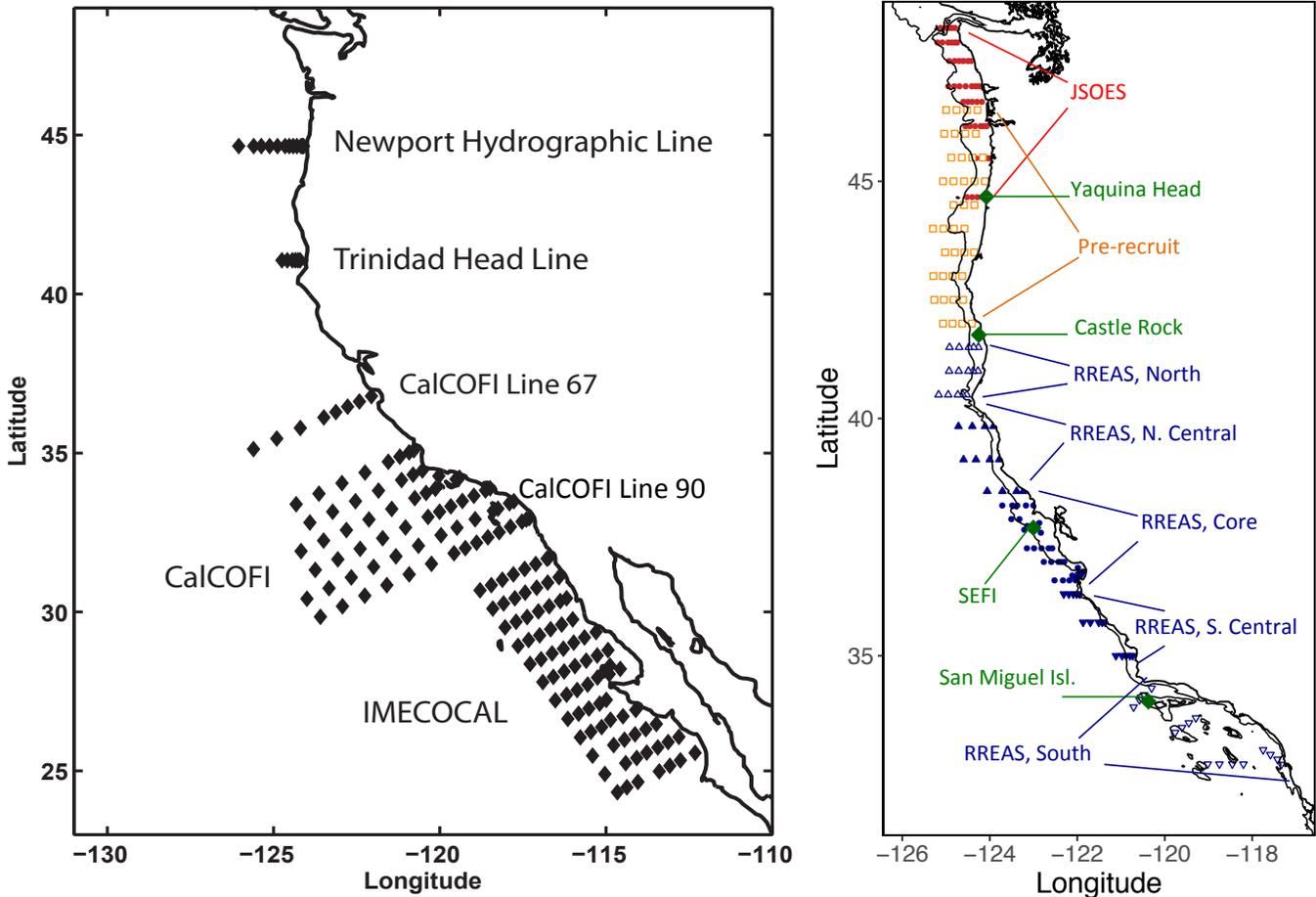


Figure 1. Left) Station maps for surveys that were conducted multiple times per year during different seasons to provide year-round observations in the California Current System. The CalCOFI survey (including CalCOFI Line 67 and 90) was occupied quarterly; the winter and spring CalCOFI survey grid usually extends just north of San Francisco. The IMECOCAL survey is conducted quarterly or semiannually. The Newport Hydrographic Line was occupied biweekly. The Trinidad Head Line was occupied at biweekly to monthly intervals. Right) Location of annual or seasonal surveys, including locations of studies on higher trophic levels, from which data were included in this report. Different symbols and colors are used to help differentiate the extent of overlapping surveys. Surveys used in this report include (Red) Juvenile Salmon and Ocean Ecosystem Survey (JSOES, NOAA/BPA rope trawl), (Orange) NWFSC Pre-recruit midwater trawl survey, and (Blue) SWFSC Rockfish Recruitment and Ecosystem Assessment Survey (RREAS) in five regions. SEFI indicates Southeast Farallon Island.

INTRODUCTION

From 2014 to 2017 the California Current System (CCS) had an unprecedented combination of warm-water conditions that may affect CCS marine life for a number of years, there was a large marine heat wave from 2014–16, influenced in part by anomalously warm conditions in the tropical Pacific that were punctuated by the 2015–16 El Niño (Leising et al. 2015; Jacox et al. 2016; Di Lorenzo and Mantua 2016; McClatchie et al. 2016; Frischknecht et al. 2017; Peterson et al. 2017). This report revisits these years when applicable to current ecosystem conditions but primarily examines the state from spring 2016–spring 2017; this report is an extension of the previous State of the California Current report (McClatchie et al. 2016). Specifically, following on previous reports, we consolidate environmental and survey data from throughout the California Current (fig. 1). These data include indicators of

basin-scale conditions, regional oceanographic conditions, and the food-web from primary production to top-predator foraging behavior, reproductive success, and condition. Although many results are preliminary and encompass dissimilar survey designs, synthesis of these diverse components provides a first approximation of the coast-wide and regional ecosystem conditions. Typical of these reports, we highlight emerging stories as supported by the available data and explore the connections between past, current, and future CCS ecosystem states. This year's report will focus on the clear disparity between ecosystem recoveries following the record 2014–16 warming of the CCS in northern and southern CCS subregions. Specifically, while the southern region trended toward a “normal” ecosystem state in 2016–17, the northern region did not (e.g., there was a persistence of the southern copepod community, limited forage availability, anomalously high salmon mortality,

TABLE 1
 State of various indicators along California Current System (CCS).
 The status represents early 2017 unless otherwise stated. Grey font indicates average production/condition, red indicates below average production/condition, and green indicates above average production/condition. Italics represent data cited from elsewhere within this report or preliminary analyses discussed in this report.
 Abbreviations: Oceanic Niño Index (ONI), Pacific Decadal Oscillation (PDO), North Pacific Gyre Oscillation (NPGO), North Pacific High (NPH), and sea surface temperature (SST).

Indicator	Basin	Northern CCS	Central CCS	Southern CCS
ONI	Average			
PDO	Above average			
NPGO	Near average			
NPH	Below average			
Upwelling		Below average	Average	Above average
Cumulative upwelling		Average	Below average	Average
SST		Above average	Average	Average
Chlorophyll		Below average	Average	Average
Harmful algal blooms		No	No	Yes
Copepods		Southern derived and rich	—	—
Forage		offshore and southern derived assemblage	Typical assemblage	Typical assemblage along with increased anchovy abundances
Salmon survival		Below average juvenile abundance at sea	<i>Ecosystem indicators related to salmon suggest average</i>	—
Seabird productivity (2016)		Reproductive failures	Below/near average	—
Seabird at-sea abundance		Well below average	Below/near average	Well above average
Sea lions (2016)			Signs of recovery after the 2013 unusual mortality event	
Whales			Humpback whales distributed shoreward	

unprecedented abundance of pyrosomes, and reduced reproductive success of seabirds) (table 1).

BASIN-SCALE CONDITIONS

North Pacific Climate Indices

The CCS experienced a marine heat wave that featured record-high sea surface temperatures (SST) in 2015, with 2014–16 the warmest 3-year period on record (Jacox et al. 2017). The exceptionally high SST anomalies declined from their peak values in spring/summer 2016. The marine heatwave was first evident in the Gulf of Alaska in late 2013 (Bond et al. 2015) and by the middle of 2014, anomalously high SST anomalies were also observed in the southern CCS as far south as Baja California (Leising et al. 2015).

El Niño/Southern Oscillation (ENSO) is a mode of interannual variability in the equatorial Pacific causing physical and ecological impacts throughout the Pacific basin and CCS, though the links between ENSO and the CCS are complex (Fiedler and Mantua 2017). The Oceanic Niño Index (ONI; <http://www.cpc.ncep.noaa.gov/data/indices/>), a three-month running mean of SST anomalies averaged over the NINO3.4 region of 5°S–5°N and 120°W–170°W, had values exceeding the 0.5°C threshold that signifies an El Niño event from April 2015 through May 2016 (fig. 2). Peak ONI values in 2015–16 rivaled those of the record 1997–98 El Niño event, but this tropical climate event was perhaps not quite as extreme (Jacox et al. 2016). Negative ONI values, indicative of a tropical La Niña event, first

appeared during July 2016, but declined only to –0.84°C indicating a modest intensity La Niña during October–November 2016. By March 2017 the ONI had transitioned to ENSO-neutral conditions, with small positive values below the 0.5°C threshold. NOAA’s Climate Prediction Center¹ has issued a report stating that El Niño neutral conditions were present during the summer of 2017 and they predict that there are growing odds for a tropical La Niña event in winter 2017–18.

The Pacific Decadal Oscillation (PDO) index describes the temporal evolution of dominant spatial patterns of SST anomalies over the North Pacific (Mantua et al. 1997). Positive PDO values are also associated with a shallower upwelling cell in the northern CCS (Di Lorenzo et al. 2008). The PDO values from January 2015 to the spring of 2016 were exceptionally high. By summer of 2016 the PDO values dropped considerably and reached their lowest values since the spring of 2014 (fig. 2). However, the winter 2016–17 PDO values were slightly elevated from these, only to decline to near-zero values in July–August 2017 (fig. 2).

The North Pacific Gyre Oscillation (NPGO) is a low-frequency signal of sea surface height, indicating variations in the circulation of the North Pacific Subtropical Gyre and Alaskan Gyre (Di Lorenzo et al. 2008). Positive values of the NPGO are linked with increased equatorward flow in the California Current, along with increased surface salinities, nutrients, and chlorophyll values in the southern-central CCS (Di Lorenzo et al. 2009). Negative

¹ <http://www.cpc.ncep.noaa.gov>

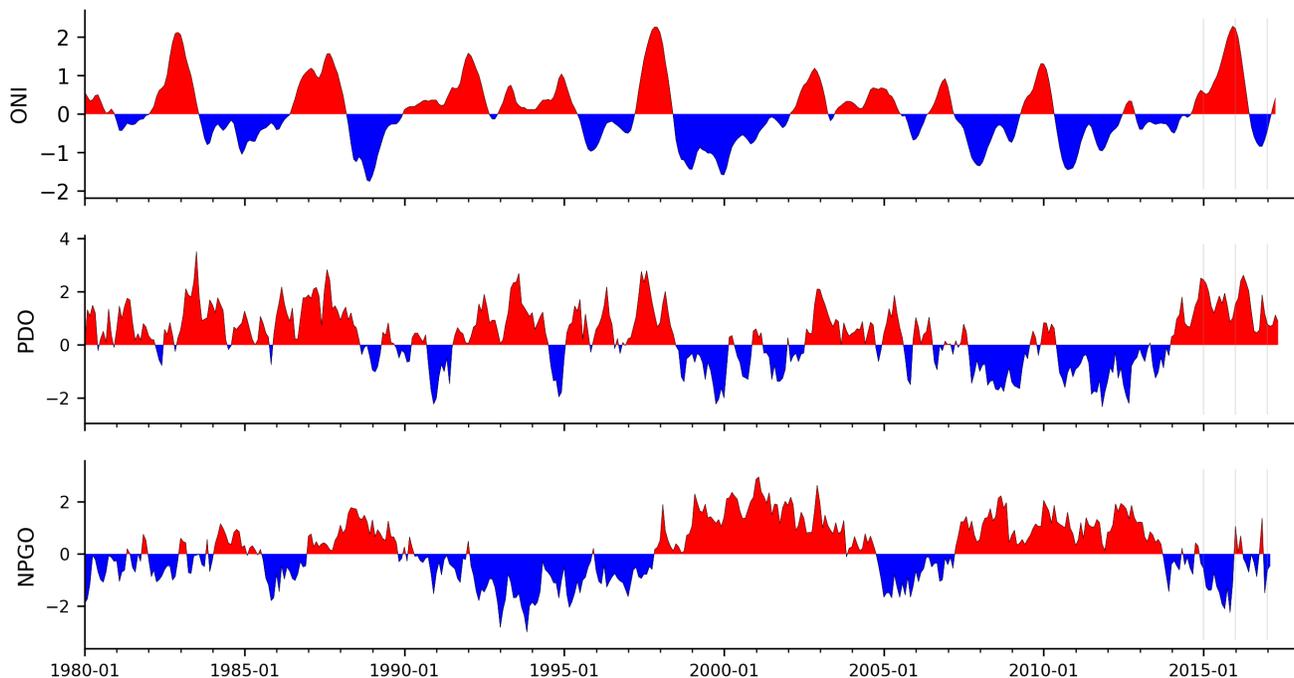


Figure 2. Time series of monthly values for three ocean climate indices especially relevant to the California Current: Oceanic Niño Index (ONI), the Pacific Decadal Oscillation (PDO), and North Pacific Gyre Oscillation (NPGO). Data are shown for January 1980 to July 2017. Vertical lines mark January 2015, 2016, and 2017.

NPGO values are associated with decreases in these variables, inferring less subarctic source waters, fewer nutrients, reduced upwelling and generally lower production in the CCS. The NPGO was negative for the entirety of 2015, with the largest negative values occurring in the fall (fig. 2). During 2016 the NPGO oscillated from positive to negative values that were very small in amplitude. The winter 2016–17 NPGO values were negative with December 2016 having the largest negative value of -1.5 . Thus, NPGO index indicated that basin-scale gyre circulation favored low to neutral production across the CCS between spring 2016–spring 2017.

In summary, 2015–16 had extreme positive ONI and PDO index values, and extremely low NPGO index values, all pointing toward increased subtropical influences and reduced subarctic influences in the CCS. Summer 2016 to spring 2017 featured a modest La Niña event and reduced amplitudes in the PDO and NPGO indices, such that these basin-scale patterns were not indicating large fluctuations on the state of the CCS ecosystem over that period.

North Pacific Climate Patterns

A basin-scale examination of SST and surface wind anomalies allows for the interpretation of the spatial evolution of climate patterns and wind forcing over the North Pacific related to trends in the basin-scale and upwelling indices (figs. 3, 4). During July 2016, negative SST anomalies in the central and eastern Equatorial Pacific marked the transition between the El Niño event

that peaked in winter 2015–16 and the La Niña event that peaked in winter 2016–17 (fig. 3). Tropical La Niña conditions dissipated by May 2017. During the summer of 2016, SST anomalies exceeding 1°C were evident in the Bering Sea and the Gulf of Alaska. These positive anomalies persisted into the winter of 2016–17. The SST approached the long-term average by May 2017 in the central and southern CCS but remained warmer than average along the northern CCS.

Wind anomalies over the Bering Sea and Gulf of Alaska were anomalously eastward in July and December 2016 and a large anti-cyclonic pattern was centered at 42°N , 160°W due to higher than average sea level pressures during July and December 2016 (fig. 3). High SST anomalies associated with the marine heatwave had dissipated along the west coast of North America by July 2016, with only the Southern California Bight and along the Baja Peninsula showing SST anomalies greater than 1°C . From December 2016 to May 2017 SST along the West Coast were near the long-term mean, with slightly elevated temperatures along the Washington and Oregon coasts and southern Baja California, Mexico (figs. 3, 4). Alongshore winds were average during July 2016, but strengthened in December 2016. February 2017 winds were anomalously northward, associated with an unusual number of winter storms and excessive rainfall along the West Coast (fig. 3)². Upwelling-favorable (southward) winds resumed by May 2017.

² <https://www.ncdc.noaa.gov/sotc/drought/201702>

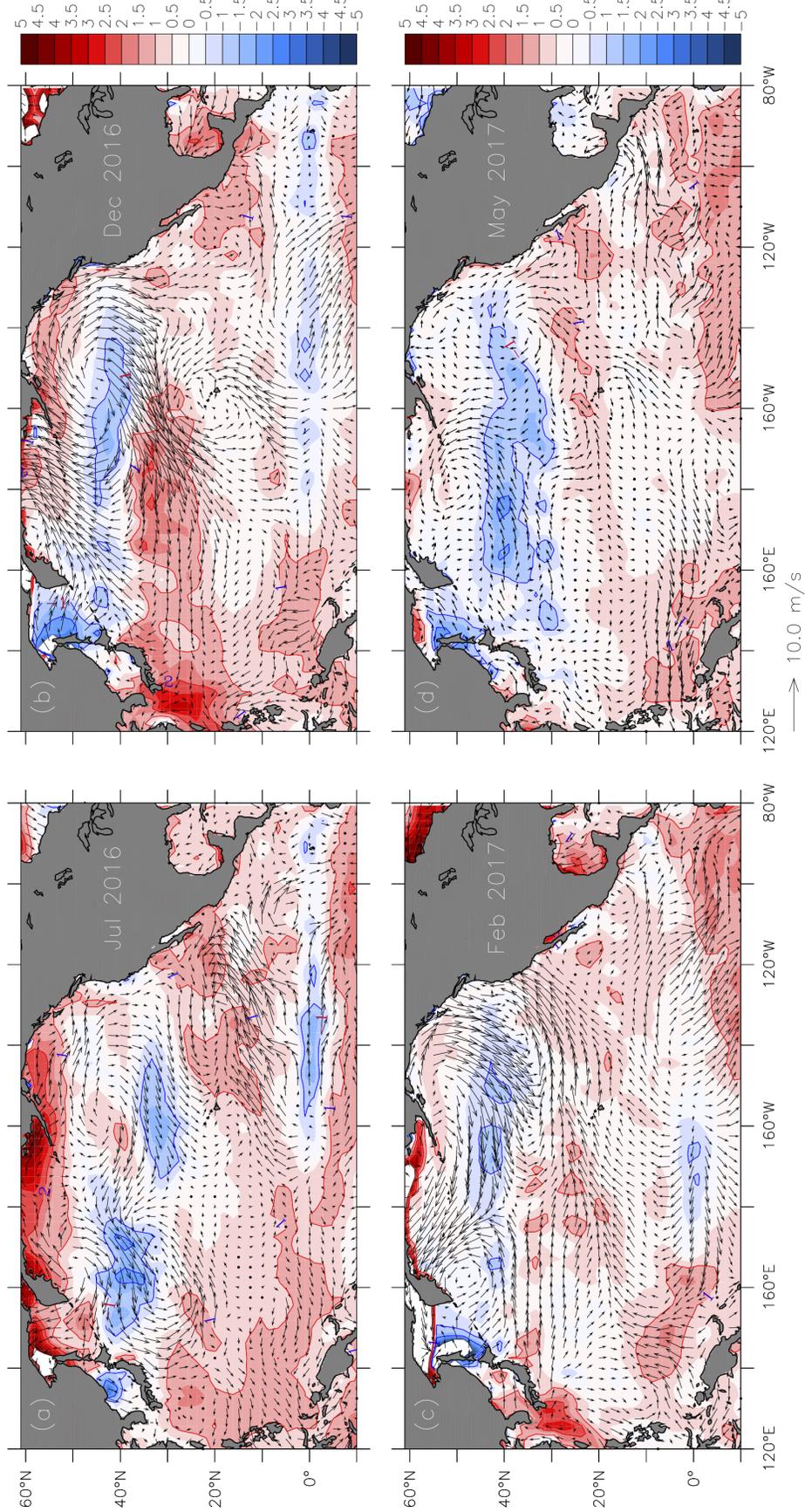


Figure 3. Anomalies of surface wind velocity and sea surface temperature (SST) in the North Pacific Ocean for July 2016, December 2016, February 2017, and May 2017. Arrows denote magnitude and direction of wind anomaly (scale arrow at bottom). Contours denote SST anomaly. Shading interval is 0.5°C and contour interval is 1 and 2°C are shown. Negative (cool) SST anomalies are shaded blue. Wind climatology period is 1968–96. SST climatology period is 1950–79. Both SST and wind data are from NCEP/NCAR Reanalysis and were obtained from <http://www.esrl.noaa.gov>.

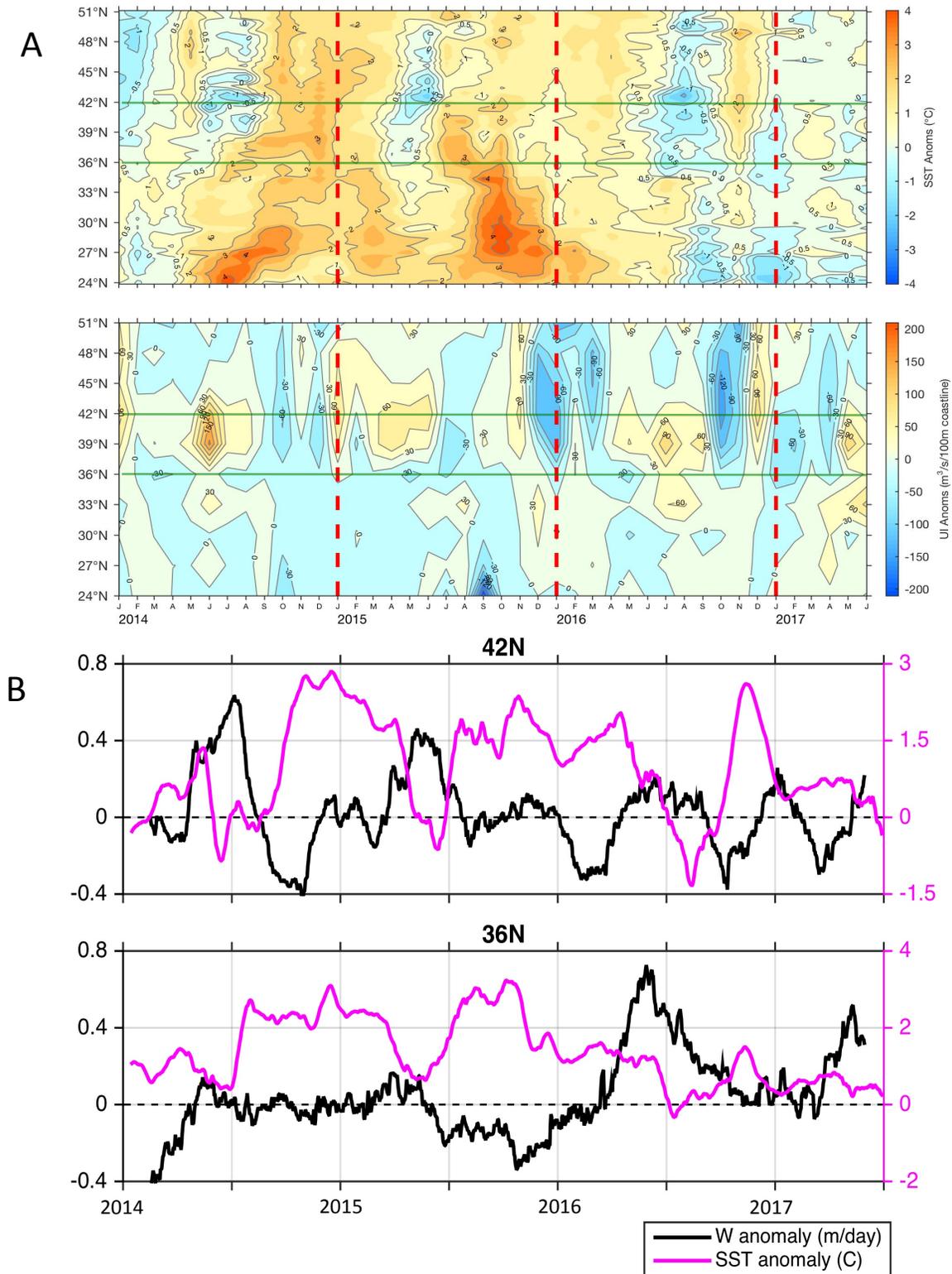


Figure 4. A) Monthly sea surface temperature (SST) anomalies (top) and upwelling index (UI) anomalies (bottom) for January 2014–June 2017. The SST anomalies are averaged from the coast to 100 km offshore. Positive and negative upwelling anomalies denote greater than average upwelling or downwelling (usually during the winter), respectively. Anomalies are relative to 1982–2017 monthly means. Daily optimum interpolation AVHRR SST data obtained from <http://coastwatch.pfeg.noaa.gov/erddap/griddap/ncdcOisst2Agg>. Six-hourly upwelling index data obtained from <http://oceanview.pfeg.noaa.gov/erddap/tabledap/>. B) Upwelling anomalies (black) and SST anomalies (magenta) relative to the 1999–2011 climatology, derived from a data assimilative ocean reanalysis of the California Current System (<http://oceanmodeling.ucsc.edu/ccsrr/>), are shown at two latitudes off the US West Coast; 36°N and 42°N (indicated by horizontal green lines in A). Values are averaged from the coast to 100 km offshore. SST is smoothed with a 30-day running mean; upwelling, which is much noisier, is smoothed with a 90-day running mean.

COAST-WIDE CONDITIONS

Upwelling in the California Current

Monthly anomalies of SST (averaged from the coast to 100 km offshore) and upwelling are used to examine anomalous coastal upwelling conditions within the CCS from January 2014 to July 2017 (fig. 4). Upwelling estimates come from two sources: the Bakun upwelling index (UI; fig. 4a; Bakun 1973; Schwing et al. 1996), and a data-assimilative regional ocean model (W; fig. 4b; Jacox et al. 2014)³. We take this approach as the UI has long been used in studies of the California Current, but in some places, particularly south of 39°N, it is a less reliable indicator of upwelling due to relatively poor estimation of the wind stress and modulation of upwelling by the cross-shore geostrophic flow (Bakun 1973; Jacox et al. 2014). SST anomalies along the coast are driven by upwelling, especially in northern latitudes due to a strong coupling between local winds and SST (Frischknecht et al. 2015). High SST anomalies due to the marine heat wave are evident in 2014 and 2015. Positive SST anomalies (>1°C) during the 2015–16 El Niño event persisted during the winter and spring of 2016 especially for locations north of 42°N. From January to May of 2017, SST anomalies north of 42°N were near the long-term average, with the exception of a few localized periods of ~0.5°C anomalies. UI anomalies from 39° to 45°N were positive during the spring and summer of 2015, but anomalously strong downwelling occurred in the winter of 2015–16 (typical of past El Niño winters). The longest period of sustained positive upwelling anomalies during 2016 occurred from July to September for latitudes between 36° and 42°N. October and November 2016 upwelling anomalies were negative north of 36°N, followed by positive anomalies (weaker downwelling) in December. On the whole, upwelling during 2017 has been about average from 39° to 42°N, weaker than average farther north, and stronger than average farther south.

The cumulative upwelling index (CUI) is the cumulative sum of the daily UI values starting January 1 and ending on December 31, and it provides an estimate of the net influence of upwelling on ecosystem structure and productivity over the course of the year (Bograd et al. 2009). In general, upwelling has been weaker for the last two years, 2016–17, than the previous two years, 2014–15 (fig. 5). During the 2016 winter, upwelling north of 39°N was low due to the El Niño and strong

upwelling only began by the summer. South of 39°N, upwelling anomalies were neutral to positive in early 2016, counter to what would be expected from a strong El Niño (Jacox et al. 2015). Upwelling during 2017 was near the long-term average for the whole coast except for the latitudes between 36°–42°N. For these latitudes, the CUI curves during the winter were below the climatological curve and stronger upwelling began by the beginning of May.

Periods of upwelling or, farther north, reduced downwelling during the winter can limit stratification and facilitate introduction of nutrients to the surface acting to precondition the ecosystem for increased production in the spring (Schroeder et al. 2009; Black et al. 2010). The area of the surface atmospheric pressures associated with the North Pacific High (NPH) can be used as an index of this winter preconditioning (Schroeder et al. 2013). Since 2014 there has been a continual weak NPH during the winter (fig. 6). The January–February mean of the NPH area has been very small since the exceptionally large area during 2013, and the 2017 area was the smallest size since 2010.

Coastal Sea Surface and Subsurface Temperatures

SSTs measured by National Data Buoy Center buoys along the West Coast were mostly above long-term averages during summer of 2015 through spring of 2016 (fig. 7). For the northern buoys, this period of warm temperature was briefly interrupted by a decrease in temperatures during August or September that coincided with a strong period of upwelling favorable winds. The decrease in temperatures associated with upwelling was also evident in April and May 2016 for the buoys located off California. For all buoys, warm to exceptionally warm temperatures were recorded during October and November 2016, which decreased greatly in December and January 2017 during a period of strong southward winds. The winter storms that brought excessive rainfall to the West Coast January–February 2017 were accompanied by episodes of strong northward winds lasting approximately a week at a time (fig. 7).

Figure 8 shows January 2014–May 2017 upper ocean temperature anomalies from ROMS averaged from the coast to 100 km offshore at latitudes of 33, 36, 39 and 42°N. From Cape Blanco (42°N) to central California (36°N) near-surface temperature was above average from the summer of 2014 through spring of 2016; yet, at depths greater than ~50 m, cool anomalies were often present. The exception of the warm surface and cool subsurface conditions was during winter 2015–16 when above average temperatures existed throughout the entire water column. This is

³ A data-assimilative configuration of the Regional Ocean Modeling System (Shepmetkin & McWilliams 2005; Haidvogel et al. 2008) has been used to produce a reanalysis of the California Current circulation extending back in time to 1980 (Neveu et al. 2016) and continuing to present in near real time (<http://oceanmodeling.ucsc.edu/ccsnrt>).

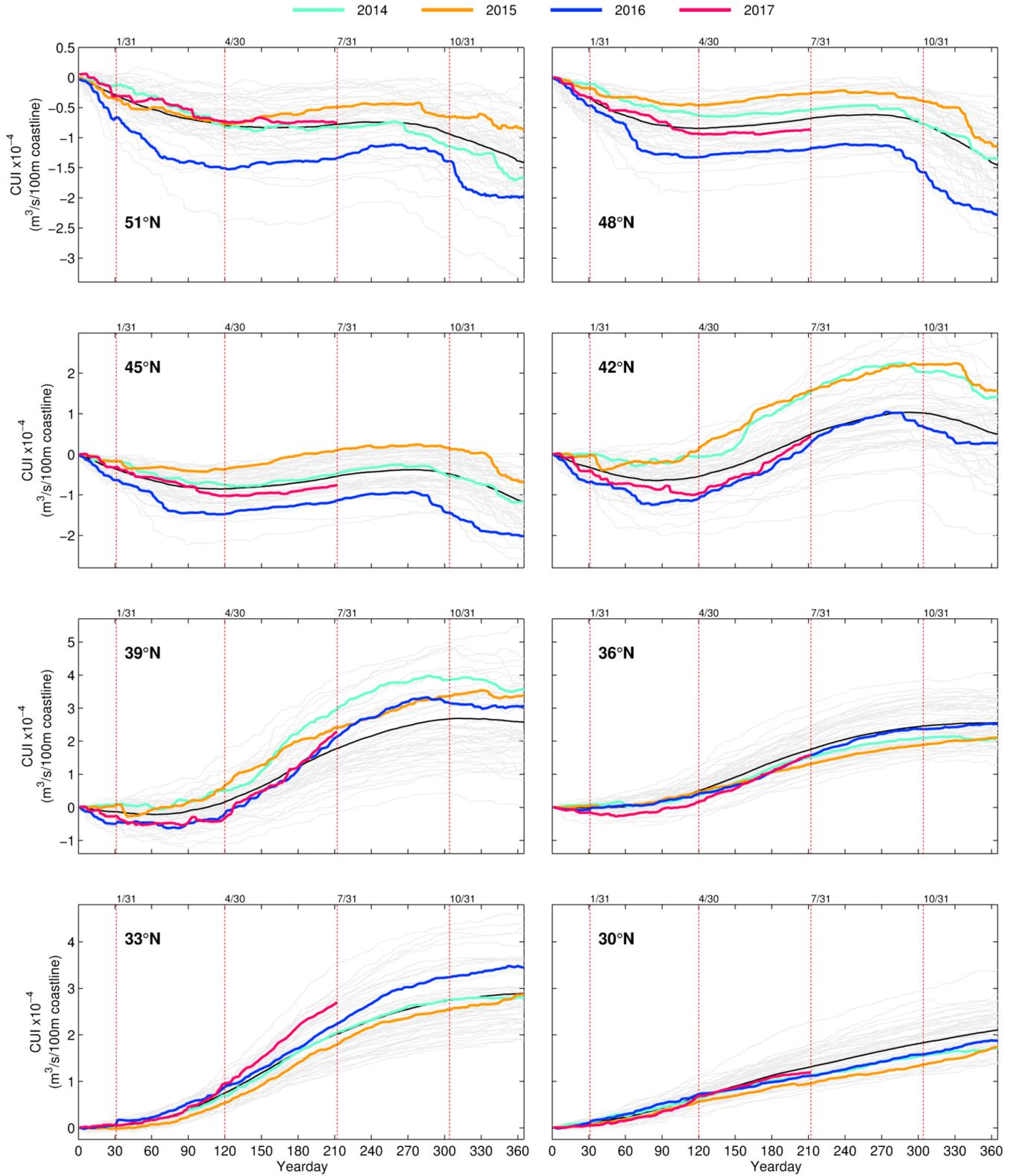


Figure 5. Cumulative upwelling index (CUI) starting on January 1 calculated from the daily upwelling index at locations along the west coast of North America. Grey lines are all yearly CUI for 1967–2016, colored CUI curves are for the years 2014–17. The climatological mean CUI is the black line. The red dashed vertical lines mark the end of January, April, July and October. Daily upwelling index data obtained from <http://upwell.pfeg.noaa.gov/erddap/>.

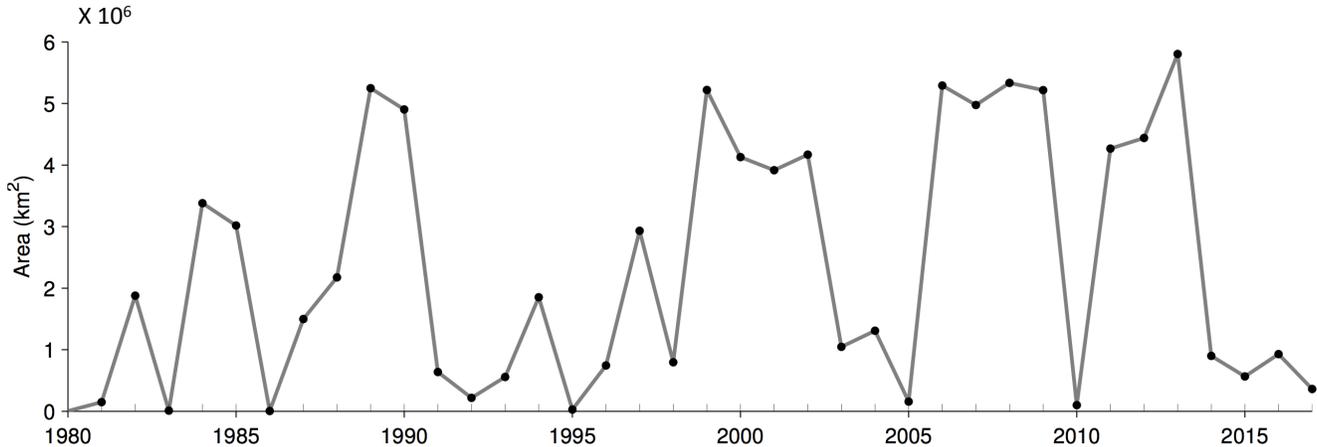


Figure 6. The area of high atmospheric pressure of the North Pacific High averaged over January and February each year (Schroeder et al. 2013). The area is the areal extent of the 1020 hPa isobar located in the eastern North Pacific.

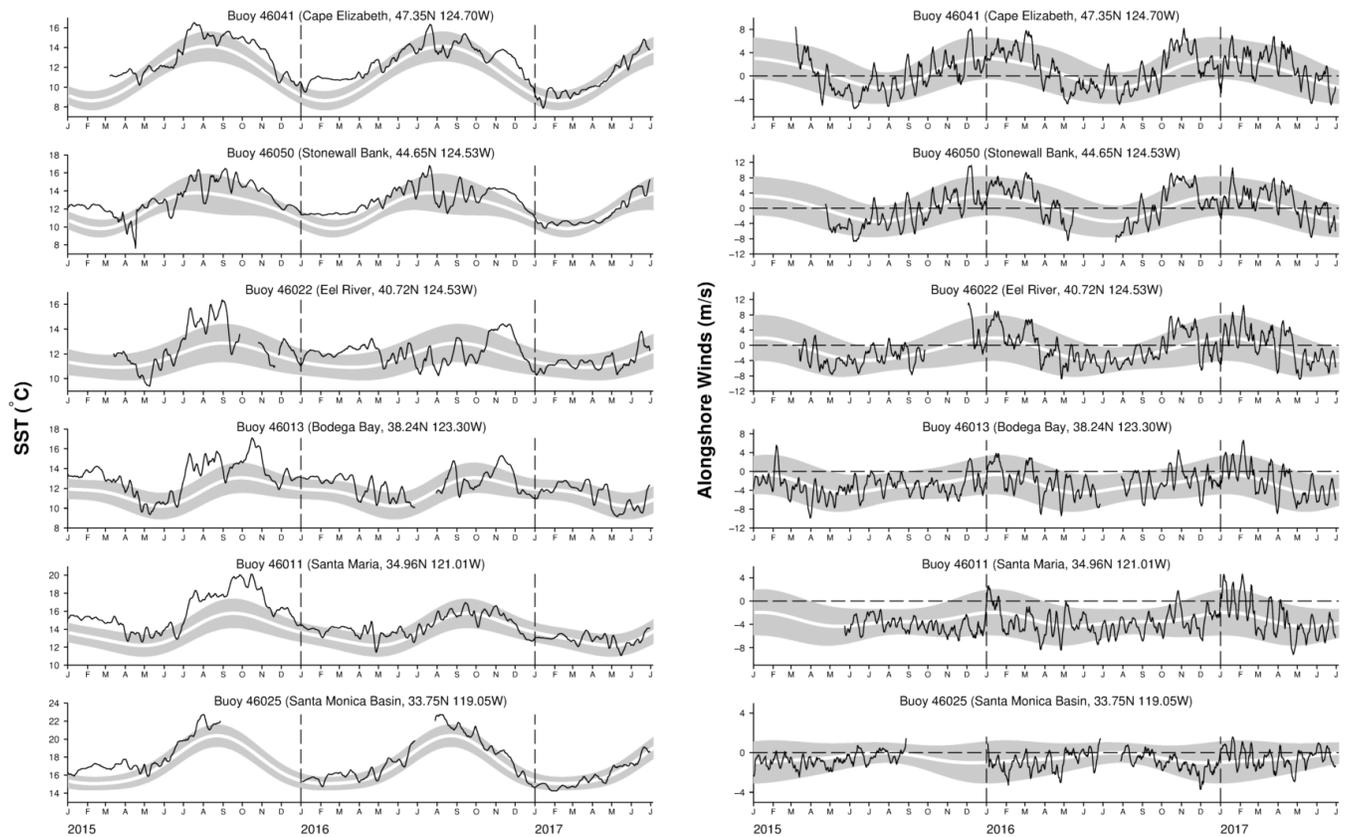


Figure 7. Time series of daily sea surface temperatures (left) and alongshore winds (right) from various National Data Buoy Center (NDBC) coastal buoys along the CCS for January 2015 to June 2017. The wide white line is the biharmonic annual climatological cycle at each buoy. Shaded areas are the standard errors for each Julian day. Series have been smoothed with a 7-day running mean. Data provided by NOAA NDBC. Additional buoy information can be found at <http://www.ndbc.noaa.gov/>.

especially evident in the southern bight and latitudes south of 39°N during the summer of 2015 and winter of 2015–16. In fact, for the line at 33°N the subsurface temperatures were anomalously high for the whole water column from spring of 2014 to the win-

ter of 2016. During the winter and early spring of 2017, near-surface temperatures (0–50 m) for all the lines were slightly above average, turning below average by the late spring for depths between the surface and 150 m.

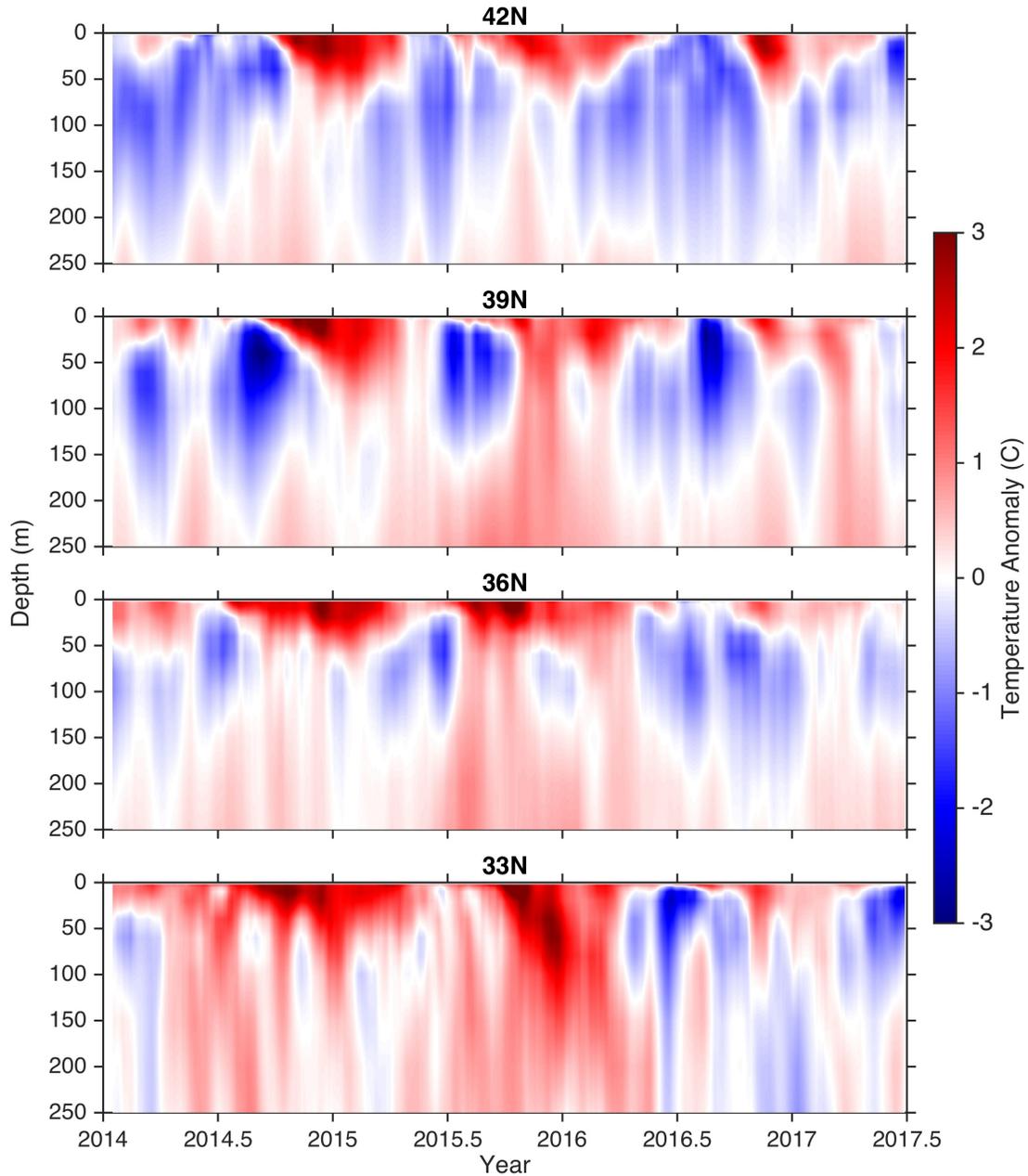


Figure 8. Temperature anomalies relative to the 1999–2011 climatology, derived from a data assimilative ocean reanalysis of the California Current System (<http://oceanmodeling.ucsc.edu/ccsrt/>), are shown at four latitudes off the US West Coast. Temperatures are averaged from the coast to 100 km offshore and smoothed with a 30-day running mean.

Primary Production in the California Current System

Anomalous high chlorophyll during the spring occurred along Central California in 2014 and along the whole coast from northern Washington to Point Conception in 2015, which likely represents, to a degree, *Pseudo-nitzschia* (see McClatchie et al. 2016 for more complete description) (fig. 9)⁴. However, during these two years chlorophyll levels were below aver-

age off southern California. Spring chlorophyll levels in 2016 were below average for the whole coast except for a few localized increases along Washington and central California coasts (McClatchie et al. 2016). Spring 2017 chlorophyll values were lower than average for the majority of the CCS but showed increases in central California and around the Channel Islands. The elevated chlorophyll in spring 2017 for the Channel Islands corresponded to significant toxin event caused by *Pseudo-nitzschia* (modeled data shown in lower panels of fig. 9).

⁴ https://www.nwfsc.noaa.gov/research/divisions/efs/microbes/hab/habs_toxins/hab_species/pn/index.cfm

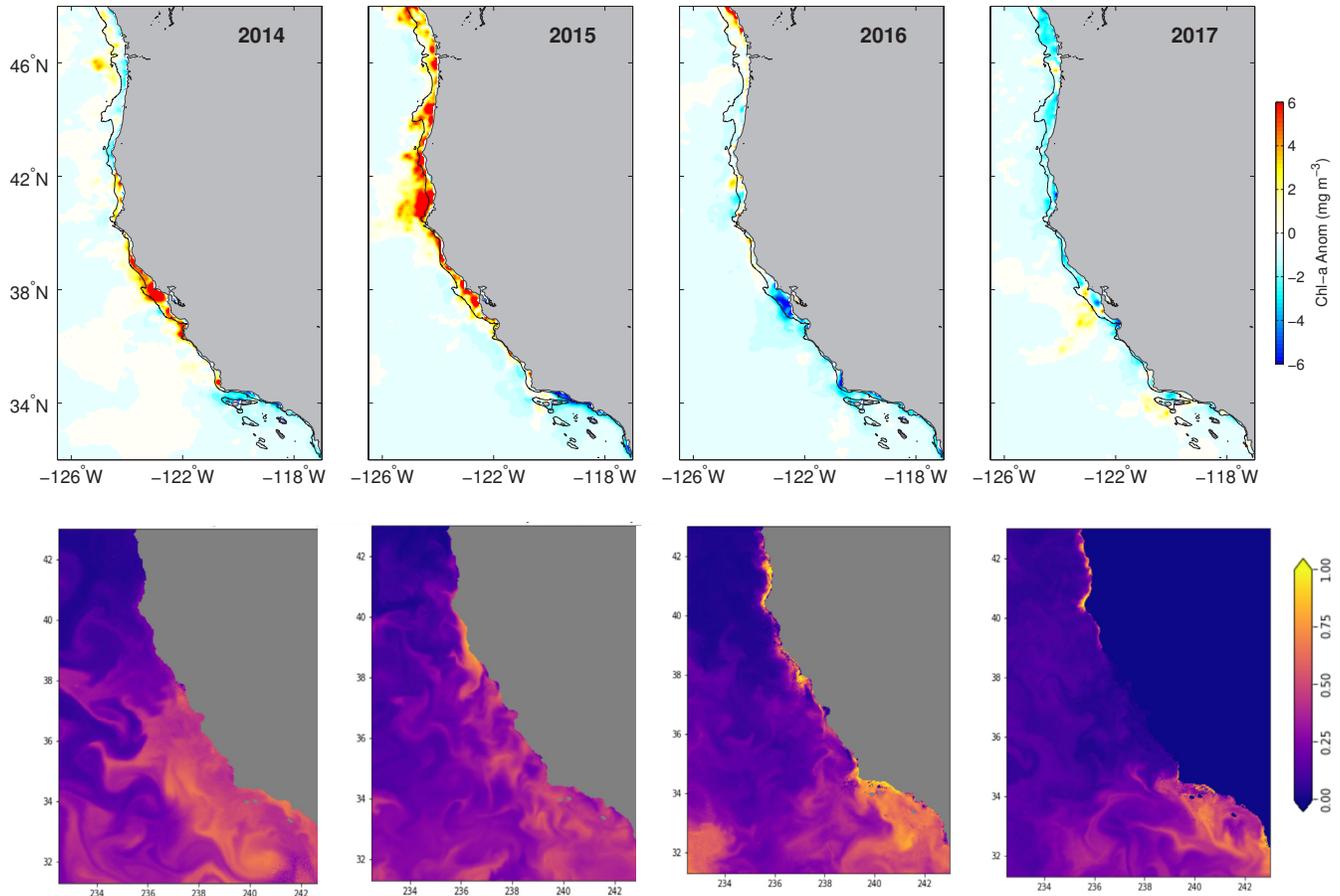


Figure 9. Top) Chlorophyll a anomalies from Aqua MODIS for spring (March–May) of 2014–2017. Monthly anomalies were averaged onto a $0.1^\circ \times 0.1^\circ$ grid and the climatology was based on the time period from 2002–17. The data were obtained from <http://coastwatch.pfel.noaa.gov/>. Bottom) predicted probability of domoic acid > 500 nanograms/L, during the same times periods as the top pane from <http://www.cencoos.org/data/models/habs/previous>.

REGIONAL OBSERVATIONS OF ENVIRONMENT AND LOWER TROPHIC LEVELS

Northern California Current: Oregon (Newport Hydrographic Line)

The warm anomalies that intruded onto the Oregon shelf surface waters in September 2014 remained throughout 2015, 2016, and continued into 2017, dominating the local hydrography and impacting pelagic communities. The upwelling season (spring transition) began early on 27 March 2016 and ended on 29 September 2016 (fig. 4), resulting in an upwelling season that was eight days longer than the 40-year climatology. Upwelling in 2016 cooled the warm temperatures that began during the winter of 2015–16 and continued into spring of 2016, resulting in neutral sea surface and deeper water temperatures on the shelf from June through September (figs. 7, 10). During this upwelling period, shelf waters were slightly saltier while deep waters on the slope were mostly neutral throughout 2016 and into 2017. Despite above average upwelling

(fig. 4), nitrogen concentrations remained below average throughout 2016 and into 2017 (fig. 10). Following the upwelling season in 2016, the shelf waters returned to anomalously warm and fresh conditions, which were similar to the previous two years.

The zooplankton community remained in a lipid-depleted state throughout 2016 and into 2017. The zooplankton community was dominated by lipid-poor tropical and subtropical copepods and gelatinous zooplankton that generally indicate poor feeding conditions for small fishes. Pyrosomes (*Pyrosoma atlanticum*), a tropical species, were first observed in the fall of 2016 and their biomass increased greatly in the spring of 2017. With the exception of the upwelling months in 2016, the biomass of lipid-rich northern (“cold water”) copepods was the lowest observed in the 21-year time series (fig. 10). During June through September, the biomass anomalies of the northern copepods were reduced slightly in response to upwelling, however the anomalies still remained strongly negative. The biomass of southern (“warm water”) copepods fluctuated greatly, with

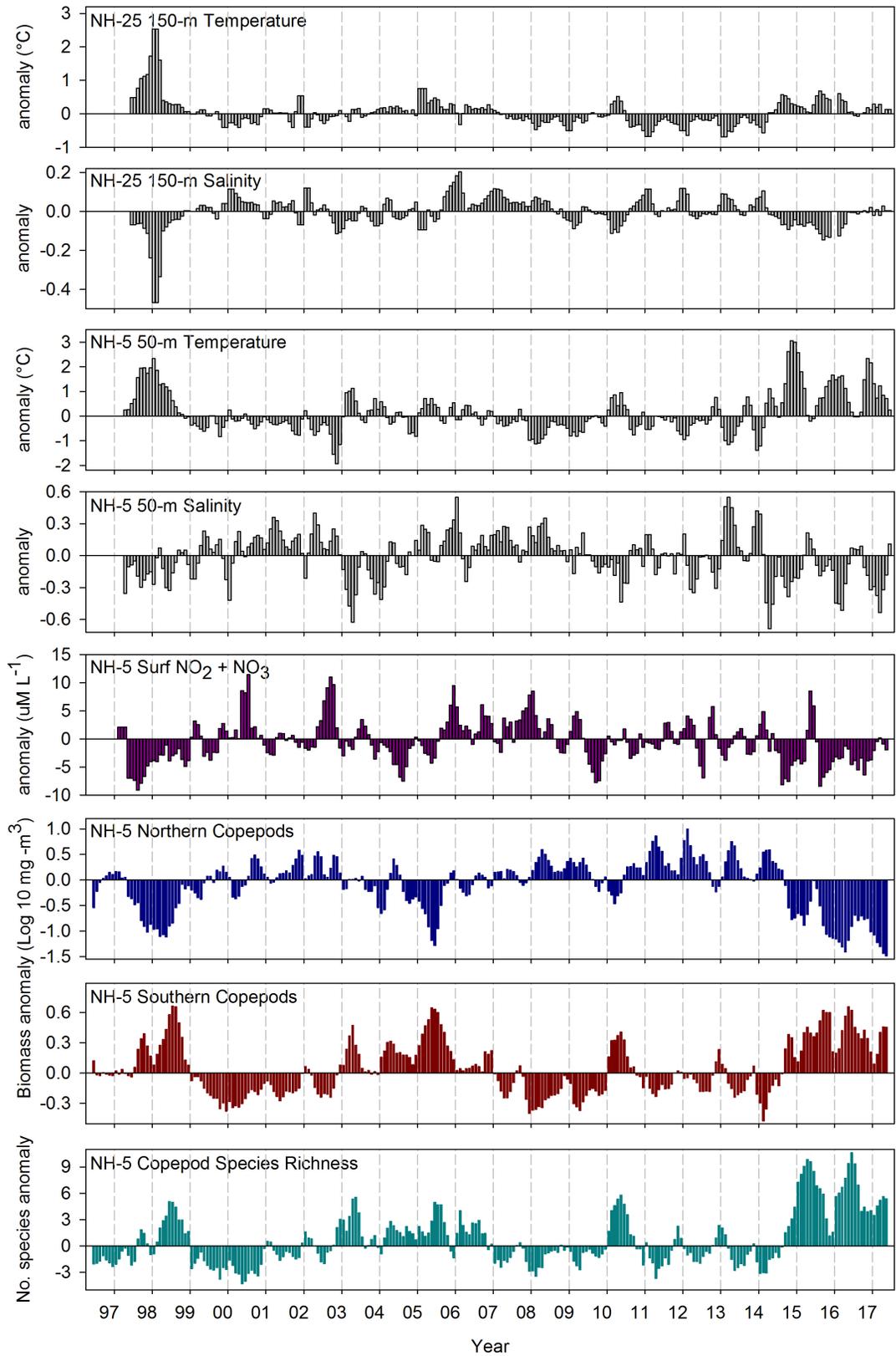


Figure 10. Time series plots of local physical and biological anomalies (monthly climatology removed) from 1997–2017 at NH-25 (Latitude: 44.6517 N Longitude: 124.65 W; top two panels) NH-5 (Latitude: 44.6517 N Longitude: 124.1770 W; lower six panels) along the Newport Hydrographic Line. Temperature and salinity from 150 m and 50 m at NH-25 and NH-5 respectively, NO₂ + NO₃ from the surface, and copepod biomass and species richness anomalies are integrated over the upper 60 m. All data were smoothed with a 3-month running mean to remove high frequency variability.

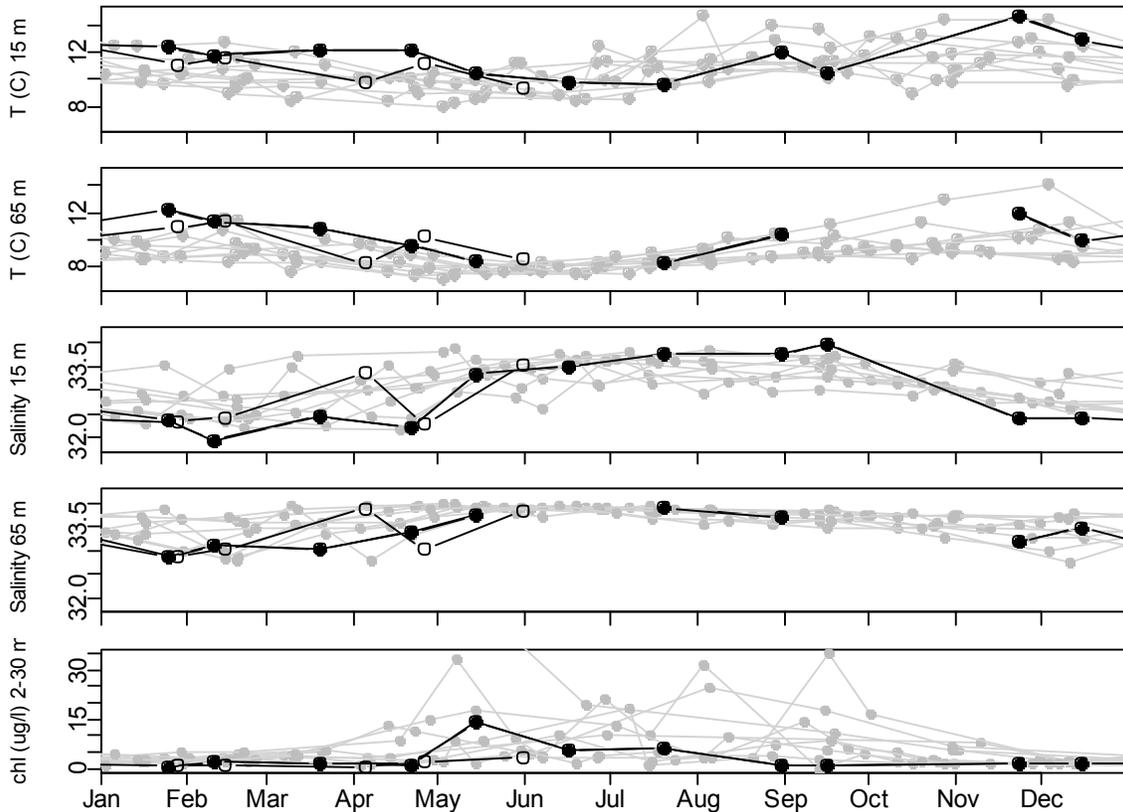


Figure 11. Hydrographic observations along the Trinidad Head (TH) Line at station TH02. Panels from top to bottom show temperature at 15 m, temperature at 65 m (near the sea floor), salinity at 15 m, salinity at 65 m, and mean (uncalibrated) chlorophyll a concentration from 2–30 m. Closed black circles represent 2016, open circles represent 2017, and grey time series represent previous years.

the highest biomass anomalies occurring during the upwelling months and lower anomalies during the winter (fig. 10). In 2015 and in 2016, the seasonal shift from a winter copepod community to a cold summer community that results from the Davidson Current in winter and its disappearance in spring did not happen (data not shown). This transition in the copepod community also did not occur during 1998, however it is unusual to remain in a warm-water copepod community for two consecutive years. This last occurred in 2003, 2004, and 2005 (fig. 10).

Copepod species richness was the highest in the time series during the summer of 2016⁵. Many of the rare species observed during this period had Transition Zone and North Pacific Gyre affinities and many of the species have never (or rarely) been observed off Newport since sampling began in 1969 (Peterson et al. 2017). The presence of these species greatly increased the species richness, which exceeded the number of species observed during the strong El Niño in 1998 (fig. 10). Like cold-water copepods, euphausiid biomass during 2016 was

among the lowest in 21 years and the coastal euphausiid, *Thysanoessa spinifera*, was largely absent (data not shown; Peterson et al. 2017).

Northern California Current: Northern California (Trinidad Head Line)

Coastal waters off northern California were warmer and fresher than usual during early 2016, but cooled in response to strong upwelling during summer. Warmer, fresher water was again observed over the shelf following relaxation from upwelling in early fall 2016. Coastal waters were slightly cooler in early 2017 relative to early 2016 (figs. 8, 11), yet remained higher than most previous observations in the record, which is consistent with larger scale patterns in the CCS (figs. 3, 8). These patterns manifested throughout the water column over the inner to midshelf (fig. 11), and extended to surface waters offshore, but did not have a strong signal at depth over the outer shelf (fig. 8). Upwelling in spring 2016 led to a phytoplankton bloom that peaked in late spring and persisted through the summer (figs. 9, 11). *Pseudo-nitzschia* were a major component of this bloom, leading to low to moderately high concentrations of particulate domoic acid (the neurotoxin produced by

⁵Copepod data were based on samples collected with a 0.5 m diameter ring net of 202 µm mesh, hauled from near the bottom to the sea surface. A TSK flowmeter was used to estimate volume of water sampled.

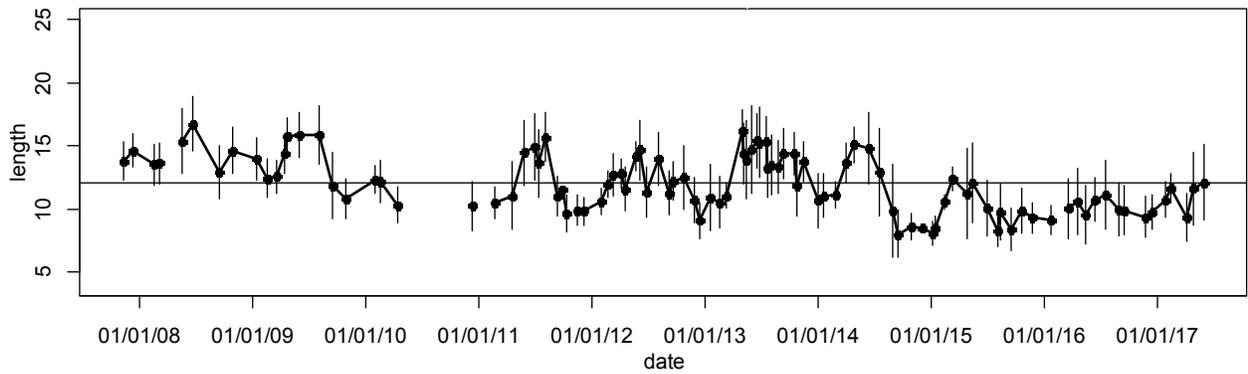


Figure 12. Density-weighted mean (points) and standard deviation (whiskers) of rostral-dorsal length of adult *Euphausia pacifica* collected along the Trinidad Head Line (aggregated over stations TH01 to TH05). Horizontal line indicates mean length taken over entire time series. Samples are collected by fishing bongo nets (505 μm mesh) obliquely from a maximum depth of 100 m (or within a few meters of the sea floor in shallower areas) to the surface.

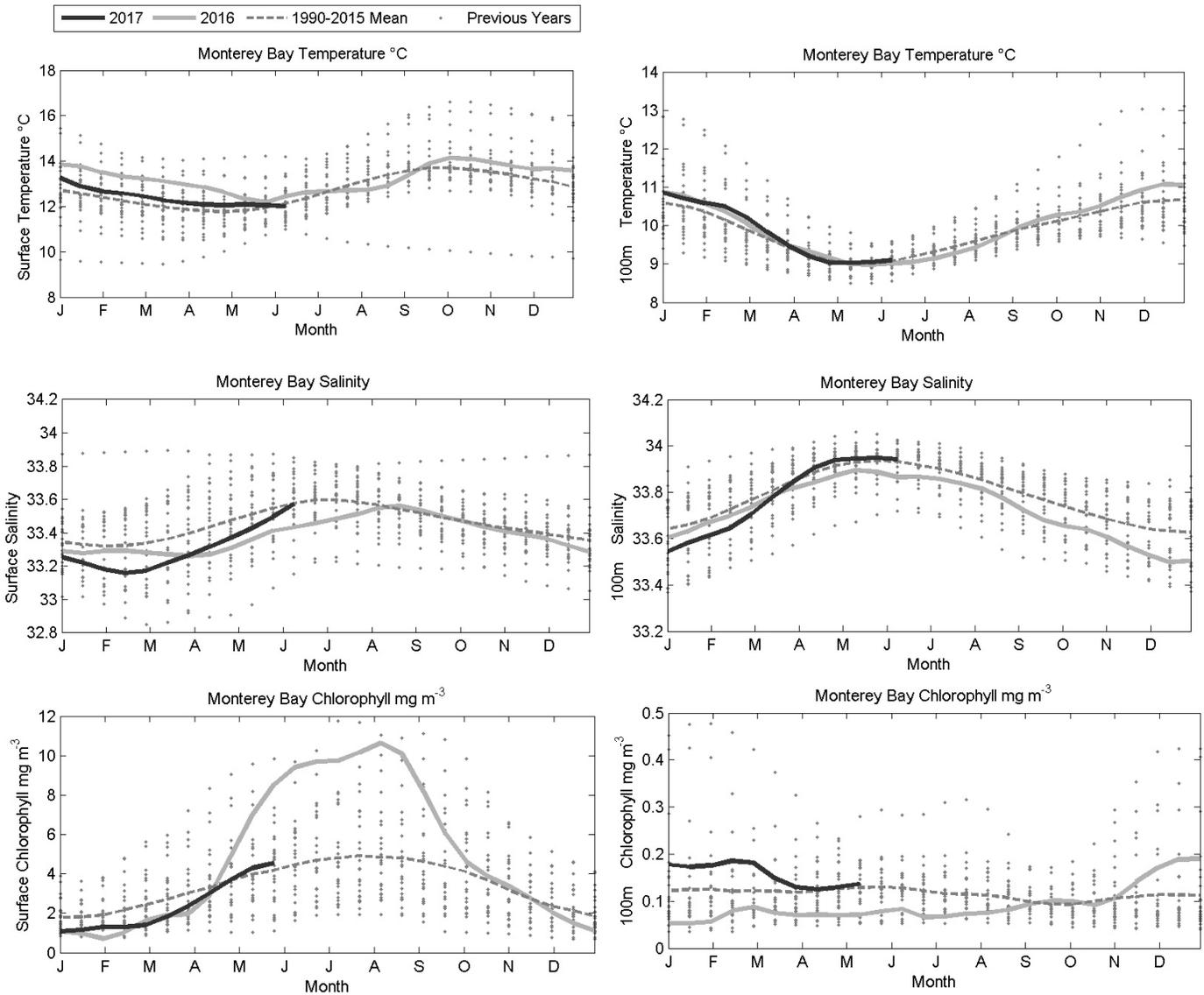


Figure 13. Temperature (top panels), salinity (middle panels) and chlorophyll a concentration (bottom panels) at the surface (left-hand column) and at 100 m (right hand column) observed at the M1 mooring in Monterey Bay, CA.

Pseudo-nitzschia; 0 to > 16,000 ng l⁻¹) in June 2016 that declined over the course of the summer. Chlorophyll concentrations have remained low through spring 2017 (figs. 9, 11). No hypoxic events were observed during 2016 and early 2017.

Zooplankton population and community data reflected the ongoing biological response to the persistence of warmer-than-usual water masses off northern California. For example, mean length of adult *Euphausia pacifica* collected along the Trinidad Head Line has remained consistently smaller than usual (fig. 12). Larger individuals were captured during periods of upwelling-driven cooling, and have been more consistently encountered during 2016 and early 2017, but the population continues to be dominated by smaller adults. The warm-water euphausiids *Euphausia recurva* and *Nyctiphanes simplex* were captured during winter and early spring 2016. Both species also occurred in winter samples from 2016–17, suggesting that warm-water zooplankton communities remained in the region but were displaced from coastal waters during periods of sustained upwelling. Copepod community data have not been updated through this period, but cursory inspection of samples and anecdotal observations made during analysis of krill samples suggest that cold-water copepods remain relatively rare or absent. Pyrosomes were present at unusually high densities throughout 2016 and early 2017, with the greatest abundance occurring during spring 2017. Large pyrosomes (i.e., individuals too large to be retained in preserved samples) were much more frequently and consistently encountered during 2016 and early 2017 than in previous years. Salps were abundant for a brief time during summer and fall 2016.

Central California Current: Monterey Bay

Temperatures at the surface and 100 m recorded at M1 (36°45'0" N 122°1'48" W) mooring in Monterey Bay were near average in 2017 and similar to the values from 2016. Surface salinities were also near the climatological average during this time period, although in early 2017 surface waters were somewhat fresher (fig. 13). Chlorophyll at the surface was low during winter 2016 but increased concomitantly with increased upwelling during summer and stayed elevated until October when upwelling weakened (fig. 4). Chlorophyll remained slightly below average until May 2017. At 100 m, chlorophyll remained below average during 2016 through November, at which point, it was near average until April 2017. Generally, aside from extremely elevated surface chlorophyll during June–September 2016 associated with anomalously strong upwelling (fig. 4), conditions at M1 were typical. In contrast to other regions, there were no significant toxic blooms in Central California,

but there were a series of “red tide” events in the near-shore caused by the dinoflagellate *Akashiwo sanguinea*.

Southern California Current: CalCOFI Survey⁶

Over the last 12 months, mixed layer temperature anomalies remained above the long-term average (fig. 14) but were 1 to 1.5°C cooler than those observed during the marine heatwave in 2014–15. The cooling of surface waters since 2015–16 is clearly shown in the Hovmoeller plots of 10 m temperatures along CalCOFI line 90, and temperatures at 100 m depth had returned to the long-term average (figs. 8, 15).

Over the last three years water column stratification in the upper 100 m was primarily driven by high surface ocean temperatures (McClatchie et al. 2016), and this trend continued over the last year (fig. 14). Mixed layer salinity was slightly below long-term averages for the last three years (fig. 14). Temperature–salinity distributions for the offshore, California Current, upwelling, and Southern California Bight areas were not dramatically different from previous years, and neither region showed the pronounced warming of the surface layer seen in 2015–16.

The depth of the σ_t 26.4 isopycnal (fig. 16), which can indicate nutrient availability and transport, was close to its long-term average over the last 12 months, contrasting with high (deep) values observed during the previous two years. Bjorkstedt et al. (2012) speculated that concentrations of oxygen at depth had been declining since the year 2000 to values not observed previously. It appears that this trend has ended (fig. 16). Indeed, one could argue that there is no trend in the O₂ time series at σ_t 26.4 from 2003 until the present (fig. 16). The same is true for the nitrate time series (fig. 16). Changes in N*, which is a biogeochemical indicator which reflects the deficit of nitrate in a system relative to concentrations of phosphate, over the last year have also been small (fig. 16).

Mixed layer concentrations of chlorophyll were extremely low during the marine heat wave and the 2015–16 El Niño. Chlorophyll concentrations returned

⁶ These results are based on four seasonal CalCOFI cruises (Ohman and Venrick 2003) in July and November of 2016 and January and April of 2017. The sampling domain encompasses the southern California Current, the Southern California Bight, the coastal upwelling region at and north of Pt. Conception and an offshore area at the edge of the North Pacific Gyre.

Results are presented as time series of averages over all 66 standard CalCOFI stations covered during a cruise or as anomalies of such values with respect to the 1984–2012 time period. When appropriate, averages from selected regions are used based on a subset of the 66 standard CalCOFI stations. The buoyancy frequency was calculated for all depths and averaged for the upper 100 m of the water column. The nitracline depth is defined as the depth where concentrations of nitrate reach values of 1 μ M, calculated from measurements at discrete depths using linear interpolation. Mesozooplankton displacement volumes for the last 12 months are not yet available. Methods used to collect and analyze samples are described in detail at www.CalCOFI.org/methods. At each station a CTD cast and various net tows were carried out. This report focuses on the hydrographic, chemical and biological data derived from ~20 depths between the surface and ~515 m, bottom depth permitting.

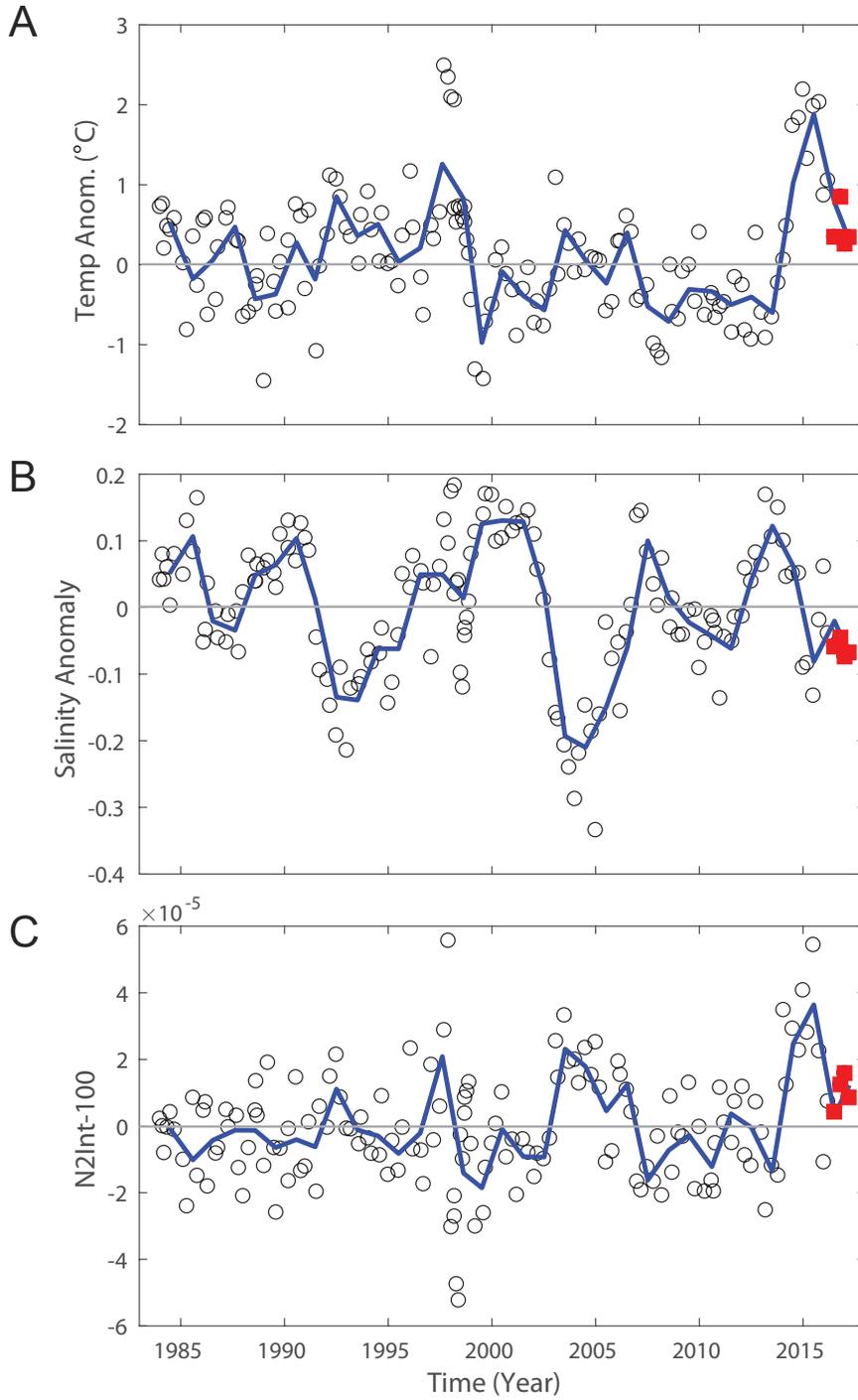


Figure 14. Cruise averages of property anomalies for the mixed layer (ML) of the 66 standard CalCOFI stations (Figure 1) for 1984 to the spring of 2017. A) ML temperature, B) ML salinity, C) buoyancy frequency squared (N2) in the upper 100 m. Data from individual CalCOFI cruises are plotted as open circles; data from the four most recent cruises, 201607 to 201704, are plotted as solid red symbols. Blue solid lines represent annual averages, grey horizontal lines the climatological mean, which is zero in the case of anomalies. Anomalies are based on the 1984 to 2012 time period.

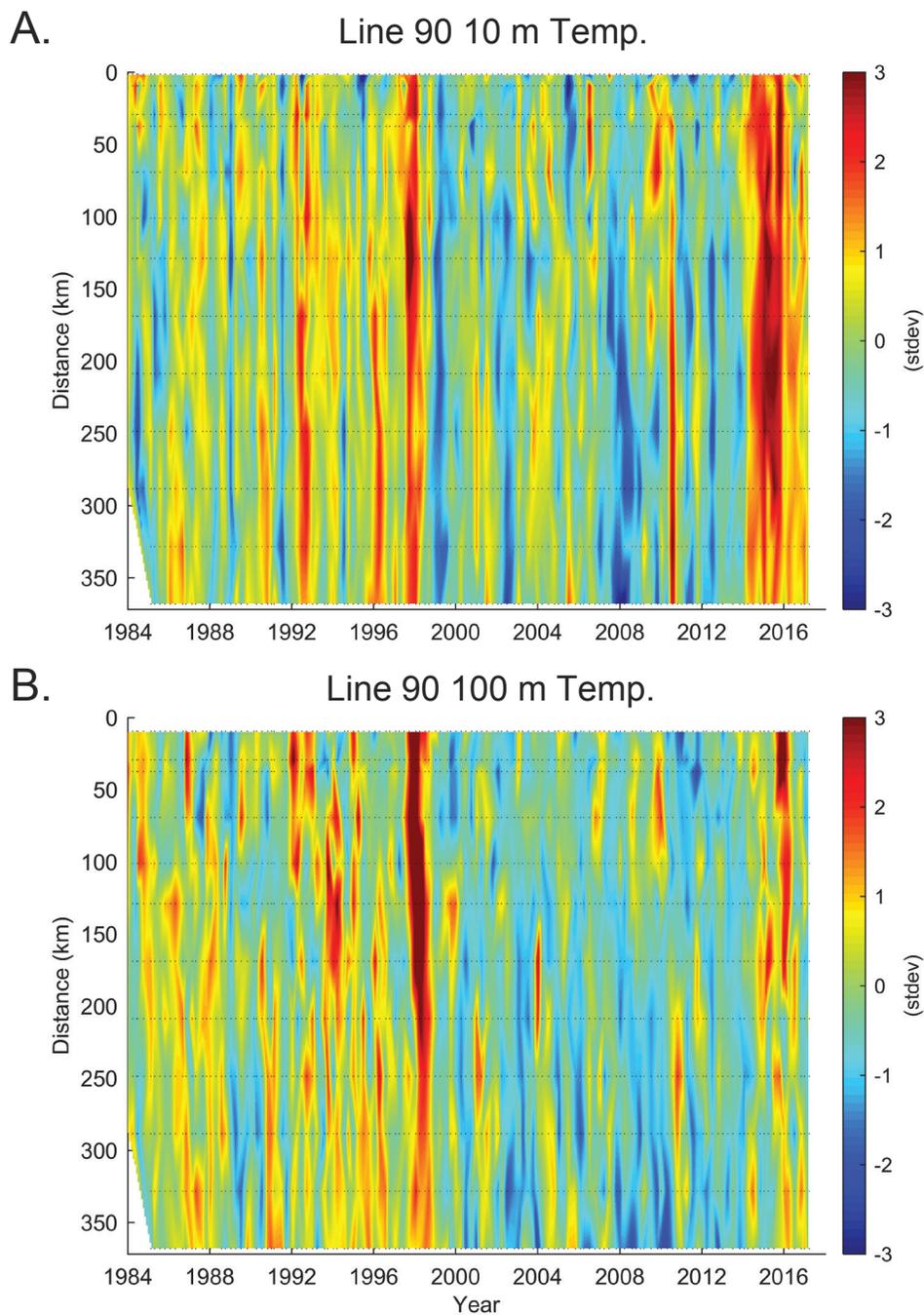


Figure 15. Standardized temperature anomalies for CalCOFI line 90 plotted against time and distance from shore for a depth of 10 m (A) and 100 m (B). Plotted data are deviations from expected values in terms of standard deviations in order to illustrate the strength of the relative changes at different depths.

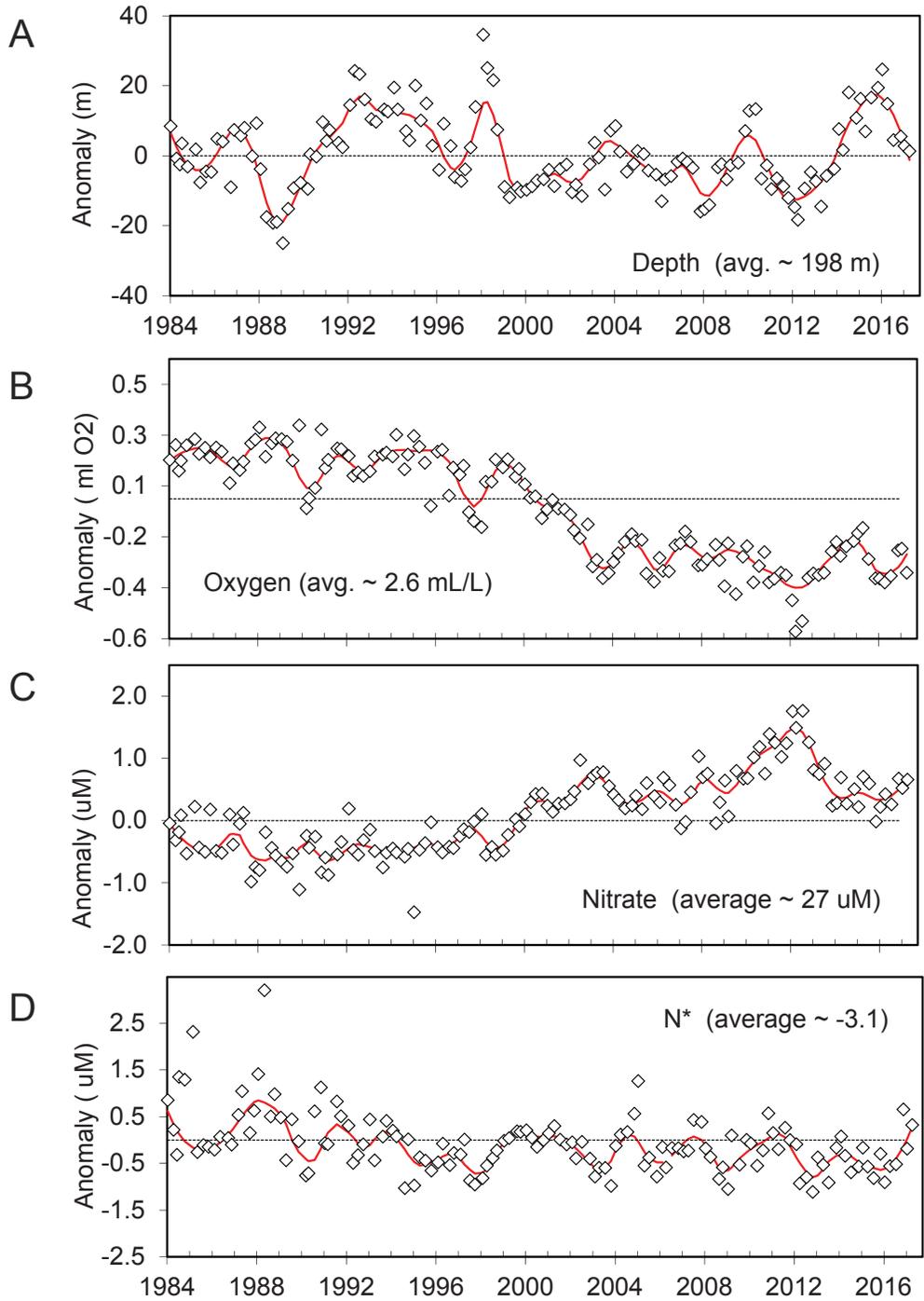


Figure 16. Anomalies of hydrographic properties at the σ_t 26.4 isopycnal (open diamonds) averaged over the 66 standard CalCOFI stations. Shown are anomalies of isopycnal depth, oxygen, nitrate, and N^* , which is a biogeochemical indicator which reflects the deficit of nitrate in a system relative to concentrations of phosphate (Gruber & Sarmiento 1997). The solid red line represents a LOESS fit to the data; average values for the properties are listed. Anomalies are based on the 1984 to 2012 time period.

to the long-term average over the last 12 months (fig. 17). Values of mixed layer nitrate concentrations and nitracline depth (fig. 17) were also close to their long-term average, consistent with the hypothesis that phytoplankton biomass in the CalCOFI study area is primarily

controlled by the availability of inorganic nutrients such as nitrate, which in turn is controlled by stratification. The depth distributions of chlorophyll in the offshore, California Current, and upwelling areas were similar to those observed between 1984 and 1997 (<http://calcofi>).

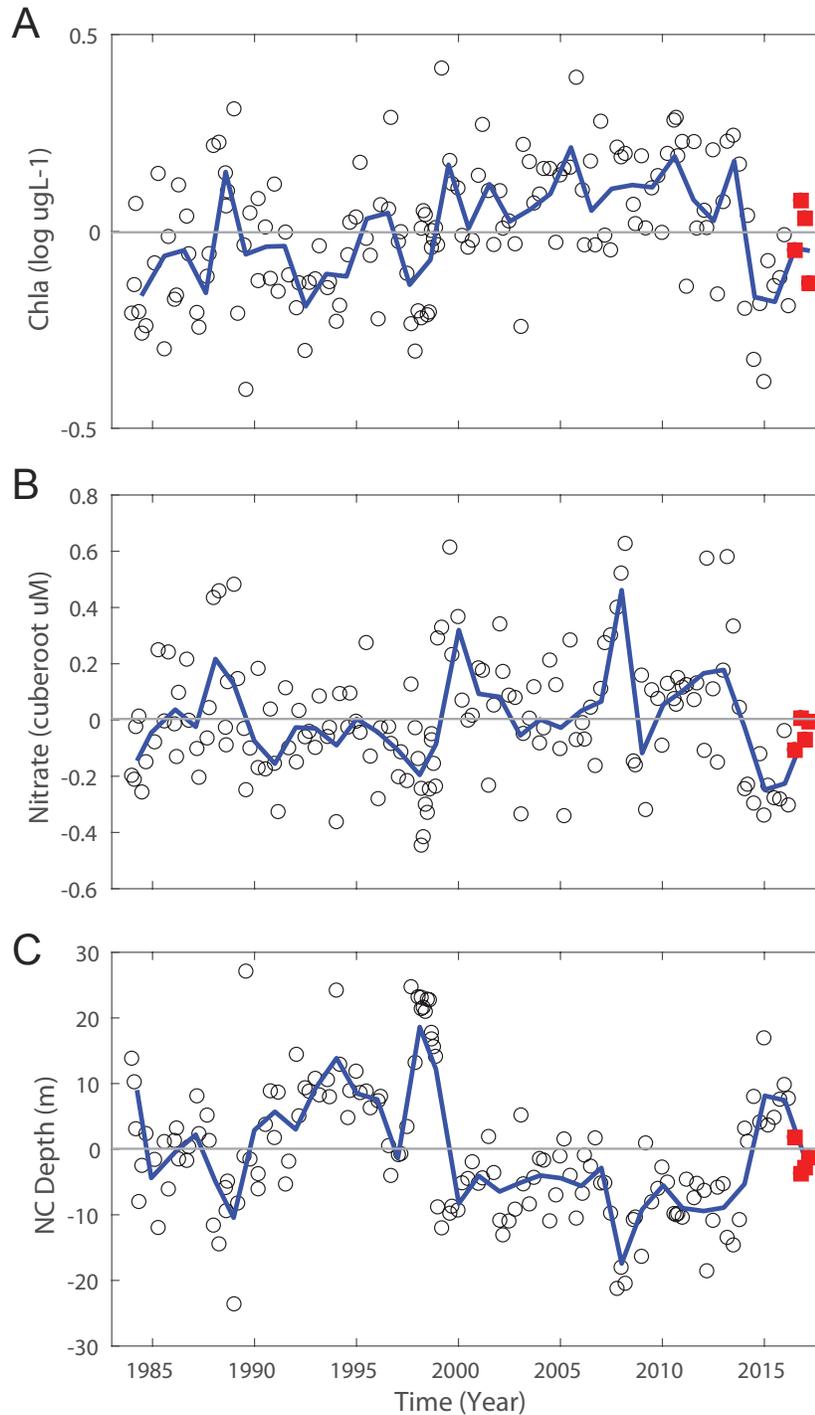


Figure 17. Cruise averages of properties for a depth of 10 m for the CalCOFI standard grid plotted as anomalies relative to the mean of the time series. A) The log₁₀ of chlorophyll a, B) the cube root of nitrate, and C) nitracline depth.

org/cruises.html). The chlorophyll maximum in the off-shore and California Current region was 10 to 20 m deeper than during the last decade. In the Southern California Bight the chlorophyll maximum was substantially stronger than maxima observed over the last 15 years but the mechanism driving these changes is unknown.

Southern California Current: Harmful Algal Blooms (HAB)

As part of the 2016 CalCOFI surveys, near-surface samples were collected for domoic acid to see if there would be an HAB response to the El Niño conditions. Toxin concentrations were negligible during 2016. In

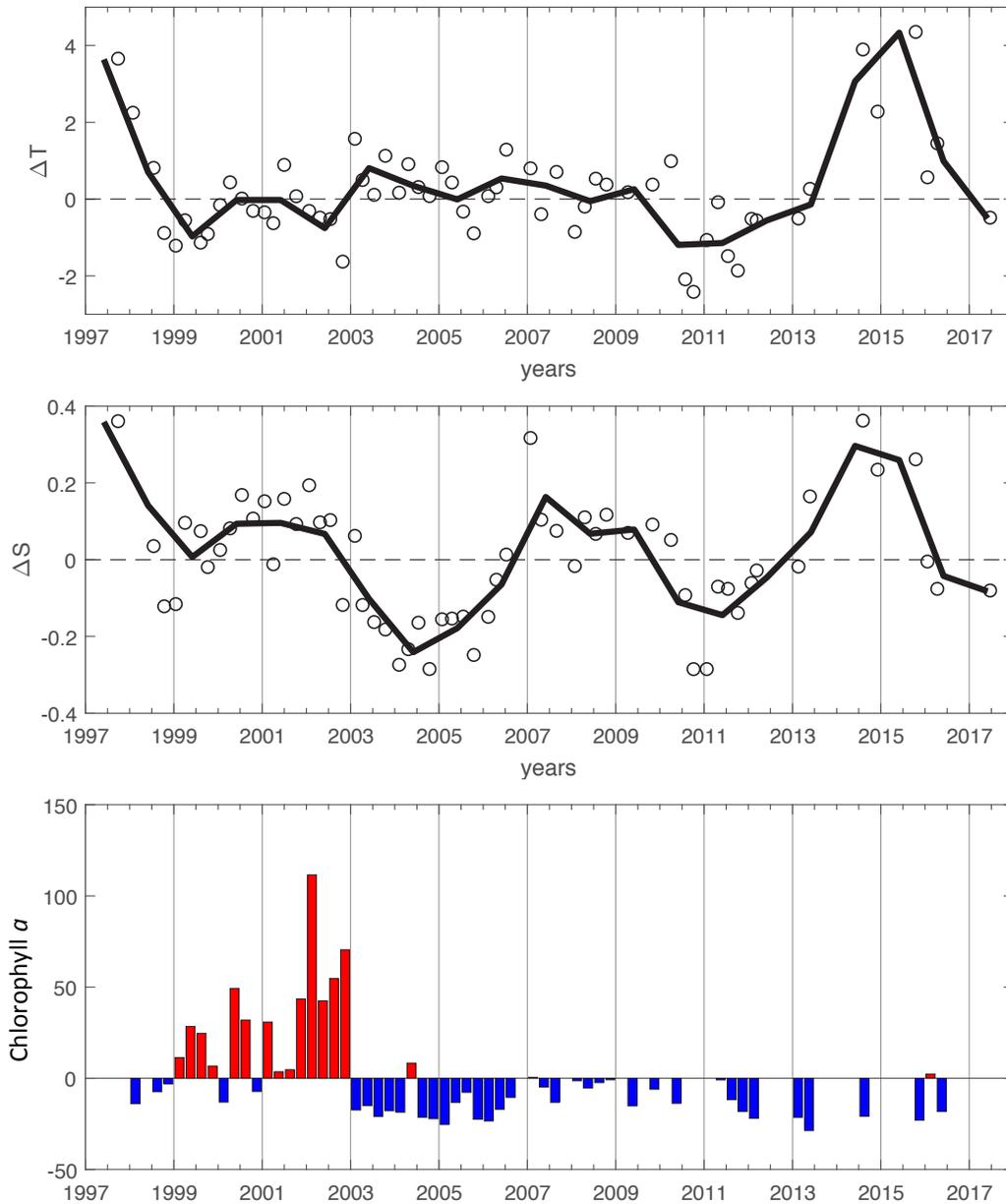


Figure 18. Interannual variability of the mixed layer temperature anomalies (°C) and salinity anomalies in the IMECOCAL region for the period 1997–2017 (white circles) and the mean of each year (thick line). Depth-integrated (0–100 m) chlorophyll a anomalies (mg m^{-2}) in the IMECOCAL region.

contrast, a significant bloom developed in April–May 2017, with numerous bird mortalities and marine mammal strandings. The bloom was localized to the Southern California Bight region, but achieved very high particulate domoic acid concentrations (exceeding 50,000 ng/L). This caused an unusual mortality event for multiple marine bird species, dominated by loons (*Gavia* spp., 75% of strandings). Sixteen loons were sampled for toxins, and all were positive for domoic acid. One loon had a sardine in its gullet at the time of death, which contained 681 ppm domoic acid. Concentrations in the loons (liver, kidney, bile) tested as high as 88 ppm (the

regulatory limit for human consumption of fish and shellfish is 20 ppm). The bloom region corresponded to the elevated chlorophyll in Figure 9.

**Southern California Current:
 Baja California (IMECOCAL)⁷**

Similar to other areas in the California Current, the magnitude of anomalously warm conditions of 2014–

⁷ The IMECOCAL program conducts quarterly cruises off the Baja California peninsula since 1997–98 El Niño. However, during 2012–17 the sampling frequency has been more sporadic and the last two years the surveys have been carried out exclusively off north Baja California.

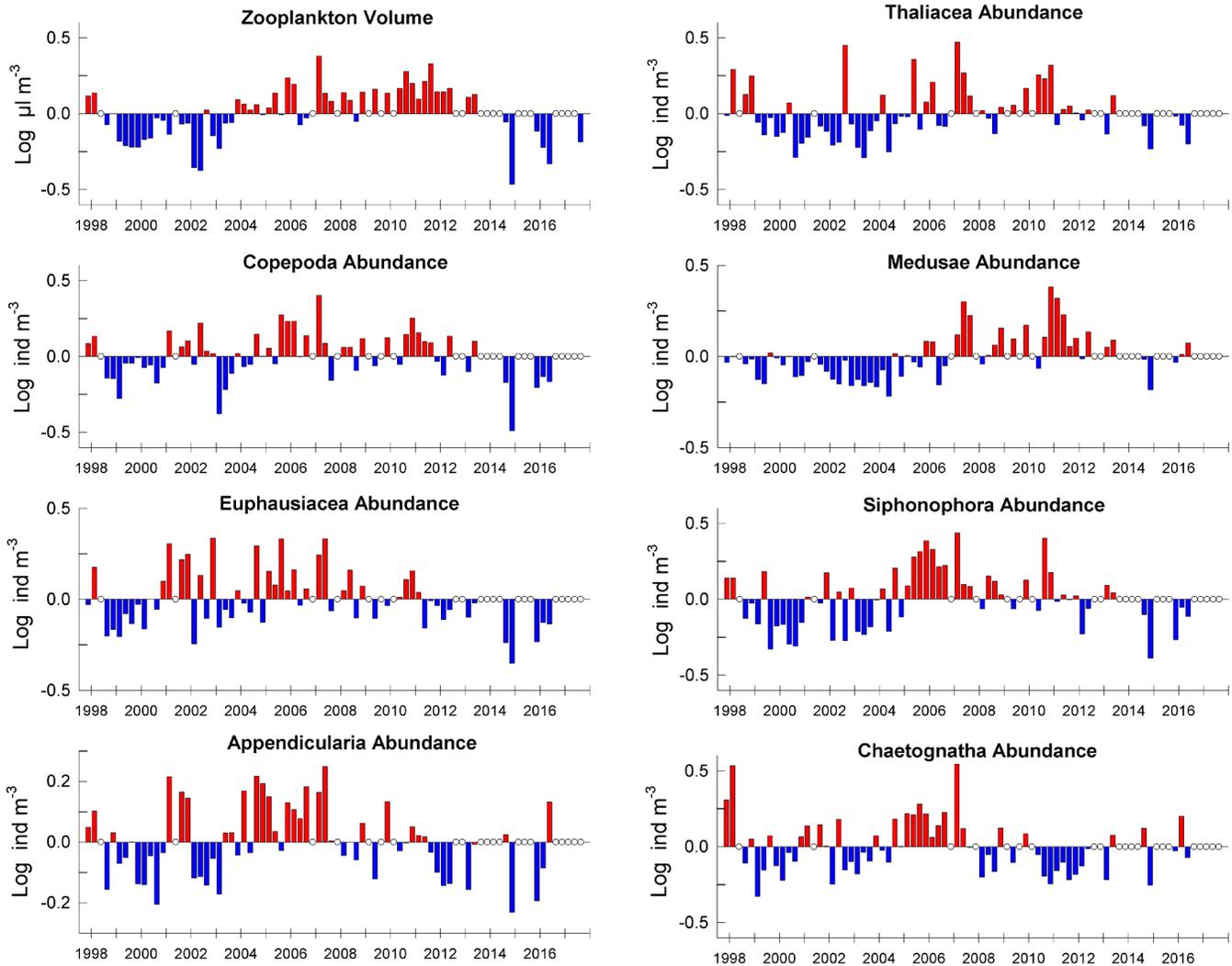


Figure 19. Zooplankton volume anomalies and abundance anomalies of zooplankton groups for the Baja California Peninsula (IMECOCAL) region. Each bar represents a single cruise and open circles represent cruises that did not take place or were omitted due to limited sampling. Data were converted to logarithms.

15 was reduced in 2016 off Baja California (fig. 18)⁸. By June 2017, surface waters transitioned to slightly cooler than average. The last result should be taken with caution because the cruise was carried out in early summer during overcast conditions. Similar to temperature, salinity anomalies of the mixed layer in April 2016 shifted from more saline waters associated with 2014–15 to fresher than average water, and remained this way into 2017 (fig. 18).

Chlorophyll from 2003–2016 remained anomalously low (fig. 18)⁹. However, there were data missing

⁸ The hydrographic data were collected using seabird sensors factory calibrated prior to each cruise. CTD data were computed by Seasoft based on EOS-80. After that, the thermodynamic variables were processed using Matlab functions from SEA-MAT. The mixed layer depth was estimated following the methodology by Jeronimo and Gomez-Valdes (2010) for the IMECOCAL grid. Harmonics were computed for mixed layer properties for all stations for which sufficient data exists. Our approach to obtain the long-term variability follows that of Bograd and Lynn (2003).

for the most productive season (spring) in recent years 2015–17. It is worth noting that anomalies presented in this updated figure differ from the figure reported in McClatchie et al. (2016) for the time interval 2008–16. This is due to a methodological error found and the application of a correction factor to values collected after 2008.

Zooplankton biomass anomalies have only recently tracked chlorophyll anomalies in this region (fig. 19)¹⁰.

⁹ Phytoplankton chlorophyll-*a* data were analyzed from water collected at discrete depths in the upper 100 m, filtering water onto Whatman GF/F filters, following the fluorometric method. Integrated chlorophyll anomalies were estimated removing seasonal means. Chlorophyll was not measured in the cruise performed in 2017.

¹⁰ Zooplankton was sampled with oblique tows of a bongo net (500 μ m of mesh width) from 210 m to the surface. Displacement volume was measured in all samples and zooplankton taxa were counted in nighttime samples only. For more reference about water samples collections and zooplankton techniques visit the IMECOCAL Web page: <http://imecocal.cicese.mx>.

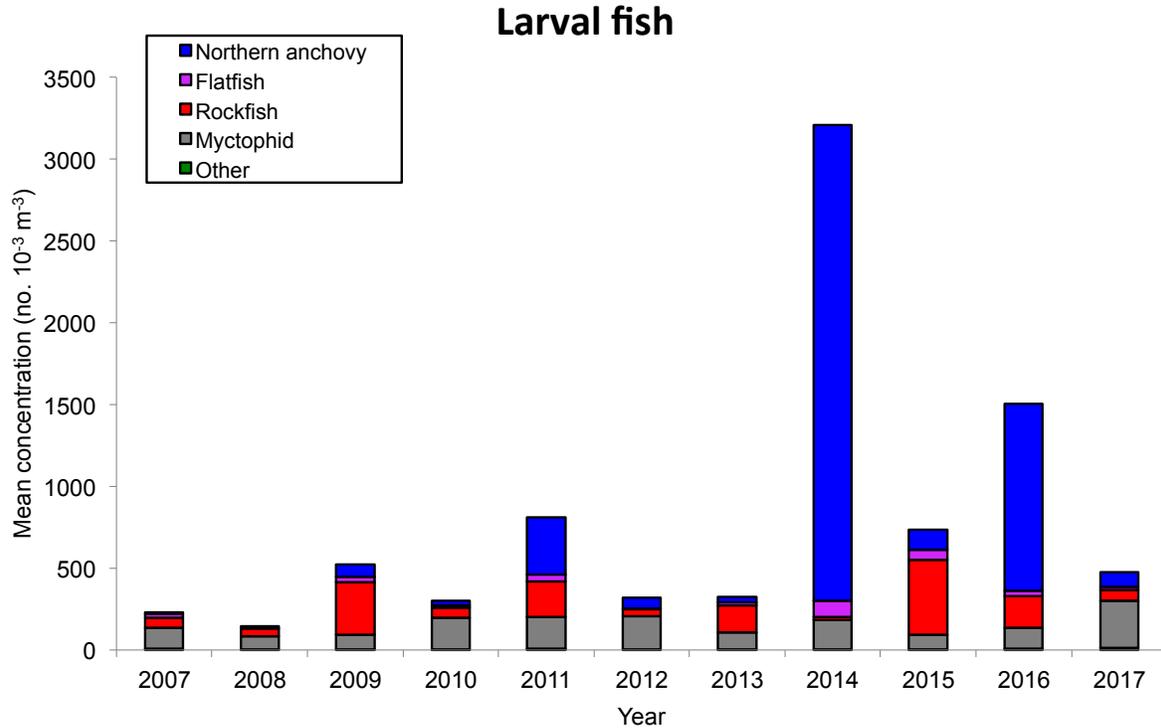


Figure 20. Mean concentrations (no. 10⁻³ m⁻³) of the dominant larval fish taxa collected during June–July in 2007–17 along the Newport Hydrographic (NH; 44.65°N, 124.35–125.12°W) and Columbia River (CR; 46.16°N, 124.22–125.18°W) lines off the coast of Oregon.

During 2014–16, an anomalously low biomass of zooplankton coincided with low chlorophyll concentrations. Prior to this (2003–13), zooplankton biomass tended to be greater than average despite the anomalously low concentration of chlorophyll over this same period. In June 2017, zooplankton biomass remained anomalously low despite cooling water temperatures. The main crustacean grazers (copepods and euphausiids) as well as gelatinous groups (tunicates, siphonophores, and medusae) may have contributed to the extremely low biomass of zooplankton observed (fig. 19). The negative anomalies of zooplankton biomass and abundances of functional groups during El Niño 2015–16 are in contrast with El Niño 1997–98 when positive anomalies of copepods, euphausiids, tunicates, and siphonophores were observed. The unique coincidence between zooplankton in the two periods were positive anomalies of chaetognaths abundance during both the 2015–16 and the 1997–98 El Niño.

It is difficult to distinguish the contribution of the marine heat wave or El Niño on the low abundance of zooplankton in the Baja California. An increase in temperature could be the result of either, producing a similar effect on subtropical species, which usually are dominant in the region (Jiménez-Pérez and Lavaniegos 2004; Lavaniegos and Ambriz-Arreola 2012). Also, negative anomalies in some groups, such as euphausiids,

appendicularians, and chaetognaths, occurred since 2011, previous to the marine heat wave event.

REGIONAL EPIPELAGIC MICRONEKTON AND SALMON OBSERVATIONS

Northern California Current: Washington and Oregon

Newport Hydrographic Line and Pre-recruit Survey

The larval epipelagic micronekton community along the central–northern coast of Oregon in June 2017 was similar to the average community structure found in the same area and season during the previous ten years in terms of composition and relative concentrations of the dominant taxa (fig. 20)¹¹. The exception was unusually

¹¹ Micronekton samples were collected from 3–4 stations representing coastal (<100 m in depth), shelf (100–1000 m), and offshore (>1000 m) regions along both the Newport Hydrographic (NH; 44.65°N, 124.35–125.12°W) and Columbia River (CR; 46.16°N, 124.22–125.18°W) lines off the coast of Oregon during June–July in 2007–17 (See Auth 2011 for complete sampling methods). In addition, post-larval (i.e., juvenile and adult) fish were collected using a modified-Cobb midwater trawl (MWT) with a 26 m headrope and a 9.5 mm codend liner fished for 15 min at a headrope depth of 30 m and ship speed of ~2 kt. MWT collections were made at 4–6 evenly-spaced, cross-shelf stations representing coastal, shelf, and offshore regions along nine (five in 2017) half-degree latitudinal transects between 42.0 and 46.0°N latitude in the northern California Current region during June–July in 2011–17 (although no sampling was conducted in 2012). Sampled volume was assumed to be uniform for all hauls. All fish collected were counted and identified to the lowest taxonomic level possible onboard, although pre-recruit rockfish were frozen and taken back to the lab for identification using precise meristic and pigmentation metrics.

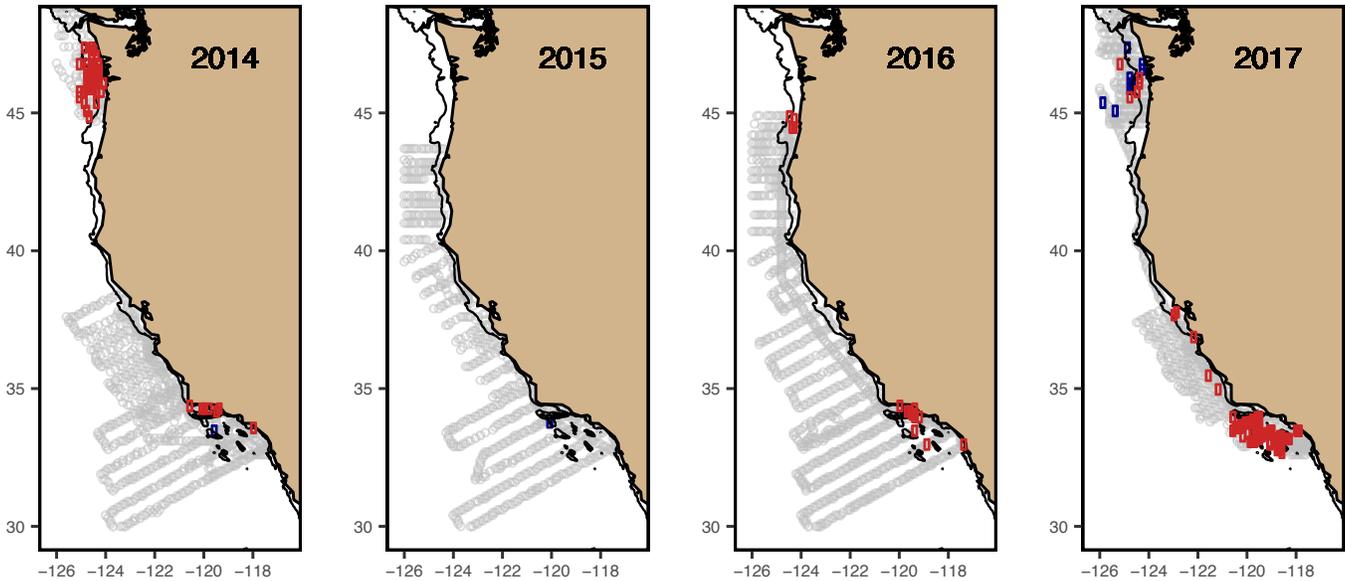


Figure 21. Northern anchovy egg density anomalies from continuous underway fish egg sampler (CUFES) surveys March–July 2014–17. Anomalies are shown for values greater than 2 eggs/m³ (red, Observation – Mean) or less than –2 eggs/m³ (blue) based on 0.1° bin spatial averages. North of 44°N there were only 12 years of data: 2003, 2004, 2006, 2007, 2008, 2010, 2011, 2012, 2013, 2014, 2016, and 2017. Note that central California southward has been surveyed since 1997.

high concentrations of larval northern anchovy (*Engraulis mordax*) in 2014 and 2016 resulting from anomalously high spawning activity in the region (fig. 21)¹². Total mean larval concentration was near average based on the 11-year time series. Larval myctophids in 2017 were found in the highest concentration since sampling began in 2007 as were “other” taxa, although other taxa still only accounted for <3% of the total mean larval concentration.

The post-larval fish community in the northern California Current in June 2017 was similar to the community structure found in the same area and season during the previous two years primarily due to the continued dominance of Pacific hake (*Merluccius productus*), which comprised 83% of the mean abundance of “other” taxa and ~ 60% of the total mean abundance of all post-larval fish (fig. 22). The abundance of smelt in 2017 was tied with that in 2016 for the lowest of the six-year time series, while the abundance of clupeiformes in 2017 was tied with that in 2016 for the highest, primarily due to the high concentration of northern anchovy collected just off the mouth of the Columbia River. Rockfish abundance in 2017 was the second highest of the time series, with the dominant species consisting of shortbelly (*S. jordani*; 50% of total rockfish), blue (*S. mystinus*), darkblotch (*S. crameri*), and widow (*Sebastes entomelas*). In addition, medusafish (*Ichthyos lockingtoni*) were collected in far higher numbers than ever before in the six-year

time series, probably due to their affinity for pyrosomes which were present in unprecedented numbers throughout the sampling area.

Columbia River plume region: Juvenile Salmon and Ocean Ecosystem Survey The June fish and invertebrate assemblage in the northern California Current during 2017 was unusual and dominated by species that normally occur in warmer ocean waters to the south of the study area¹³. A nonmetric multidimensional scaling (NMDS) ordination clearly showed that the 2015–17 assemblages were outliers, distinct not only from the 1999 La Niña assemblages, but also from the assemblage sampled during the 2005 warm event in the northern California Current (fig. 23).

The fish and invertebrate community in 2017 was similar to the past two warm years of 2015 and 2016 (fig. 23). Taxa indicative of 2017 included the pyrosome, Pacific pompano (*Peprilus simillimus*), Pacific chub mackerel (*Scomber japonicus*), and jack mackerel (*Trachurus symmetricus*). Pyrosomes are tunicates that are normally

¹² Egg data is from continuous underway fish egg sampler (CUFES). While the southern/central region has been surveyed since 1997, the survey expanded north of 44°N only in 12 years: 2003, 2004, 2006, 2007, 2008, 2010, 2011, 2012, 2013, 2014, 2016, and 2017. Spatial anomalies are estimated on 0.1° bins.

¹³ Pelagic fish and invertebrate catch data were collected by the Juvenile Salmon and Ocean Ecosystem Survey (JSOES, NWFSC NOAA/Bonneville Power Administration) surveys using surface trawls on standard stations along transects between northern Washington and Newport, OR, in June from 1999 to 2016. All tows were made during the day at predetermined locations along transects extending off the coast to the shelf break (Brodeur et al. 2005). We restricted the data set to stations that were sampled consistently over the sampling time period (>9 y). Numbers of individuals were recorded for each species caught in each haul and were standardized by the horizontal distance sampled by the towed net as CPUE (number/km towed). A log(x+1) transformation was applied to the species at each station and then averaged by year for each species. The species data matrix included the 27 most abundant species captured over the 18 years sampled years (27 species x 18 years). A nonmetric multidimensional scaling (NMDS) ordination was used to describe the similarity of each year's community in species space.

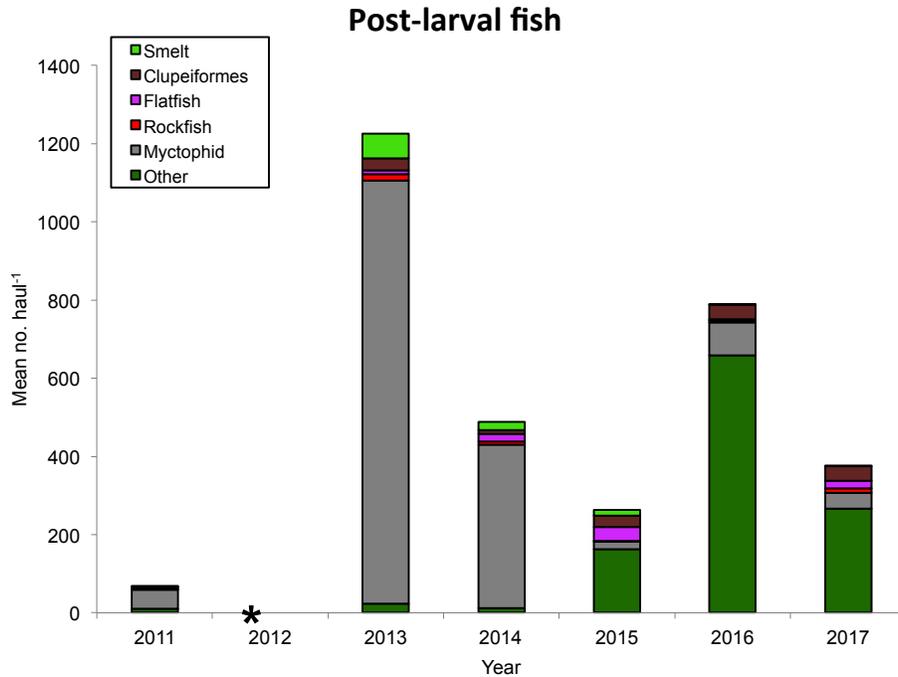


Figure 22. Mean catches (no. haul⁻¹) of the dominant post-larval fish taxa collected during June–July in 2011–17 along nine half-degree latitudinal transects between 42.0° and 46.0°N latitude in the northern California Current region. * = no samples were collected in 2012.

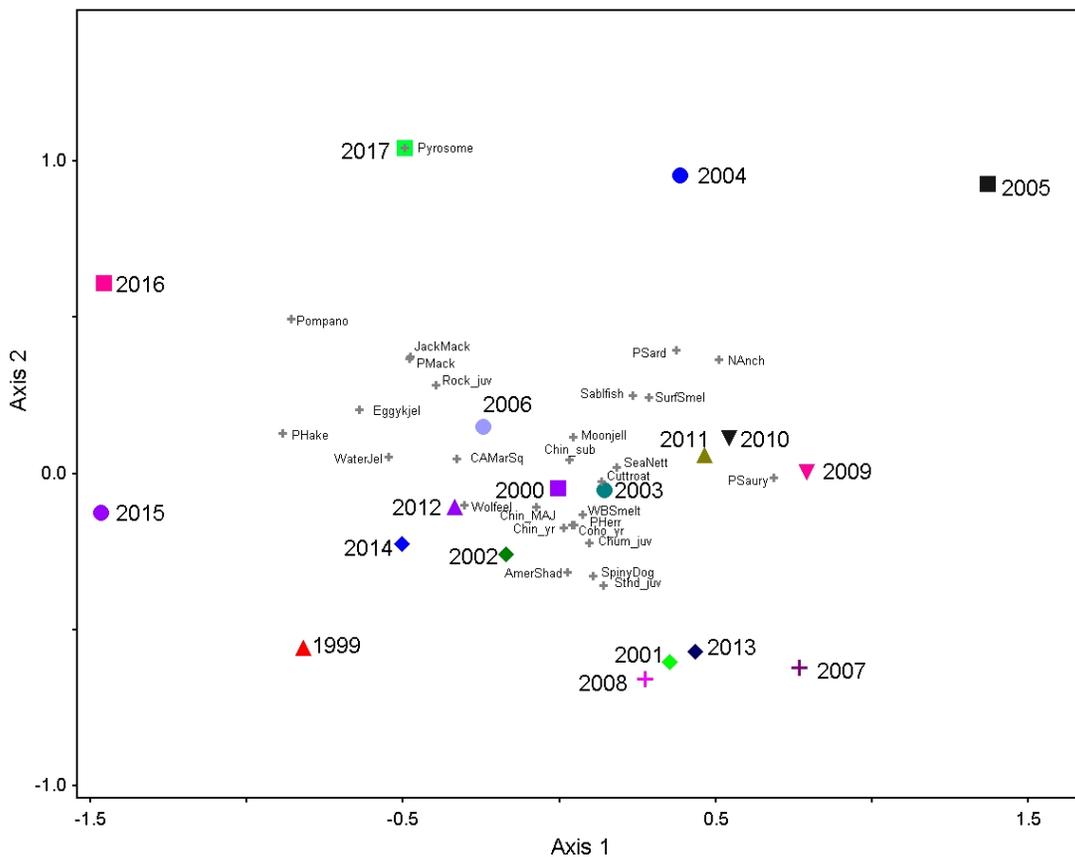


Figure 23. NMDS ordination of northern California Current pelagic assemblages. The NMS ordination explained 80.8% of the total variability in the first two dimensions. Pelagic fish and invertebrate catch data were collected by the NWFSC NOAA/Bonneville Power Administration surveys using surface trawls on standard stations along transects between northern Washington and Newport, OR, in June from 1999 to 2016. All tows were made during the day at predetermined locations along transects extending off the coast to the shelf break (Brodeur et al. 2005).

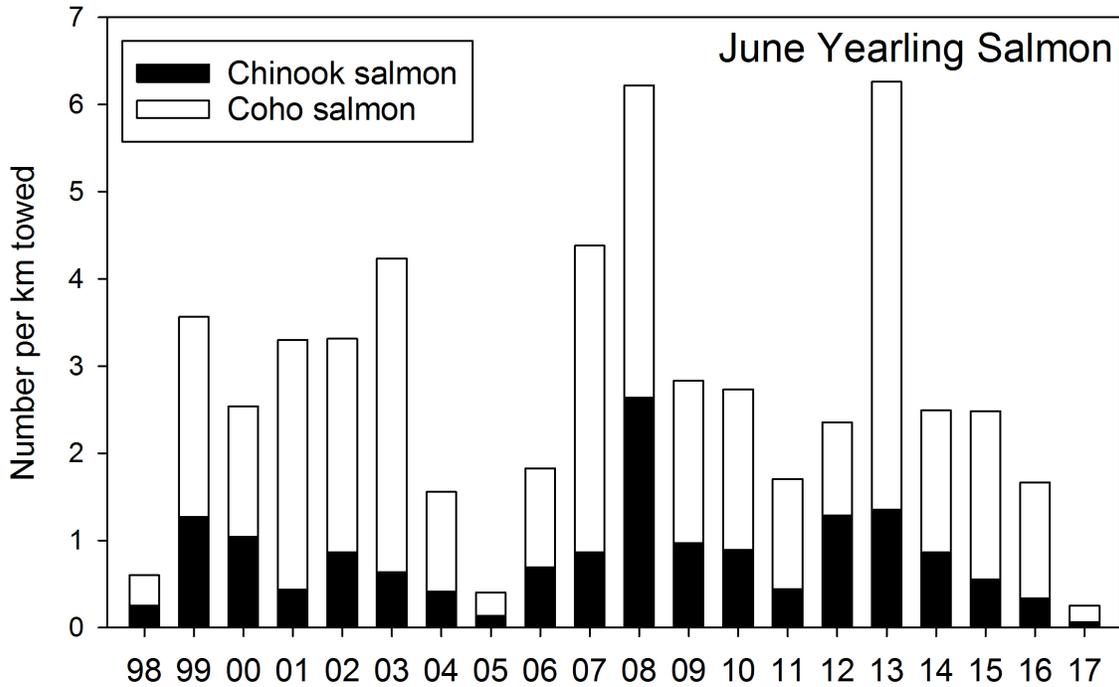


Figure 24. Catches of juvenile coho (black bars) and Chinook (white bars) salmon off the coast of Oregon and Washington in June from 1998–present.

found in the tropics, and have never been captured on the continental shelf during this survey or any previous surveys off central Oregon to northern Washington to our knowledge, although in recent years it has been found increasingly farther north off the shelf in other surveys¹⁴. But during June 2017 pyrosomes were present in 37% of the hauls, sometimes exceeding hundreds of individuals.

The jellyfish community off Washington and Oregon was also quite different than previous years. The usual numerically dominant large jellyfish is a cool-water associated scyphozoan species, sea nettle (*Chrysaora fuscescens*). However, during the warm ocean years of 2015 and 2016, the more offshore taxa of Hydromedusae, the water jelly (*Aequorea* spp.) was much more abundant and densities of *Chrysaora* were low. In June 2017 both *Chrysaora* and *Aequorea* were caught in average densities.

Salmon and salmon forage indicators in northern California Current Catches of yearling salmon off Washington and Oregon in June may be a good indicator of early ocean survival of yearling Chinook (*Oncorhynchus tshawytscha*) and coho salmon (*O. kisutch*). The abundance of yearling Chinook salmon during June is positively related to spring Chinook jack and adult salmon counts at the Bonneville Dam (with 1 and 2 year lags, respectively), as does the abundance of yearling coho salmon to subsequent coho smolt to adult

survival¹⁵ (Morgan et al. 2017). Catch per unit effort (number per km trawled) of both yearling Chinook and coho salmon during the June 2017 survey was the lowest of the 20-year time series from 1998 to 2017 (fig. 24). This suggests that adult returns of both spring Chinook in 2019 and coho salmon in 2018 will be significantly lower than average.

The biomass of fish larvae in late winter from the Newport Hydrographic Line provides an index of fish that are the common prey of juvenile salmon when they enter the ocean in spring and summer, and correlates with juvenile salmon survival and return as adults (Daly et al. 2013, 2017)¹⁶. The food biomass for out-migrating juvenile salmon in winter (January–March) 2017 was the highest in the 20-year time series (fig. 25), largely attributable to presence of young-of-the-year (YOY) rockfishes.

In addition to the increased biomass of fish prey potentially available to out-migrating juvenile salmon, the type of fish prey (assemblage) that are available for salmon also influences salmon survival. Importantly, the overall community composition of winter ichthyoplankton in 2017 was similar to 2015 and 2016 and predicted a poor food community for the salmon (fig. 26).

¹⁴ <http://news.nationalgeographic.com/2017/06/pyrosome-fire-body-bloom-eastern-pacific-warm-water>

¹⁵ [https://www.nwfsc.noaa.gov/oceanconditions/Juvenile Salmon Catch](https://www.nwfsc.noaa.gov/oceanconditions/Juvenile%20Salmon%20Catch)

¹⁶ Ichthyoplankton samples were collected from 5 stations spaced ~9 km apart along the NH line. Sampling was conducted approximately every 2 wk between January and March. Only samples from January–March were used, assuming that larvae collected during these months would have had sufficient time to grow to the average size of prey eaten by juvenile salmon in late spring and early summer.

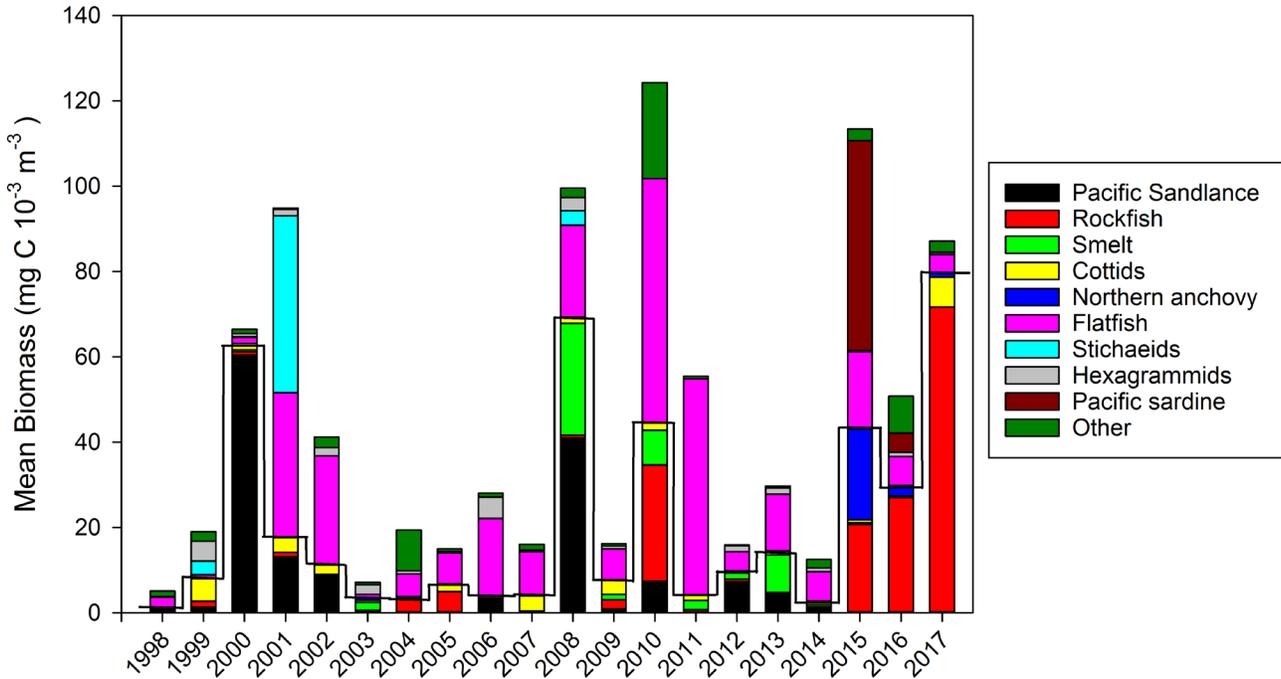


Figure 25. Annual mean biomass ($\text{mg C } 10^{-3} \text{ m}^{-3}$) of the five important salmon prey taxa (below solid line) and five other dominant larval fish taxa (above solid line) collected during winter (January–March) in 1998–2017 along the Newport Hydrographic line off the coast of Oregon (44.65°N, 124.18–124.65°W). Figure expanded from one presented in Daly et al. (2013).

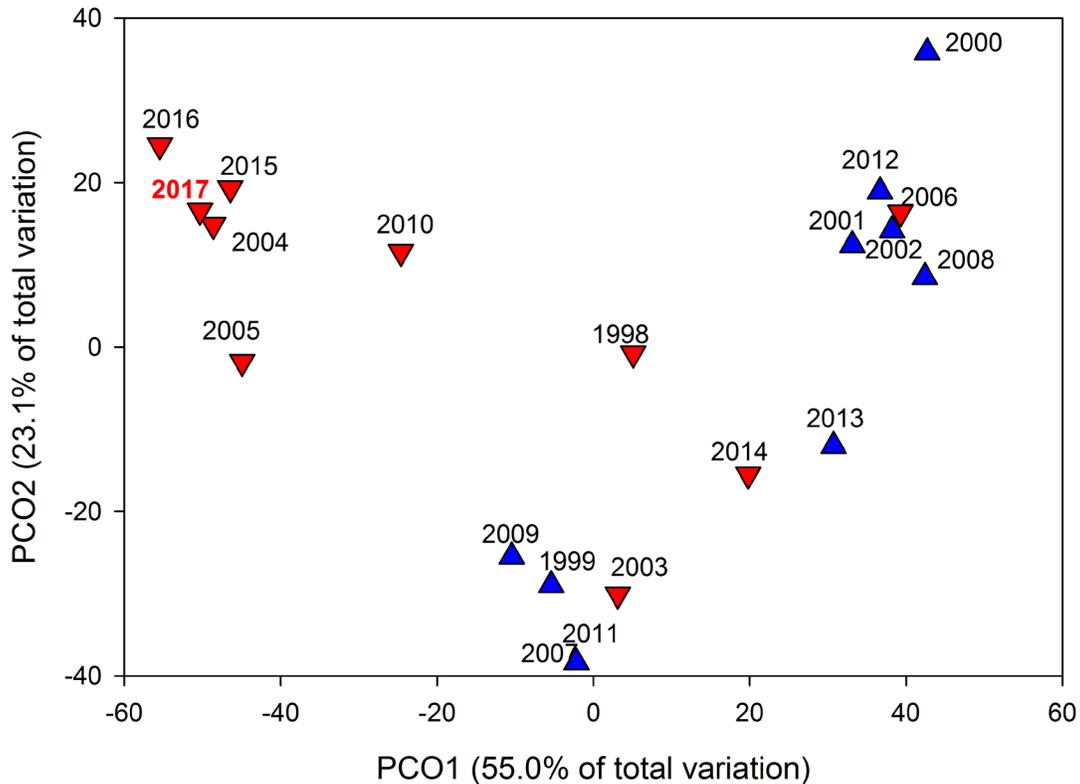


Figure 26. Principal coordinate analysis of the prey composition of winter ichthyoplankton that are important prey for out-migrating juvenile salmon (Pacific sand lance, osmerids, cottids, northern anchovy, and rockfishes). Red symbols indicate positive winter PDO (warm ocean temperatures) and blue indicates negative winter PDO (cold ocean temperatures). The larvae were collected during winter (January–March) in 1998–2017 along the Newport Hydrographic line off the coast of Oregon (44.65°N, 124.18–124.65°W). Figure expanded from one presented in Daly et al. (2017).

Based on axis 1 values (55% variance explained along this axis) from principal coordinate analysis of the prey composition of winter ichthyoplankton, the index of the 2017 prey composition predicts poor prey conditions for currently out-migrating juvenile salmon. In 2017, 90% of the winter ichthyoplankton composition was warm ocean condition taxa consisting of rockfishes and northern anchovy larvae. The relationship between the principle component 1 (PC1) axis values (prey composition) with spring Chinook salmon adult returns to Bonneville Dam two years later is: $P = 0.003$; $R^2 = 48.0\%$ (1998–2014; 1999 outlier year excluded). The biomass of ichthyoplankton in winter predicts returns of spring Chinook salmon to Bonneville Dam in 2019 to be just below ~230,000, and the prey composition prediction is one of the lowest of the time series at ~74,000.

Higher than average ichthyoplankton biomass but poor ichthyoplankton composition occurred in the warm ocean years 2015–17. Of particular note during January–March 2017, southern California winter-spawned larvae were present for the third winter in a row (e.g., Pacific hake and Pacific sardine [*Sardinops sagax*]; Auth et al. 2017). Sardine larvae were present in winter 2017, but not in high amounts, and were located at inshore stations (NH 1 and 10) and some were >10 mm long (Auth unpublished data). Of note, juvenile sardine were eaten for the first time in the time series by coho and Chinook salmon in May and June 2016 (Daly and Brodeur unpublished data), indicating that sardine are a new prey resource for the salmon in warm ocean conditions.

Summary of epipelagic micronekton and salmon in northern CCS Taken as a whole, the micronekton community and juvenile salmon abundance during winter to June 2017 off Washington and Oregon indicate continued perturbation from “normal” conditions. The abundance of pyrosomes may have indicated abnormal water transport in 2017. It is not yet clear whether the findings of 2017 are a result of the marine heat wave combined with the 2015–16 El Niño or whether ocean processes unique to 2017 combined with the previous warm years resulted in the altered community structure.

Central California¹⁷

Above average catches of YOY rockfishes were observed off central California in late spring 2017, although these catches were lower than the high catches

observed in 2015 and 2016 (fig. 27). Catches in the southern region increased from below average values in 2016 to the greatest values in the (shorter) 13-year record in that region in 2017. Catches of YOY rockfish in north-central California were below average, such that there was a gradient in relative catch rates from record highs in the Southern California Bight to below average (but above historic low levels) in northern California.

In the Southern California Bight during 2017, catches of adult northern anchovy were comparable to past (2004) high levels, while catches continued to be very sparse in other regions of the California Current sampled by this survey (fig. 27). The survey also samples YOY northern anchovy and YOY Pacific sardine, for which catches of both increased during the 2015–16 warm event, and, in 2017, stayed above previous low levels in northern and central areas while continuing to increase to very high levels in the Southern California Bight (data not shown, but see Sakuma et al. 2016). Although the sparse catches for adult Pacific sardine and adult northern anchovy north of Southern California Bight indicate that the biomass of each may be too low to be meaningfully indexed by the survey, the increase in catches of YOY northern anchovy, in particular, are consistent with an increase in that population which is likely more concentrated in nearshore habitats not sampled by the survey. An increase in adult northern anchovy nearshore is also consistent with the egg enumeration data in 2017 (fig. 21) and seabird diets (presented below), both of which indicated above average adult northern anchovy abundance in the region. The abundance of both krill and market squid (*Doryteuthis opalescens*), increased significantly in all regions in 2017, both ranked at the third highest value since 1990 in the core region (fig. 27).

Thetys as well as other salps were less abundant than recent years in all but the southern region, where other salps increased relative to 2016 (fig. 28). Pyrosomes continue to be caught in very large numbers across all regions (fig. 28), with particularly high catches (of primarily very small pyrosomes) in the southern region. Catches of scyphozoan jellyfish (primarily *Aurelia* spp. and *Chrysaora* spp.) continued to be unusually low in 2017, a pattern that emerged in 2015 (fig. 28). The high numbers of pelagic red crabs (*Pleuroncodes planipes*) and California lizardfish observed in 2015 and 2016 (Leising et al. 2015; McClatchie et al. 2016) were not observed in 2017 possibly indicating cooler water regionally.

There are sharp differences in principal component (PC) loadings between coastal pelagic (Pacific sardine, northern anchovy) and mesopelagic species (myctophids) relative to most of the YOY groundfish, krill, and cephalopods. The two leading PCs for the assemblage are shown in a phase plot (fig. 29). The dramatic separation of the 2013–16 period was apparent as those years were

¹⁷ Epipelagic micronekton samples were collected during May and June by the Southwest Fisheries Science Center Rockfish Recruitment and Ecosystem Assessment Survey and the Northwest Fisheries Science Center Pre-recruit Groundfish Survey, covering a geographic range from the US/Mexico border (32.5°N) to southern Washington (46.5°N). A modified midwater Cobb trawl (10–30 m headrope depth) was used to sample pelagic species along the CCE in the mixed layer where juvenile salmon are typically found. Methods were standardized between regions beginning in 2011 (Sakuma et al. 2016).

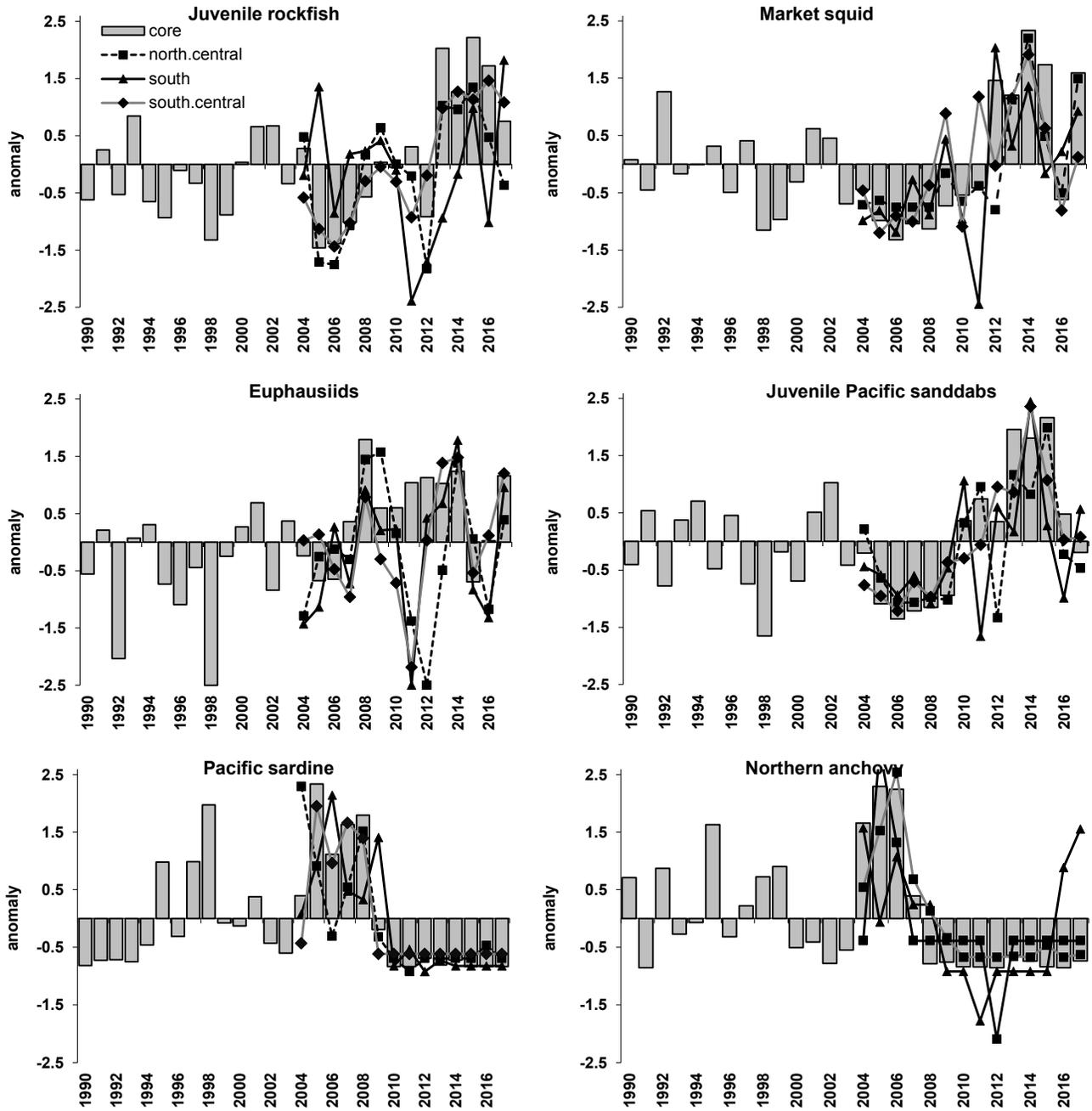


Figure 27. Long-term standardized anomalies of several of the most frequently encountered pelagic forage species from rockfish recruitment survey in the core (central California) region (1990–2017) and the southern, south-central and north-central survey areas (2004–17). Forage groups are YOY rockfish, market squid, krill (primarily *Euphausia pacifica* and *Thysanoessa spinifera*), YOY Pacific sanddab, Pacific sardine and northern anchovy.

extremely orthogonal to the low productivity years of 1998, 2005, and 2006. However, in 2017 the observed community switched to what might be considered a “normal” state, centrally located among the years 1990–2016. The switch in the forage base has important implications for seabirds, marine mammals, salmon and adult groundfish that forage primarily, or exclusively, on one or another component of the forage assemblage.

Southern California Current: CalCOFI region

The spring coastal pelagic fish survey in 2017 on NOAA ship *Reuben Lasker* was focused on northern anchovy rather than Pacific sardine and consequently the offshore extent of transects was reduced. No trawling was conducted offshore and unlike 2015 and 2016, no sampling was conducted north of San Francisco in 2017. The spring CalCOFI cruise on NOAA ship

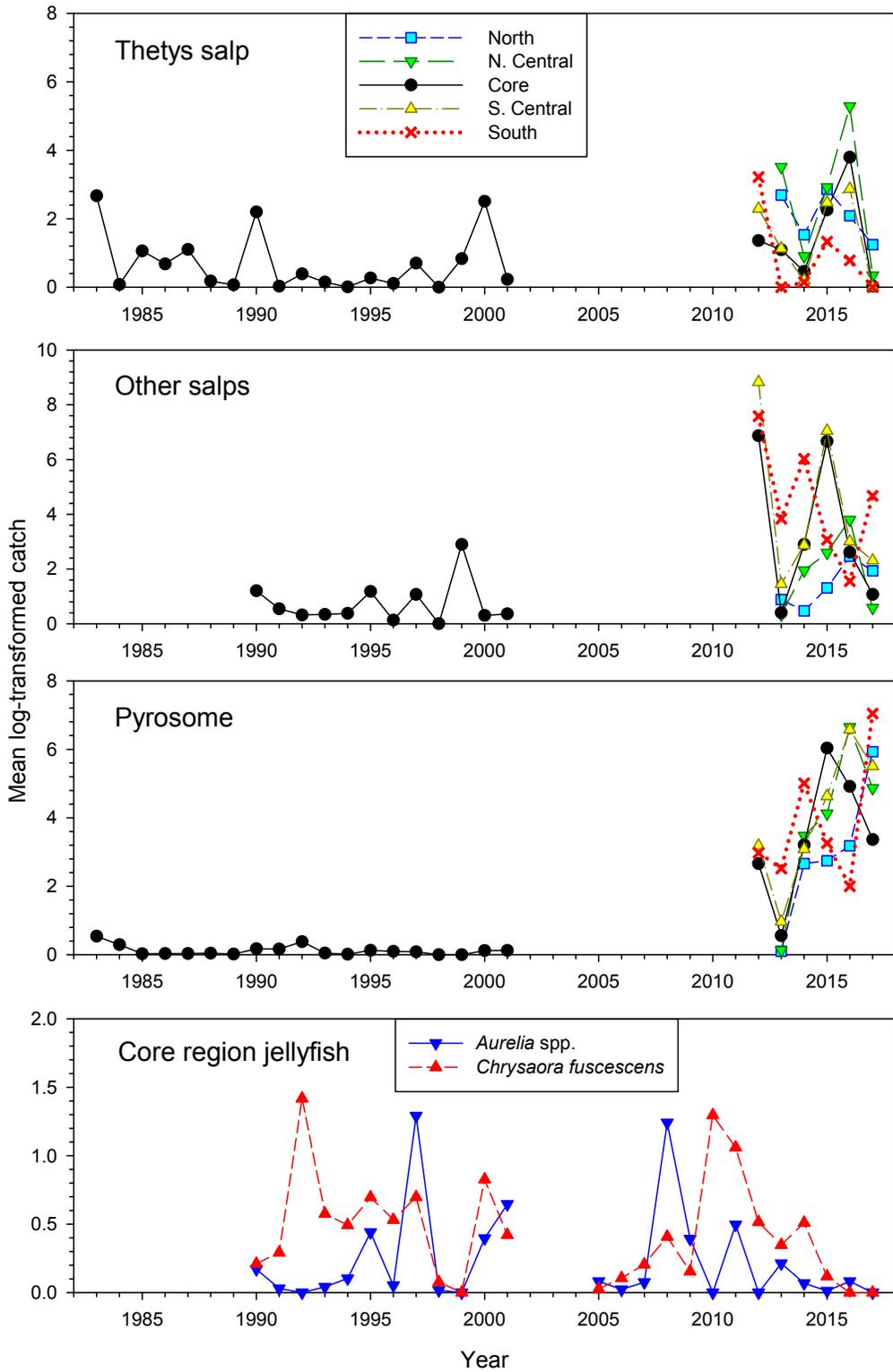


Figure 28. Standardized catches of jellyfish (*Aurelia* and *Chrysaora* spp.) and pelagic tunicates in the core and expanded survey areas.

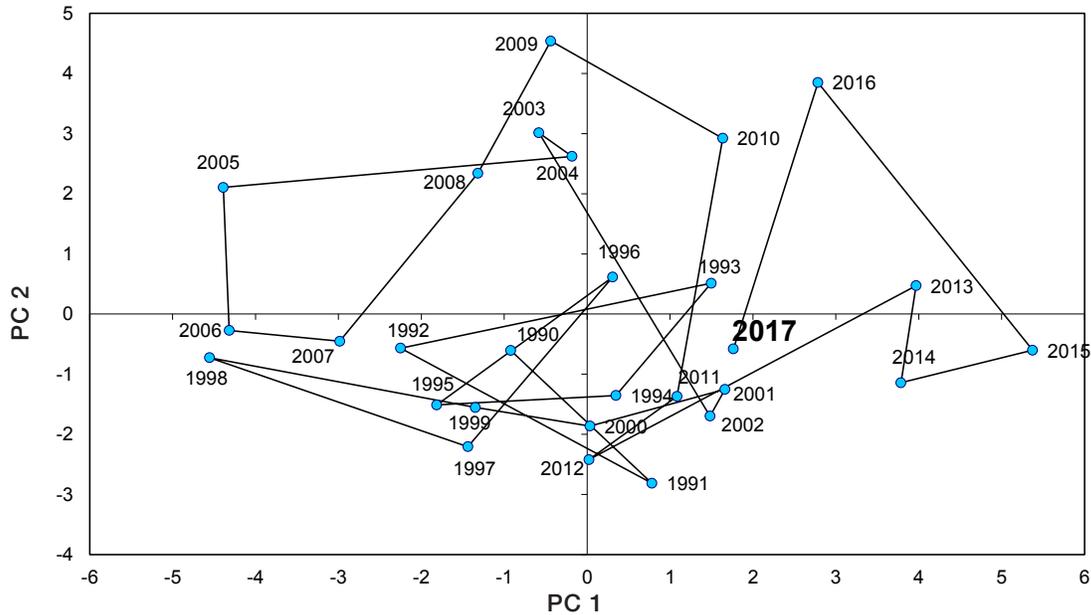


Figure 29. Principal component scores plotted in a phase graph for the nine key taxonomic groups of forage species sampled in the central California core area in the 1990-2017 period.

Bell M. Shimada sampled the usual 113-station winter and spring pattern (San Diego to San Francisco) (fig. 30).

Anchovy eggs in spring 2017 were notably more abundant than in 2016 (fig. 31). Anchovy eggs were also an order of magnitude more abundant in spring 2016 compared to 2015, but the increase was spatially restricted to small areas off Ventura, California and Newport, Oregon. By contrast, in spring 2017 anchovy eggs were widespread in the Southern California Bight, indicating that eggs were both more widely distributed and present at higher density than in 2016. It is notable that the highest egg count was very localized (again, off Ventura, California) and was associated with an extreme trawl catch of more than 600 kg of almost pure anchovy. This single catch was an order of magnitude larger than all of the other forage fish trawl catches on the entire cruise, and presumably represented a large school of northern anchovy.

In 2017, few anchovy eggs, and no adults, were collected north of Point Conception (fig. 30) although other continuous underway fish egg sampler surveys demonstrate concentrations of northern anchovy eggs off the Columbia River (fig. 21). Peak northern anchovy spawning off California generally occurs during March, so spawning patterns detected by the spring cruise may not be representative of the full northern anchovy spawning season.

Sardine and jack mackerel eggs were found at very low concentrations in the spring of 2017, consistent with the long-term trend. Sardine eggs were most abundant off the central California coast, south of Monterey, California (fig. 30). In 2016 the spawning distribution of

sardine eggs was centered farther north (43°–44.5°N, off Oregon) than in spring 2015 (41°–43°N, California-Oregon border), but we are unsure if there was significant sardine spawning off Oregon in 2017 (fig. 31).

Whereas the ichthyoplankton assemblage (larval; an earlier stage than represented in fig. 27) in 2014–16 (based on spring samples from lines 80 and 90) was characterized by high abundances of southern, off-shore mesopelagic fishes such as *Ceratospelus townsendi*, *Gonostomatidae* (mostly in the genus *Cyclothone*), *Triphoturus mexicanus*, and *Vinciguerria* spp. (mostly *V. lucetia*; these taxa are colored red on fig. 32), the 2017 assemblage was more “normal” (fig. 32). In multivariate space based on NMDS, NMDS 1 largely separated years when southern species (red font, fig. 32) were predominant (high NMDS 1) from years with primarily northern species (low NMDS 1; blue font on fig. 32), and NMDS 2 distinguished years with high Pacific sardine (high NMDS 2) and high northern anchovy (low NMDS 2). The 2017 assemblage fell in the middle of both NMDS axes 1 and 2, indicating that the assemblage was characterized by species with cosmopolitan distributions (colored green in fig. 32) and unexceptional abundances of both Pacific sardine and northern anchovy across the sampled region.

Evaluation of common mesopelagic taxa indicated that warm-water taxa generally declined between 2016 and 2017 while abundances of cool-water taxa were similar between these years. The southern warm-water taxa *Vinciguerria* spp. and *C. townsendi* fell to relatively low abundances in the spring of 2017 (fig. 33). The southern myctophid *T. mexicanus* declined dramatically from 2016

**FSV Bell M. Shimada and FSV Reuben Lasker
 21 March to 21 April 2017**

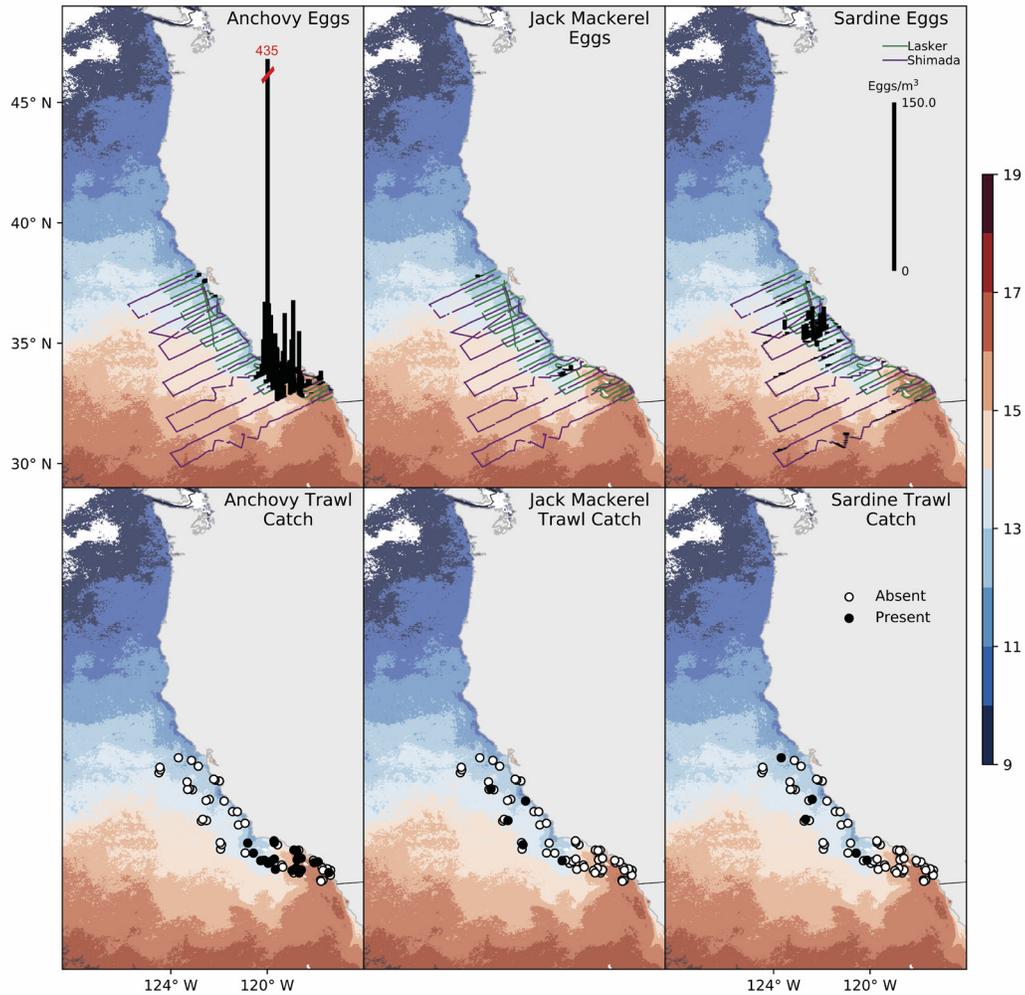


Figure 30. Density of eggs of northern anchovy, jack mackerel, and sardine collected with the continuous underway fish egg sampler (CUFES) during the spring 2017 CalCOFI and coastal pelagic fish cruises overlaid on satellite sea surface temperatures (°C). Lower panels represent trawls in which anchovy, jack mackerel, and sardine where absent or present.

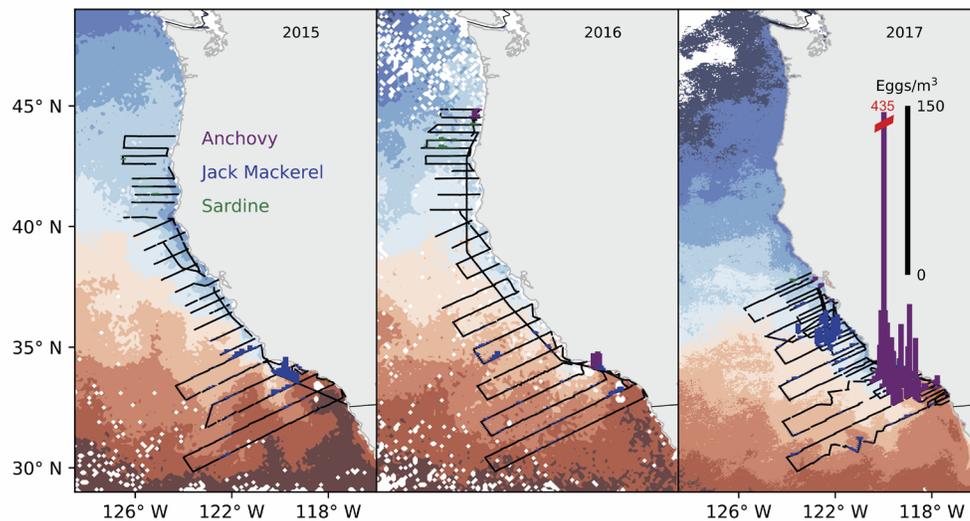


Figure 31. Density of eggs of northern anchovy, jack mackerel, and sardine collected with the continuous underway fish egg sampler (CUFES) during the spring 2015–17 CalCOFI and coastal pelagic fish cruises overlaid on satellite sea surface temperatures (°C; scale bar is shown in Figure 30).

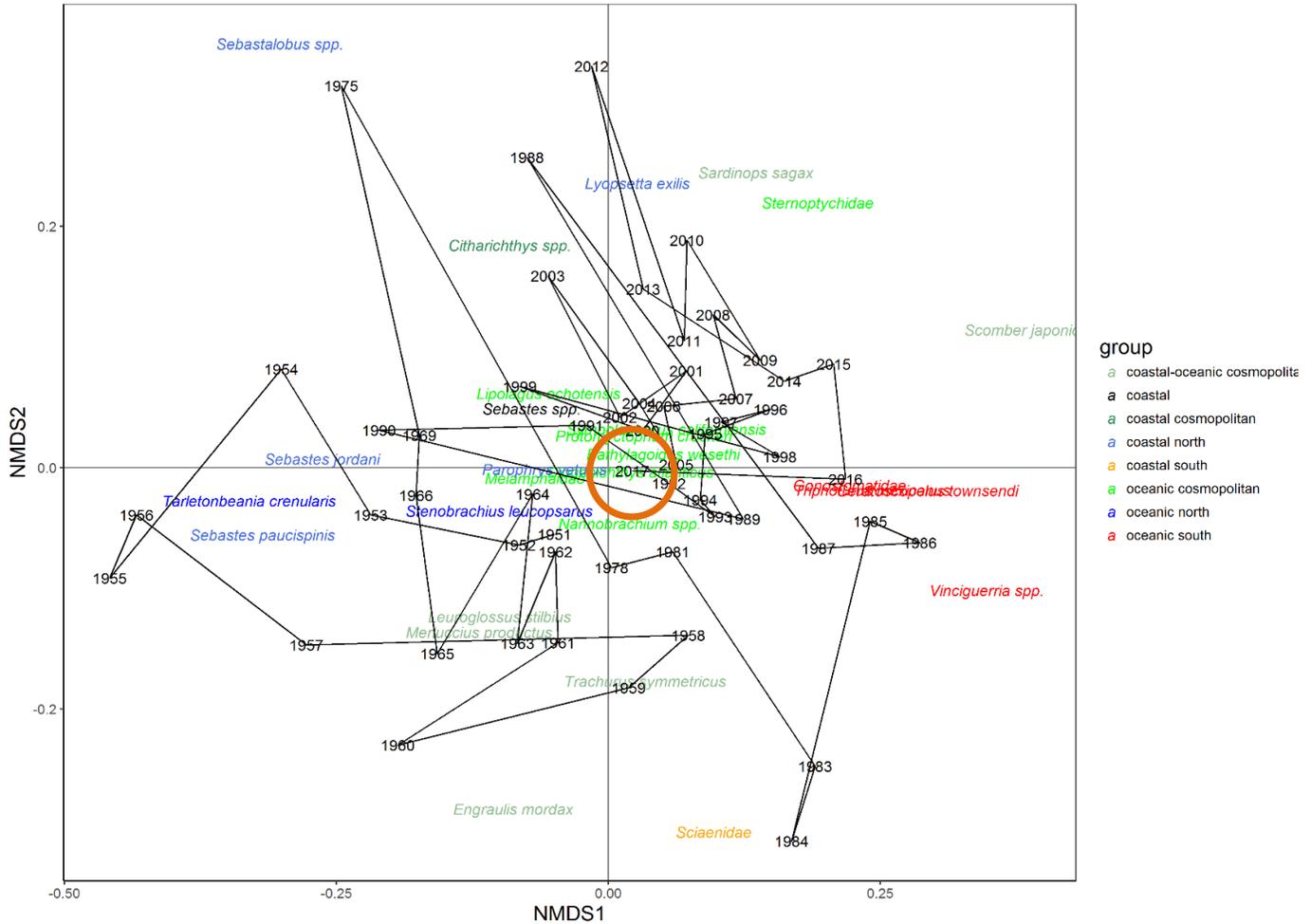


Figure 32. NMDS analysis depicting the composition of forage assemblage from lines 80 and 90 during the spring among years. The color of the species names characterizes their habitat affiliation and biogeographic range. Species in red or orange font are southern California Current, blue font are northern California Current, and green font are cosmopolitan. Open orange circle denotes the location of 2017.

but was still high relative to most years, while Gonostomatidae declined in 2017 to approximately average abundances (fig. 33). The northern cool-water myctophid *Stenobranchius leucopsarus* increased a bit relative to 2015–16 to near average levels (fig. 33), while another northern myctophid, *Tarletonbeania crenularis*, remained low (fig. 33).

For coastal pelagic species that are fished to varying degrees, northern anchovy abundance in spring was very similar to 2016 (fig. 34). Northern anchovy abundance from spring samples has been low since the early 1990s (with the exception of 2005), and 2017 had the third highest abundance of this species since 1994 (fig. 34). Abundance of northern anchovy in 2017, however, was still low relative to peaks between the 1950s and 1994. Pacific sardine, jack mackerel, and Pacific chub mackerel abundances were low in 2017 (fig. 34).

Shannon-Weaver diversity was almost exactly at a median level in spring of 2017 (fig. 35). This index tends to be low when coastal pelagic species are very

abundant (e.g., correlation $r = -.70$ between Shannon-Weaver and northern anchovy) and high when southern mesopelagics are relatively abundant (e.g., $r = .35$ between Shannon-Weaver and *T. mexicanus*). The median diversity reflects results of the multivariate analysis on individual taxa suggesting that 2017 was characterized by having unexceptional abundances of both the southern mesopelagic taxa and northern anchovy. Overall species richness based on an estimated asymptote from bootstrap species accumulation curves was at the upper 75th quantile in 2017 and increased by approximately 8 species in comparison with 2016. Species richness also correlates positively with abundances of southern offshore species (e.g., $r = .53$ between Gonostomatidae and richness). Although the southern offshore species were down from 2015–16, some taxa (e.g., *T. mexicanus*, Gonostomatidae) were still relatively abundant (fig. 34). In addition, while a few commonly found taxa such as *Citharichthys* spp., shortbelly rockfish, and *Sebastes*

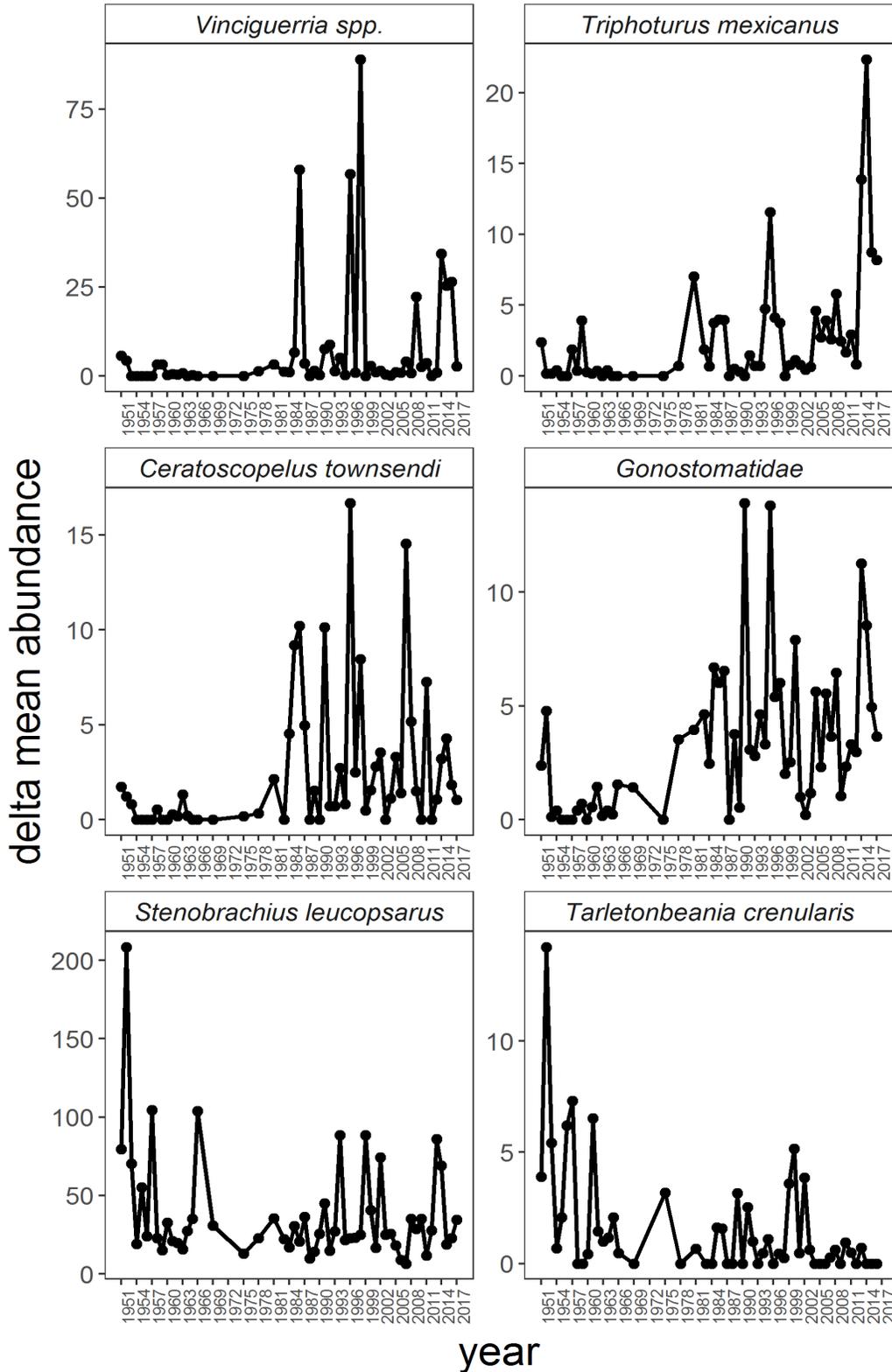


Figure 33. Delta-mean abundances of common mesopelagic taxa in spring between 1951 and 2017. Delta-mean calculations are used to estimate mean values from data with high numbers of samples that contain zero values (Pennington 1996). The four taxa in the top panels (*Vinciguerria* spp., *Triphoturus mexicanus*, *Ceratoscopelus townsendi*, and *Gonostomatidae*) have southern distributions relative to southern California and the two in the bottom panels (*Stenobrachius leucopsarus* and *Tarletonbeania crenularis*) are more broadly distributed to the north.

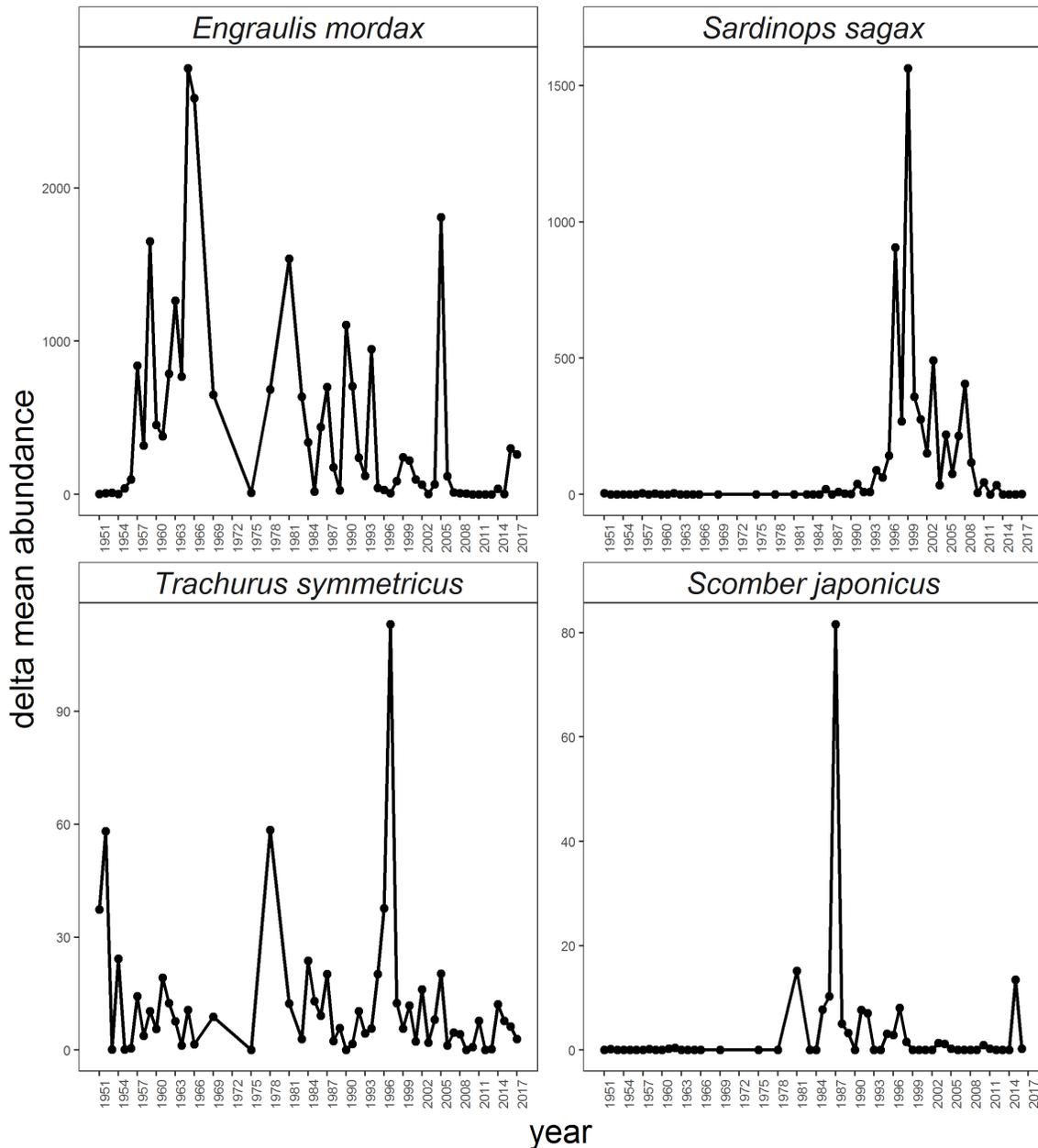


Figure 34. Delta-mean abundances of the most common coastal pelagic species that are to some extent commercially fished. Delta-mean calculations are used to estimate mean values from data with high numbers of samples that contain zero values.

paucispinis were completely absent in 2016, these taxa were again present in 2017.

REGIONAL PATTERNS IN BIRDS AND MARINE MAMMALS

Northern California Current: Yaquina Head, Oregon

Common murre (*Uria aalge*) at Yaquina Head experienced reproductive failure in 2016, as they had in 2015. Most (97%) murre eggs laid ($n = 183$) were not

incubated long enough to hatch chicks. This was the second consecutive year of almost complete reproductive failure, and the only times this occurred during the 15 years of data collection. Murres at Yaquina Head exhibited a 6-year run (2011–16) of low reproductive success that is approximately a quarter the success of the first 9 years of our study (1998–2002, 2007–10, fig. 36). Murre reproductive success during the 2014–16 are the lowest on record. As in previous years, the reproductive failure is a combination of top-down predation and bottom-up food limitation. While the top-

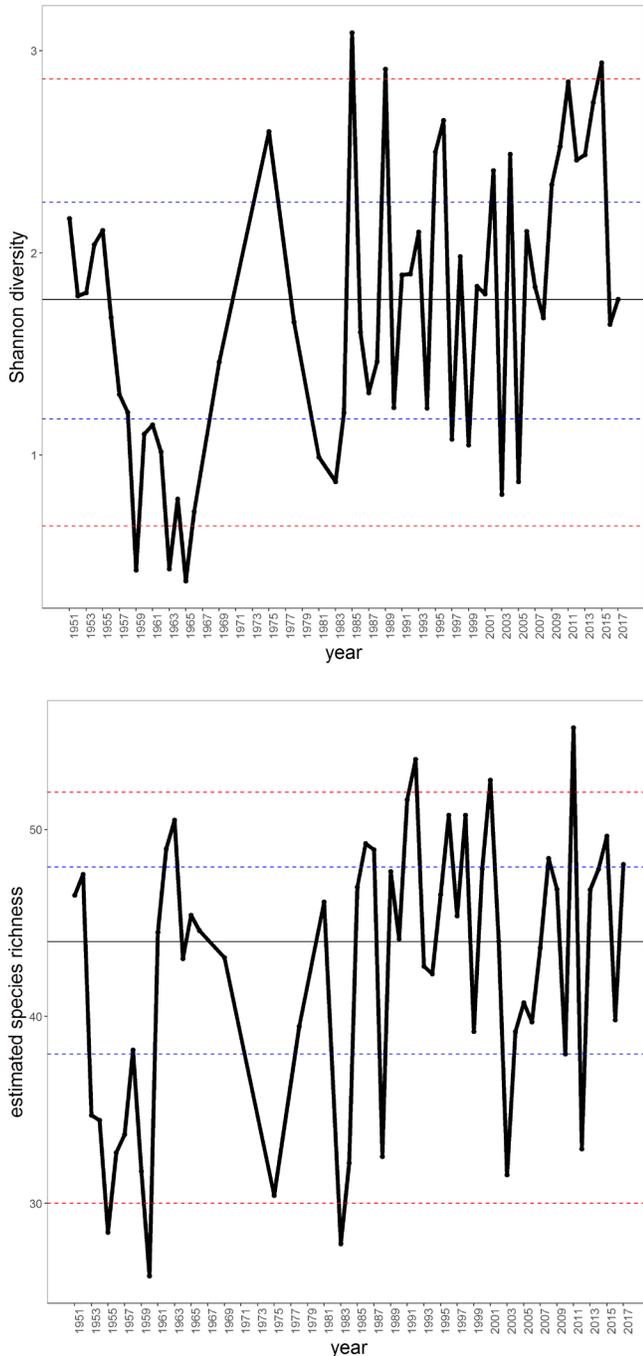


Figure 35. Shannon-Weaver diversity and estimated taxa richness of the larval assemblage. Dashed, horizontal blue lines depict 25th and 75th quantiles, dashed red lines 5th and 95th quantiles, and solid, horizontal black lines the median values.

down signal is most prominent, the bottom-up signal is evident. For example, the only location where a few murre chicks fledged in 2015 and 2016 was a small rock near sea level, not used for rearing chicks in previous years, and generally out of the way of predators. Even at this mostly predator-free site where a new study plot was added in 2016, the murre reproductive

success was only 0.21 fledglings/pair, which is among the lowest recorded for the whole colony in our time series and similar to reproductive success during the 1998 El Niño (Gladics et al. 2015).

Since 2011 much of the reproductive loss for murres has been due to egg and chick predators (Horton 2014), however, 2016 had the highest rate of murre egg and adult loss, with 4.21 eggs destroyed and 0.28 adult murre fatalities per hour of observation (n = 243 hours). As in 2015, the disturbance by primarily bald eagles (95%; *Haliaeetus leucocephalus*) in 2016 was so intense early in the breeding season that most eggs were not incubated long enough to hatch chicks. Persistent eagle disturbance early season is also in part responsible for the later chick hatching dates of murres.

Brandt's (*Phalacrocorax penicillatus*) and pelagic (*P. pelagicus*) cormorant were both successful at rearing young. Brandt's cormorants reproductive success (0.87 fledglings/nest) was lower than 2015 (1.70 fledglings/nest), but greater than 2014 (0.72 fledglings/nest) and overall slightly above the long-term mean (fig. 37). Median hatch date (June 27th) was among the earliest recorded in our time series (fig. 37). Average brood size (1.65 chicks) was close to the long-term average (fig. 37).

Pelagic cormorants had their second highest reproductive success (1.37 fledglings/nest), only surpassed by 2013 (2.13 fledglings/nest; fig. 36). There were 30 nests visible from observation platforms, also second only to 2013 (34 nests) and more than double 2015 (11 nests). Pelagic cormorant reproductive success has been highly variable during our time series. Median hatch date (July 13th) was close to the long-term average (fig. 37).

The three main forage fish species fed to murre chicks in the Yaquina Head region have been smelt (*Osmeridae*), Pacific herring or sardine (*Clupeidae*), and Pacific sand lance (*Ammodytes hexapterus*). The relative proportion of the three species can be similar or one species may be numerically dominant in a given year. The failure of most of the colony prior to chick rearing provided an added challenge for diet data collection in 2015 and 2016. We were able to collect diet data, however, very few of these samples were likely fed to chicks, but instead simply adults flying into the colony with fish. Diets in 2016 were again dominated by smelt (82%), continuing a trend of smelt-dominated diets for six of the past seven years (since 2010; fig. 38). Murre diets in 2016 had the highest proportion of smelt (82%) recorded in a single year, with sand lance a distant second (16%). Pacific sand lance continues to be minimal in diets since 2010. The dominance of smelt, and lack of herring and sand lance is even notably different than diets during the 1998 El Niño (fig. 38). Sand lance are generally more prom-

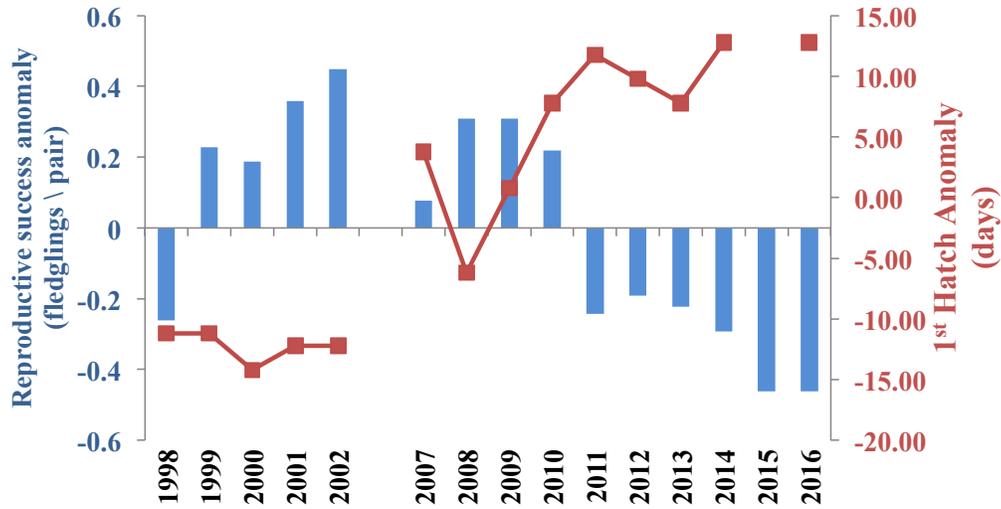


Figure 36. Anomalies of first chick hatch date and reproductive success for common murrelets nesting at Yaquina Head, Oregon, 1998–2016. 2016 was the second year that the colony failed to produce chicks from all but one small area where <10 chicks fledged each year.

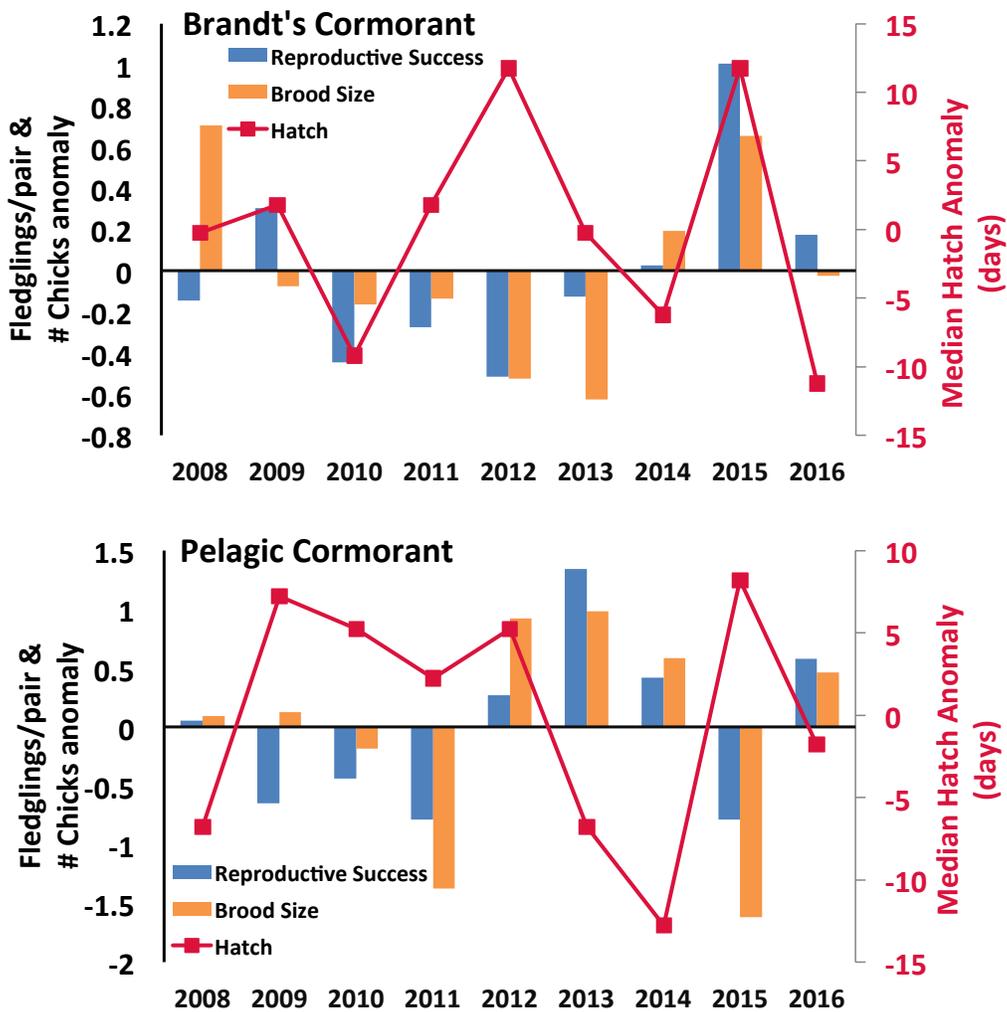


Figure 37. Anomalies of reproductive success and brood size for cormorants nesting at Yaquina Head, Oregon, 2008–16. Cormorants had average to above average reproductive success and brood size. Red lines indicate hatch date anomalies for cormorants.

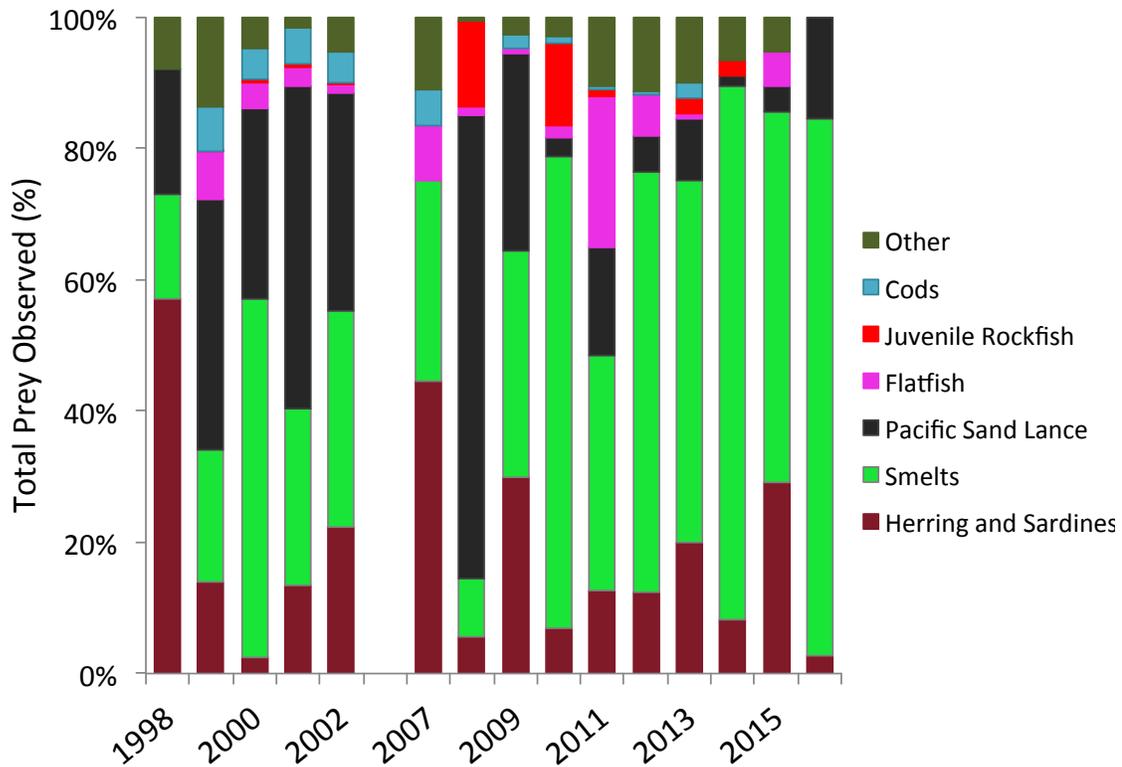


Figure 38. Prey fed to common murre chicks (% occurrence) at Yaquina Head Oregon, 1998–2016.

inent in murre diets during cold water years (Gladics et al. 2014, 2015), as highlighted by their prevalence in 2008 (fig. 38). Clupeids (primarily Pacific herring, *Clupea pallasii*), are generally associated with warmer water and positive PDO (Gladics et al. 2015), although their occurrence in recent warm water years has been lower than expected.

Northern California Current: Cape Flattery, Washington to Newport, Oregon

Notably, mean bird densities at sea for the 2017 strip transect surveys between Cape Flattery and Newport were the lowest observed during the 13-year data set and may indicate continued poor reproductive performance of resident breeders in 2017 (i.e., common murre)¹⁸. There was an apparent downward trend in common murre abundance at sea since 2015, with the third lowest mean density value on the record (9.27 birds per km²) occurring in 2017 (fig. 39). This species was also aggregated near the Columbia River mouth, with 70.5% of all individuals observed on the three transects closest to the Columbia River (Willapa Bay, WA and Columbia River/Cape Mears, OR). Common murre are usually

the most numerous breeding species found in the California Current during the upwelling season. Murre may have been affected by low forage fish availability beyond the Columbia River plume. The region near the Columbia River mouth where common murre were observed was also the area where northern anchovy were collected in surveys, including the same survey as the bird observations, and where above-average egg densities were observed with continuous underway fish egg sampler (fig. 21).

Sooty shearwater (*Ardenna grisea*) abundance in 2017, although very similar to that in 2011, was the lowest value yet observed in all 2003–17 June surveys (8.96 birds per km²) (fig. 39). Sooty shearwaters were highly aggregated in their distribution, with almost all (85.8%) individuals observed during the survey found on two transect lines immediately north of the Columbia River mouth (Grays Harbor and Willapa Bay, WA) where adult northern anchovy were observed during the same period. Given that sooty shearwaters are the most numerous non-breeding piscivorous species found in the California Current during upwelling season (May–September), their absence may reflect a lack of available prey in the offshore oceanic and Oregon waters found on the shelf in 2017, an hypothesis supported by the unusual micronekton assemblage observed in the same survey (fig. 23).

¹⁸ Seabird observations from an annual June survey encompassing 8 cross-shelf transects (extending ~30–50 km offshore) between Cape Flattery, WA and Newport, OR provide information on density patterns for the northern domain of the California Current.

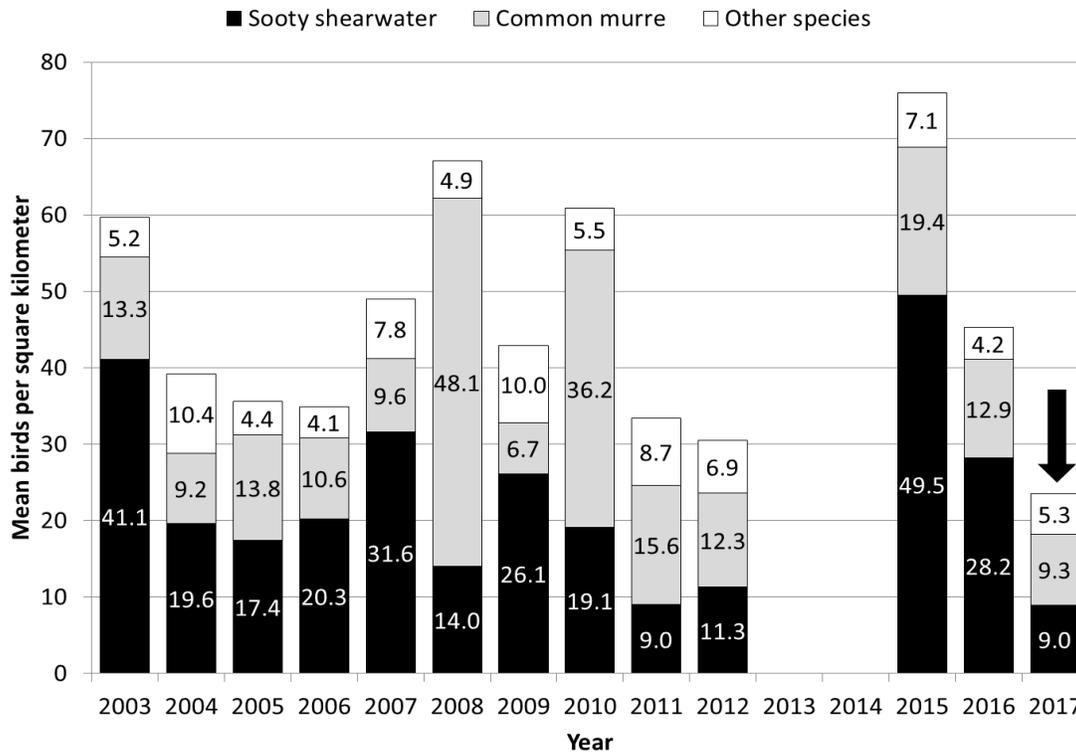


Figure 39. Seabird observations from an annual June survey encompassing 8 cross-shelf transects (extending ~30–50 km offshore) between Cape Flattery, WA and Newport, OR provide information on density patterns for the northern domain of the California Current.

Northern California Current: Castle Rock National Wildlife Refuge¹⁹

Common Murre are the most abundant surface-nesting seabird at Castle Rock and their reproductive success, nesting phenology, and chick diet have been studied since 2007. The percent of nesting pairs that successfully fledged young in 2016 was based on 93 breeding pairs monitored every other day for the duration of nesting. During 2016, murre only produced 0.16 fledglings per pair, which was 78% lower than the long-term average for this colony and the poorest year observed during the 10-year time-series (fig. 40). Although many murre hatched eggs (63%), chick starvation was frequent and 74% of chicks died prior to fledging. While the bottom-up food limitation was the primary cause of mortality, this food limitation caused murre to frequently leave chicks alone at the colony in search of prey, and these unprotected chicks were sometimes predated opportunistically by western gulls (*Larus occidentalis*) also

¹⁹ In recent times, Castle Rock National Wildlife Refuge (hereafter Castle Rock) has frequently been the most populous single-island seabird breeding colony in California (Carter et al. 2001). This island is located off the coast of Crescent City, just south of Point St. George, in the northern California Current System. To facilitate long-term monitoring of seabirds nesting at this colony, a remotely-controlled video monitoring system was installed at this island in 2006. For purposes of assessing the state of the California Current, the reproductive performance of common murre and Brandt's cormorants is provided. For common murre, nesting phenology and chick diet between 2007 and 2016 is also provided.

nesting at the island. Reproductive failure of common murre at Castle Rock is consequential for the overall population of murre nesting in the California Current as this island is one of the most populous colonies south of Alaska (Carter et al. 2001).

In 2016, the average nest initiation date was 19 May, which was 10 days later than the long-term average at this colony (fig. 40) likely due to the later onset of upwelling-favorable winds (fig. 4) and weaker NPH and preconditioning (Schroeder et al. 2009, fig. 6). Although the timing of nesting by murre is not a direct response to the onset of upwelling, the increased availability of food associated with upwelling improves the body condition of egg-laying females and thereby influences the timing of nesting (Reed et al. 2006; Schroeder et al. 2009).

In 2016, the diversity of prey fed to chicks was lower than usual, (11 of 21 prey types observed), and no new prey types were observed²⁰. Proportion of northern anchovy was 23x greater than the long-term average in 2016. Despite this increased prevalence of anchovy, smelt remained the predominant prey fed to chicks (fig. 40). Notably, the total number of prey observed at the colony was much less than usual because most chicks starved

²⁰ To determine prey composition fed to common murre chicks, 2-hour diet surveys were conducted 6 days per week during the murre chick-rearing period (approximately 23 hours surveyed in 2016).

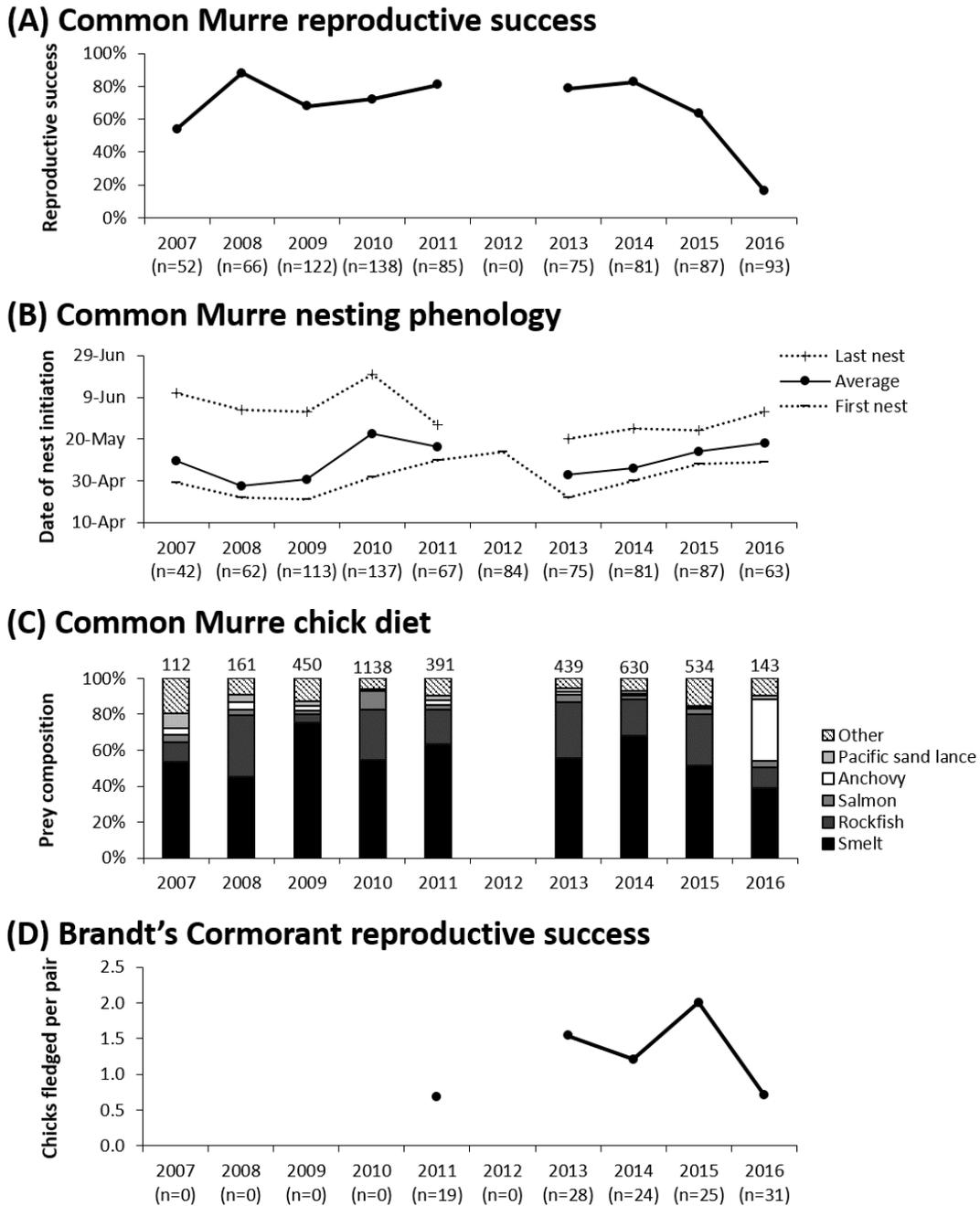


Figure 40. Reproductive data for seabirds nesting at Castle Rock National Wildlife Refuge (hereafter Castle Rock), Del Norte County, CA between 2007 and 2016; (A) Percent of common murre nesting pairs that successfully fledged young. The sample size (n) represents the total number of nesting pairs observed per year, and this figure does not include the success of replacement clutches. (B) First, average, and last dates for nests initiated by common murre. The date of nest initiation was defined as the day that an egg was laid at a nest-site. The sample size (n) represents the total number of nests observed each year where nest initiation dates were accurate to ± 3.5 days. (C) Composition of prey delivered to chicks by common murre. Numbers above each bar indicate the total number of prey identified each year. (D) Chicks fledged per nesting pair of Brandt's cormorant. The sample size (n) represents the total number of nesting pairs observed per year, and this figure does not include the success of replacement clutches. For each section, data from 2012 is lacking due to premature failure of the video monitoring system.

before they reached fledging age. Interestingly, murre diet data from Castle Rock and Yaquina Head continued to show northerly shifts in the forage fish community during 2016. Specifically, murre at Castle Rock had a dramatic increase in northern anchovy (more typical of central California colonies to the south) and Yaquina

Head remain dominated by smelt (more typical of Castle Rock to the south).

Brandt's cormorant are the second-most abundant surface-nesting seabird at Castle Rock and their reproductive success has been studied since 2011. Based on 31 nests observed every three days throughout the 2016

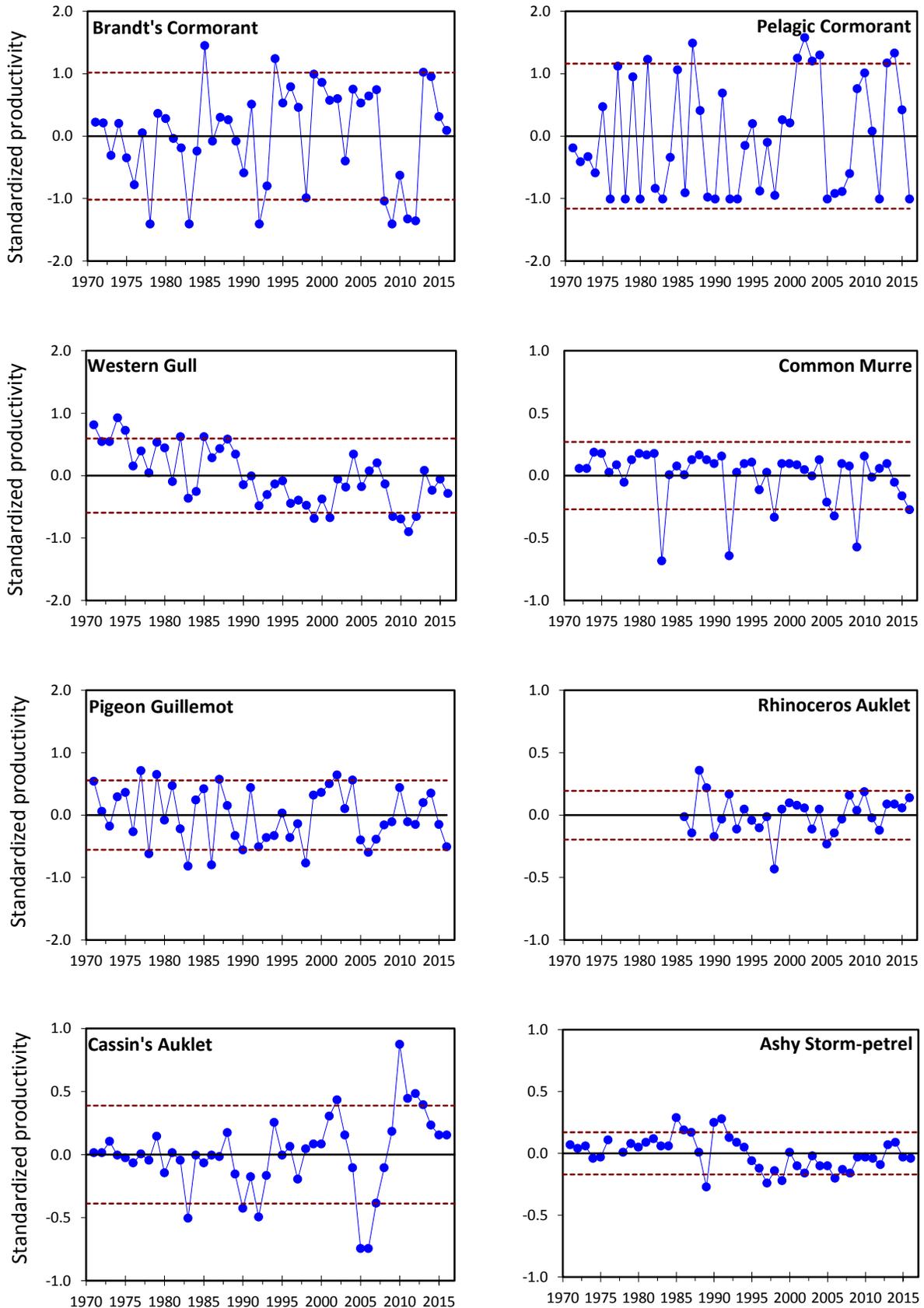


Figure 41. Standardized productivity anomalies (annual productivity minus 1971–2017 mean productivity) for 8 species of seabirds on Southeast Farallon Island.

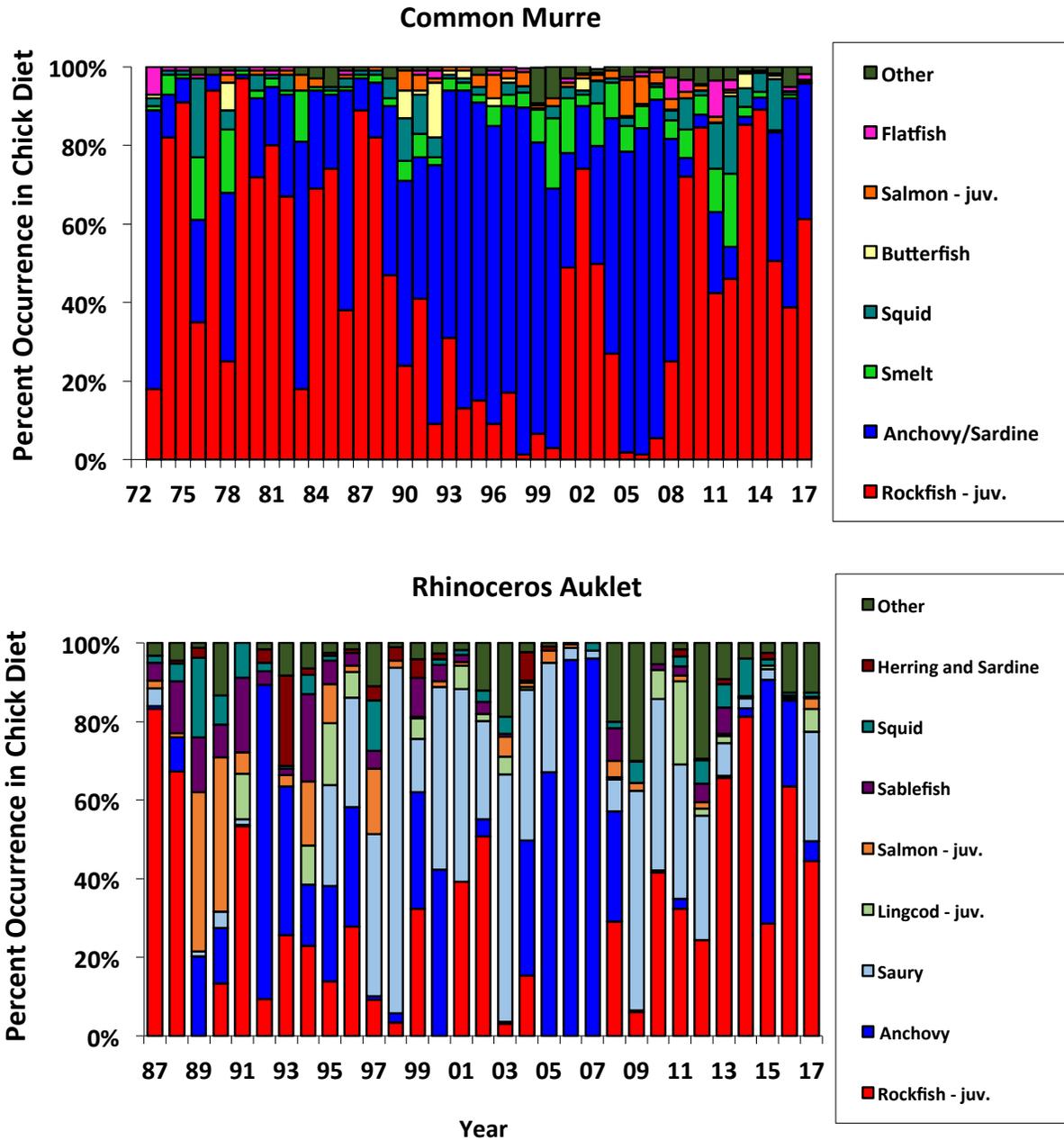


Figure 42. Diets of common murre and rhinoceros auklets returning to feed chicks 1987–2017. Note bar color differences between panels.

season, breeding pairs produced 0.71 chicks on average which was 1.9x lower than the long-term average at this colony and the second lowest observation since monitoring began (fig. 40). This reduction in success between 2015 and 2016 mirrored observations at Yaquina Head.

Central California: Southeast Farallon Island

Warm water conditions, such as those observed during the recent El Niño, typically lead to very low breeding success and even breeding failure for seabirds (fig. 41). This generally proved to be true in 2016 with reduced breeding populations and reproductive suc-

cess for most species. However, the availability of common forage taxa such as rockfishes and krill muted the response relative to previous El Niño events such as 1998 during which these forage taxa were well below average (fig. 27). Overall breeding success of seabirds during the 2016 breeding season at Southeast Farallon Island can best be classified as a below average year for most species. Reproductive success was lower for most species when compared to 2015, including complete breeding failure for pelagic cormorants and the lowest success for pigeon guillemots (*Cephus columba*) in 10 years. Common murres, Brandt’s cormorant, and west-

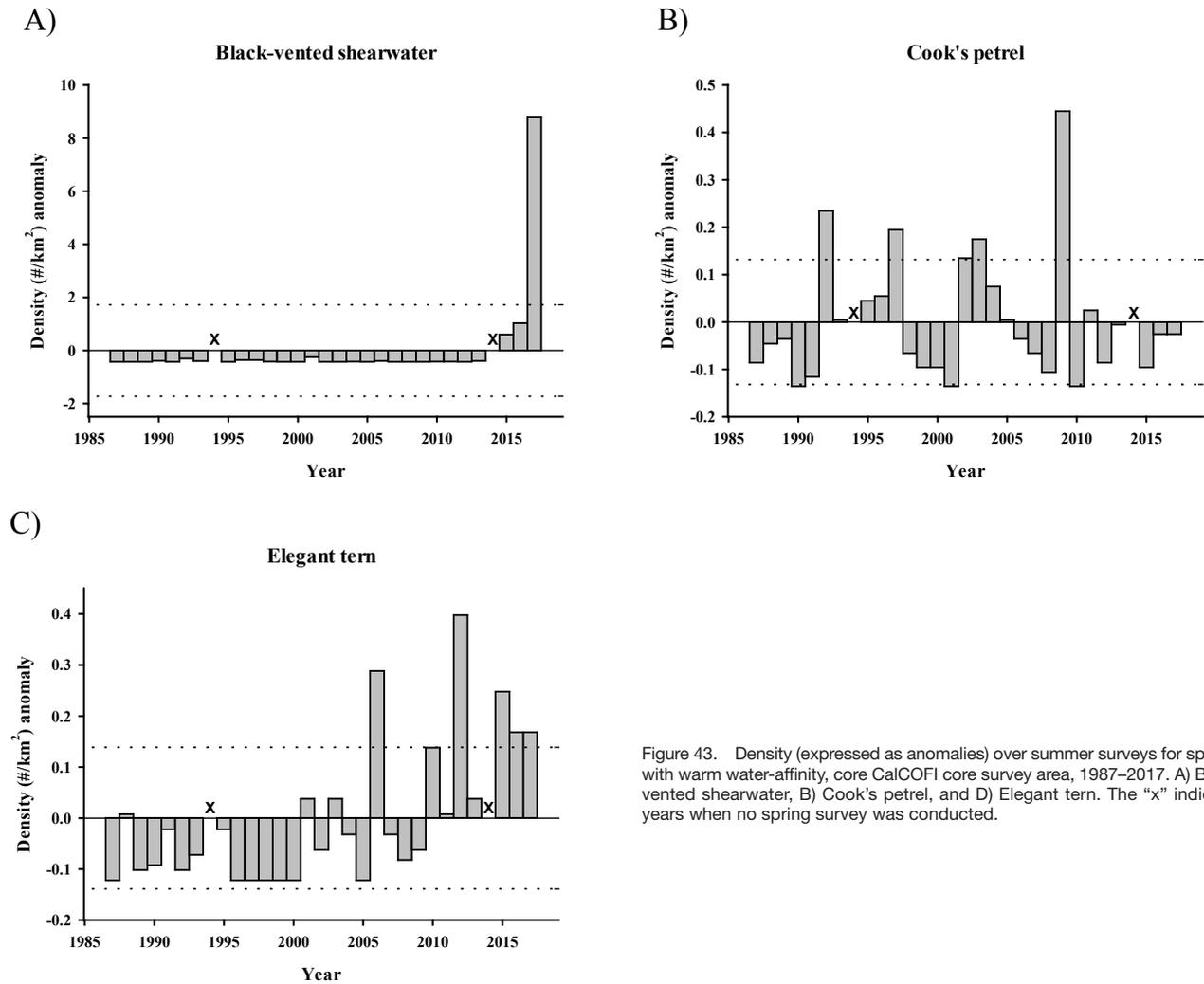


Figure 43. Density (expressed as anomalies) over summer surveys for species with warm water-affinity, core CalCOFI core survey area, 1987–2017. A) Black-vented shearwater, B) Cook's petrel, and D) Elegant tern. The "x" indicates years when no spring survey was conducted.

ern gull likewise suffered lower than average breeding success. Cassin's auklets (*Ptychoramphus aleuticus*) and rhinoceros auklets (*Cerorhinca monocerata*) were the only species to have higher than average breeding success. Cassin's auklets attempted few second broods but did manage to successfully fledge chicks from two of them, typically a sign of productive ocean conditions. Though the second broods did not significantly contribute to overall productivity this season, a high success rate for first broods resulted in an overall productive season.

Effects on breeding populations were mixed. Brandt's cormorants, Cassin's auklets, pigeon guillemots and western gulls all decreased whereas pelagic cormorants, double-crested cormorants (*Phalacrocorax auritus*) and tufted puffins (*Fratercula cirrhata*) increased. The western gull breeding population estimate was the lowest observed during our 46 years of monitoring while pigeon guillemots, Brandt's cormorants and Cassin's auklets were the lowest they have been in the last five years.

Following the strong upwelling periods in late March and April 2016 (fig. 4), zooplankton abundance (primarily krill) was average (fig. 27). Although diet analysis has not been completed, preliminary visual inspection of Cassin's diet samples indicated that krill remained the dominant item in auklet prey. This likely allowed for the higher than expected breeding in 2016 for Cassin's auklets. Similarly, the diets of common murre and rhinoceros auklet can be indicative of the current-year preyscape and resultant foraging behavior (Wells et al. 2017) and, ultimately, the reproductive success (Wells et al. 2008). Juvenile rockfish, a preferred prey, remained a significant portion of the diet fed to chicks in 2016 and 2017 (fig. 42) suggesting that significant reproductive failure is unlikely in 2017.

In general, although the 2015–16 El Niño may not have had as great an impact as previous events, the number of birds attempting to breed and their breeding success were both reduced during 2016. Chicks generally took longer to grow and fledged at lower weights

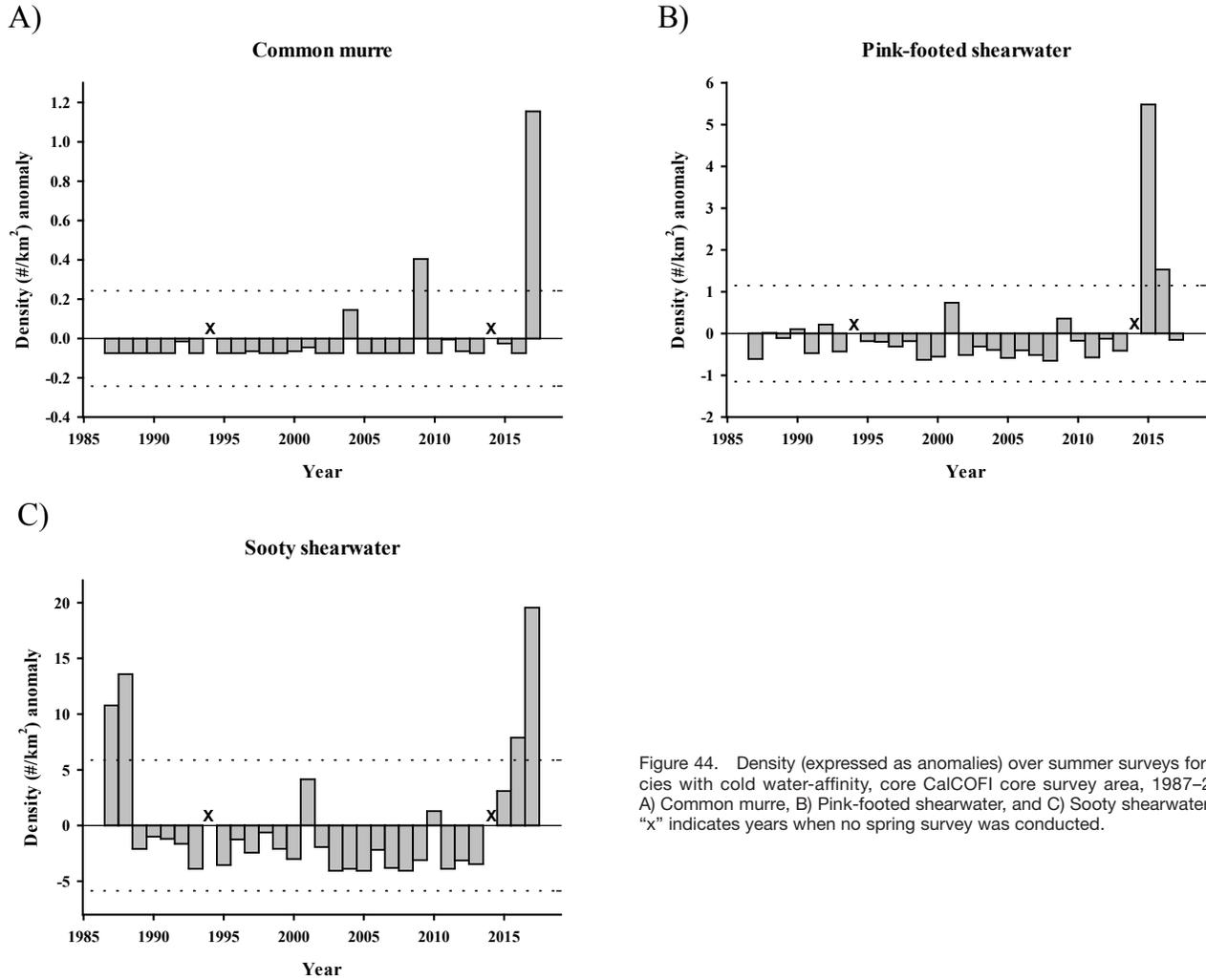


Figure 44. Density (expressed as anomalies) over summer surveys for species with cold water-affinity, core CalCOFI core survey area, 1987–2017. A) Common murre, B) Pink-footed shearwater, and C) Sooty shearwater. The “x” indicates years when no spring survey was conducted.

than in the past few seasons. Warm water continued to bring unusual species into the region. These included record numbers of brown boobies (*Sula leucogaster*), a few persistent blue-footed boobies (*Sula nebouxi*) and the first island record for least storm-petrel (*Oceanodroma microsoma*), all species that are normally found in more tropical regions.

Southern California Current: CalCOFI

Seabird distribution and abundance was surveyed during the 2017 summer CalCOFI cruise and seabird densities are presented here for the core survey area (defined here as the six CalCOFI lines, 77–93), 1987–2017. Anomalies of seabird species density in summer are indicative of species with affinities for warm and cold-water conditions (Hyrenbach and Veit 2003; Sydeman et al. 2009; Santora and Sydeman 2015). For summer, species with warm water-affinity include black-vented shearwater (*Puffinus opisthomelas*), Cook’s petrel (*Pterodroma cookii*), and elegant tern (*Sterna elegans*) (fig. 43²¹).

Cold water-affinity species include common murre, pink-footed shearwater (*Ardenna creatopus*), and sooty shearwater (fig. 44). Notable results from the 2017 summer survey indicate higher than average density of the warm-water species black-vented shearwater (highest density since 1992) and elegant tern. Interestingly, two of the three cool water-affinity species’ (sooty shearwater and common murre) densities are well above any observed summer values since 1987. This is in stark contrast to results from northern California Current surveys that observed record low densities and may reflect superior foraging conditions within the core survey region during the 2017 spring CalCOFI cruise.

Sea Lions: San Miguel Island

California sea lions (*Zalophus californianus*) are permanent residents of the CCS, breeding in the California Channel Islands and feeding throughout the CCS

²¹ https://static1.squarespace.com/static/56a6b01dd8af105db2511b83/t/5931b5aa59cc68dd30ae919b/1496429995317/FI_Report_CAC_2017_summer.pdf

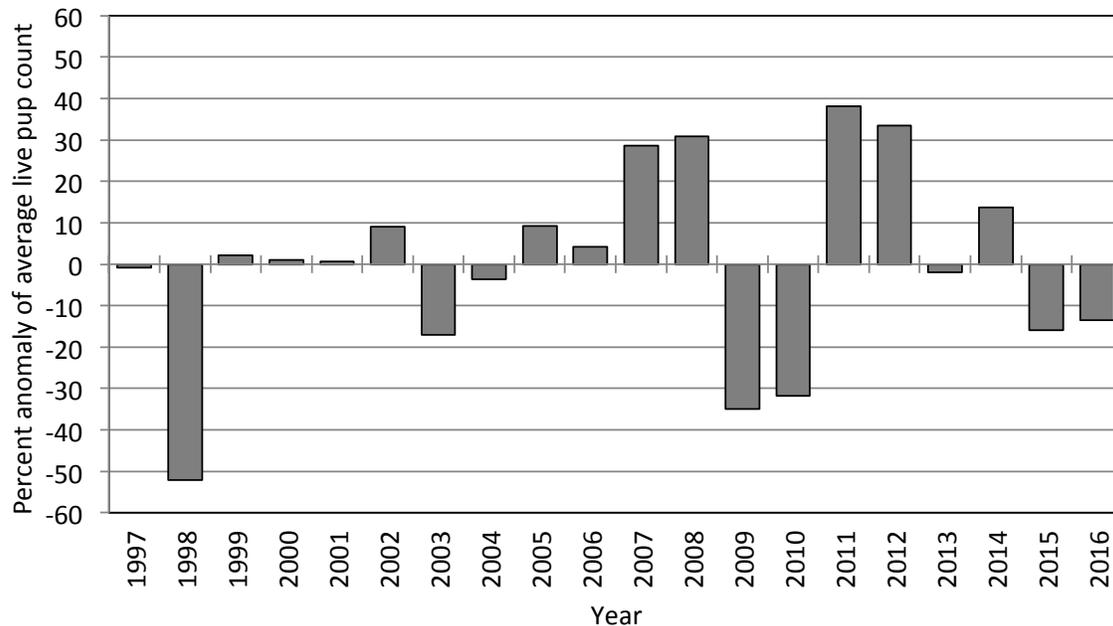


Figure 45. The percent anomaly of live California sea lion pup counts at San Miguel Island, California, based on a long-term average of live pup counts between 1997–2016 in late July when surviving pups were about 6 weeks old.

in coastal and offshore habitats²². They are also sensitive to changes in the CCS on different temporal and spatial scales and so provide a good indicator species for the status of the CCS at the upper trophic level (Melin et al. 2012). Two indices are particularly sensitive measures of prey availability to California sea lions: pup production and pup growth during the period of maternal nutritional dependence²³. Pup production is a result of successful pregnancies and is an indicator of prey availability to and nutritional status of nursing females from October to the following June. Pup growth from birth to 7 months of age is an index of the transfer of energy from the mother to the pup through lactation between June and the following February which is related to prey availability to nursing females during that time²⁴.

In 2016, California sea lion pup births at San Miguel Island were 14% below the long-term average between

1997 and 2016 but showed a slight improvement from 2015 (16% below) (fig. 45)²⁵. Pup condition and pup growth for the 2016 cohort increased from the record lows for the 2015 cohort. The average weights of three-month-old pups were 1.7 kg and 2.0 kg higher than the long-term average for female and male pups, respectively (fig. 46), representing a 10% increase in pup condition in 2016 compared to 2015. After two years of extremely low growth rates in 2014 and 2015, pup growth rates from three to seven months of age for female and male pups were similar to the 20-year average in 2016, marking a significant improvement in growth rates (fig. 47).

Since 2009, the California sea lion population has experienced low pup survival, low pup births, or both (Melin et al. 2012; McClatchie et al. 2016; DeLong et al. 2017). In March 2013, an unusual mortality event was declared for California sea lions in southern California in response to unusually high numbers of young pups from the 2012, 2014, and 2015 cohorts stranding along the coast and at San Miguel Island and other rookeries (Wells et al. 2013; Leising et al. 2014; Leising et al. 2015; McClatchie et al. 2016)²⁶. The unusual mortality event was associated with poor foraging conditions for

²² San Miguel Island, California (34.03°N, 120.4°W) is one of the largest colonies of California sea lions, representing about 45% of the US breeding population. As such, it is a useful colony to measure trends and population responses to changes in the marine environment.

²³ We used the number of pups alive at the time of the live pup census conducted in late July and the average weights of pups at 4 months and 7 months of age between 1997 and 2016 as indices of the population response to annual conditions in the CCS. The number of live pups in late July represents the number of pups that survived from birth to about 6 weeks of age. Live pups were counted after all pups were born (between 20–30 July) each year. A mean of the number of live pups was calculated from the total number of live pups counted by each observer. A long-term average live pup count based on counts between 1997 and 2016 was used to create annual anomaly percentages from the long-term average.

²⁴ Each year, between 200 and 500 pups were weighed when about 4 months old. Pups were sexed, weighed, tagged, branded, and released. Up to 60 pups were captured in February and weighed and measured at 7 months of age. Of the 60 pups captured in February, up to 30 pups were branded and provided a longitudinal dataset for estimating a daily growth rate between 4 months and 7 months old.

²⁵ We used a linear mixed-effects model fit by REML in R to predict average weights on 1 October and 1 February in each year because the weighing dates were not the same among years. The model contained random effects with a sex and days interaction (days = the number of days between weighing and 1 October and 1 February) which allowed the growth rate to vary by sex and year, and a full interaction fixed effects of sex and days. The average weights between 1997 and 2016 were compared to the long-term average for the average pup weights between 1975 and 2016.

²⁶ <http://www.nmfs.noaa.gov/pr/health/mmume/californiasealions2013.htm>

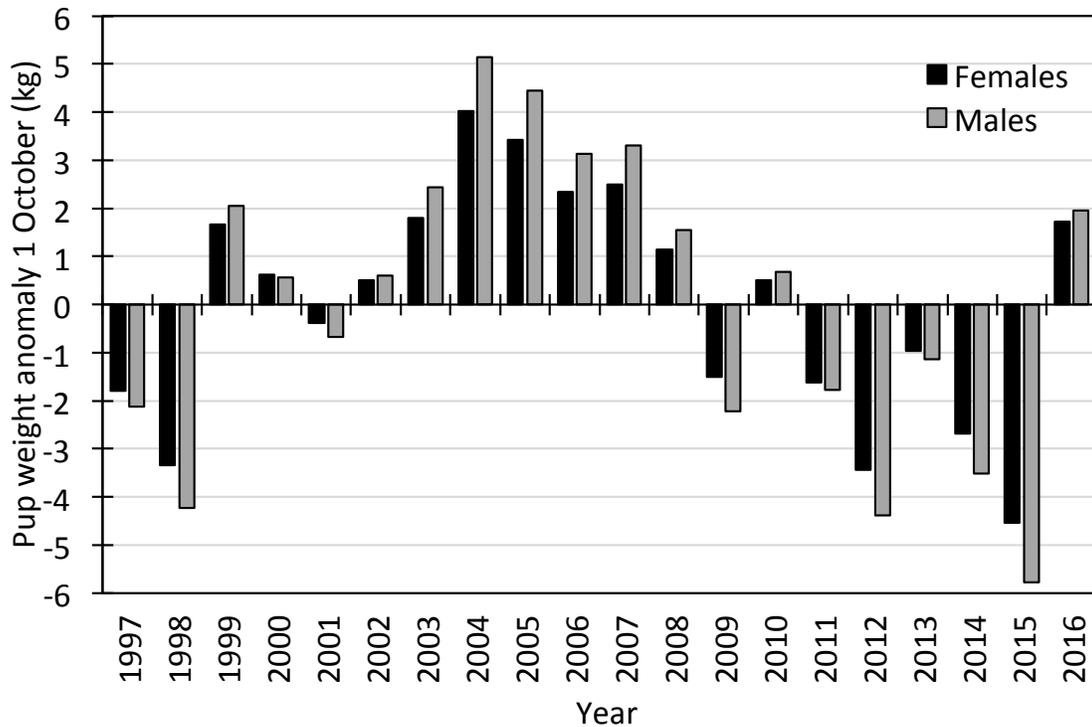


Figure 46. Average pup weight anomaly (kg) from predicted average weights of 3-month-old female and male California sea lion pups at San Miguel Island, California, from the long-term average between 1997 and 2016.

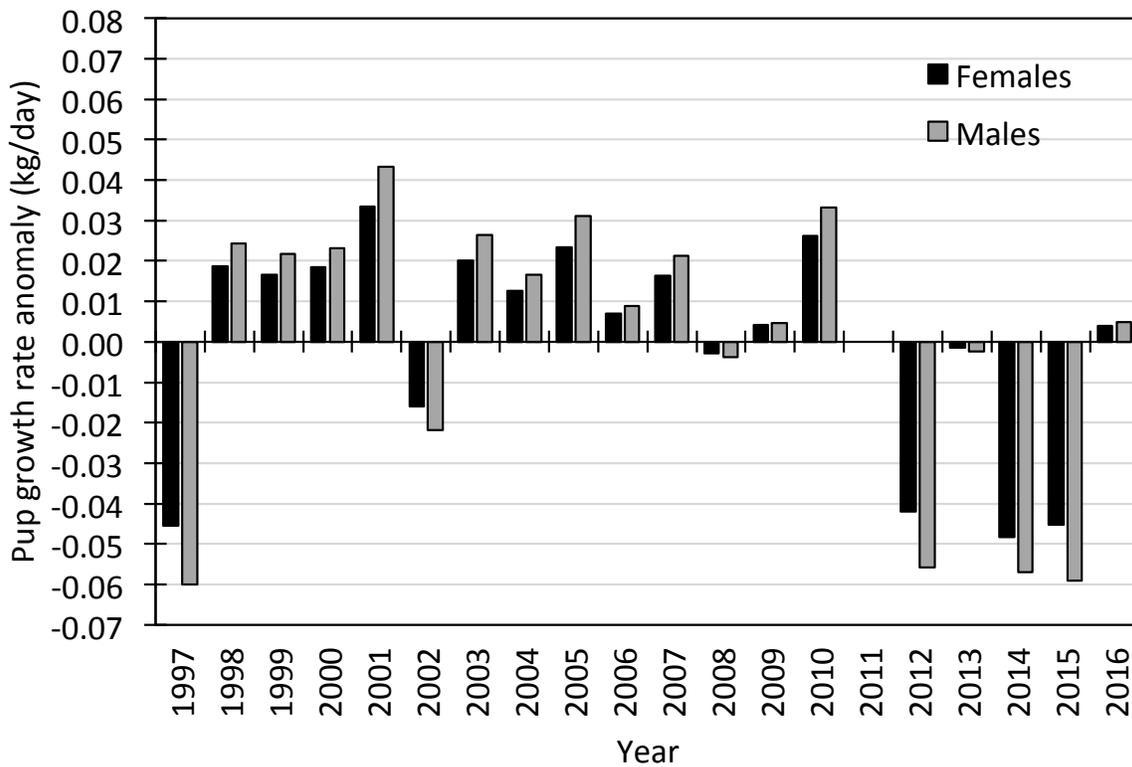


Figure 47. Average daily growth rate anomaly of female and male California sea lion pups between 3 and 7 months old at San Miguel Island, California, from the long-term average between 1997 and 2016.

nursing females due to shifts in the availability of prey and prey community composition in the central and southern CCS during the period of pup nutritional dependence. The low numbers of births in 2016 reflect the effects of low numbers of births and poor pup and juvenile survival since 2009 that have reduced the number of reproductive females in the population. However, the improved condition of pups in 2016 indicates that nursing females experienced better foraging conditions during the 2016–17 nursing period and were able to support the nutritional demands of their pups. The improved condition of pups in 2016 coincided with the return to a nursing female diet with high frequencies of northern anchovy (92%) and Pacific hake (63%) compared to a diet rich in juvenile rockfish and market squid that dominated the food habits during the unusual mortality event.

Marine Mammal Surveys: CalCOFI Surveys

On-effort visual detections of baleen whales for 2014–17 are shown in fig. 48²⁷. During winter and spring cruises, most baleen whale sightings occurred within 200 nm of the shoreline. A nearshore shift in distribution of humpback whales (*Megaptera novaeangliae*) was seen during the spring in the 2016 and 2017 cruises. During summer, there were more baleen whale sightings along the continental slope and in offshore waters. During fall cruises in 2015 and 2016 baleen whale sighting were concentrated in the Channel Islands region.

Odontocete detections for 2014–17 are shown in Figure 49. In general, short-beaked common dolphins (*Delphinus delphis*) were detected offshore more frequently than inshore. In 2015, short-beaked common dolphins were not observed in the offshore areas, but they were present in the offshore areas during the summer and fall of 2016.

DISCUSSION

In this paper, we have not attempted to develop a quantitative model integrating all these data series. However, when we examine them in total, bolstered by current literature, we can make assertions about the temporal and spatial evolution of the California Current ecosystem encompassing the majority of links between environmental influences, population productivity, reproductive and foraging dynamics of top-predators, and the overall trophic structure. We finish with a comment regarding unanticipated ecosystem inter-

actions resulting from recent anomalous ocean conditions and the realized and potential impact they have on coastal communities.

A weak La Niña in 2016, and stormy winter and sluggish upwelling in 2017

From spring 2016–spring 2017, the NPGO was at near-average values and the PDO remained positive, with values lower than the exceptionally high values of 2014–16. A weak tropical La Niña event was marked by modest negative ONI values from summer 2016–winter 2017. Together, these indices suggest that basin-scale patterns did not likely favor strong coast-wide productivity anomalies from spring 2016 to spring 2017. Above average upwelling north of 36°N persisted from the spring to the fall of 2016 (March–September). By January and February 2017, stronger-than-average downwelling winds occurred in northern California Current (fig. 4) related to a continued weak NPH (fig. 6). As upwelling began in March and April 2017 it was weaker than typical north of 36°N. Ultimately, chlorophyll during the March–May of 2017 was below average throughout much of the CCS with localized areas with positive chlorophyll anomalies in central California and the Channel Islands (fig. 9). The positive chlorophyll anomalies in central California may have been associated with strongly positive upwelling anomalies that began in May (fig. 4). As late-winter and spring conditions influence productivity of the forage base across the CCS (Logerwell et al. 2003; Schroeder et al. 2009, 2014) and structuring of the ecosystem (Wells et al. 2016, 2017), the observed weak upwelling conditions north of 36°N during March–April 2017 could negatively affect the availability of forage to predators through 2017.

Dissimilar conditions emerged in the south and the north

Regional surveys during the 2016 El Niño found that surface waters were anomalously warm across the CCS and were also anomalously warm at depth south of Cape Mendocino (figs. 4, 7, 8). Through 2016, northern CCS copepod communities had an anomalously high abundance of subtropical species (fig. 10). Chlorophyll concentrations were low across the California Current in 2016. At Trinidad Head there was a *Pseudo-nitzschia* bloom in spring that abated by June. In the central and southern CCS domoic acid concentrations were negligible during 2016 (fig. 9).

Early in 2017 physical and biological conditions were dissimilar between the northern, central, and southern CCS. Surface conditions north of Cape Mendocino remained anomalously warm (fig. 4), chlorophyll was very low (fig. 9), and copepod species richness patterns

²⁷ Marine mammal surveys were initiated as part of the CalCOFI cruises in 2004. Visual monitoring incorporates standard line-transect survey protocol which includes two experienced observers scanning for marine mammals during transits between CalCOFI stations. Information on all cetacean sightings was logged systematically, including species, group size, reticle of cetacean position relative to the horizon, relative angle from the bow, latitude, longitude, ship's heading, behavior, environmental data and comments.

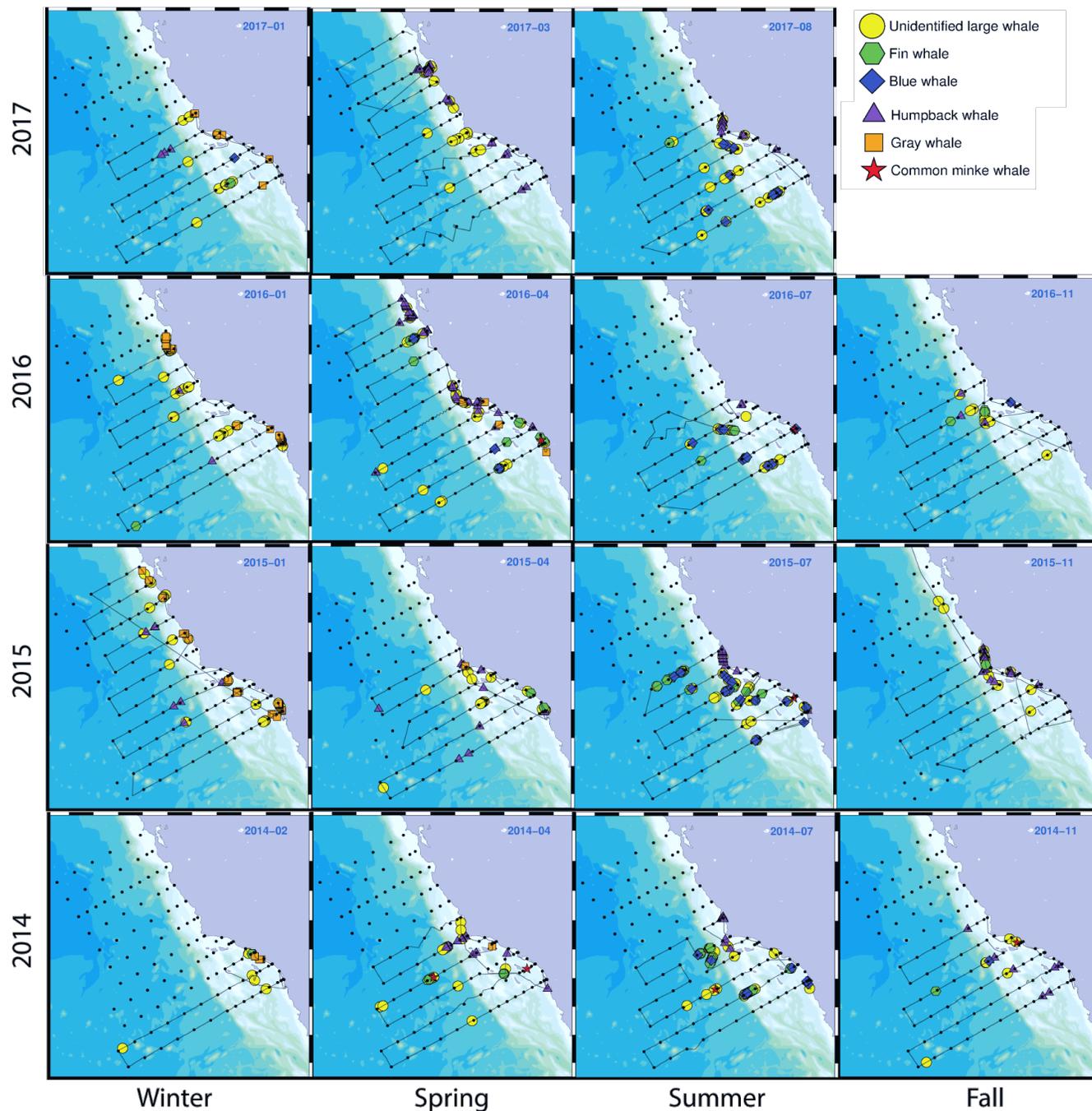


Figure 48. On-effort baleen whale sightings during CalCOFI cruises 2014–17. CalCOFI stations are represented by black dots and the ship’s trackline is represented as a solid black line between stations. Symbol shapes and colors denote different species, as per legend.

were representative of southern assemblages in 2017 (table 1, fig. 10). Further, in January–April 2017 downwelling anomalies were evident along the West Coast from Monterey Bay to Vancouver Island, which were associated with increased storm events especially in California (figs. 3, 4). Southern and central regional surveys indicated that environmental conditions were typical for the longer time series, which suggests that central

and southern regions may be returning to “normal.” However, atypically, the increased chlorophyll in spring 2017 around the Channel Islands during April–May corresponded with a significant toxic event linked to increased estimates of *Pseudo-nitzschia* abundance (fig. 9). The event was responsible for an unusual mortality event for a number of seabirds and exceeded the regulatory limit for human consumption of fish and shellfish.

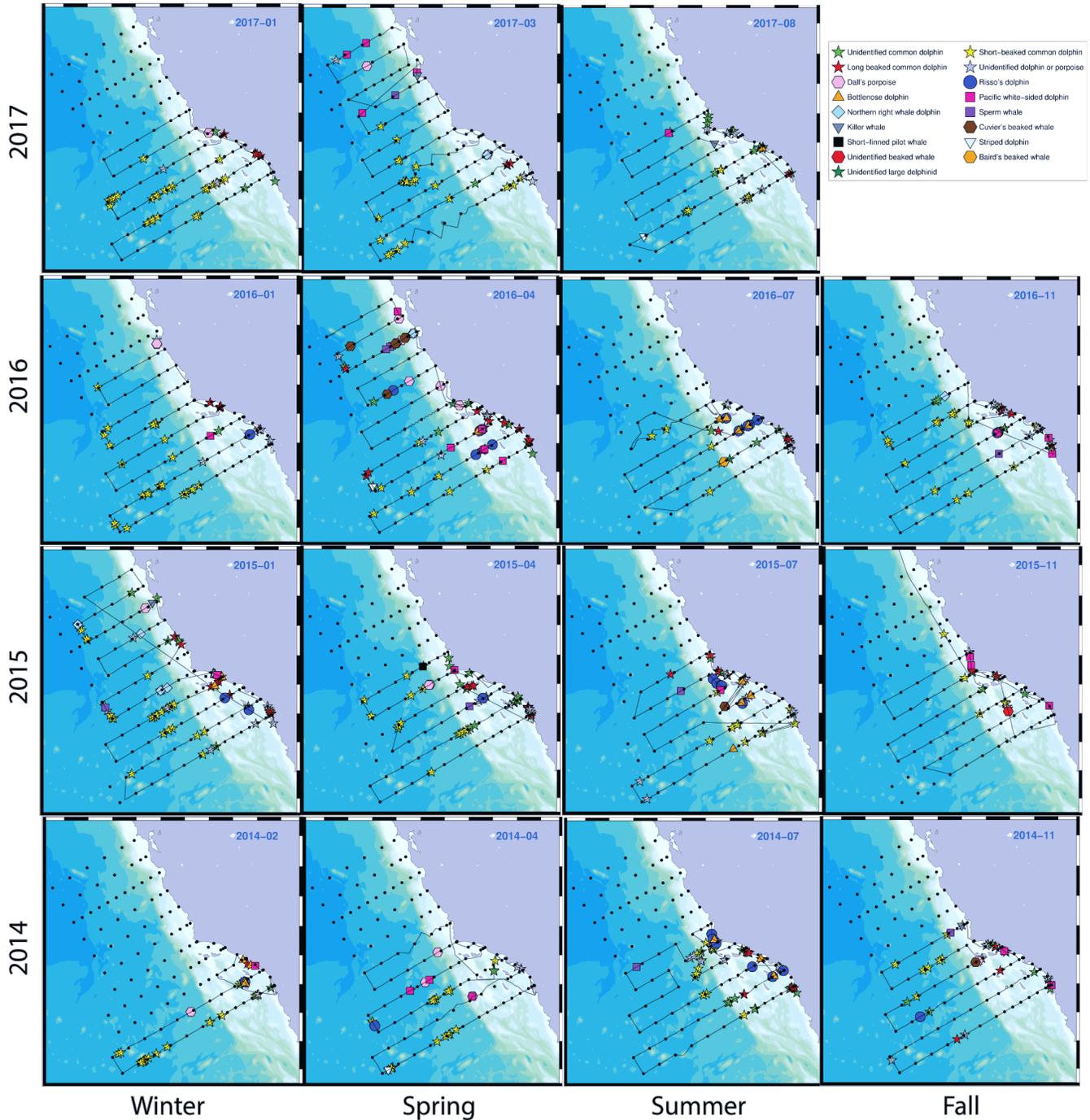


Figure 49. On-effort odontocete sightings during CalCOFI cruises 2014–17. CalCOFI stations are represented by black dots and the ship's trackline is represented as a solid black line between stations. Symbol shapes and colors denote different species, as per legend.

Micronekton communities responded to regional conditions and northern anchovy had notable spawning events

Micronekton abundance, distribution, and community structure reflect the larger patterns in environmental and zooplankton variability observed throughout the CCS. Namely, while conditions south of Cape Men-

docino were typical of the longer times series, the northern regions did not return to a “normal” state following the end of the 2014–16 marine heatwave (Auth et al. 2017; Peterson et al. 2017). Specifically, the northern CCS was anomalously warm at the surface and the micronekton community was dominated by taxa originating from the south and off the shelf (e.g.,

pompano, myctophids, YOY Pacific hake, and YOY rockfishes) (Auth et al. 2017). In 2017 the dominant signal of warm-water taxa on the shelf included the extreme abundance of pyrosomes, which have been found with increasing frequency since 2014 in the northern California Current, but never in the extreme densities on the shelf region as observed this year (Brodeur, unpub.). The anomalously strong northward winds and the associated downwelling that occurred in the northern CCS in January–February 2017 (figs. 3, 4, 7) may have led to poor preconditioning of coastal waters (Hickey et al. 2006; Logerwell et al. 2003) and directly contributed to the presence of offshore and southern taxa on the shelf in winter and spring. There may also be a biological reason for the reduction in typical fish taxa. Specifically, many of these fishes are short-lived and are regional residents. It is not unreasonable to expect that the preceding three years of poor productivity (due to the marine heat wave and El Niño) may have simply reduced their spawning stock biomass.

It is also notable that a greater than average abundance of northern anchovy has been observed in the northern CCS since 2014. As well, egg enumeration data indicates their spawning activity has been high (fig. 21). Interestingly, the most anomalous event in the southern CCS was the increased spawning activity of northern anchovy (fig. 31). While the greatest spawning activity was in the Southern California Bight and Columbia River shelf regions, greater than average spawning activity was also observed at a few isolated locations nearshore in central California (fig. 21). The mechanisms driving these dense spawning aggregations largely in the northern and southern parts of the CCS are to yet be determined, but they are consistent with the predictions of the Basin Model (MacCall 1990), which states that as the overall population abundance is reduced, as has been observed in recent years²⁸, dense spawning aggregations may be concentrated in areas of particularly suitable habitat. In the case of northern anchovy, they would be impinged along the remaining good habitats nearshore and expand to less optimal habitat as the population increases; such expansion may now be occurring in the core anchovy habitat within Southern California Bight.

Salmon habitat and observations

Recent climate extremes contributed to sharp downturns in the abundance (catch + escapement) of many West Coast Chinook and coho salmon populations. Historically poor freshwater conditions were caused by California's extreme "hot drought" from 2012–15. A broader "western snow drought" in 2015 related to

a combination of precipitation and record high surface air temperatures contributed to extreme high freshwater temperature in many western rivers in 2015 that will impact catches and escapement during 2017–20. Record high coastal ocean temperature from 2014–16 and the associated ecosystem impacts that included shifts to more subtropical forage communities and shifting predator distributions likely contributed to sharp declines in survival rates for many US West Coast salmon populations. Fishery impacts included sharply reduced Chinook salmon landings in West Coast commercial fisheries and very low escapements in California's Klamath and Sacramento Rivers in 2016 (PFMC 2017a). The Klamath River fall Chinook ocean abundance forecast was the lowest on record (since 1985). This low abundance forecast and conservation concerns for other weak stocks led to heavily constrained or closed commercial, recreational, and tribal fisheries in California and Oregon (PFMC 2017b).

Results from northern surveys indicate that 2017 likely had anomalously high early-marine mortality for Columbia Basin origin coho and Chinook salmon. Specifically, 2017 had the lowest catch for juvenile Chinook and coho salmon in coastal surveys in the 20-year times series (1998–2017; fig. 24). The record-low catch is likely related to the forage composition (fig. 26) for out-migrants soon after they entered marine waters (Daly et al. 2017) rather than river conditions as the springtime stream flow was about average as the majority of smolts out-migrated in 2017. Early marine survival for 2017 out-migrants will influence the bulk of the adult coho salmon returns in 2018 and the bulk of the Columbia River Chinook salmon returns in 2019.

For the central CCS, environmental conditions in freshwater, estuaries and the coastal ocean from spring 2016 to summer 2017 were notably different than those during the 2012–15 hot drought and 2014–15 marine heat wave and 2016 El Niño. Out-migration flows in the Sacramento River were exceptionally low in spring 2014, 2015, and 2016. They were so low that emergency measures were taken that included trucking hatchery juveniles to the Bay-Delta for release^{29,30}. By contrast, flows were high in spring 2017. Sacramento River stream temperature in 2014–15 was exceptionally high and contributed to record-low egg-to-fry survival for Central Valley winter-run Chinook salmon (Martin et al. 2016), while from spring 2016–summer 2017 stream temperatures were much more favorable for salmon. The improved freshwater conditions in 2016–17 likely resulted in improved salmon growth and condition at the time of out-migration to sea, thus improving their likelihood of survival (Woodson et al. 2013). Unfortunately,

²⁸ http://usa.oceana.org/sites/default/files/maccall_et_al_anch_biomass_remains_low_2012-2015.pdf

²⁹ https://www.fws.gov/sfbaydelta/fisheries/salmon_trucking_and_release.htm

³⁰ https://www.fws.gov/sfbaydelta/documents/2015_coleman_salmon_trucking_nr.pdf

at-sea observations of juvenile salmon from California are unavailable. However, ocean ecosystem indicators of early salmon survival have been developed for central California (Wells et al. 2016, 2017). For both spring 2016 and spring 2017 conditions in the Gulf of the Farallons were near normal. Likewise, the forage community supporting central California salmon in spring 2016 and 2017 was not significantly below average. Similarly, seabird diets on the Farallon Islands in springs 2016 and 2017, which have been linked to early salmon survival (fig. 42; Wells et al. 2017), were typical (i.e., largely rockfishes and northern anchovy) and did not demonstrate a significant increase in predation on juvenile salmon. Considering this suite of indicators based on ecosystem conditions related to key freshwater and marine salmon life stages, a Central Valley fall-run Chinook salmon fishery impact like that observed in 2007–08 (or 2016–17) appears to be unlikely for 2018–19.

Seabird reproductive success and foraging behavior reflect forage communities regionally

The reproductive success of seabirds in 2016 (the most current year available) was negatively related to latitude. In addition, there existed a northward shift in the prey field. In the northern California Current, at Yaquina Head and Castle Rock breeding colonies, some of the lowest reproductive success rates on record were observed. Nest failures were attributed to a combination of bottom-up and top-down forces. At Castle Rock, most chicks died of starvation, whereas at Yaquina Head, most nests failed due to predation by bald eagles seeking alternate prey. At-sea surveys of distribution and abundance of seabirds in northern California Current indicate that the reproductive success in 2017 may also be catastrophic. Namely, extremely low abundances were observed for migrant and central-place feeders. The few occurrences of common murre and sooty shearwaters observed at sea in 2017 in the north were at the locations where rare concentrations of forage (i.e., northern anchovy) were also observed, indicating close coupling of available forage patches and seabird aggregations. Preliminary observations at Castle Rock and Yaquina Head in 2017 also corroborate this speculation of catastrophic reproductive failure; fledging success of murrelets was 0%, with most chicks starving in the first few days, and it is likely Brandt's cormorants at Castle Rock also failed to produce young.

South of Cape Mendocino seabird reproductive success was generally below average. However, the significant decreases noted in the north were unapparent. Examination of the prey field (fig. 27) and the diets (fig. 42) indicate that the availability of primary forage taxa to seabirds remained average although the overall community was diverse (Santora et al. 2017a) and, in

2016, atypical (fig. 29) likely resulting from the inclusion of offshore forage taxa on the shelf during the El Niño event.

In 2017 the divergent characteristics of the environment, forage assemblages, and seabird abundances were apparent. For example, in southern California where forage communities were typical and the surface waters only slightly warmer than typical, the abundance of sooty shearwater was far above average. Yet, in the northern CCS abundance of sooty shearwater was the lowest in the observed record; observations also confirm lower abundance in central California (but within 1 SD of mean)³¹. As sooty shearwater migrate northward along the California Current, it is possible that they stopped their migration in southern California to benefit from persistent trophic hot spots there (Santora et al. 2017b) rather than continue to the northern California Current to lower quality forage assemblages. In addition, forage may have been reduced on their main foraging grounds in the Alaskan Bering-Sea Aleutian Islands ecosystem. Although unconfirmed, the seabirds in the south may be responding to the increased abundance of northern anchovy in the Southern California Bight (figs. 21, 27, 31); in the northern surveys the increased density of anchovy was isolated to the region of Columbia River mouth where the few seabirds were observed (fig. 21).

California sea lions show signs of recovery since the unusual mortality event

Increases in the abundance of northern anchovy coincided with improved condition of pups in 2016. Namely, lipid-rich northern anchovy and Pacific hake occurred in greater frequencies in the nursing female diet compared to the diet during the unusual mortality event that was dominated by juvenile rockfishes and market squid, which have low caloric value. The superior diet of nursing females translated into better condition of their dependent pups. If foraging conditions continue to improve, pup condition and survival should also improve. However, pup production will likely remain suppressed for several more years because the smaller cohorts produced from the unusual mortality event will comprise a greater proportion of the breeding population.

Whales shifting to nearshore habitats

There was a shoreward shift in the distribution of baleen whales. This distributional shift is quite apparent in central and southern California where there has been a recent, dramatic increase in whale entanglements with fixed fishing gears³². Humpback whales likely forag-

³¹ https://static1.squarespace.com/static/56a6b01dd8af105db2511b83/t/59cd54e09f7456363177e20d/1506628834109/FI_Report_NMFS_JRES_2017.pdf

³² http://www.westcoast.fisheries.noaa.gov/mediacenter/WCR%202016%20Whale%20Entanglements_3-26-17_Final.pdf

ing on the increased nearshore abundances of northern anchovy are the most at risk³³. However, gray (*Eschrichtius robustus*) and blue (*Balaenoptera musculus*) whales have also been increasingly encountering gear. While yet to be determined, there are several potential causes for the increased interactions such as increased population abundance and increased predation on anchovy as an alternative prey. For example, humpback whales shift their foraging patterns between nearshore and offshore prey communities (Ainley and Hyrenbach 2010), focusing their foraging effort on krill during cool, productive years and on northern anchovy more inshore during years of delayed upwelling or lower productivity (Fleming et al. 2016).

Human dimensions

The ecosystem conditions observed during the last few years demonstrate the impacts that ocean variability and unanticipated environmental–food web–fishery interactions can have on coastal communities. For example, the marine heat wave was associated with coast-wide blooms of *Pseudo-nitzschia australis* that resulted in fishery season delays and closures (e.g., Dungeness crab, razor clams, rock crab) (Leising et al. 2015, McClatchie et al. 2016, McCabe et al. 2016). Further, due to increased SST, adult northern anchovy and associated spawning aggregations nearshore became more common in the northern CCS. Presumably, while foraging on the nearshore schools of northern anchovy, a dramatic increase of human–predator interactions occurred, including whale entanglements with fixed fishing gears that were deployed in greater density during the condensed and delayed Dungeness crab season of 2016. The risk for these interactions may increase if northern anchovy, a nearshore resident, continues to increase in abundance, or if there are further delays (or increased late-season effort) in Dungeness crab and other fixed-gear fisheries. Beyond fishery impacts, there could also be a need for alteration of coastal shipping lanes in trophic hot spots to reduce ship strikes on whales (Redfern et al. 2013, Santora et al. 2017b).

The low catches of juvenile salmon in the northern CCS survey may indicate a significant impact on the fisheries and dependent communities. Salmon represent an example of how unanticipated, negative synergistic interactions can emerge. Salmon recruitment is reliant on ocean and river conditions the salmon experience early in life. In 2007–08, Central Valley Chinook salmon fishery collapsed requiring a Congressional appropriation of \$170,000,000 from disaster relief (Lindley et al. 2009). The proximate cause of that collapse was poor ocean conditions in central California during 2005–06 (Lindley et al. 2009). Specifically, the anomalous ocean conditions

and low productivity reduced forage availability that motivated a switch by predators, such as common murre, from preferred prey to adult northern anchovy nearshore. This switch in foraging behavior led to increased incidental predation on juvenile salmon as they outmigrated to sea. This interaction between ocean environment whereby bottom-up influences in the ocean environment led to top-down impacts on salmon was largely responsible for the extreme mortality of juvenile salmon and the subsequent collapse of the fishery (Wells et al. 2017). Similar mechanisms have been argued for salmon in the northern California Current (Percy 1992; Emmett et al. 2006; Phillips et al. 2017) and could be a contributor to the low juvenile salmon numbers observed in the northern survey during 2017. As predator populations increase, especially for potential salmon predators such as common murre (Wells et al. 2017) and humpback whales (Chenoweth et al. 2017), the impacts of poor ocean conditions on salmon may be magnified. One potential mitigation effort is to improve freshwater conditions such that more, larger, and an increased portfolio of salmon life histories contribute to increased diversity in the smolt out-migration to sea (e.g., more diversity in ocean-entry timing, smolt size, or migration routes) (Carlson and Satterthwaite 2011; Woodson et al. 2013). However, improvements to inland habitat would not be disconnected from interactions with agriculture, hydropower, and flood control. Regardless, the ocean is not always the primary determinant of recruitment. The “hot drought” affecting California from 2012–15 is considered a dominant driver of the lowest escapement to Central Valley since the collapse of the fishery a decade ago (PFMC 2017a). In such cases, recruitment of salmon to the fishery may rely on mitigation of mortality in freshwater by exceptional ocean ecosystem productivity where smaller (Woodson et al. 2013) and ill-timed (Satterthwaite et al. 2014) out-migrants have a better opportunity of survival.

Ultimately, given the highly variable CCS ecosystem and its variety of interacting components, management actions aimed at sustainability in living marine resources and resource systems will require an ecosystem-based fishery management approach. Efforts to better understand ecosystem interactions and the cascading consequences of anomalous ocean conditions will be critical to the ability of managers to respond effectively to variable ocean conditions while avoiding undesirable impacts to fisheries, protected resources and coastal communities.

Extending the empirical results of these and similar integrative programs to quantitative models capable of evaluating competing management scenarios may be a key aspect of affective management in a variable environment.

³³ <http://www.sfchronicle.com/bayarea/article/Why-eye-popping-whale-shows-off-the-California-12172489.php>

LITERATURE CITED

- Ainley, D. G., and K. D. Hyrenbach. 2010. Top-down and bottom-up factors affecting seabird population trends in the California current system (1985–2006). *Progress in Oceanography* 54:242–254.
- Auth, T. D. 2011. Analysis of the Spring–Fall Epipelagic Ichthyoplankton Community in the Northern California Current in 2004–09 and Its Relation to Environmental Factors. California Cooperative Oceanic Fisheries Investigations Reports 52:148–167.
- Auth, T. D., E. A. Daly, R. D. Brodeur, and J. L. Fisher. 2017. Phenological and distributional shifts in ichthyoplankton associated with recent warming in the northeast Pacific Ocean. *Global Change Biology* doi: 10.1111/gcb.13872.
- Bakun, A. 1973. Coastal upwelling indices, West Coast of North America, 1946–71. NOAA Tech. Rep., NMFS SSRF-671, 114 pp.
- Bjorkstedt, E., R. Goericke, S. McClatchie, E. Weber, W. Watson, N. Lo, B. Peterson, R. Emmett, R. Brodeur, J. Peterson, M. Litz, J. Gomez-Valdez, G. Gaxiola-Castro, B. Lavaniegos, F. Chavez, C. A. Collins, J. Field, K. Sakuma, P. Warzybok, R. Bradley, J. Jahncke, S. Bograd, F. Schwing, G. S. Campbell, J. Hildebrand, W. Sydeman, S. Thompson, J. Largier, C. Halle, S. Y. Kim, and J. Abell. 2012. State of the California Current 2010–2011: Regional Variable Responses to a Strong (But Fleeting?) La Niña. California Cooperative Oceanic Fisheries Investigations Report 52:36–68.
- Black, B. A., I. D. Schroeder, W. J. Sydeman, S. J. Bograd, and P. W. Lawson. 2010. Wintertime ocean conditions synchronize rockfish growth and seabird reproduction in the central California Current ecosystem. *Canadian Journal of Fisheries and Aquatic Sciences* 67:1149–1158.
- Bograd, S. J., and R. J. Lynn. 2003. Anomalous subarctic influence in the southern California Current during 2002. *Geophysical Research Letters* 30:doi: 8020, doi:8010.1029/2003GL017446.
- Bograd S. J., I. D. Schroeder, N. Sarkar, X. M. Qiu, W. J. Sydeman, and F. B. Schwing. 2009. Phenology of coastal upwelling in the California Current. *Geophys Res Lett* 36:doi: 10.1029/2008gl035933.
- Bond, N. A., M. F. Cronin, H. Freeland, and N. Mantua. 2015. Causes and impacts of the 2014 warm anomaly in the NE Pacific. *Geophysical Research Letters* 42:3414–3420.
- Brodeur, R. D., J. P. Fisher, R. L. Emmett, C. A. Morgan, and E. Casillas. 2005. Species composition and community structure of pelagic nekton off Oregon and Washington under variable oceanographic conditions. *Marine Ecology Progress Series* 298:41–57.
- Carlson, S. M., and W. H. Satterthwaite. 2011. Weakened portfolio effect in a collapsed salmon population complex. *Canadian Journal of Fisheries and Aquatic Sciences* 68:1579–1589.
- Carter, H. R., U. W. Wilson, R. W. Lowe, D. A. Manuwal, M. S. Rodway, J. E. Takekawa, and J. L. Yee, editors. 2001. Population trends of the Common Murre (*Uria aalge californica*). U.S. Geological Survey, Information and Technology Report, USGS/BRD/ITR–2000–0012, Washington, D.C.
- Chenoweth, E. M., J. M. Straley, M. V. McPhee, S. Atkinson, and S. Reifensstuhl. 2017. Humpback whales feed on hatchery-released juvenile salmon. *Royal Society Open Science* 4:170180.
- Daly, E. A., T. D. Auth, R. D. Brodeur, and W. T. Peterson. 2013. Winter ichthyoplankton biomass as a predictor of early summer prey fields and survival of juvenile salmon in the northern California Current. *Marine Ecology Progress Series* 484:203–217.
- Daly, E. A., R. D. Brodeur, and T. D. Auth. 2017. Anomalous ocean conditions in 2015: impacts on spring Chinook salmon and their prey field. *Marine Ecology Progress Series* 566:169–182.
- DeLong, R. L., S. R. Melin, J. L. Laake, P. Morris, A. J. Orr, and J. D. Harris. 2017. Age- and sex-specific survival of California sea lions (*Zalophus californianus*) at San Miguel Island, California. *Marine Mammal Science*. doi:10.1111/mms.12427.
- Di Lorenzo, E., N. Schneider, K. M. Cobb, P. J. S. Franks, K. Chhak, A. J. Miller, J. C. McWilliams, S. J. Bograd, H. Arango, E. Curchitser, T. M. Powell, and P. Riviere. 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophysical Research Letters* 35:doi 10.1029/2007gl032838.
- Di Lorenzo, E., J. Fiechter, N. Schneider, A. Bracco, A. J. Miller, P. J. S. Franks, S. J. Bograd, A. M. Moore, A. C. Thomas, W. Crawford, A. Pena, and A. J. Hermann. 2009. Nutrient and salinity decadal variations in the central and eastern North Pacific. *Geophysical Research Letters* 36.
- Di Lorenzo, E., and N. Mantua. 2016. Multi-year persistence of the 2014/15 North Pacific marine heatwave. *Nature Clim. Change* 6:1042–1047.
- Emmett, R. L., G. K. Krutzikowsky, and P. Bentley. 2006. Abundance and distribution of pelagic piscivorous fishes in the Columbia River plume during spring/early summer 1998–2003: Relationship to oceanographic conditions, forage fishes, and juvenile salmonids. *Progress in Oceanography* 68:1–26.
- Fiedler, P. C., and N. J. Mantua. 2017. How are warm and cool years in the California Current related to ENSO? *Journal of Geophysical Research: Oceans* 122:5936–5951.
- Fleming, A. H., C. T. Clark, J. Calambokidis, and J. Barlow. 2016. Humpback whale diets respond to variance in ocean climate and ecosystem conditions in the California Current. *Global Change Biology* 22:1214–1224.
- Frischknecht, M., M. Münnich, and N. Gruber. 2017. Local atmospheric forcing driving an unexpected California Current System response during the 2015–2016 El Niño. *Geophysical Research Letters* 44:304–311.
- Gladics, A. J., R. M. Suryan, R. D. Brodeur, L. M. Segui, and L. Z. Filliger. 2014. Constancy and change in marine predator diets across a shift in oceanographic conditions in the Northern California Current. *Marine Biology* 161:837–851.
- Gladics, A. J., R. M. Suryan, J. K. Parrish, C. A. Horton, E. A. Daly, and W. T. Peterson. 2015. Environmental drivers and reproductive consequences of variation in the diet of a marine predator. *Journal of Marine Systems* 146:72–81.
- Gruber, N., and J. L. Sarmiento. 1997. Global patterns of marine nitrogen fixation and denitrification. *Global Biogeochemical Cycles* 11:235–266.
- Haidvogel, D. B., H. Arango, W. P. Budgell, B. D. Cornuelle, E. Curchitser, E. Di Lorenzo, K. Fennel, W. R. Geyer, A. J. Hermann, L. Lanerolle, J. Levin, J. C. McWilliams, A. J. Miller, A. M. Moore, T. M. Powell, A. F. Shchepetkin, C. R. Sherwood, R. P. Signell, J. C. Warner, and J. Wilkin. 2008. Ocean forecasting in terrain-following coordinates: Formulation and skill assessment of the Regional Ocean Modeling System. *Journal of Computational Physics* 227:3595–3624.
- Hickey, B., A. MacFadyen, W. Cochlan, R. Kudela, K. Bruland, and C. Trick. 2006. Evolution of chemical, biological and physical water properties in the northern California current in 2005: Remote or local wind forcing? *Geophysical Research Letters* 33:L22S02. doi:10.1029/2006GL026782.
- Horton, C. A. 2014. Top-down influences of Bald Eagles on Common Murre populations in Oregon. Oregon State University.
- Hyrenbach, K. D., and R. R. Veit. 2003. Ocean warming and seabird communities of the southern California Current System (1987–98): response at multiple temporal scales. *Deep-Sea Research Part II—Topical Studies in Oceanography* 50:2537–2565.
- Jacox, M. G., A. M. Moore, C. A. Edwards, and J. Fiechter. 2014. Spatially resolved upwelling in the California Current System and its connections to climate variability. *Geophysical Research Letters* 41:3189–3196.
- Jacox, M. G., J. Fiechter, A. M. Moore, and C. A. Edwards. 2015. ENSO and the California Current coastal upwelling response. *Journal of Geophysical Research: Oceans*, 120:1691–1702.
- Jacox, M. G., E. L. Hazen, K. D. Zaba, D. L. Rudnick, C. A. Edwards, A. M. Moore, and S. J. Bograd. 2016. Impacts of the 2015–2016 El Niño on the California Current System: Early assessment and comparison to past events. *Geophysical Research Letters* 43:7072–7080.
- Jacox, M. G., M. A. Alexander, N. J. Mantua, J. D. Scott, G. Hervieux, R. S. Webb, and F. E. Werner. 2017. Forcing of multiyear extreme ocean temperatures that impacted California Current living marine resources in 2016. *Bulletin of the American Meteorological Society*. Accepted.
- Jeronimo, G., and J. Gomez-Valdes. 2010. Mixed layer depth variability in the tropical boundary of the California Current, 1997–2007. *Journal of Geophysical Research—Oceans* 115.
- Jimenez-Perez, L. C., and B. E. Lavaniegos. 2004. Changes in dominance of copepods off Baja California during the 1997–99 El Niño and La Niña. *Marine Ecology Progress Series* 277:147–165.
- Lavaniegos, B. E., and I. Ambriz-Arreola. 2012. Interannual variability in krill off Baja California in the period 1997–2005. *Progress in Oceanography* 97:164–173.
- Leising, A., I. D. Schroeder, S. J. Bograd, E. Bjorkstedt, J. Field, K. Sakuma, J. Abell, R. R. Robertson, J. Tyburczy, W. Peterson, R. D. Brodeur, C. Barcelo, T. D. Auth, E. A. Daly, G. S. Campbell, J. A. Hildebrand, R. M. Suryan, A. J. Gladics, C. A. Horton, M. Kahru, M. Manzano-Sarabia, S. McClatchie, E. D. Weber, W. Watson, J. A. Santora, W. J. Sydeman, S. R. Melin, R. L. DeLong, J. Largier, S. Y. Kim, F. P. Chavez, R. T. Golightly, S. R. Schneider, P. Warzybok, R. Bradley, J. Jahncke, J. Fisher, and J. Peterson. 2014. State of the California Current 2013–14: El Niño

- looming. California Cooperative Ocean and Fisheries Investigations Reports 55.
- Leising, A. W., I. D. Schroeder, S. J. Bograd, J. Abell, R. Durazo, G. Gaxiola-Castro, E. P. Bjorkstedt, J. Field, K. Sakuma, R. R. Robertson, R. Goericke, W. T. Peterson, R. Brodeur, C. Barceló, T. D. Auth, E. A. Daly, R. M. Suryan, A. J. Gladics, J. M. Porquez, S. McClatchie, E. D. Weber, W. Watson, J. A. Santora, W. J. Sydeman, S. R. Melin, F. P. Chavez, R. T. Golightly, S. R. Schneider, J. Fisher, C. Morgan, R. Bradley, and P. Warzybok. 2016. State of the California Current 2014–15: Impacts of the warm-water “Blob.” California Cooperative Oceanic Fisheries Investigations Reports 56:31–68.
- Lindley, S. T., C. B. Grimes, M. S. Mohr, W. Peterson, J. Stein, J. T. Anderson, L. W. Botsford, D. L. Bottom, C. A. Busack, T. K. Collier, J. Ferguson, J. C. Garza, A. M. Grover, D. G. Hankin, R. G. Kope, P. W. Lawson, A. Low, R. B. MacFarlane, K. Moore, M. Palmer-Zwahlen, F. B. Schwing, J. Smith, C. Tracy, R. Webb, B. K. Wells, and T. H. Williams. 2009. What caused the Sacramento River fall Chinook stock collapse? NOAA Tech. Memo. NOAA-TM-NMFS-SWFSC-447.
- Logerwell, E. A., N. Mantua, P. W. Lawson, R. C. Francis, and V. N. Agostini. 2003. Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (*Oncorhynchus kisutch*) marine survival. Fisheries Oceanography 12:554–568.
- MacCall, A. 1990. Dynamic geography of marine fish populations. University of Washington Press, Seattle 153 pp.
- Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78:1069–1079.
- Martin, B. T., A. Pike, S. N. John, N. Hamda, J. Roberts, S. T. Lindley, and E. M. Danner. 2017. Phenomenological vs. biophysical models of thermal stress in aquatic eggs. Ecology Letters 20:50–59.
- McCabe, R. M., B. M. Hickey, R. M. Kudela, K. A. Lefebvre, N. G. Adams, B. D. Bill, F. M. D. Gulland, R. E. Thomson, W. P. Cochlan, and V. L. Trainer. 2016. An unprecedented coastwide toxic algal bloom linked to anomalous ocean conditions. Geophysical Research Letters 43:10,366–310,376.
- McClatchie, S., R. Goericke, A. Leising, T. D. Auth, E. Bjorkstedt, R. R. Robertson, R. D. Brodeur, X. Du, E. A. Daly, C. A. Morgan, F. P. Chavez, A. J. DeBich, J. Hildebrand, J. Field, K. Sakuma, M. G. Jacox, M. Kahru, R. Kudela, C. Anderson, B. E. Lavanigos, J. Gomez-Valdes, S. P. A. Jiménez-Rosenberg, R. McCabe, S. R. Melin, M. D. Ohman, L. M. Sala, B. Peterson, J. Fisher, I. D. Schroeder, S. J. Bograd, E. L. Hazen, S. R. Schneider, R. T. Golightly, R. M. Suryan, A. J. Gladics, S. Lored, J. M. Porquez, A. R. Thompson, E. D. Weber, W. Watson, V. Trainer, P. Warzybok, R. Bradley, and J. Jahncke. 2016. State of the California Current 2015–16: Comparisons with the 1997–98 El Niño. California Cooperative Ocean and Fisheries Investigations Reports 57:5–61.
- Melin, S. R., A. J. Orr, J. D. Harris, J. L. Laake, and R. L. DeLong. 2012. California sea lions: An indicator for integrated ecosystem assessment of the California Current System. California Cooperative Ocean and Fisheries Investigations Reports 53:140–152.
- Morgan, C. A., B. R. Beckman, R. D. Brodeur, B. J. Burke, K. C. Jacobson, J. A. Miller, W. T. Peterson, D. M. Van Doornik, L. A. Weitkamp, J. E. Zamon, A. M. Baptista, E. A. Daly, E. M. Phillips, and K. L. Fresh. 2017. Ocean Survival of Salmonids RME, 1/1/2016–12/31/2016, Annual Report, 1998-014-00. 71pp. Available at: <https://www.cbfish.org/Document.mvc/Viewer/P154622>.
- Neveu, E., A. M. Moore, C. A. Edwards, J. Fiechter, P. Drake, W. J. Crawford, M. G. Jacox, and E. Nuss. 2016. An historical analysis of the California Current circulation using ROMS 4D-Var: System configuration and diagnostics. Ocean Modelling 99:133–151.
- Ohman, M. D., and E. Venrick. 2003. CalCOFI in a changing ocean. Oceanography 16:76–85.
- Pearcy, W. G. 1992. Ocean ecology of North Pacific salmonids. Washington Sea Grant Program, Seattle, WA.
- Pennington M. 1996. Estimating the mean and variance from highly skewed marine data. Fisheries Bulletin 94:498–505.
- Peterson, W. T., J. L. Fisher, P. T. Strub, X. Du, C. Risien, J. Peterson, and C. T. Shaw. 2017. The pelagic ecosystem in the Northern California Current off Oregon during the 2014–2016 warm anomalies within the context of the past 20 years. Journal of Geophysical Research: Oceans 122:doi:10.1002/2017JC012952.
- PFMC. 2017a. Preseason Report I: Stock Abundance Analysis and Environmental Assessment Part 1 for 2017 Ocean Salmon Fishery Regulations. Portland, Oregon.
- PFMC. 2017b. Preseason Report III, Council Adopted Management Measures and Environmental Assessment Part 3 for 2017 Ocean Salmon Fishery Regulations. Portland, Oregon.
- Phillips, E. M., J. K. Horne, and J. E. Zamon. 2017. Predator-prey interactions influenced by a dynamic river plume. Canadian Journal of Fisheries and Aquatic Sciences 74:1375–1390.
- Redfern, J. V., M. F. McKenna, T. J. Moore, J. Calambokidis, M. L. Deangelis, E. A. Becker, J. Barlow, K. A. Forney, P. C. Fiedler, and S. J. Chivers. 2013. Assessing the Risk of Ships Striking Large Whales in Marine Spatial Planning. Conservation Biology 27:292–302.
- Reed, T. E., S. Wanless, M. P. Harris, M. Frederiksen, L. E. B. Kruuk, and E. J. A. Cunningham. 2006. Responding to environmental change: plastic responses vary little in a synchronous breeder. Proceedings of the Royal Society B-Biological Sciences 273:2713–2719.
- Sakuma, K. M., J. C. Field, N. J. Mantua, S. Ralston, B. B. Marinovic, and C. N. Carrion. 2016. Anomalous Epipelagic Micronekton Assemblage Patterns in the Neritic Waters of the California Current in Spring 2015 during a Period of Extreme Ocean Conditions. California Cooperative Oceanic Fisheries Investigations Reports 57:163–183.
- Santora, J. A., E. L. Hazen, I. D. Schroeder, S. J. Bograd, K. M. Sakuma, and J. C. Field. 2017a. Impacts of ocean climate variability on biodiversity of pelagic forage species in an upwelling system. Marine Ecology Progress Series doi: 10.3354/meps12278.
- Santora, J. A., and W. J. Sydeman. 2015. Persistence of hotspots and variability of seabird species richness and abundance in the southern California Current. Ecosphere 6.
- Santora, J. A., W. J. Sydeman, I. D. Schroeder, J. C. Field, R. R. Miller, and B. K. Wells. 2017b. Persistence of trophic hotspots and relation to human impacts within an upwelling marine ecosystem. Ecological Applications 27:560–574.
- Satterthwaite, W., S. Carlson, S. Allen-Moran, S. Vincenzi, S. Bograd, and B. Wells. 2014. Match-mismatch dynamics and the relationship between ocean-entry timing and relative ocean recoveries of Central Valley fall run Chinook salmon. Marine Ecology Progress Series 511:237–248.
- Schroeder, I. D., B. A. Black, W. J. Sydeman, S. J. Bograd, E. L. Hazen, J. A. Santora, and B. K. Wells. 2013. The North Pacific High and wintertime pre-conditioning of California Current productivity. Geophysical Research Letters 40:541–546.
- Schroeder, I. D., W. J. Sydeman, N. Sarkar, S. A. Thompson, S. J. Bograd, and F. B. Schwing. 2009. Winter pre-conditioning of seabird phenology in the California Current. Marine Ecology Progress Series 393:211–223.
- Schwing, F. B., M. O’Farrell, J. M. Steger, and K. Baltz. 1996. Coastal upwelling indices, West Coast of North America, 1946–1995. NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-231, 144 pp.
- Shchepetkin, A. F., and J. C. McWilliams. 2005. The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. Ocean Modelling 9:347–404.
- Sydeman, W. J., K. L. Mills, J. A. Santora, S. A. Thompson, D. F. Bertram, K. H. Morgan, J. M. Hipfner, B. K. Wells, and S. G. Wolf. 2009. Seabirds and Climate in the California Current—a Synthesis of Change. California Cooperative Oceanic Fisheries Investigations Reports 50:82–104.
- Sydeman, W. J., J. A. Santora, S. A. Thompson, B. Marinovic, and E. D. Lorenzo. 2013. Increasing variance in North Pacific climate relates to unprecedented ecosystem variability off California. Global Change Biology 19:1662–1675.
- Wells, B. K., J. C. Field, J. A. Thayer, C. B. Grimes, S. J. Bograd, W. J. Sydeman, F. B. Schwing, and R. Hewitt. 2008. Untangling the relationships among climate, prey and top predators in an ocean ecosystem. Marine Ecology Progress Series 364:15–29.
- Wells, B. K., J. A. Santora, M. J. Henderson, P. Warzybok, J. Jahncke, R. W. Bradley, D. D. Huff, I. D. Schroeder, P. Nelson, J. C. Field, and D. G. Ainley. 2017. Environmental conditions and prey-switching by a seabird predator impact juvenile salmon survival. Journal of Marine Systems 174:54–63.
- Wells, B. K., J. A. Santora, I. D. Schroeder, N. Mantua, W. J. Sydeman, D. D. Huff, and J. C. Field. 2016. Marine ecosystem perspectives on Chinook salmon recruitment: a synthesis of empirical and modeling studies from a California upwelling system. Marine Ecology Progress Series 552:271–284.
- Wells, B. K., I. D. Schroeder, J. A. Santora, E. L. Hazen, S. J. Bograd, E. P. Bjorkstedt, V. J. Loeb, S. McClatchie, E. D. Weber, W. Watson, A. R. Thompson, W. T. Peterson, R. D. Brodeur, J. Harding, J. Field, K. Sakuma, S. A. Hayes, N. Mantua, W. J. Sydeman, M. Losekoot, S. A. Thompson,

J. Largier, S. Y. Kim, F. P. Chavez, C. Barceló, P. Warzybok, R. Bradley, J. Jahncke, R. Georricke, G. S. Campbell, J. A. Hildebrand, S. R. Melin, R. L. DeLong, J. Gomez-Valdes, B. E. Lavaniegos, G. Gaiola-Castro, R. T. Golightly, S. R. Schneider, N. Lo, R. M. Suryan, A. J. Gladics, C. A. Horton, J. Fisher, C. Morgan, J. Peterson, E. A. Daly, T. D. Auth, and J. Abell. 2013. State of the California Current 2012–13: No such thing as an “average” year. CalCOFI 54:37–71.

Woodson, L. E., B. K. Wells, P. K. Weber, R. B. MacFarlane, G. E. Whitman, and R. C. Johnson. 2013. Size, growth, and origin-dependent mortality of juvenile Chinook salmon *Oncorhynchus tshawytscha* during early ocean residence. Marine Ecology Progress Series 487:163–175

ARE THERE TEMPORAL OR SPATIAL GAPS IN RECENT ESTIMATES OF ANCHOVY OFF CALIFORNIA?

P. C. DAVISON, W. J. SYDEMAN, AND J. A. THAYER

Farallon Institute
101 H St., Suite Q
Petaluma, CA 94952
ph: (707) 981-8033
jthayer@faralloninstitute.org

ABSTRACT

MacCall et al. (2016) recently published an estimate of the biomass of the central stock of northern anchovy (*Engraulis mordax*) off the coast of California, and found that this stock experienced a population crash from 2009–15. However, anecdotal observations concurrent to the collapse suggested that anchovy were extremely abundant. We used central and southern California data from two trawling surveys, ichthyoplankton time series, and aerial surveys to investigate whether or not any anchovy spawning was missed by MacCall et al. We found no evidence using additional and more recent data that 1) anchovy adults migrated north of the study area, 2) there was a large biomass of anchovies near shore, or 3) spawning was temporally missed by MacCall et al. Thus, we conclude that the 2009–15 population crash is real and that the anchovy population remnant contracted to extremely nearshore habitat where it appeared paradoxically abundant to observers.

INTRODUCTION

MacCall et al. (2016) recently estimated the biomass of the central stock of northern anchovy (*Engraulis mordax*) off California from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton time series calibrated to past stock estimates made using the daily egg production method (Lo 1985a; Jacobson et al. 1994). MacCall et al. found that the California anchovy stock is experiencing a population crash, and that the stock size may be as low as 15,000 t (2009–11; 95% CI <100,000 t). However, recent anecdotal reports state that anchovy are abundant (Bartolone 2014; Gaura 2015). Thus, it is possible that the MacCall et al. estimate missed spawning that was inshore, north of their study area off central California, or outside of their study periods (Parrish 2015). We examine the evidence in support of and against the argument that there remains a significant anchovy stock off central and southern California that was not observed by MacCall et al.

The anchovy is a schooling coastal pelagic fish species that has undergone large oscillations in abundance for thousands of years, with periodicity of ~60 y (Baumgartner et al. 1992; MacCall 1996; Field et al. 2009). Several

authors have linked population oscillations to climate influences (Lehodey et al. 2006; Lindegren et al. 2013). Indeed, the current collapse described by MacCall et al. (2016) occurred in the absence of a significant fishery, and occurred ~60 y after the last anchovy population crash in the early 1950s. Anchovy are a relatively small and short-lived species (most <16 cm in length; most fishes <5 y in age; Schwartzlose et al. 1999), with high fecundity and mortality, and are thought to do well in colder waters associated with high coastal upwelling (Ryckaczewski and Checkley 2008; Lindegren et al. 2013). There are historically three population centers for anchovy on the Pacific coast of North America: a northern stock near the Columbia River mouth, a central stock concentrated in the Southern California Bight (SCB) and Monterey Bay (Schwartzlose et al. 1999; Zwolinski et al. 2012), and a southern stock off the Baja California coast.

MacCall et al. (2016) developed their anchovy biomass estimate using CalCOFI ichthyoplankton data from southern California. Although one cannot logically prove that there is no “hidden stock” of anchovies in the California Current system (CCS) that eluded the methods of MacCall et al., it is possible to test whether their conclusions are consistent with independent data and data that were excluded from their analysis. We compared egg, larval, and adult anchovy abundance and distribution in years when stock assessments were high, moderate, and low and logically tested whether the reported ichthyoplankton decline was consistent with migration of the SCB population inshore or north to central California. To address the possibility that spawning was missed temporally we looked at monthly means of CalCOFI ichthyoplankton abundance, and discuss the results in context with the phenology of anchovy in the CCS.

METHODS

We use data collected from several large-scale anchovy sampling programs operating approximately annually in the study area: CalCOFI ichthyoplankton, CalCOFI continuous underwater fish egg sampler (CUFES), the National Marine Fisheries Service (NMFS) Southwest Fisheries Science Center (SWFSC) juvenile rockfish sur-

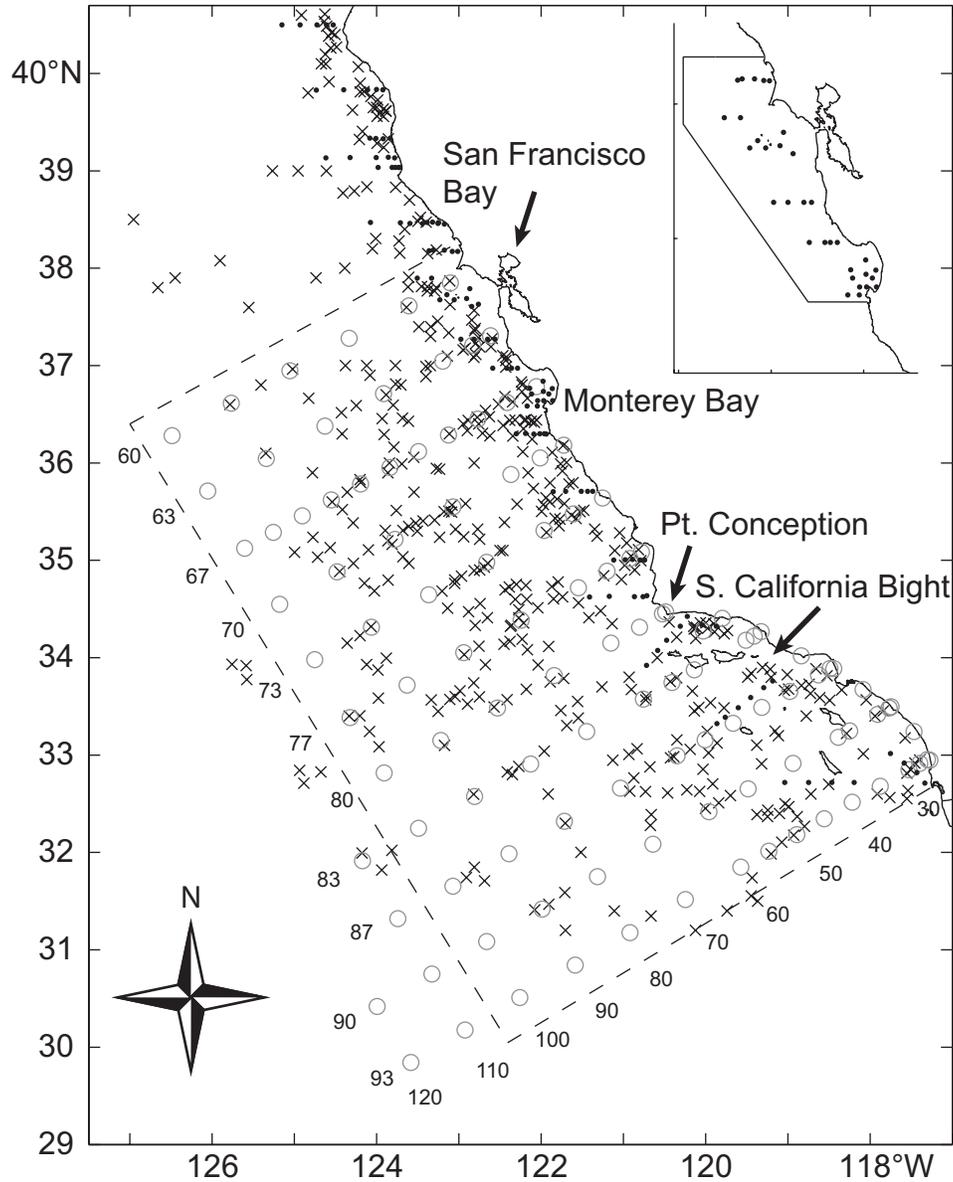


Figure 1. Central and southern California sampling. JRS stations are indicated with black dots, CalCOFI and SCCOOS stations are indicated with grey circles, CalCOFI ichthyoplankton data were used from within the dashed box, and the Spring CPS rope trawls are indicated as black crosses. The inset shows the “core” JRS region and stations. AT transects are not shown, but they generally cover the CalCOFI region and extend north of the displayed area. CalCOFI line numbers are indicated to the west of the study region, and station numbers to the south.

vey (JRS), the SWFSC Spring Coastal Pelagic Species (Spring CPS) rope trawl program, and we discuss the SWFSC acoustic trawl (AT) and California Department of Fish and Wildlife aerial surveys of coastal pelagic fishes (fig. 1). The methods for these data are presented by survey, whereas the results and discussion are organized into a comparison between central and southern California, long-term changes in abundance, abundance inshore of the standard CalCOFI stations, and seasonal patterns in anchovy abundance. Extensive time series are available for two of these surveys, the JRS and CalCOFI ichthyo-

plankton. We also use the underway CUFES data (2012–15) to assess the possibility that the anchovy stock has recently recovered. We compare anchovy abundance at several points in time, chosen from four published biomass estimate time series (Methot 1989; Jacobson et al. 1994; Fissel et al. 2011; MacCall et al. 2016). For “high” anchovy stock, we use 1975, for “moderate” biomass we use 1984, and for “low” biomass we use 2011 (fig. 2). We also use 2005 for an alternate period of “high” biomass, as there was a short-term recovery of the stock 2005–06 (fig. 2). We used the methods of MacCall et al. (2016)

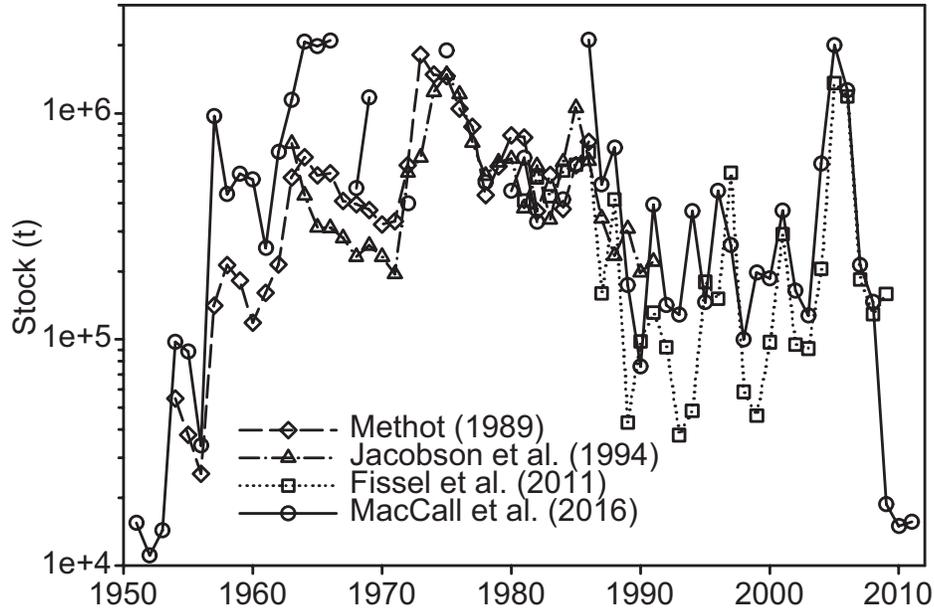


Figure 2. Published stock estimates for the central anchovy stock.

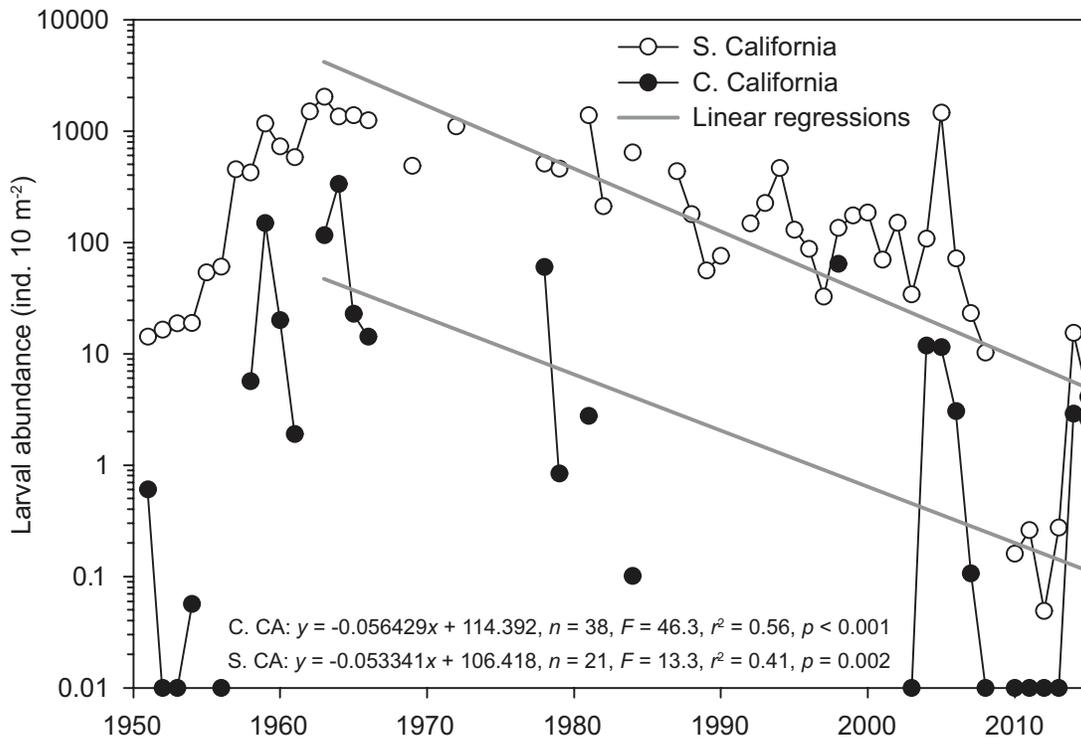


Figure 3. Spring CalCOFI mean anchovy larval abundance (ind. 10 m⁻²) for central California (north of Pt. Conception; closed circles) and southern California (open circles). Linear regressions for 1963–2015 are shown as grey lines, neither passed the test for constant variance ($p < 0.05$).

to extend their spring larval abundance estimates to the year 2015 (fig. 3), and compared standard CalCOFI station results to those using the inshore Southern California Coastal Ocean Observing System (SCCOOS) stations for the period 2005–15.

CalCOFI

CalCOFI ichthyoplankton data were collected with plankton nets 1951–2015. During the early part of the time series, cruises were monthly, and during the later part quarterly. Between 1969 and 1981 CalCOFI cruises

were made triennially. We did not group data collected in different months.

There were two major changes in sampling methods over the course of the time series; in 1969 the sampling depth was changed from 140 m to 210 m, and in 1978 the net design was changed from a 1 m ring net to a 0.7 m bongo net. The capture efficiency of the two net designs is roughly the same for the size classes of anchovy larvae that make up 90% of the catch (Hewitt 1980). For this reason, and because 100% of anchovy larvae were found shallower than 122 m (Ahlstrom 1959), the changes in sampling methods should have little effect on the abundance time series.

Anchovy abundance estimates based upon CalCOFI data are subject to spatial hyperstability bias because neither the fish nor the sampling stations are evenly distributed within the study area (MacCall et al. 2016; fig. 1). Spatial hyperstability was corrected by assigning sample locations to a 10 x 10 km grid, filling unoccupied grid elements using linear interpolation, and then averaging the entire interpolated grid. Multiple occupations of the same grid cell in the same month were averaged prior to interpolation. Only larval abundance was used, rather than larval and egg abundance, to better detect evidence of inshore spawning and to reduce any temporal mismatch between spawning and sampling. Larvae are more likely to be detected than eggs at widely spaced sampling stations and times due to advection and diffusion processes (Richardson 1981) because the egg stage is ~3 d duration in comparison to the 70–90 d spent as a larva (Hunter and Coyne 1982; Lo 1985b; Smith 1985).

We used CalCOFI station larval abundance in three ways: mean central California spring larval abundance north of Pt. Conception (lines 60–77 offshore to station 100) was compared with the southern California index of MacCall et al. (2016); we compared spring anchovy larval abundance in the SCB at the inshore SCCOOS stations to that at the inshore ends of CalCOFI lines 80–93; and we used mean monthly larval abundance data off southern California (1951–2015, all cruises, lines 77–93, stations \leq 100) to study seasonality of spawning.

Underway anchovy egg concentration has been recorded during CalCOFI cruises using CUFES since 1996 (NOAA 2015). The CUFES device filters water pumped at ~650 l min⁻¹ from an intake 3 m below the surface while the vessel is underway (Checkley et al. 1997). Fish eggs from the filtered samples were usually identified and counted every 5–30 min.

JRS

The NMFS SWFSC conducts an annual spring–summer survey in the CCS over the continental shelf and slope that is designed to collect juvenile rockfishes, although many other taxa are recorded (Ralston et al.

2015). The data used here span the years 1983–2013. Trawls made in August or later were excluded for seasonal consistency with the Spring CPS rope trawl. Marine fauna were collected at night with ~15 min tows of a modified Cobb midwater trawl with a mouth area of ~144 m² and a variable mesh terminating with a cod end liner mesh of 9.5 mm. The trawl was fished at ~2 knots at a station-specific standard depth (headrope at ~10 m or ~30 m). Nonstandard tows, tows made to nonstandard depths, and tows for which an error was noted were not used. JRS cruises occupy specific stations, often more than once per cruise, and central California stations that were added or dropped mid-series were not included in this study. An exception was made for two stations, which were combined because they are only ~7 km apart and were occupied for complementary halves of the time series. The “core” region of the survey off central California as defined above then consists of 32 stations that are occupied approximately three times annually (fig. 1). We used the mean station catch per unit effort (CPUE; ind. trawl⁻¹), and all “core” station means were then averaged to produce an annual mean. Additionally, mean station CPUE was calculated over several similar years corresponding to the “moderate” (1983–85) and “low” (2010–13) anchovy biomass periods in order to decrease trawl catch variability. JRS data north and south of the core area were available 2004–13 and processed similarly.

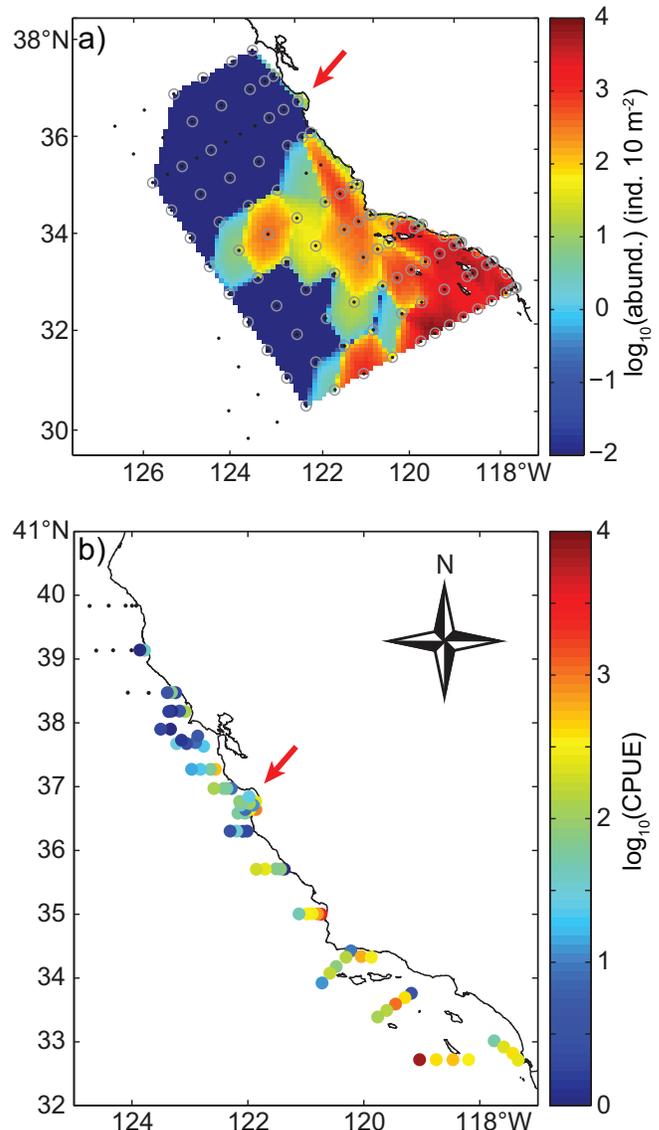
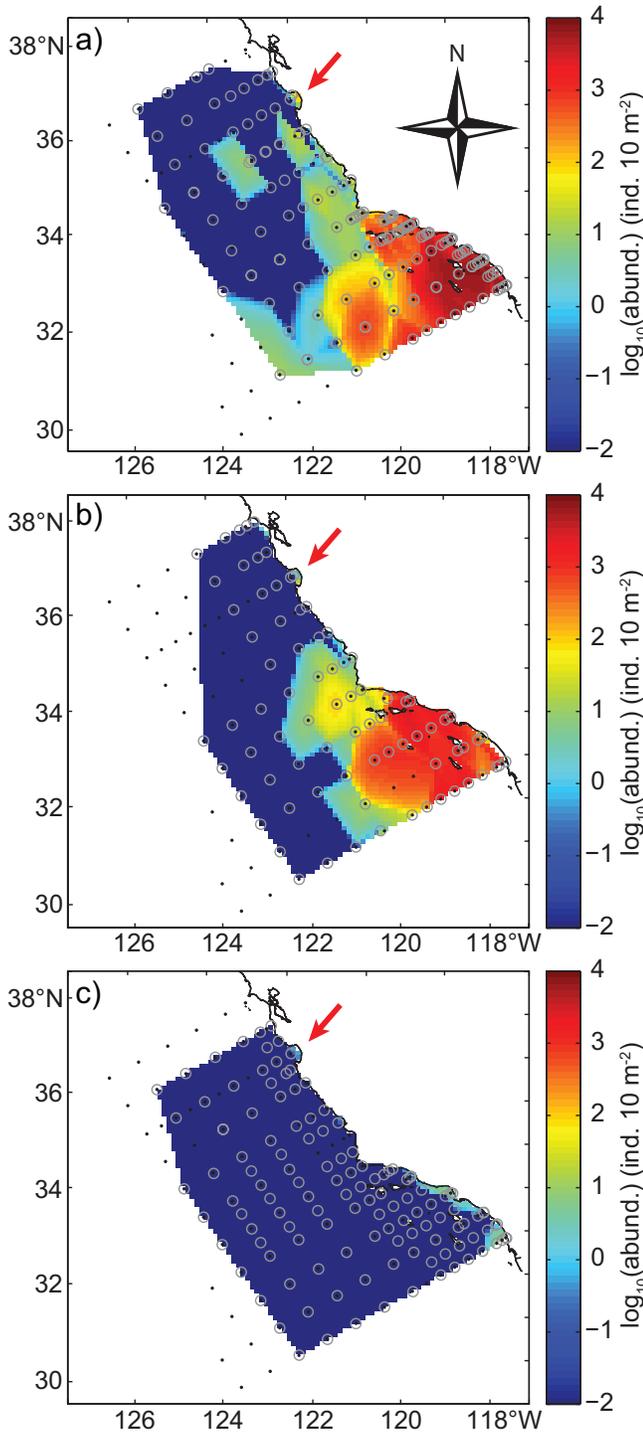
CPS

Spring CPS cruises sample pelagic nekton at night using a Nordic 264 rope trawl (Griffith 2008; Dotson et al. 2010). The rope trawl has a working mouth area of ~600 m² and is fished near the surface at ~3.5 knots. It has a variable mesh concluding with 8 mm mesh in the cod end liner. Because the sampling was somewhat sparse, and because several trawls may be made within a small area in the same night, we mapped the data to a 50 x 50 km square grid to avoid spatial bias, and used the mean of samples within each grid element. Data from the entire time period (2010–13) were grouped together to reduce the inherent variability in trawl catches.

RESULTS

CalCOFI spring anchovy larval abundance in 1975, 1984, 2005, and 2011 was greatest in the SCB, with lower concentrations of larvae found north of Pt. Conception (figs. 4–5). The area of greatest larval concentration in 1975 and 1984 abutted the southern boundary of the study area.

CUFES data were not available from 1975 or 1984, but were available from the alternate “high” stock year of 2005 and the “low” years of 2010–15 (NOAA 2015). Anchovy egg distribution was predominantly in the



(Above) Figure 5. The short 2005–06 anchovy recovery showing a) spring 2005 CalCOFI anchovy larval abundance (standard stations are indicated with black dots, occupied stations with grey circles, and axes origin is 29.5°N 127.5°W), and b) 2005–06 JRS mean CPUE (stations with zero catch are shown as black dots). Monterey Bay is marked with a red arrow in both panels.

(Left) Figure 4. CalCOFI spring anchovy larval abundance for a) high biomass (1975), b) moderate biomass (1984), and c) low biomass (2011) years. Standard stations are indicated with black dots, and occupied stations with grey circles. The axes origin is 29.5°N 127.5°W. Monterey Bay is marked with a red arrow in panels a–c).

SCB in 2005, with few eggs found off central California (fig. 6). Anchovy eggs were rare and local 2010–15 off both central and southern California, with the greatest concentrations in 2014 near shore in the SCB.

The JRS anchovy CPUE off central California was greatest inshore between Pt. Conception and San Francisco Bay (figs. 5, 7). The JRS anchovy catch was not

evenly distributed within the “core” area, and anchovy were significantly concentrated to the southeast (fig. 7 inset; Wilcoxon signed rank test, $n = 31$, $Z = 4.52$, $p < 0.001$). Within this subregion (1983–2013), anchovy CPUE was 196 (30% of the total nekton catch), but in the remaining portion of the “core” area anchovy CPUE was 15 (2% of the total catch).

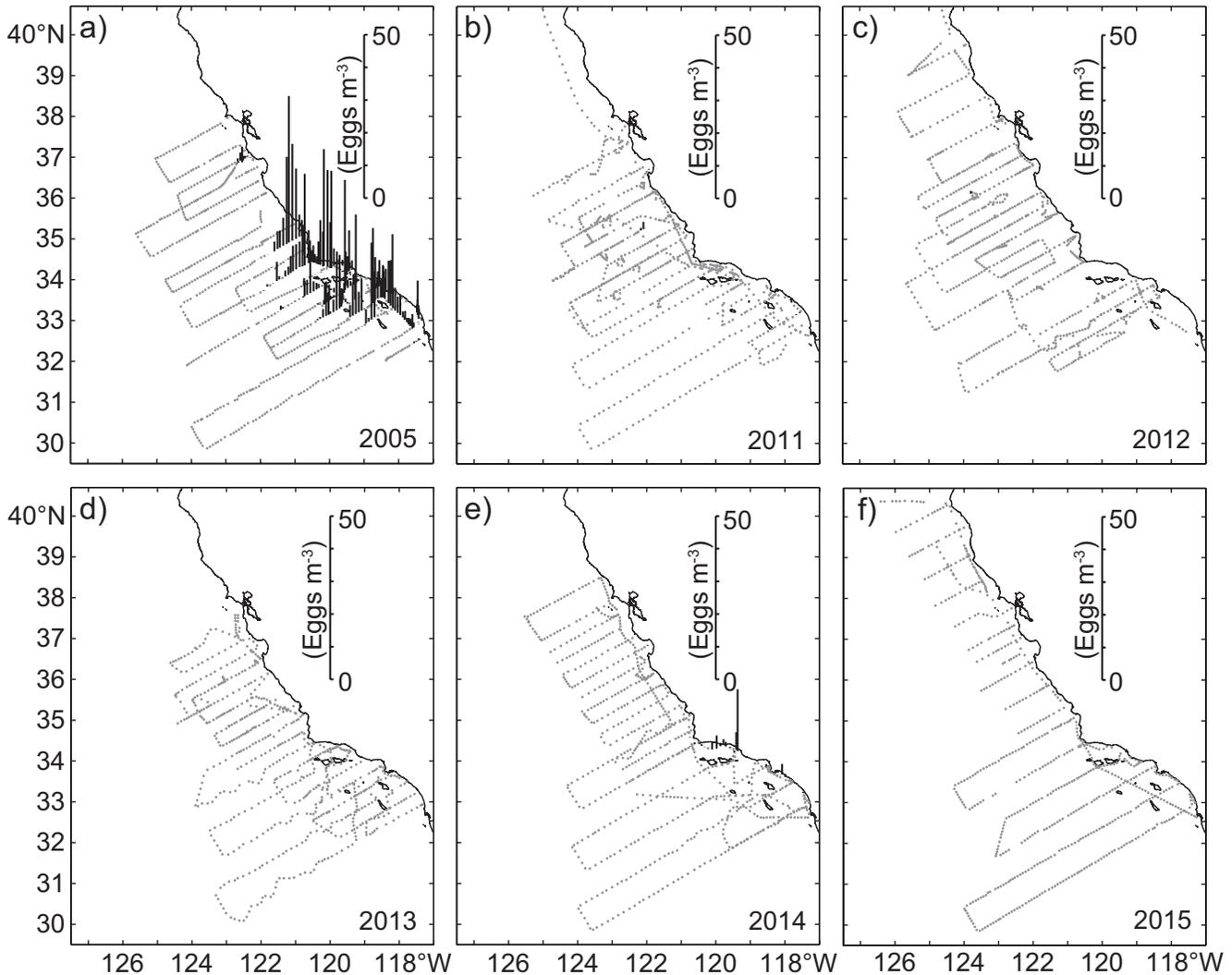


Figure 6. CalCOFI spring CUFES counts of anchovy egg density (2005, 2011–15). Zero concentration is indicated by grey dots. Data from 2015 (panel f), are preliminary and do not include seven unanalyzed stations. Data from 2010 (not shown) are similar to those from 2011–13.

A total of 524 Spring CPS rope trawl deployments were made off the entire US West Coast 2010–13 (fig. 8). Anchovy were only captured inshore in the SCB, near Pt. Conception, and off Washington State. No anchovy were collected off central California, despite the fact that it was the region of greatest effort (fig. 8).

Central and southern California anchovy abundance

April larval concentrations were compared north and south of Pt. Conception 1951–2015, with “north” defined as CalCOFI lines 60–77, north of the Pt. Conception, and “south” as the standard CalCOFI area. Larval anchovy abundance was significantly greater to the south (Wilcoxon signed rank test, $n = 26$, $Z = -4.457$, $p < 0.001$), and the north:south ratio of the mean abundance was 0.07 (fig. 3). Larval abundance was signifi-

cantly greater to the south in years 1975, 1984, 2005, and 2011 (Table 1).

Only 18 of 738 CUFES samples were positive for anchovy eggs in 2011 (maximum 2.3 eggs m^{-3}), whereas in 2005, 228 of 851 samples were positive (maximum 44.9 eggs m^{-3} ; fig. 6). Mean concentration was 144-fold greater in 2005 than in 2011. Egg concentrations were significantly higher to the south in 2005, but not in 2011 because there were few positive samples anywhere (table 1).

JRS anchovy CPUE was significantly greater south of Pt. Conception for both 2005–06 and 2010–13 (table 1), although in 2010–13 the median and mean were greater to the north due to the two large catches just north of Pt. Conception (fig. 7).

There was only one positive catch for anchovy off central California from the spring CPS 2010–13 (fig. 8),

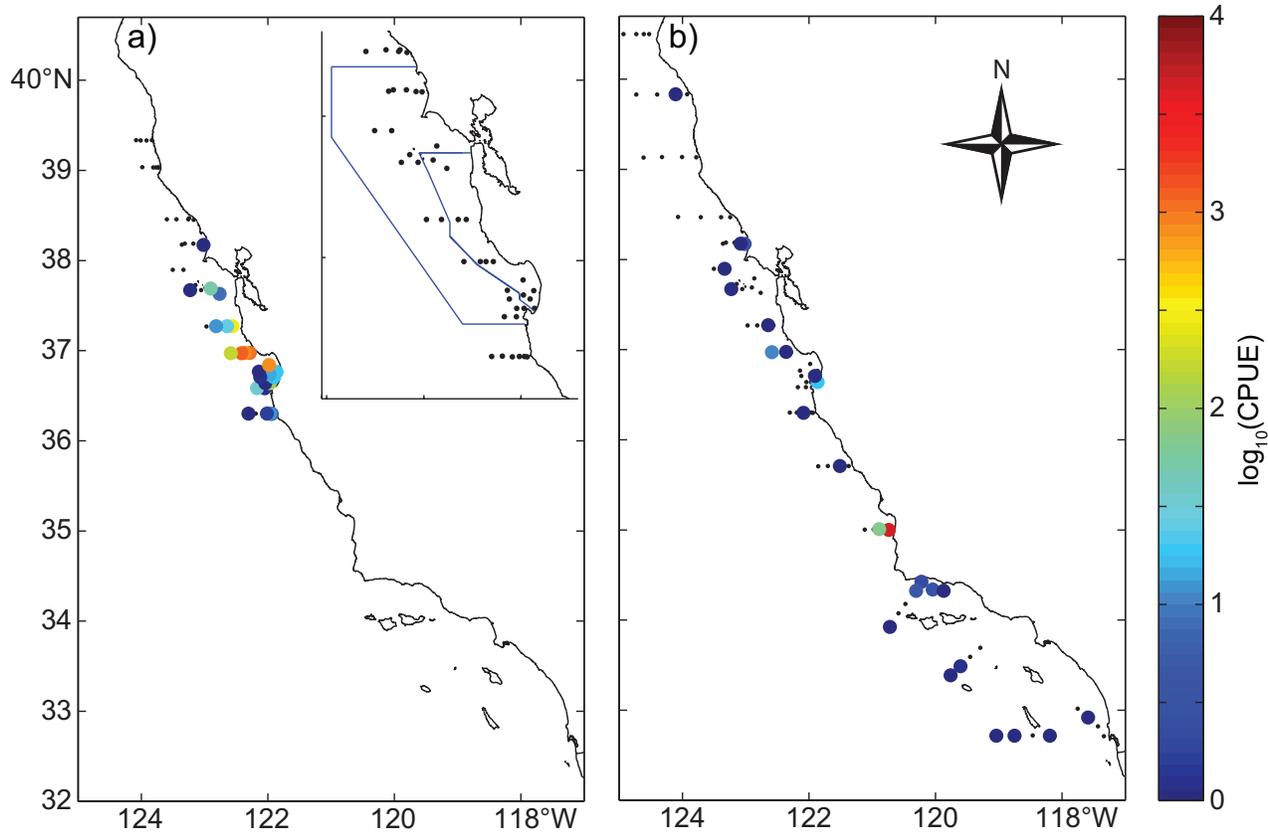


Figure 7. JRS station mean CPUE for a) moderate biomass (1983–85), and b) low biomass (2010–13) years. Stations with zero mean catch are shown as black dots. Inset in panel a) shows JRS stations off Central California as black dots. The outer blue polygon encloses the “core” stations, and the inner blue polygon encloses the region with elevated anchovy CPUE.

TABLE 1
 Wilcoxon signed rank tests of anchovy abundance north (N) and south (S) of Pt. Conception.

	year	mean (N)	mean (S)	median (N)	median (S)	n (N)	n (S)	Z	p
CalCOFI larvae	1975	1.60	869.29	0	69.14	1500	1416	-36.89	<0.001
	1984	2.32	350.39	0	11.96	1198	1462	-26.96	<0.001
	2005	47.12	655.98	0	59.01	1541	1468	-22.15	<0.001
	2011	0.00	0.08	0	0	1260	1466	-4.68	<0.001
CUFES eggs	2005	0.60	1.59	0	0	325	536	-7.71	<0.001
	2011	0.01	0.01	0	0	343	415	0.89	0.375
JRS adults	2005–06	165.11	626.61	32.00	234.13	47	20	-3.45	0.001
	2010–13	103.98*	0.90	0	0.33	46	19	-2.31	0.021
CPS adults (inshore)	2010–13	0.08	53.07	0	1.05	12	8	-2.99	0.003

*Dominated by two extreme catches near Pt. Conception (fig. 7).

and southern California had significantly greater CPUE (table 1). Because there were no positive catches >50 km from shore off central or southern California, we used only the inshore grid elements between Pt. Conception and Pt. Reyes to reduce zero inflation.

Temporal patterns in abundance

The CalCOFI anchovy ichthyoplankton spring time series can be roughly divided into two temporal segments: a period of increasing abundance (1951–63), and a period of generally declining abundance (1964–2015). From 1963–2015 there is an exponential decline

in anchovy larval abundance in both central and southern California (fig. 3). January–May monthly abundances all exhibit the same long-term pattern (fig. 9).

JRS pelagic trawl data off central California also suggest a long-term exponential decline in anchovy abundance 1983–2013, with a decreasing slope on a semilog scale (fig. 10). In the “moderate” biomass period (1983–85) anchovy were captured at more stations and in 1–2 orders of magnitude greater numbers than from 2010–13, even in their good habitat near Monterey Bay (fig. 7). JRS anchovy CPUE also declined over time as a fraction of nekton captured by trawls in the subregion of good

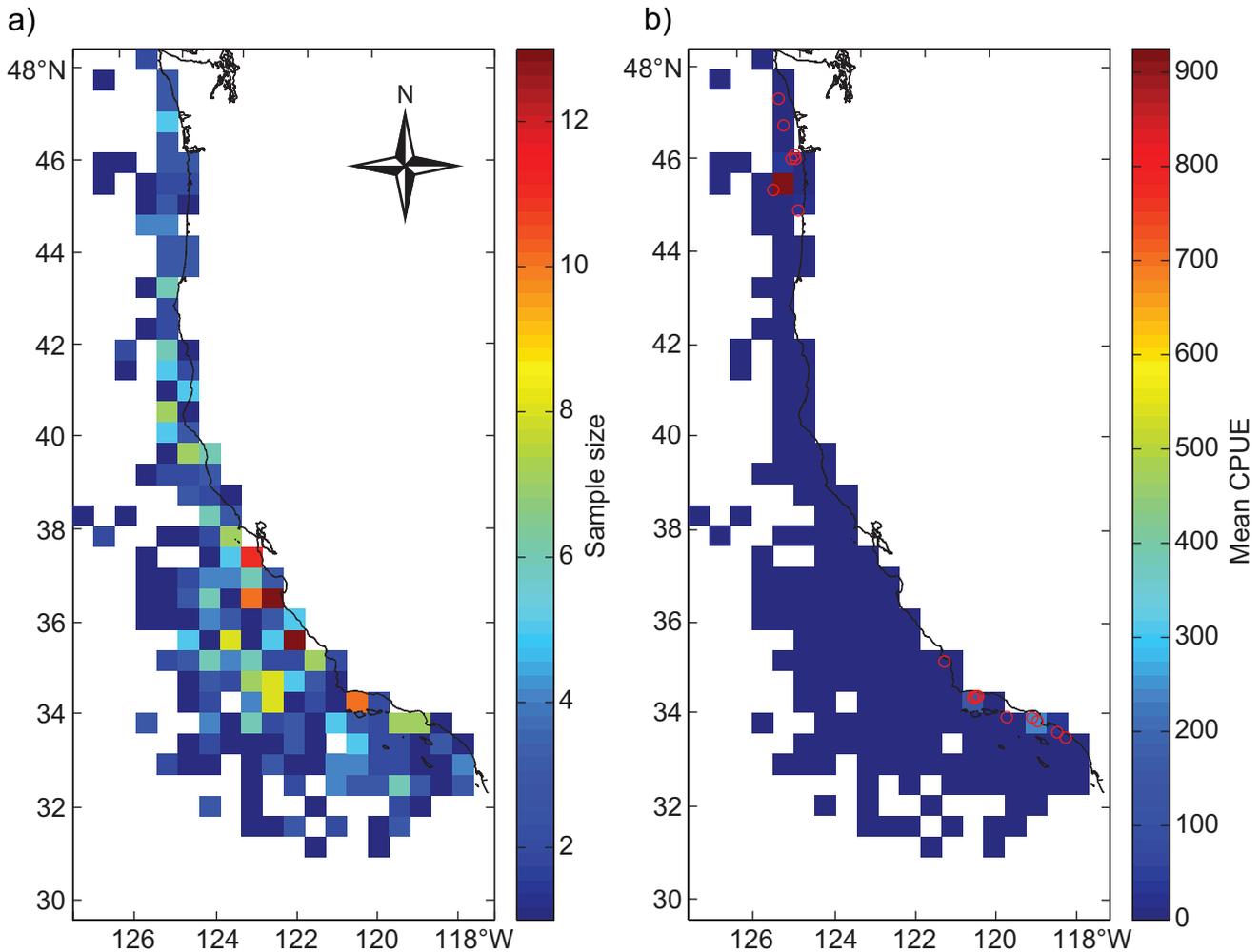


Figure 8. Spring CPS rope trawl a) spatially-averaged sample size, and b) anchovy mean CPUE (2010–13). The axes origin is 29.5°N 127.5°W, and the grid size is 50 x 50 km. Non-zero catches are marked with red circles.

habitat (fig. 7 inset). Anchovies comprised >40% of the overall CPUE in the 1980s and 1990s, 18% 2000–09, and only 0.1% 2010–13.

No CUFES data were available prior to 1996, so we used 2005 as an alternate “high” anchovy biomass year. Underway data from the CalCOFI CUFES program showed high anchovy egg abundance in 2005 throughout the SCB and north around Pt. Conception, whereas in the “low” biomass years (2010–15), few anchovy eggs were collected anywhere (fig. 6).

Undetected inshore spawning

April anchovy egg and larval abundance at nine nearshore SCCOOS stations (mean distance to shore 1.5 km) were compared to the innermost six CalCOFI stations between lines 80 and 93 (mean distance to shore 7.3 km) for the time period in which SCCOOS stations were occupied (2005–15). Neither egg nor larval abundance were significantly different between

these two groups of stations (Wilcoxon signed rank test, $n = 8$; $Z = -0.14$, $p = 0.89$ for eggs; $Z = -0.84$, $p = 0.40$ for larvae). Inclusion of SCCOOS stations using the methods of MacCall et al. (2016) did not result in a significant difference in larval abundance estimates ($n = 8$, $t = -0.81$, $p = 0.45$).

Seasonal patterns in spawning

Over the course of the whole time series (1951–2015), monthly larval abundance was elevated January–May, with a peak in March (fig. 9). Egg abundance was also elevated January–May, but with peak abundance in April. January–May larval concentrations all exhibited the same long-term pattern, and (excluding April) had similar magnitudes clustering around a 1:1 ratio against April concentrations (fig. 9). Outliers from the ~1:1 ratio indicate relatively poor winter (1961, 1981, 2000–08) or spring spawning (2010–11, 2013), and most outliers were from the time period 2000–13.

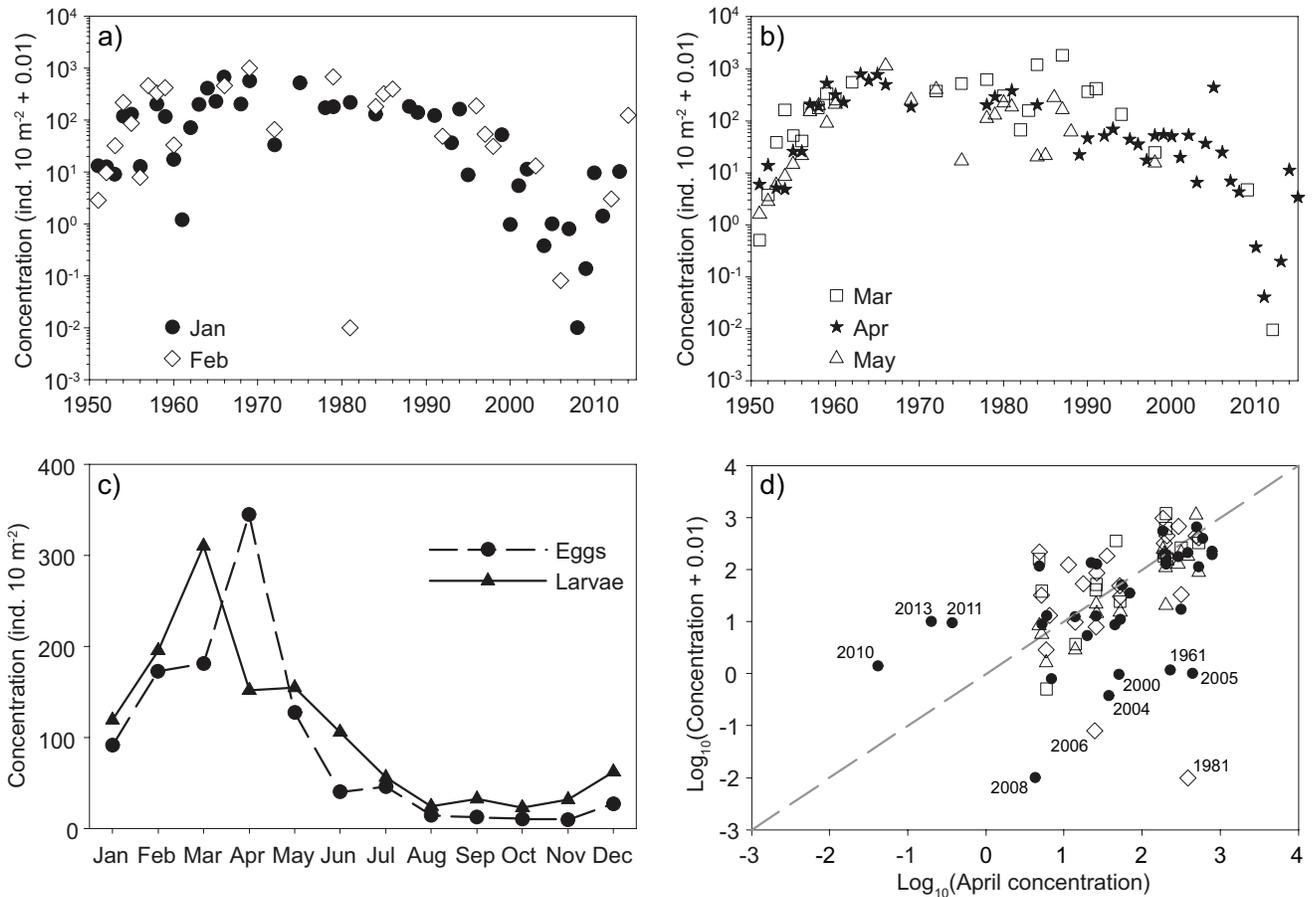


Figure 9. Southern California anchovy ichthyoplankton abundance showing a) winter larval concentration by month and year, b) spring larval concentration by month and year, c) mean concentration of larvae and eggs by month (1951–2015), and d) January–May (excluding April) monthly larval concentrations plotted against April concentration with outlier years labeled. Panel d) uses the same legend symbols as panels a) and b). The 1:1 ratio is plotted as a grey dashed line.

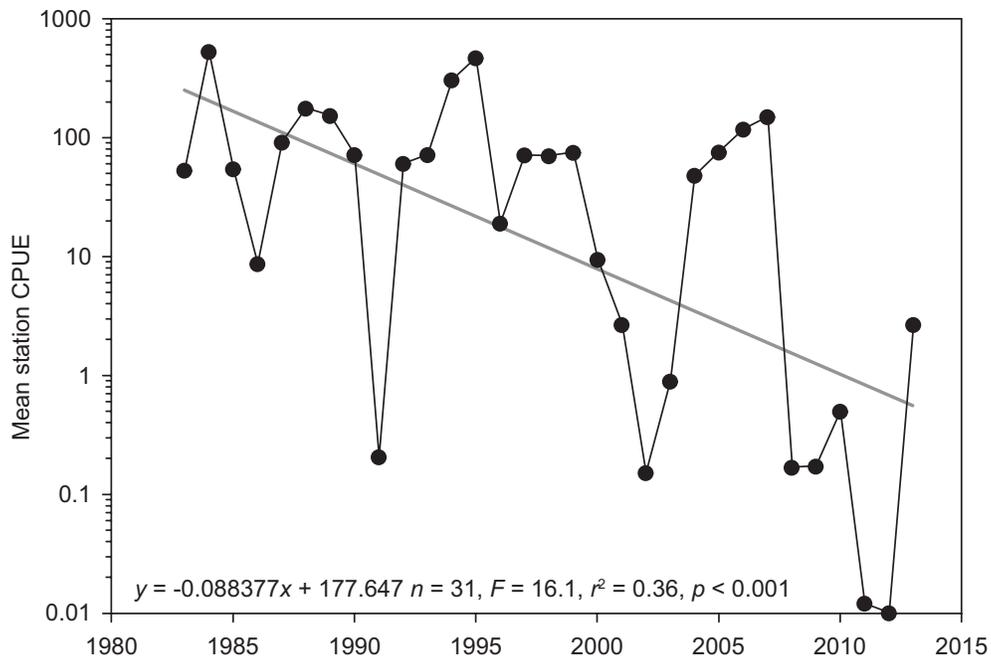


Figure 10. JRS central California “core” station anchovy CPUE. The linear regression is (grey line) was significant, but failed the constant variance assumption ($p = 0.018$).

DISCUSSION

Recent central and southern California anchovy populations

The central California coast from San Francisco Bay to Monterey Bay has been noted anecdotally and scientifically as a hotspot for anchovy and their cetacean predators (Santora et al. 2012; Drake 2013). The region of good anchovy habitat with elevated CPUE (fig. 7 inset) is relatively small, ~3,500 km², whereas the surface area of the SCB inside the Channel Islands is ~30,000 km². Larval concentrations were at least one order of magnitude lower off central California than they were in the SCB in years of high, moderate, and low biomass (1975, 1984, 2005, and 2011; figs. 3–5; table 1). Mean annual anchovy larval concentration (1951–2015) north of Pt. Conception was 7% of that to the south. Adult and egg abundance were also lower north of Pt. Conception, although from 2010–13 the data were sensitive to outliers or amounted to a comparison of zeros (figs. 6–7; table 1).

It has been known for decades that most of the central anchovy stock resides in or about the SCB (Smith 1972; MacCall and Prager 1988; Jacobson et al. 1994; Schwartzlose et al. 1999). The most important spawning habitat for anchovy is in the SCB, both in terms of larval concentrations and areal extent (figs. 3–5). The CPUE of both pelagic trawls and underway egg density sampling have consistent spatial distribution with that of larval abundance (figs. 5–6, 8). Anchovy were captured in the SCB by the Spring CPS rope trawl 2010–13, but no adult anchovy were captured off central California, despite greater effort there (fig. 8). Anchovy egg, larval, and adult abundance between Pt. Conception and Cape Mendocino was so low 2010–13 as to be inconsequential to the central stock as a whole (figs. 3–4, 6, 8). During the period of high anchovy biomass (1966–79), the fraction of total larval catch from waters north of Pt. Conception was estimated to be 0%–6% (Hewitt 1980).

Even a cursory glance at anchovy larva distribution indicates that there may be substantial spawning or advected ichthyoplankton in Mexican waters just south of San Diego (figs. 4–5). This fraction was variable and estimated to be 11%–59% of the total larval catch 1966–79 (Hewitt 1980). It is not clear whether some CalCOFI ichthyoplankton were from the southern stock. The Baja California coast has not been surveyed by CalCOFI cruises after 1981, although it has been sampled by the Mexican investigations of the California Current (IMECOCAL) program 1998–present. Thus, the current “standard” CalCOFI station pattern (lines 77–93) does not cover the full range of anchovy spawning habitat when the stock is large. If a variable amount of spawn-

ing occurs outside the standard CalCOFI station plan, this will introduce error into stock estimates based only upon US ichthyoplankton data.

Temporal patterns in abundance

The various anchovy stock estimates were in approximate agreement for the “high” (mid-1970s), and “moderate” (early 1980s) biomass periods (fig. 2). Our observation of increasing anchovy ichthyoplankton abundance 1951–63 (fig. 3) was consistent with reports of an increasing anchovy stock 1951–69 (Smith 1972). The low 2011–15 anchovy ichthyoplankton abundances (figs. 3–4, 6; MacCall et al. 2016) were consistent with catches of adults. Only two JRS net tows off southern California 2010–13 captured many anchovy (both near Pt. Conception; fig. 7), in contrast to the many trawls over a wide area that captured anchovy in a year when anchovy were abundant (fig. 5). Few anchovy off southern California and none off central California were captured by the Spring CPS rope trawl (2010–13; fig. 8). An acoustic estimate of anchovy stock size in the study area was attempted by the NMFS AT survey (2006–11), which concluded that anchovy were too low in abundance and too patchily distributed for a good estimate from 2006–10 (Zwolinski et al. 2012), and that the anchovy biomass was <10,000 t in 2011 (Demer et al. 2013).

Despite short recoveries in 1986 and 2005–06 (fig. 2), both adult and larval anchovy spring abundance have declined exponentially since the early 1960s (figs. 3, 10). Adult anchovy off central California have also declined over time as a fraction of nekton CPUE. Because both central and southern California ichthyoplankton abundances have declined together (fig. 3), few eggs have been observed between Pt. Conception and Cape Mendocino (fig. 6), and catches of adults off central California have similarly declined or are nil (figs. 7–8), there is no evidence that the anchovy stock has migrated north out of the southern California study area of MacCall et al. (2016). There is also no evidence from ichthyoplankton, trawling, or CUFES data that the stock has recovered 2012–15 after the period covered by MacCall et al. (2016).

Inshore anchovy population

The CalCOFI ichthyoplankton sampling may miss anchovy spawning close to shore. However, southerly winds in the study area advect surface water offshore, and the moving surface water can be expected to transport weakly swimming anchovy larvae. A ~5-fold inshore/offshore difference in abundance of the smallest (youngest) size classes of anchovy larvae is evidence of this larval advection offshore (Smith 1972). Prior studies of the distribution of anchovy ichthyoplankton relative to the

coast found that larval abundance (ind. m⁻²) increased with bottom depth from 8–70 m (Brewer and Smith 1982; Barnett et al. 1984), that nearshore habitat (8–36 m bottom depth) was not preferred for spawning by anchovy in comparison to the CalCOFI sampling area (Brewer and Smith 1982), and that the peak abundance of anchovy larvae was 60 km from shore (Richardson 1981). The inner stations of the five CalCOFI lines in the SCB (plus the Santa Barbara Basin station) are 2–19 km from shore at a median bottom depth of 63 m (depth range 34–578 m). The nine SCCOOS stations in the SCB are 0.1–3.7 km from shore at 20 m bottom depth, but these stations were not used by MacCall et al. (2016) because they were only occupied since 2005. There was no significant difference in larval or egg concentrations between the SCCOOS stations and the inner CalCOFI stations, or between abundance estimates made with and without SCCOOS stations, and thus there is no evidence that inshore spawning was missed by MacCall et al. (2016) in the SCB.

Egg concentrations are a more accurate index of parent stock size than larval concentration due to variable mortality rates in the egg and larval stages (MacCall et al. 2016), but are less precise due to greater patchiness. Indeed, there has been a sharp increase in anchovy egg/larva mortality in recent years (Fissel et al. 2011; MacCall et al. 2016). We used anchovy larval concentration here, rather than egg concentration, in order to reduce patchiness effects and better detect “missing” evidence of inshore spawning. The anchovy egg stage lasts 2–7 d, whereas the larval stage lasts 70–90 d (Hunter and Coyne 1982; Lo 1985b; Smith 1985). Thus, larvae are more dispersed than eggs due to movements of the water and more likely than eggs to be detected by sampling at CalCOFI stations some distance from possible close-to-shore spawning habitat (Richardson 1981).

The recent period of very low anchovy catches contrasts with newspaper reports of huge anchovy schools close to shore in Monterey Bay 2013–15 (Drake 2013; Goode 2013; Bartolone 2014; Gaura 2015) and in the SCB (Herreria 2014), and it may be argued that these fishes were missed by the mostly deeper-water CalCOFI and JRS surveys. In low biomass periods, anchovy are known to contract their range inshore (Schwartzlose et al. 1999; MacCall et al. 2016). Aerial surveys are well-suited to observe these inshore shoals. Aerial surveys of the SCB, the population center of the central anchovy stock, showed that in the “low” biomass period (2012–14) anchovy were almost entirely found <4 km from shore (Lynn et al. 2015). The maximum biomass observed aurally was 14,532 t in 2013. Thus, it is clear that even though there is a dense population of anchovy nearshore, it doesn’t amount to a large biomass due to the restricted spatial distribution. Sporadic,

large catches of anchovy at inshore stations by the AT survey (Zwolinski et al. 2012; Demer et al. 2013), JRS (fig. 7), and Spring CPS rope trawl (fig. 8) are consistent with a small but dense population of anchovy close to shore in low biomass years. CUFES data from 2014–15 are also consistent with a population distribution very close to shore (fig. 6). Anchovies were essentially absent from their historical offshore habitat 2009–15 (figs. 4–5), yet they paradoxically appeared unusually abundant to nearshore observers.

Seasonality of spawning

Anchovy spawn all year with a peak March–April (fig. 9; Parrish et al. 1986; MacCall and Prager 1988; Asch 2015). The use of winter and spring (January and April) anchovy ichthyoplankton abundance generally captures the peak spawning season, and the January–May monthly abundances are similar in both magnitude and long-term pattern (fig. 9). The period of steepest decline in larval abundance is characterized by relatively poor winter (2000–09) or spring abundances (2010–13), consistent with a shortening of the spawning season and perhaps match-mismatch processes (Cushing 1990).

Monthly averages of anchovy abundance (fig. 9c) were lower but otherwise similar to previously published material (Moser et al. 2001) for larvae, but differed for eggs in that February and March averages were also relatively lower in comparison to April concentrations. The overall reduced abundance is due to extension of the time series to include the recent anchovy collapse. The sharpening of the egg abundance peak resulted from our correction for spatial bias in sampling locations relative to anchovy spawning habitat (Moser et al. used an average of occupied stations).

Peak anchovy spawning in the CalCOFI area is (non-significantly) shifting -3 d decade⁻¹ (Asch 2015), or ~ 18 days across the whole CalCOFI time series. Because February larval densities were greater than those from January, May larval densities were similar to those from April, and MacCall et al. (2016) incorporated many February, March, and May cruises in their indices, the phenological shift in the timing of peak spawning would not be expected to greatly change their results. Indeed, recent CalCOFI January larval abundances would be expected to increase with such a shift relative to the early portion of the time series, producing an overestimate of the anchovy stock.

Parrish et al. (1986) found striking seasonal differences in individual anchovy fecundity from histological samples (1977–84) and the age distribution of commercial landings and scientific catches (1966–80). Therefore, Parrish (2015) argued that the use of January ichthyoplankton indices for anchovy stock assessments is difficult to justify because January egg production (1%–3%

of annual) is so small in comparison to the spring peak, and may thus be sensitive to small shifts in spawning seasonality or range. However, the great seasonal fecundity difference observed in dissected specimens (Parrish et al. 1986) is not consistent with what was observed in the water on CalCOFI cruises (fig. 9). Mean annual CalCOFI January egg concentrations were 44% of the April concentration for the period 1977–84 corresponding to Parrish et al.'s data, and 45% for all years with both January and April cruises.

Calibration

Ichthyoplankton concentration is not a direct measurement of biomass and thus requires calibration to a benchmark stock assessment in order to estimate biomass from the index. It does not matter if the index incorporates data from the time and location of maximum abundance, as long as the relationship between the benchmark and index does not change. Because the calibration stock assessments were only performed in three years overlapping with the CalCOFI ichthyoplankton surveys (MacCall et al. 2016), there is likely some error in the calibration. The accuracy of future stock estimates made from ichthyoplankton surveys will improve with additional benchmark stock assessments for calibration.

In low population years, anchovy landings may be similar to or even exceed stock assessments (Parrish 2015). Non-breeding migration of other stocks to the survey area may inflate local landings data relative to the local stock size. In addition, if the calibration stock assessment did not incorporate all anchovy habitat (e.g., extremely nearshore or waters off Mexico) then ichthyoplankton abundance is calibrated to an underestimated stock. While the calibration error may be small in years when the stock is large, it will grow in relative size as the population declines, and can lead to apparent paradoxes in low biomass years.

CONCLUSION

In regards to the question of whether or not there is an unobserved spawning population of anchovy off central California, the answer is likely “no,” or at least not a big one. Both the JRS and Spring CPS rope trawl sampling programs focus their effort in central California waters (figs. 7–8). The JRS anchovy CPUE exponentially declined 1983–2013 off central California (fig. 10). The Spring CPS rope trawl captured zero anchovy off central California 2010–13 (fig. 8). Anchovy egg sampling (CUFES) observed moderate concentrations of eggs off central California in high biomass years, and few to none when the population was low (fig. 6). Larvae were present off central California in both high and low biomass years, but their concentration was not only 1–2 orders of

magnitude lower than the SCB concentration but spread out over a much smaller area (figs. 3–5). Although there were anecdotal reports of large anchovy schools close to shore (Goode 2013; Herreria 2014), even if anchovy spawned there unobserved by CalCOFI ichthyoplankton sampling, underway CUFES egg sampling, JRS trawls, Spring CPS rope trawls, and the AT survey, it must have been confined to a narrow strip along the shore. A large concentration of fishes multiplied by a small surface area results in a small biomass at oceanic scales. However, there may have been substantial spawning activity in Mexican waters just south of San Diego (figs. 4–5), and it is not clear what fraction of anchovy spawning by the central stock was south of the survey area.

ACKNOWLEDGEMENTS

Funding for this research was provided by the Pew Charitable Trusts. The authors would like to thank the NMFS SWFSC for providing access to acoustic and trawl data from several ongoing programs, and for helpful advice from A. MacCall, S. McClatchie, D. Griffith, and S. Ralston.

LITERATURE CITED

- Ahlstrom, E. H. 1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. *Fishery Bulletin of the Fish and Wildlife Service*. 60:107–146.
- Asch, R. G. 2015. Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. *Proc. Natl. Acad. Sci.* 112:E4065–E4074.
- Barnett, A. M., A. E. Jahn, P. D. Sertic, and W. Watson. 1984. Distribution of ichthyoplankton off San Onofre, California, and methods for sampling very shallow coastal waters. *Fish. Bull.* 82:97–111.
- Bartolone, P., 2014. Massive schools of anchovies drawing humpback whales to California's coast. <http://www.caprudio.org/articles/2014/09/02/massive-schools-of-anchovies-drawing-humpback-whales-to-californias-coast/>.
- Baumgartner, T. R., A. Soutar, and V. Ferreirabartrina. 1992. Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara Basin, California. *Calif. Coop. Oceanic Fish. Invest. Rep.* 33:24–40.
- Brewer, G. D., and P. E. Smith. 1982. Northern anchovy and Pacific sardine spawning off southern California during 1978–80: preliminary observations on the importance of the nearshore coastal region. *CalCOFI Reports*. 23:160–171.
- Checkley, D. M., P. B. Ortner, L. R. Settle, and S. R. Cummings. 1997. A continuous, underway fish egg sampler. *Fish. Oceanogr.* 6:58–73.
- Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Adv. Mar. Biol.* 26:249–293.
- Demer, D. A., J. P. Zwolinski, G. R. Cutter, K. A. Byers, B. J. Macewicz, and K. T. Hill. 2013. Sampling selectivity in acoustic-trawl surveys of Pacific sardine (*Sardinops sagax*) biomass and length distribution. *ICES J. Mar. Sci.* 70:1369–1377.
- Dotson, R. C., D. A. Griffith, D. L. King, and R. L. Emmett. 2010. Evaluation of a marine mammal excluder device (MMED) for a Nordic 264 midwater rope trawl. NOAA Tech. Memo. NOAA-TM-NMFS-SWFSC-455:1–14.
- Drake, N. 2013. Feeding frenzy fills Monterey Bay with humpback whales. <http://www.wired.com/2013/09/whales-in-monterey-bay/>.
- Field, D. B., T. R. Baumgartner, V. Ferreira, D. Gutierrez, H. Lozano-Montes, R. Salvatelli, and A. Soutar. 2009. Variability from scales in marine sediments and other historical records. In *Climate change and small pelagic fish*, D. M. Checkley, J. Alheit, Y. Oozeki, C. Roy eds. New York: Cambridge University Press, pp. 45–63.

- Fissel, B. E., N. C. H. Lo, and S. F. Herrick Jr. 2011. Daily egg production, spawning biomass and recruitment for the central subpopulation of northern anchovy 1981–2009. *Calif. Coop. Oceanic Fish. Invest. Rep.* 52:116–129.
- Gaura, M. 2015. Whale watching in Monterey Bay just got really close. <http://www.sfgate.com/food/article/Whale-watching-in-Monterey-Bay-just-got-really-6207281.php>.
- Goode, E. 2013. With extra anchovies, deluxe whale watching. http://www.nytimes.com/2013/11/25/us/with-extra-anchovies-deluxe-whale-watching.html?_r=0.
- Griffith, D.A. 2008. Collecting adult coastal pelagic fish using the Nordic 264 rope trawl: a guide to deployment and sample processing. Department of Commerce, NOAA NMFS, Southwest Fisheries Science Center. NOAA Unpub. Rep.:1–12.
- Herrera, C. 2014. Enormous school of anchovies makes rare appearance at Scripps Pier in San Diego. http://www.huffingtonpost.com/2014/07/11/school-of-anchovies-san-diego_n_5572928.html.
- Hewitt, R. (Ed.) 1980. Distributional atlas of fish larvae in the California Current region: northern anchovy, *Engraulis mordax* Girard, 1966–79, CalCOFI Atlas No. 28.
- Hunter, J. R., and K. M. Coyne. 1982. The onset of schooling in northern anchovy larvae, *Engraulis mordax*. *CalCOFI Reports*. 23:246–251.
- Jacobson, L.D., N. C. H. Lo, and J.T. Barnes. 1994. A biomass-based assessment model for northern anchovy, *Engraulis mordax*. *Fish. Bull.* 92:711–724.
- Lehodey, P., J. Alheit, M. Barange, T. Baumgartner, G. Beaugrand, K. Drinkwater, J. M. Fromentin, S. R. Hare, G. Ottersen, R. I. Perry, C. Roy, C. D. Van der Lingen, and F. Werner. 2006. Climate variability, fish, and fisheries. *J. Clim.* 19:5009–5030.
- Lindgren, M., D. M. Checkley, T. Rouyer, A. D. MacCall, and N. C. Stenseth. 2013. Climate, fishing, and fluctuations of sardine and anchovy in the California Current. *Proc. Natl. Acad. Sci.* 110:13672–13677.
- Lo, N. C. H. 1985a. Egg production of the central stock of northern anchovy, *Engraulis mordax*, 1951–82. *Fish. Bull.* 83:137–150.
- Lo, N. C. H. 1985b. A model for temperature-dependent northern anchovy egg development and an automated procedure for the assignment of age to staged eggs. In *An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy (Engraulis mordax)*, R. Lasker ed. NOAA Tech. Rep. NMFS-36, pp. 43–50.
- Lynn, K., D. Porzio, A. Kesaris, and A. Holder. 2015. California Department of Fish and Wildlife report on aerial survey observations of northern anchovy in the Southern California Bight. Pacific Fishery Management Council Agenda Item G.3.a, Supplemental CDFW Report, pp. 1–6.
- MacCall, A. D. 1996. Patterns of low-frequency variability in fish populations of the California current. *Calif. Coop. Oceanic Fish. Invest. Rep.* 37:100–110.
- MacCall, A. D., and M. H. Prager. 1988. Historical changes in abundance of six fish species off southern California, based on CalCOFI egg and larva samples. *Calif. Coop. Oceanic Fish. Invest. Rep.* 29:91–101.
- MacCall, A. D., W. J. Sydeman, P. C. Davison, and J. A. Thayer. 2016. Recent collapse of northern anchovy biomass off California. *Fish. Res.* 175:87–94.
- Method, R. D. 1989. Synthetic estimates of historical abundance and mortality for northern anchovy. *Am. Fish. Soc. Symp.* 6:66–82.
- Moser, H. G., R. L. Charter, P. E. Smith, D. A. Ambrose, W. Watson, S. R. Charter, and E. M. Sandknop. 2001. Distributional atlas of fish larvae and eggs in the Southern California Bight region: 1951–98, CalCOFI Atlas No. 34. 166 p.
- NOAA, 2015. <https://swfsc.noaa.gov/textblock.aspx?Division=FRD&id=1121>.
- Parrish, R. H., 2015. Comments on Non-fishery related collapse of northern anchovy off California MacCall, A. D., W. J. Sydeman, P. C. Davison, and J. A. Thayer. Pacific Fishery Management Council Agenda Item H.3.b, Supplemental Public Comment 4, pp. 1–7.
- Parrish, R. H., D. L. Mallicoate, and R. A. Klingbeil. 1986. Age dependent fecundity, number of spawnings per year, sex ratio, and maturation stages in northern anchovy, *Engraulis mordax*. *Fish. Bull.* 84:503–517.
- Ralston, S., J. C. Field, and K. M. Sakuma. 2015. Long-term variation in a central California pelagic forage assemblage. *J. Mar. Syst.* 146:26–37.
- Richardson, S. L. 1981. Spawning biomass and early life of northern anchovy, *Engraulis mordax*, in the northern sub-population off Oregon and Washington. *Fish. Bull.* 78:855–876.
- Rykaczewski, R. R., and D. M. Checkley. 2008. Influence of ocean winds on the pelagic ecosystem in, upwelling regions. *Proc. Natl. Acad. Sci.* 105:1965–70.
- Santora, J. A., J. C. Field, I. D. Schroeder, K. M. Sakuma, B. K. Wells, and W. J. Sydeman. 2012. Spatial ecology of krill, micronekton and top predators in the central California Current: Implications for defining ecologically important areas. *Prog. Oceanogr.* 106:154–174.
- Schwartzlose, R. A., J. Alheit, A. Bakun, T. R. Baumgartner, R. Cloete, R. J. M. Crawford, W. J. Fletcher, Y. Green-Ruiz, E. Hagen, T. Kawasaki, D. Lluch-Belda, S. E. Lluch-Cota, A. D. MacCall, Y. Matsuura, M. O. Nevarez-Martinez, R. H. Parrish, C. Roy, R. Serra, K. V. Shust, M. N. Ward, and J. Z. Zuzunaga. 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. *S. Afr. J. Mar. Sci.* 21:289–347.
- Smith, P. E. 1972. Increase in spawning biomass of northern anchovy, *Engraulis mordax*. *Fish. Bull.* 70:849–874.
- Smith, P. E. 1985. Year class strength and survival of 0-group clupeoids. *Can. J. Fish. Aquat. Sci.* 42:69–82.
- Zwolinski, J. P., D. A. Demer, K. A. Byers, G. R. Cutter, J. S. Renfree, T. S. Sessions, and B. J. Macewicz. 2012. Distributions and abundances of Pacific sardine (*Sardinops sagax*) and other pelagic fishes in the California Current Ecosystem during spring 2006, 2008, and 2010, estimated from acoustic-trawl surveys. *Fish. Bull.* 110:110–122.

CALIFORNIA ANCHOVY POPULATION REMAINS LOW, 2012–16

J. A. THAYER, A. D. MACCALL, AND W. J. SYDEMAN

Farallon Institute
101 H Street, Suite Q
Petaluma, CA
ph: (707) 981-8033
jthayer@faralloninstitute.org

P. C. DAVISON

Scripps Institution of Oceanography affiliation
San Diego, CA

ABSTRACT

Updated abundance estimates of the central subpopulation of northern anchovy (*Engraulis mordax*) are developed from California Cooperative Oceanic Fisheries Investigations (CalCOFI) data on egg and larval densities for 1951–2011, with new estimates for 2012–15. We followed the approach of MacCall et al. (2016; Fish. Res.) which corrected for a hyperstability bias due to nearshore concentration of CalCOFI stations and the tendency of the anchovy population to contract into this area when abundances are low. We corrected previous estimates based on calibration using an erroneous absolute biomass value from the 1980s, and extended estimates up through 2015. Anchovy spawning biomass remains below 100,000 metric tons, at an average of 20,700 metric tons over the past 7 years. Although the most recent 2016 CalCOFI data are not yet available, recent results from the continuous underway fish egg sampler (CUFES) do not indicate any substantial recovery of the anchovy population to date.

INTRODUCTION

Northern anchovy is an important component of the forage fish community of the California Current ecosystem (CCE). Anchovy are schooling coastal pelagic fish that have undergone large oscillations in abundance for thousands of years, with periodicity of ~60 y (Baumgartner et al. 1992; MacCall 1996; Field et al. 2009) which have been linked to climate influences (Lehodey et al. 2006; Lindegren et al. 2013). Anchovy are a relatively small and short-lived species (most <16 cm in length; most fishes <5 y in age; Schwartzlose et al. 1999), with high fecundity and mortality, and are thought to do well in colder waters associated with high coastal upwelling (Rykaczewski and Checkley 2008; Lindegren et al. 2013). There are historically three oceanic population centers for anchovy along the Pacific coast of North America: a northern stock near the Columbia River mouth, a central stock concentrated in the Southern California Bight (SCB) and Monterey Bay, and a southern stock off of Baja California (Huppert 1980; Schwartzlose et al. 1999; Zwolinski et al. 2012).

Anchovy is an important prey resource for many upper trophic level predators in the CCE (Szloboszlai et al. 2015), and supported historically significant fish-

eries in California and Mexico (CDFG 2001). Anchovy stock assessments were conducted until 1995 (Jacobson et al. 1995); since then, only spawning biomass estimates exist (MacCall et al. 2016). After a spike in estimated spawning biomass briefly exceeding a million metric tons (MT) in 2005–06, the population subsequently collapsed by 2009 (MacCall et al. 2016). The systemic causes of the recent decline in abundance are not clear, although one of the proximal causes of the decline has been hypothesized to be the decrease in egg and larval survivorship during the 2000s (Fissel et al. 2011; MacCall et al. 2016). The cause of that mortality is not presently known, but intensified filter feeding cannibalism by the parents is a likely possibility (i.e., high density of adults can occur from the range contraction at low population sizes; MacCall 1990). The consequence was a severe reduction in the production of recruitment-age fish. Given the short timing and the magnitude of the decline in abundance, it happened faster than could be explained by poor recruitment alone, indicating that the natural mortality rate of adults also probably increased. The estimation approach of MacCall et al. (2016) excluded data from the extreme inshore region because those trawl stations were not sampled continuously through time, but separate analyses of these inshore stations revealed egg and larval densities similar to those in the continuously sampled area (Davison et al. 2017). Therefore, an unknown but probably large portion of the remaining remnant population thereafter consisted of conspicuous, concentrated, nearshore shoals, where it has been vulnerable to predators and the fishery as well as appearing paradoxically abundant to shore-based observers such as members of the public (MacCall et al. 2016; Davison et al. 2017).

Herein, we correct previous biomass estimates for the central subpopulation of northern anchovy, which were based on calibration using an erroneous absolute biomass value from the early 1980s. We also extend the spawning biomass estimates to 2015 as additional data have become available. We follow the MacCall et al. (2016) method that corrected for hyperstability bias (Hilborn and Walters 1992) due to the nearshore concentration of CalCOFI stations and the tendency of the anchovy population to contract into this area when abundances are low (MacCall 1990).

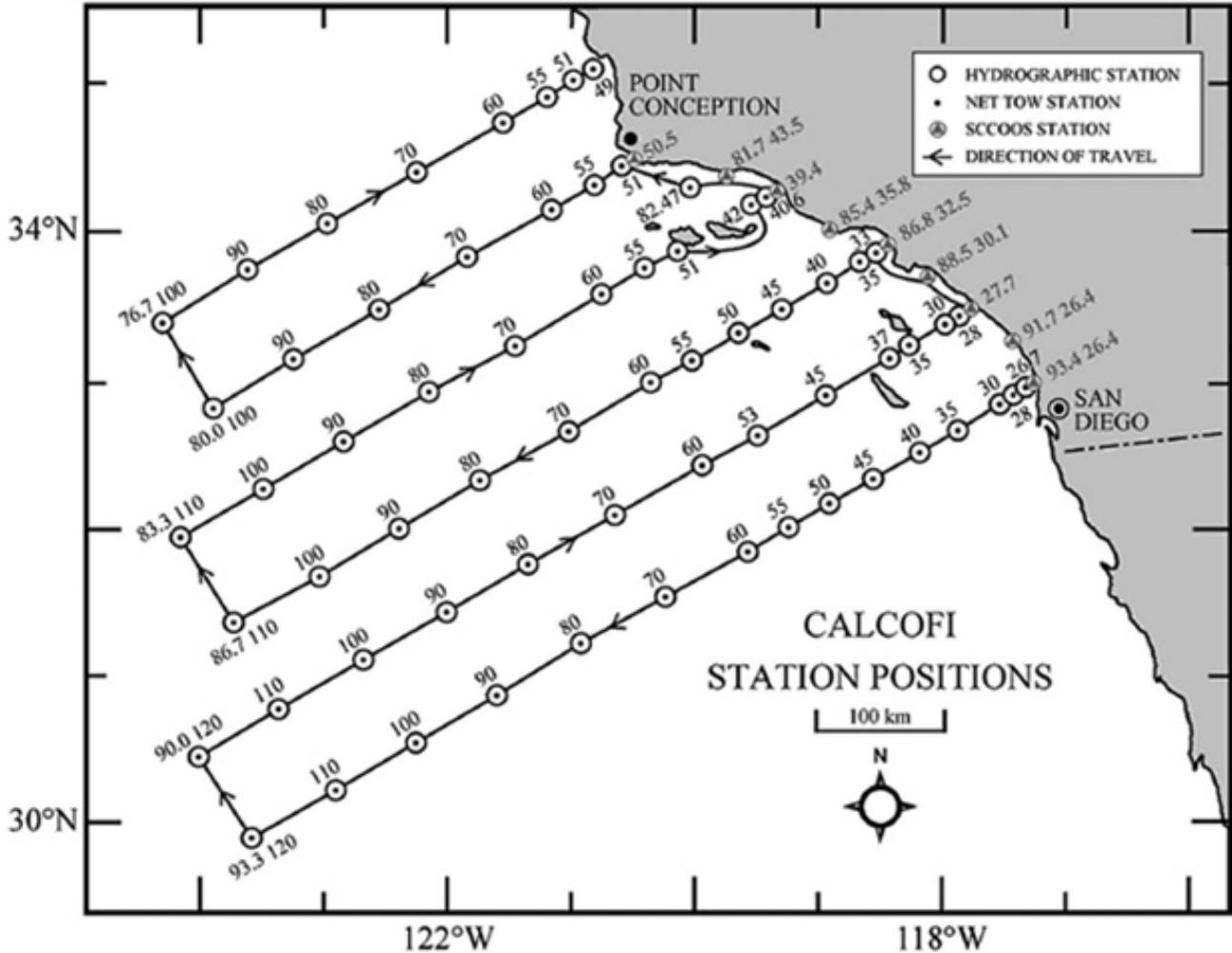


Figure 1. Locations of core southern California CalCOFI sampling stations (from MacCall et al. 2016), also showing location of the nine nearshore SCCOOS stations added in Fall 2004, but not included in our long-term timeseries due to standardization of survey locations.

METHODS

Following the methods of MacCall et al. (2016), egg and larval sample densities from core CalCOFI surveys (fig. 1) for January and April were geo-spatially weighted, summed to obtain total abundance, developed into a combined index of productivity, and then calibrated to early 1980s absolute biomass estimates based on the daily egg production method (DEPM). These DEPM estimates spanned CalCOFI line 60 (off Pt. Reyes, California), to CalCOFI line 110.0 (at Bahia del Rosasio, Baja California, Mexico) (Lasker 1985; Bindman 1986), allowing the core survey results to be scaled up to population biomass (Methot et al. 1989; Jacobson et al. 1994). DEPM estimates were corrected here prior to calibration. The erroneous spawning biomass value for year 1982 (used in all previous assessments) was due to the value in short tons estimated by Picquelle and Hewitt (1983) having been reported as metric tons in a summary by Bindman (1986).

The DEPM method includes sampling of spawning adult (mature) anchovies during ichthyoplankton collections to obtain information on size and age structure and female fecundity. Since such data were not available recently, we had to rely here on historical average values for such data, acknowledging that for indeterminate spawners such as anchovy where egg production is largely a function of adult condition, this is not ideal. However, there was no trend evident in spawning phenology, only a slight nonsignificant shift (-3 d decade $^{-1}$; Asch 2015). Since the CalCOFI data used included surveys with any days in January or any days in April, so incorporating many February, March, and May data, the slight shift in peak spawning would not be expected to greatly affect results (Davison et al. 2017; MacCall et al. 2016).

Both egg and larval samples were used for biomass estimates in 1951–99 and 2012–15, although larval samples had to be dropped in 2000–11 due to exception-

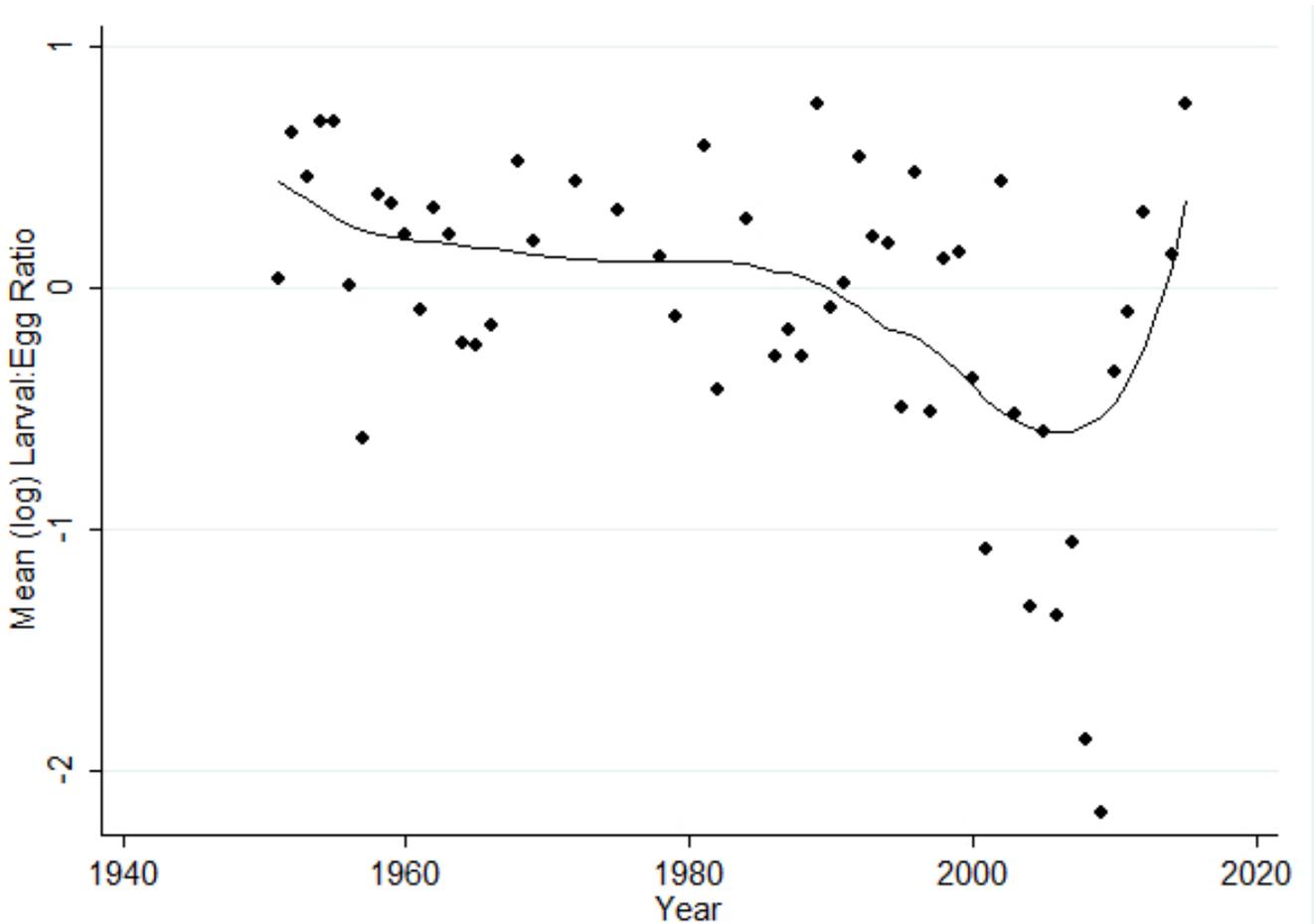


Figure 2. Geometric mean of January and April larvae to egg ratio for northern anchovy sampled by the CalCOFI program, 1951–2015. The ratio for 2013 was dropped as this value was an outlier: $\log(65) = 1.8$. Lowess smoothing function (bandwidth 0.6) shown.

ally low larvae to egg ratios (MacCall et al. 2016; fig. 2). The extended estimates included April and January data as was available in 2012–14. Only partial cruise track data were available in January 2014 due to ship engine malfunction. As of this analysis, January data were not yet available for 2015. Precision of abundance estimates was calculated using a jackknife procedure that provided variance estimates for each of our two to four indices (depending on the year and data available), January egg and larvae and April egg and larvae, and subsequent approximation to produce a variance estimate for the combined index, which tended to overestimate the variance (MacCall et al. 2016).

RESULTS

Revised and extended northern anchovy spawning biomass estimates for the central subpopulation, with coefficients of variation, are presented in Appendix I. The biomass remains very low and probably at an all-time low since CalCOFI sampling began in 1951. Although the abundance estimates are imprecise at this low level, the biomass is almost certainly less than 100,000 mt.

Larvae to egg ratios decreased in the early 2000s, indicating poor survival. Post-2011, the larvae to egg ratio returned to values within the range seen in 1951–99 (fig. 2). Therefore, both egg and larval samples were utilized for updating biomass estimates for 2012 through 2015.

The extended time series (2012–15) shows that stock remains low after a collapse after 2005 (i.e., two orders of magnitude below the 2005 value; fig. 3). The coefficients of variation of recent biomass estimates are high due to low numbers of positive stations, etc., and therefore estimates for recent single years are imprecise and should not be used individually for interpretation. In the past 7 years, annual estimates for anchovy spawning biomass had an equally weighted average of 20,700 mt. In the past 4 years since the last anchovy biomass update, estimated biomass averaged 24,300 mt.

DISCUSSION

Although it was not possible to estimate spawning biomass precisely with available data, the analysis clearly supports the conclusion that abundance of the northern anchovy central subpopulation is at the lowest val-

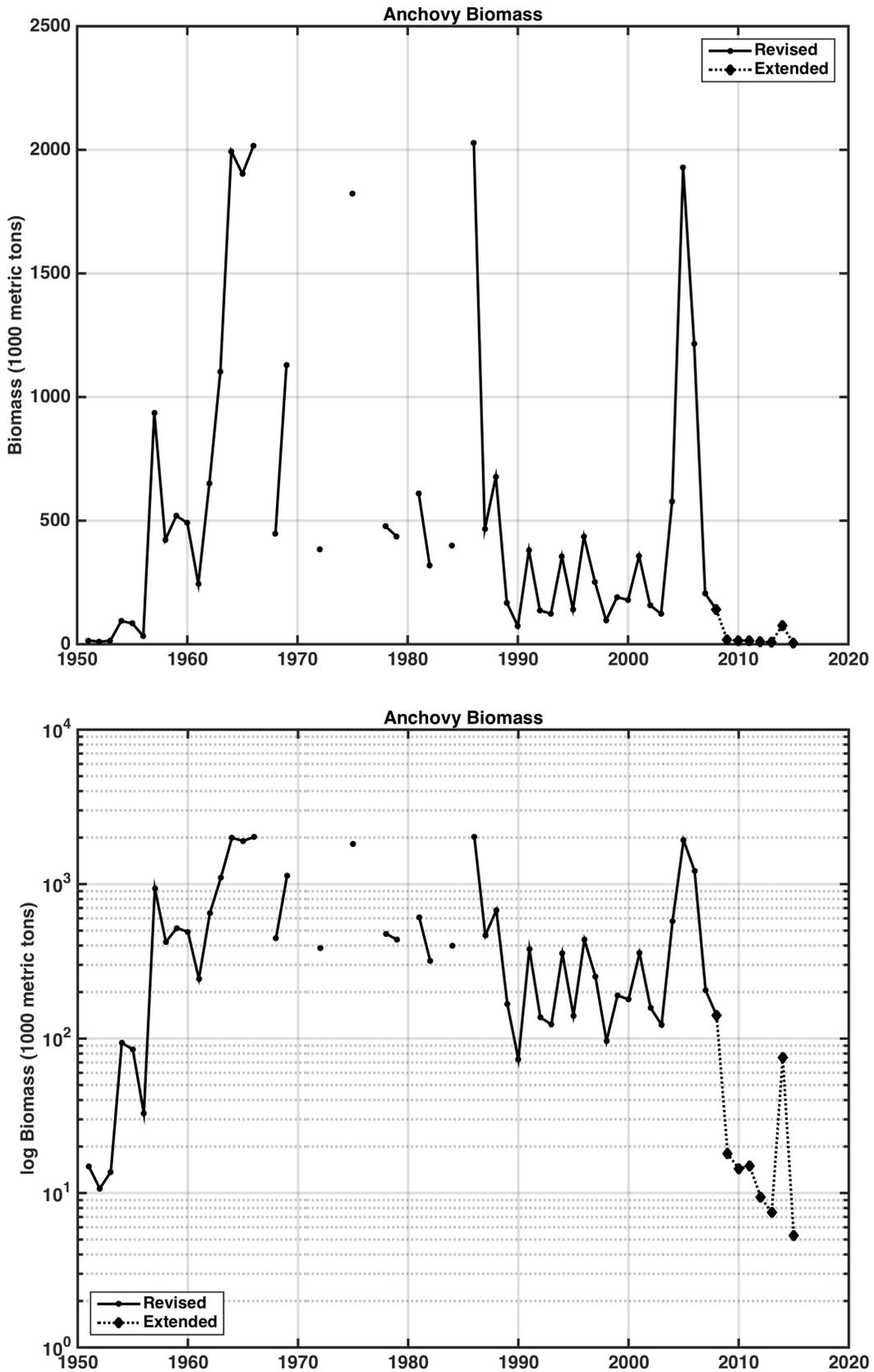


Figure 3. Anchovy biomass estimates on (a) numeric and (b) log scale. As extended estimates are based on few positive stations, CVs are imprecise. After removing larvae from estimates in 2000–11, adding larvae back into estimates for 2012–15 (dotted lines) does not change the pattern, but does improve precision.

ues since the beginning of CalCOFI surveys. Anchovy spawning biomass remains below 100,000 metric tons, at a multiyear average of 20,000–25,000 metric tons. Other fisheries-independent trawl survey results and predator responses also support this.

There were not sufficient spatial data with which to separately estimate biomass for central California and/or northern Baja, Mexico (see Lasker 1985; MacCall et al. 2016). The available core CalCOFI data covered most of the anchovy biomass in most years, but historical patterns suggest that our estimates may be relatively less precise at very low biomasses. For this reason, we suggest using an average of recent years rather than an annual point estimate.

Recent independent trawl survey data supported our results of sustained low anchovy spawning biomass. Spring CalCOFI cruises sample pelagic nekton at night using a Nordic 264 rope trawl (Davison et al. 2017; Griffith 2008; Dotson et al. 2010). Rope trawl survey results from 2010–13 showed that anchovy were only captured inshore in the Southern California Bight, near Pt. Conception, and off of Washington State. No anchovy at all were collected off of central California, despite the fact that it was the region of greatest effort (Davison et al. 2017). The National Marine Fisheries Service (NMFS) Rockfish Recruitment and Ecosystem Assessment Survey (RRS) also had very low catches of age 0 and age 1+ anchovy in 2010–13 (Sakuma 2015). In 2014–15, adult northern anchovy catches remained low in all areas, including inshore sampling stations. Catches of larvae and pelagic juveniles, however, increased in the southern California region in 2014, and in all regions of California in 2015 (southern, central and northern; Sakuma 2015). The NMFS Acoustic-Trawl Survey (ATS) estimated a low total anchovy biomass for the central subpopulation in 2015 (<35,000 mt; Zwolinski et al. 2016). The ATS catch had a range of <4–13 cm with a mode of 6 cm indicating primarily young-of-the-year; this included almost exclusively small anchovy (<10 cm) in the central California region.

Recent available predator data included unusual mortality events for California sea lions in southern California in 2009–10 (Melin et al. 2010, 2012). Declines in seabird abundance at sea (Sydeman et al. 2015; Santora and Sydeman 2015) and reductions of anchovy in seabird diets in both central and southern California were seen at least through 2012 (e.g., Elliott et al. 2015). More recently, poor breeding performance of brown pelicans off southern California (Henry 2015) and reductions in anchovy in sea lion diets in central California were observed up through 2014 (J. Thayer, unpublished data). Increases in anchovy in predator diets in central California were observed in 2015, almost exclusively age-0 fish (Beck et al. 2015; J. Thayer/Farallon Institute,

unpublished data), mirroring increased catch of age-0 anchovy in 2015 acoustic and trawl surveys.

Anecdotal observations (mostly visual) suggested that anchovy were extremely abundant in recent years (e.g., newspaper reports summarized in Davison et al. 2017). Davison et al. (2017) examined not only RRS and CalCOFI rope trawls, but additional data from the CalCOFI ichthyoplankton time series, nearshore Southern California 85 Coastal Ocean Observing System (SCCOOS) stations and aerial surveys. He explored whether anchovy adults migrated north of the study area, whether there was a large biomass of anchovies nearshore, or whether spawning was temporally missed in our analyses, yet found no evidence of any of the above. Thus, we adhered to our previous methodology, and maintain with the current updates/corrections that the 2009–16 population crash is real and that the remnant anchovy population contracted to extremely nearshore habitat where it has appeared paradoxically abundant to observers.

Another seeming contradiction was that fishery catch of anchovy in 2015 surpassed the estimate of spawning biomass that year. Similar anomalies were observed at low spawning biomasses in the early 1950s, but we now understand better how they can be explained. As detailed in Davison et al. (2017), such an anomaly can result from a small calibration error and bias in the biomass estimate due to nearshore refuges from fisheries-independent surveys but not from fishers. While our spawning biomass estimate represents the entire central subpopulation, core CalCOFI station data were collected in southern California and calibrated using the 1980s DEPM data, which span from Baja California to Pt. Reyes in the north. Fishery catch in 2015 occurred largely in central California (CDFW 2016). Furthermore, direct comparison of CalCOFI-based spawning biomass estimates with fishery catches is misleading because it assumes they have similar age structure, which is not necessarily the case. To the extent that the catch includes pre-spawning anchovies (immature) and occurs in the fall and winter, the total biomass available to the fishery could substantially exceed the spawning biomass estimated as of January–April. (Indeed, 2015 trawls and predator diet contained a high proportion of immature anchovy; Sakuma 2015; Zwolinski et al. 2016; Beck et al. 2015; J. Thayer unpublished data.) Therefore, a more meaningful comparison is between catch and total biomass—2015 fishery catch was just over half of the preliminary total biomass estimate from southern and central California ATS data (Zwolinski et al. 2016). The anchovy population crash occurred in the near-absence of fishing and therefore was a natural phenomenon (MacCall et al. 2016; McClatchie et al. 2017), yet fishing pressure at the current low population levels may be high.

The tendency of anchovy to contract inshore at low population sizes makes them more susceptible to fishing and many predators. Landings may actually go up when the population is depressed (Beverton 1990). Many anchovy predator populations have been increasing (Szloboszlai et al. 2015; Caretta et al. 2014; Grandin et al. 2016), and sequential poor recruitment events have likely had substantive impacts on anchovy abundance and trends. The population spiked in 2005–06, then crashed from 2007–09; a linear regression of the log of biomass vs. year yields a slope of -1.15 . If we ignore fishery catches and assume there was no recruitment, this would mean that mortality M was nearly double the value of 0.6 used by Jacobson et al. (1994). These anchovies live about 4 years (longer in very cold water but such conditions have not occurred since before 1975; Mais 1981; McGowan et al. 2003). Anchovy M increases with age (MacCall 1974), so the older age structure after several years of recruitment failure could also contribute to an increase in population M .

It is still unknown if a 2015 increase of age-0 anchovy in central California acoustic and trawl surveys and reflected in predator diet resulted in much survival of anchovy to age 1+. Although the most recent 2016 CalCOFI data are not yet available, results from the continuous underway fish egg sampler (CUFES) from recent surveys indicated egg distribution nearshore in a small area at very low peaks of ~ 15 eggs/m² (fig. 4). Thus, there is no indication of substantial recovery of the anchovy population in 2016.

It remains that the core CalCOFI survey does not completely cover the range of the central anchovy sub-population. While estimates may be relatively precise in large biomass years, they are more imprecise at low population sizes. However, Davison et al. (2017) showed that neither northern nor nearshore concentrations have substantially altered recent overall spawning biomass estimates. More could be done in the future, such as using the central California and nearshore SCOOS station ichthyoplankton data along with the core CalCOFI region to estimate biomass in 2016 (NOAA 2016), for which new calibrations would be needed. Additional effort to collaborate with Mexico is needed to determine present and recent biomass in Mexican waters, potentially from the IMECOCAL program (Investigaciones Mexicanas de la Corriente de California). At present, however, all available data point to continued extraordinarily low spawning biomass of the central subpopulation of northern anchovy.

ACKNOWLEDGEMENTS

We thank the Pew Charitable Trusts and the National Fish and Wildlife Foundation for funding this study. S. A. Thompson assisted with editing and M. Garcia-Reyes

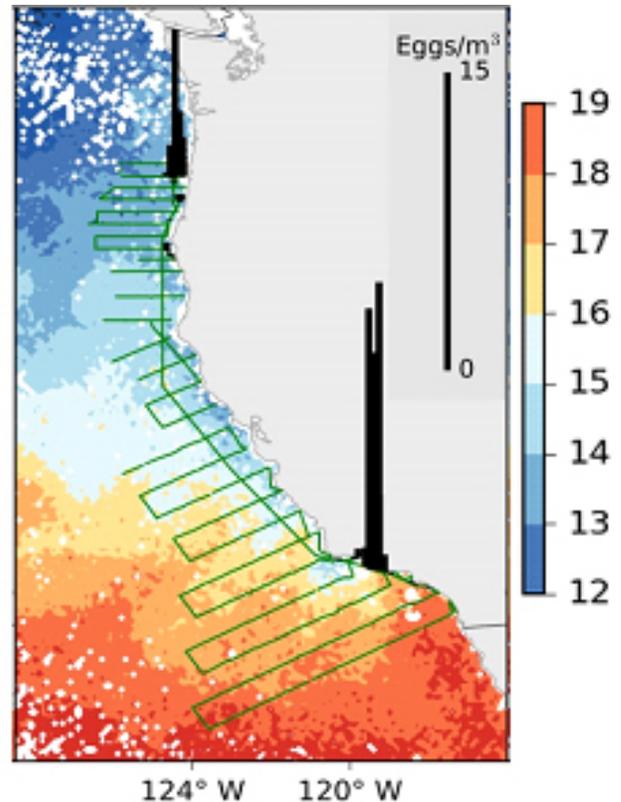


Figure 4. Preliminary CUFES survey results from spring 2016 showing anchovy egg catch and distribution. Note the continued very nearshore distribution and low values of 15 eggs/m² or less. (<https://swfsc.noaa.gov/textblock.aspx?Division=FRD&id=1121>).

helped with figures. We also thank the many people who for decades have contributed to CalCOFI surveys, and who have made the data available for analysis.

LITERATURE CITED

- Baumgartner, T. R., A. Soutar, and V. Ferreira-Bartrina. 1992. Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara Basin, California. Calif. Coop. Oceanic Fish. Invest. Rep. 33:24–40.
- Beck, J., R. Carle, D. Calleri, and M. Hester. 2015. Año Nuevo State Park Seabird Conservation and Habitat Restoration Report 2015. Oikonos - Ecosystem Knowledge Report. 45 pp. <http://oikonos.org/wp-content/uploads/2013/06/2015-Año-Nuevo-Island-Seabird-Conservation-Report.pdf>.
- Beverton, R. J. H. 1990. Small marine pelagic fish and the threat of fishing: are they endangered? J. Fish Biol. 37(Supplement A):5–16.
- Bindman, A. G. 1986. The 1985 spawning biomass of the northern anchovy. Calif. Coop. Ocean. Fish. Invest. Rep. 27:16–24.
- California Department of Fish and Game. 2001. Northern anchovy *Engraulis mordax*. In: California's living marine resources: A status report, pp. 303–305.
- California Department of Fish and Wildlife. 2016. Final California commercial landings for 2015. <https://www.wildlife.ca.gov/Fishing/Commercial/Landings#260041375-2015>.
- Carretta, J. V., E. Oleson, D. W. Weller, A. R. Lang, K. A. Forney, J. Baker, B. Hanson, K. Martien, M. M. Muto, M. S. Lowry, J. Barlow, D. Lynch, L. Carswell, R. L. Brownell Jr., D. K. Mattila, and M. C. Hill. 2014. U.S. Pacific Marine Mammal Stock Assessments: 2012. NOAA Tech. Memo. NOAA-TM-NMFS-SWFSC-504. Southwest Fisheries Science Center, 378 pp.
- Davison, P. C., W. J. Sydeman, and J. A. Thayer. 2017. Are there temporal or spatial gaps in recent estimates of anchovy off California? Calif. Coop. Oceanic Fish. Invest. Rep. 58:1–13.

- Dotson, R. C., D. A. Griffith, D. L. King, and R. L. Emmett. 2010. Evaluation of a marine mammal excluder device (MMED) for a Nordic 264 mid-water rope trawl. NOAA Tech. Memo. NOAA-TM-NMFS-SWFSC-455. Southwest Fisheries Science Center, 14 pp.
- Elliott, M. L., R. W. Bradley, D. P. Robinette, and J. Jahncke. 2015. Changes in forage fish community indicated by the diet of the Brandt's cormorant (*Phalacrocorax penicillatus*) in the central California Current. *J. Mar. Sys.* 146:50–58.
- Field, J. C., T. R. Baumgartner, V. Ferreira, D. Gutierrez, H. Lozano-Montes, R. Salvateci, and A. Soutar. 2009. Variability from scales in marine sediments and other historical records. In *Climate Change and Small Pelagic Fish*, D. M. Checkley Jr., J. Alheit, Y. Oozeki, and C. Roy, eds. Cambridge University Press, Cambridge, U.K., pp. 45–63.
- Fissel, B. E., N. C. H. Lo, and S. F. Herrick Jr. 2011. Daily egg production, spawning biomass and recruitment for the central subpopulation of northern anchovy 1981–2009. *Calif. Coop. Oceanic Fish. Invest. Rep.* 52:116–129.
- Grandin, C. J., A. C. Hicks, A. M. Berger, A. M. Edwards, N. Taylor, I. G. Taylor, and S. Cox. 2016. Status of the Pacific Hake (whiting) stock in U.S. and Canadian waters in 2016. Prepared by the Joint Technical Committee of the U.S. and Canada Pacific Hake/Whiting Agreement, National Marine Fisheries Service and Fisheries and Oceans Canada. 165 pp.
- Griffith, D. A. 2008. Collecting adult coastal pelagic fish using the Nordic 264 rope trawl: a guide to deployment and sample processing. Department of Commerce, NOAA NMFS, Southwest Fisheries Science Center. NOAA Unpub. Rep., 12 pp.
- Henry, S. P. 2015. Pacific Fishery Management Council Agenda Item G.3–Anchovy Update. Agenda Item G.3. USFWS Report. http://www.pcouncil.org/wp-content/uploads/2015/05/G3a_USFWS_Rpt_JUN2015_BB.pdf.
- Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: Choice, dynamics and uncertainty. Kluwer Academic Publishers, Boston/Dordrecht/London. 570 pp.
- Huppert, D. D., A. D. MacCall, G. D. Stauffer, K. R. Parker, J. A. McMillan, H. W. Frey. 1980. California's northern anchovy fishery: Biological and economic basis for fishery management. NOAA Tech. Memo. NOAA-TM-NMFS-SWFSC-1, 242 pp.
- Jacobson, L. D., N. C. H. Lo, S. F. Herrick Jr., and T. N. Bishop. 1995. Spawning biomass of the northern anchovy in 1995 and status of the coastal pelagic fishery during 1994. Southwest Fisheries Science Center, National Marine Fisheries Service Administration Report LJ-95-11. 52 pp.
- Lehodey, P., J. Alheit, M. Barange, T. Baumgartner, G. Beaugrand, K. Drinkwater, J. M. Fromentin, S. R. Hare, G. Ottersen, R. I. Perry, C. Roy, C. D. Van der Lingen, and F. Werner. 2006. Climate variability, fish, and fisheries. *J. Clim.* 19:5009–5030.
- Lindegren, M., D. M. Checkley Jr., T. Rouyer, A. D. MacCall, and N. C. Stenseth. 2013. Climate, fishing, and fluctuations of sardine and anchovy in the California Current. *Proc. Nat. Acad. Sci. U.S.A.* 110:13672–13677.
- MacCall, A. D. 1974. The mortality rate of *Engraulis mordax* in southern California. *Calif. Coop. Oceanic Fish. Invest. Rep.* 17:131–135.
- MacCall, A. D. 1990. Dynamic geography of marine fish populations. Washington Sea Grant, Seattle. 163 pp.
- MacCall, A. D. 1996. Patterns of low-frequency variability in fish populations of the California current. *Calif. Coop. Oceanic Fish. Invest. Rep.* 37:100–110.
- MacCall, A. D., W. J. Sydeman, P. C. Davison, and J. A. Thayer. 2016. Recent collapse of northern anchovy biomass off California. *Fish. Res.* 175:87–94.
- McClatchie, S., I. L. Hendy, A. R. Thompson, and W. Watson. 2017. Collapse and recovery of forage fish populations prior to commercial exploitation. *Geophys. Res. Lett.* 10.1002/2016GL071751.
- Mais, K. F. 1981. Age-composition changes in the anchovy, *Engraulis mordax*, central population. *Calif. Coop. Ocean. Fish. Invest. Rep.* 22:82–87.
- McGowan, J. A., S. J. Bograd, R. J. Lynn, and A. J. Miller. 2003. The biological response to the 1977 regime shift in the California Current. *Deep-Sea Res. Pt. II* 50:2567–2582.
- Melin, S. R., A. J. Orr, J. D. Harris, J. L. Laake, and R. L. DeLong. 2010. Unprecedented mortality of California sea lion pups associated with anomalous oceanographic conditions along the central California coast in 2009. *Calif. Coop. Ocean. Fish. Invest. Rep.* 51:182–194.
- Melin, S. R., A. J. Orr, J. D. Harris, J. L. Laake, and R. L. DeLong. 2012. California sea lions: An indicator for integrated ecosystem assessment. *Calif. Coop. Ocean. Fish. Invest. Rep.* 52:140–152.
- NOAA National Marine Fisheries Service. 2016. Egg and larval production of the central subpopulation of the northern anchovy in the southern California Bight. Report to the Pacific Fisheries Management Council. 31 pp. http://www.pcouncil.org/wp-content/uploads/2016/09/anchovy_egg_larval_production-1-Watermarked.pdf.
- Picquelle, S. J., and Hewitt, R. P. 1983. The northern anchovy spawning biomass for the 1982–83 California fishing season. *Calif. Coop. Ocean. Fish. Invest. Rep.* 24:16–28.
- Rykaczewski, R. R., and D. M. Checkley Jr. 2008. Influence of ocean winds on the pelagic ecosystem in upwelling regions. *Proc. Nat. Acad. Sci. U.S.A.* 105:1965–70.
- Sakuma, K. 2015. National Marine Fisheries Service Rockfish Recruitment and Ecosystem Assessment Cruise Report, April 30–June 14, 2015. NOAA Tech. Memo. 18 pp. https://swfsc.noaa.gov/publications/CR/2015/2015_Sakuma.pdf.
- Santora, J. A., W. J. Sydeman, 2015. Persistence of hotspots and variability of seabird species richness and abundance in the southern California Current. *Ecosphere* 6:214.
- Schwartzlose, R. A., J. Alheit, A. Bakun, T. R. Baumgartner, R. Cloete, R. J. M. Crawford, W. J. Fletcher, Y. Green-Ruiz, E. Hagen, T. Kawasaki, D. Lluch-Belda, S. E. Lluch-Cota, A. D. MacCall, Y. Matsuura, M. O. Nevarez-Martinez, R. H. Parrish, C. Roy, R. Serra, K. V. Shust, M. N. Ward, and J. Z. Zuzunaga. 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. *S. Afr. J. Mar. Sci.* 21:289–347.
- Sydeman, W. J., S. A. Thompson, J. A. Santora, J. A. Koslow, R. Goericke, and M. D. Ohman. 2015. Climate-ecosystem change off southern California: Time-dependent seabird predator-prey numerical responses. *Deep-Sea Res. Pt. II* 112:158–170.
- Szoboszlai, A. I., J. A. Thayer, S. A. Wood, W. J. Sydeman, and L. E. Koehn. 2015. Forage species in predator diets: Synthesis of data from the California Current. *Ecol. Inform.* 29:45–56.
- Zwolinski, J. P., and D. A. Demer. 2012. A cold oceanographic regime with high exploitation rates in the Northeast Pacific forecasts a collapse of the sardine stock. *Proc. Nat. Acad. Sci. U.S.A.* 109:4175–4180.
- Zwolinski, J. P., D. A. Demer, B. J. Macewicz, G. R. Cutter Jr., S. Mau, D. Murnin, J. S. Renfree, T. S. Sessions, and K. Stierhoff. 2016. The distribution and biomass of the central-stock Northern anchovy during Summer 2015, estimated from acoustic-trawl sampling. Draft NOAA Technical Report. Appendix 1 of Agenda Item G.4.a. Supplemental SWEFSC Report. http://www.pcouncil.org/wp-content/uploads/2016/11/G4a_Sup_SWFSC_Rpt2_NOV2016BB.pdf

APPENDIX I

Table 1. Previously published (MacCall et al. 2016) and updated biomass values and coefficients of variation for the central subpopulation of northern anchovy. Blank cells indicate no data available. Note that both egg and larval abundances were used for estimating 1951–99 and 2012–15 (light gray), while larval abundances were dropped in 2000–11 when larvae to egg ratios declined (dark gray).

Year	Published Values		New Values		Year	Published Values		New Values	
	Biomass (1000 mt)	total CV	Biomass (1000 mt)	total CV		Biomass (1000 mt)	total CV	Biomass (1000 mt)	total CV
1951	15.5	1.51	14.9	1.51	1984	415.5	0.33	400.0	0.31
1952	11.1	1.78	10.7	1.78	1985				
1953	14.3	1.57	13.7	1.57	1986	2106.6	0.30	2028.0	0.28
1954	97.5	0.62	93.8	0.61	1987	483.4	0.56	465.4	0.55
1955	88.3	0.65	85.0	0.64	1988	703.9	0.27	677.6	0.25
1956	34.0	1.02	32.8	1.02	1989	173.9	0.47	167.4	0.46
1957	972.3	0.41	936.0	0.40	1990	76.0	1.36	73.2	1.36
1958	438.3	0.32	422.0	0.31	1991	394.8	0.61	380.1	0.61
1959	539.6	0.29	519.4	0.28	1992	142.2	0.52	136.9	0.51
1960	510.0	0.30	491.0	0.29	1993	128.4	0.54	123.6	0.54
1961	253.3	0.40	243.8	0.39	1994	369.4	0.34	355.6	0.33
1962	675.2	0.27	650.0	0.26	1995	146.2	0.51	140.7	0.50
1963	1145.4	0.23	1102.7	0.21	1996	452.6	0.31	435.7	0.30
1964	2070.9	0.20	1993.7	0.18	1997	261.4	0.39	251.7	0.39
1965	1976.3	0.20	1902.6	0.18	1998	100.0	0.61	96.3	0.60
1966	2093.6	0.20	2015.5	0.18	1999	197.6	0.45	190.3	0.44
1967					2000	186.2	0.88	179.3	0.87
1968	465.1	0.57	447.8	0.56	2001	371.7	0.63	357.9	0.63
1969	1173.8	0.23	1130.1	0.21	2002	164.3	0.93	158.1	0.93
1970					2003	127.6	1.06	122.8	1.05
1971					2004	599.6	0.50	577.2	0.50
1972	399.2	0.33	384.3	0.32	2005	2002.5	0.30	1927.7	0.29
1973					2006	1263.6	0.68	1216.4	0.68
1974					2007	213.2	0.82	205.2	0.82
1975	1892.7	0.31	1822.1	0.30	2008	146.6	0.99	141.1	0.98
1976					2009	18.7	5.47	18.0	5.47
1977					2010	15.0	3.06	14.4	3.06
1978	495.5	0.30	477.0	0.29	2011	15.6	3.00	15.0	3.00
1979	453.1	0.31	436.2	0.30	2012			9.4	0.12
1980					2013			7.5	0.50
1981	634.5	0.28	610.9	0.26	2014			75.3	1.30
1982	330.5	0.67	318.2	0.66	2015			5.3	1.23
1983									

TRENDS IN THE PACIFIC HERRING (*CLUPEA PALLASII*) METAPOPOPULATION IN THE CALIFORNIA CURRENT ECOSYSTEM

SARAH ANN THOMPSON

Farallon Institute
101 H St. Ste. Q
Petaluma, CA 94952

and
Climate Impacts Group
University of Washington
Box 355674
Seattle, WA 98195

sathompson@faralloninstitute.org

WILLIAM J. SYDEMAN,

JULIE A. THAYER

Farallon Institute
101 H St. Ste. Q
Petaluma, CA 94952

ANNA WEINSTEIN,

KATHERINE L. KRIEGER

Audubon California
220 Montgomery St., Ste. 1000
San Francisco, CA 94104

DOUG HAY

Pacific Biological Station
Fisheries and Oceans Canada
3190 Hammond Bay Rd.
Nanaimo, BC
V9T 6N7 Canada

ABSTRACT

Pacific herring are important to fisheries and trophic interactions in the California Current Ecosystem (CCE). In this paper we test the hypothesis that herring biomass across the ecosystem has declined over the past three decades. Overall, herring spawning stock biomass has decreased since the mid to late 1980s, though some populations at the local to regional scale appear stable or have even increased. For regional populations in the northern CCE studied over a much longer time period (six decades), cyclic patterns of abundance are evident, suggesting that the shorter-term trend may be part of a longer-term, Pacific Decadal Oscillation (PDO)-scale cycle. In the southern part of the herring range (California and Oregon), population fluctuations are increasing, which may be related to increasing climate variability there (Sydeman et al. 2013; Black et al. 2014). Large-scale trophic mechanisms to local distribution shifts are implicated in metapopulation fluctuations. Future abundance assessments for herring in the CCE should address how climate and fisheries may synergistically impact populations.

INTRODUCTION

Pacific herring (*Clupea pallasii*) occur from Baja California, Mexico, north to the Beaufort Sea and the Arctic Ocean, and west to Japan. Pacific herring have been extremely important to humans; archeological evidence suggests human exploitation of herring at least 8,000 years ago (Thornton et al. 2010), they were the most utilized fish species by communities of the northwest coast during the last several thousand years (McKechnie et al. 2014), and fisheries for this species persist today. All life stages of herring also support key trophic relationships for North Pacific piscivorous fish, seabirds, and mammals (Womble and Sigler 2006; Rice et al. 2010; Schweigert et al. 2010; Koehn et al. 2016); a recent meta-analysis showed that herring ranks fourth in importance to all predators in the California Current Ecosystem and second in importance for

seabirds (Szoboszlai et al. 2015), thus there is potential for competition between human fisheries and marine consumers for this resource.

In the California Current Ecosystem (CCE) off the west coast of North America, some other forage fish species, notably sardine (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*), are currently at very low abundance (e.g., Hill et al. 2016; MacCall et al. 2016). An assessment of herring population trends for this ecosystem has yet to be implemented. Centers of herring spawning biomass are found in localized, sheltered inlets, bays, and estuaries, and population centers may shift. In British Columbia, for example, spawning location changes in any given year, but generally occurs on less than 2% of coastline (Hay et al. 2009). Industrial-scale commercial fishing of CCE herring began in the late 19th century with substantial harvest for many decades (McKechnie et al. 2014). Peak harvest in British Columbia and Washington occurred around 1930, and populations in these regions collapsed by the late 1960s (Outram and Humphreys 1974; Boxberger 2000; McKechnie et al. 2014). Today, fisheries supply markets for sac roe (“kazunoko,” exported for sale in Japan) and whole fish that are used for bait in other fisheries (e.g., salmon) (DFO 2015). Most current herring fisheries occur in spawning locations during the spawning season. In British Columbia, two large management areas—Prince Rupert District and Strait of Georgia—support the majority of commercial landings which typically extract up to ~20,000 metric tons (MT) per year (DFO 2015). In Washington, commercial landings take place in Puget Sound and recently ranged from 222–462 MT (Stick et al. 2014). Commercial landings in Oregon have recently ranged from 0–250 MT, with the majority of landings taking place in Yaquina Bay (Leal 2008; T. Buell, pers. comm.). In California, recent commercial landings have ranged from 0–3,000 MT (CDFW 2014).

Starting in the 1950s, annual or periodic stock assessments have been conducted to inform management

TABLE 1

From south to north in the CCE, descriptive characteristics for each region and Washington primary sites. Shown are approximate latitude for the region/site, time period covered by the data, mean \pm standard deviation (S.D.) and sample size (N years) for spawning stock biomass (given in tonnes), and the management authority for the region. CA: California; OR: Oregon; WA: Washington; BC: British Columbia; CDFW: California Department of Fish and Wildlife; ODFW: Oregon Department of Fish and Wildlife; WDFW: Washington Department of Fish and Wildlife; FOC: Fisheries and Oceans Canada.

Regions	Approx. Latitude °N	Time Period	Biomass Mean \pm S.D. (N years)	Management Authority
San Francisco Bay, CA	37.8	1979–2012	52079 \pm 28610 (33)	CDFW
Yaquina Bay, OR	44.6	1979–2011	487 \pm 501 (31)	ODFW
South Puget Sound, WA	47.2	2000–2013	2802 \pm 1454 (14)	WDFW
Hood Canal, WA	47.7	1976–2013	3317 \pm 1077 (22)	WDFW
Olympic, WA	48.1	1980–2011	814 \pm 956 (17)	WDFW
Whidbey, WA	48.3	1996–2013	2394 \pm 1029 (18)	WDFW
Anacortes, WA	48.6	1996–2013	932 \pm 458 (16)	WDFW
Whatcom, WA	48.8	1975–2013	5009 \pm 3058 (35)	WDFW
Strait of Georgia, BC	49.1	1951–2012	93756 \pm 39274 (62)	FOC
WC Vancouver Island, BC	49.4	1951–2012	41100 \pm 24290 (62)	FOC
Central Coast, BC	51.9	1951–2012	34142 \pm 17156 (62)	FOC
Haida Gwaii, BC	53.1	1951–2012	25125 \pm 19129 (62)	FOC
Prince Rupert District, BC	54.4	1951–2012	28353 \pm 16398 (62)	FOC
WA Primary Sites				
Quartermaster Harbor,				
S. Puget Sound	47.4	1976–2013	990 \pm 536 (38)	WDFW
Port Gamble, Hood Canal	47.9	1976–2013	1702 \pm 766 (38)	WDFW
Discovery Bay, Olympic	48.0	1976–2013	880 \pm 938 (38)	WDFW
Port Susan, Whidbey	48.1	1982–2013	654 \pm 533 (32)	WDFW
Fidalgo Bay, Anacortes	48.5	1980–2013	615 \pm 417 (31)	WDFW
Cherry Point, Whatcom	48.8	1973–2013	4809 \pm 3926 (41)	WDFW

decisions, including harvest quotas, but these data have yet to be synthesized across the entire ecosystem and many time series vary in duration; most stocks, however, have been assessed annually since the early 1980s. Herring stocks are discrete enough to be assessed individually and managed on small-scale stock-by-stock basis (Miller and Schmidtke 1956; Hay and McCarter 1999; Stick et al. 2014), although overlap in some stocks suggests the need for regional management. Spawning stock biomass is calculated primarily by assessing the area occupied and amount of egg deposition yearly in relation to the abundance of adult fish (Hay 1985; Stick and Lindquist 2009; Stick et al. 2014). In this study, we tested the hypothesis that herring biomass in the CCE has declined in a monotonic fashion over the past three decades. To address this hypothesis, we assessed trends in summed herring biomass at sites and regions in British Columbia, Washington, Oregon, and California. This study is significant as to date there has been no synthesis of available herring biomass data across the entire CCE, and given the central role of herring in trophic interactions, particularly for species in the northern CCE, updating and understanding trends in herring abundance can contribute to an ecosystem approach to herring fisheries management.

METHODS

Data Preparation

We obtained spawning biomass data spanning 14–62 years. Information for each site is given in Table 1, and field survey methods are described in the supplementary material. We included information on northern British Columbia populations in this analysis (i.e., as part of the CCE) as in some years the bifurcation of the North Pacific Current, which may be taken as the northern boundary of the CCE, may shift as far north as Haida Gwaii (formerly known as the Queen Charlotte Islands) (Sydeman et al. 2011). All time series were based on existing and ongoing annual surveys. The uncertainty of annual abundance estimates is generally unknown due to the methods used, so weighting analyses by precision was not possible.

Herring spawning biomass data in California were provided by the California Department of Fish and Wildlife. We excluded Humboldt Bay and Tomales Bay from our analysis due to limitation of the time series (<10 years). The time series for San Francisco Bay included 33 years of data. In Oregon, data from Yaquina Bay were provided by Oregon Department of Fish and Wildlife and covered 31 years.

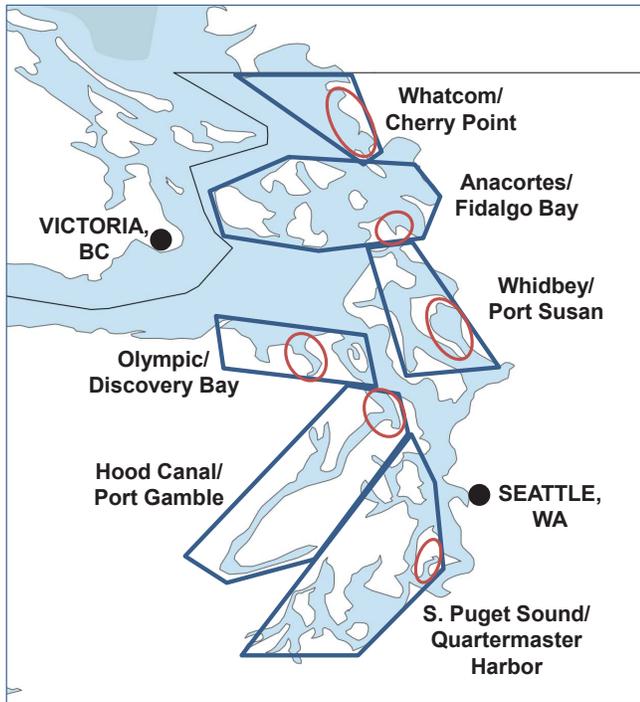


Figure 1. Map of herring spawning regions in Washington State (blue). Also shown are the primary sites examined for each region (red). Labels indicate region/site.

Data for herring spawning biomass in the Puget Sound area were provided by Washington Department of Fish and Wildlife. Due to well-known interactions among spawning populations in Puget Sound, we summarized these data by grouping them into six regions, and summing the biomass for years in which all sites in each region were surveyed. Regions were delineated based on local geographic and oceanographic characteristics (fig. 1). The southernmost region was South Puget Sound, encompassing sites in the central and south basins, south of Whidbey Island. Two sites in this region were excluded from the study for having very short time series compared to the other sites ($n = 2$ and 6 years). The Hood Canal region contained data from three sites. The Whidbey region contained data from sites on the eastern side of Whidbey and Camano Islands. The Olympic region encompassed sites on the northeast portion of the Olympic Peninsula on the Strait of Juan de Fuca. Sites in the San Juan Islands and Samish and Padilla Bays were included in the Anacortes region. Our northernmost region was Whatcom, encompassing herring spawning sites along Cherry Point and in Semiahmoo Bay. In addition to having regional sums, we also retained data from one primary spawning site in each region that, with one exception, had no gaps in its time series (Fidalgo Bay in the Anacortes region was missing three consecutive years of data). We used the longer time series available

from primary sites to verify regional patterns of change. The primary sites by region were: Quartermaster Harbor in South Puget Sound, Port Gamble in Hood Canal, Discovery Bay in Olympic, Port Susan in Whidbey, Fidalgo Bay in Anacortes, and Cherry Point in Whatcom. The longest time series in Washington was for Cherry Point (41 years), and the shortest time series was for the summed region South Puget Sound (14 years; table 1). In order to understand change in Washington overall, we also summed the data for the years 1980–2013 from the six primary sites. There were a few years for two sites that were without data. To have a complete time series for 1980–2013, we used the value from 1982 as a proxy for 1980 and 1981 at Point Susan. Fidalgo Bay was missing data for 1988–90, and for those years we used the average value for the adjacent six years (average of 1985–87 and 1991–93).

We used herring spawning biomass data for five regions in British Columbia for the years 1951–2012 (62 years). The British Columbia regions (fig. 2) were delineated by Fisheries and Oceans Canada, who provided the data for this study. The Strait of Georgia region covered spawning areas on the east side of Vancouver Island and the mainland coast along the strait. The West Coast (WC) Vancouver Island region encompassed spawning areas along the west coast of Vancouver Island. The Central Coast region covered spawning sites along the central mainland coast, while the Prince Rupert District encompassed sites on the northern mainland coast. The Haida Gwaii region covered spawning areas around the islands that comprise Haida Gwaii.

Trends in Biomass

All data were \ln -transformed prior to analysis. We used linear and quadratic regression to assess monotonic trends over time for each region, as well as the Washington primary sites, for 1980–2013. Additionally, we analyzed the British Columbia regions with linear and quadratic regression by their full time series ($n = 62$ years). To compare and select the best model (linear or curvilinear/quadratic), we used the Akaike Information Criterion (AIC); the lowest score indicates the best model (Akaike 1974). From the linear regression results we calculated the annual rate of population growth/decline (λ) by back-transforming regression coefficients. Following the regressions, we synthesized herring biomass across the ecosystem and examined commonalities in trends using Principal Component Analysis (PCA; Jolliffe 2002) (the Washington summed time series was not included to avoid replication of the primary sites). We also calculated the coefficient of variation (CV) in biomass by decade for each region. When there were fewer than six years of data available in a decade, those years were included in the next

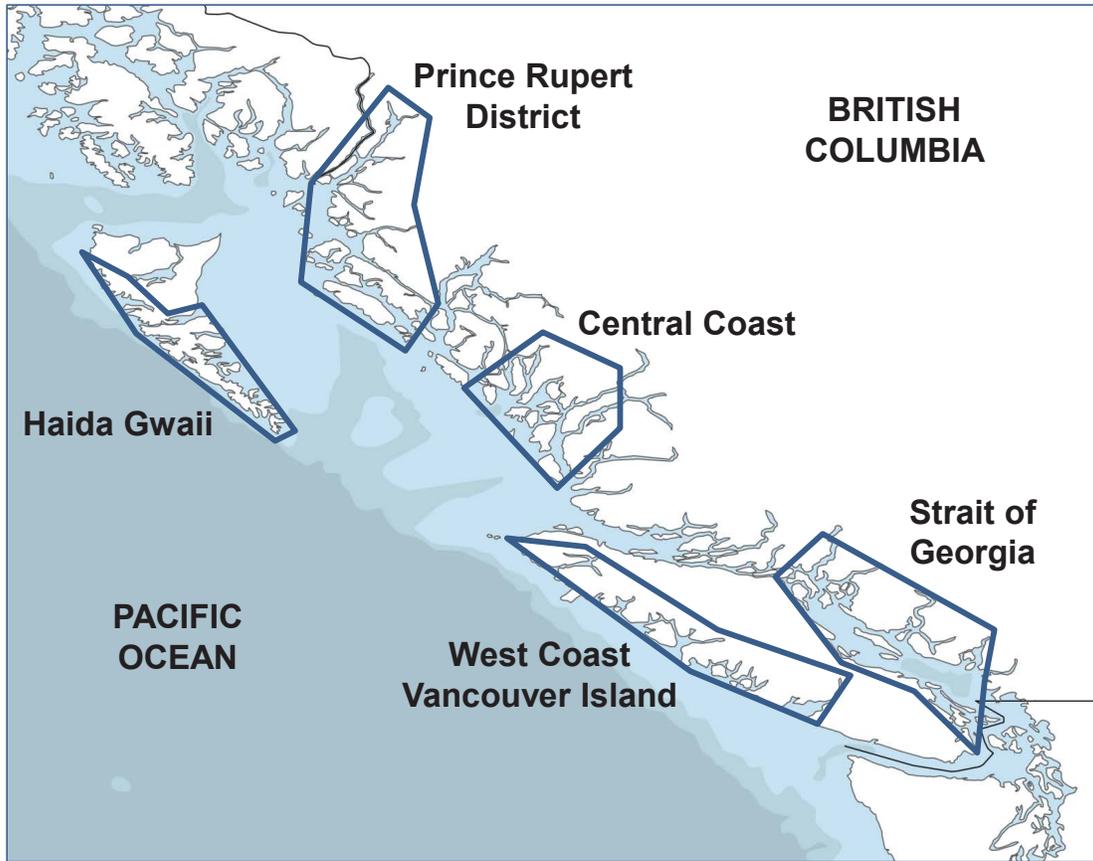


Figure 2. Map of herring spawning regions in British Columbia.

complete decade. To assess whether there was change in the variability in biomass, we used Spearman rank correlations to look for trends in the decadal-scale CV.

RESULTS

Trends in Biomass, 1980–2013

In most regions, herring spawning biomass declined since 1980 (table 2, fig. 3). Among the regions with statistically significant declines, $\lambda = -1\%$ to -12% per year (table 2). All Washington primary sites also had trends of decreasing spawning biomass, and for those sites λ ranged from -5% to -15% per year (table 2, fig. 4). Many of the regions and sites showed curvilinear declines, but most were monotonic within this time period (table 2, figs. 3–4). In all of these cases, the quadratic regression was supported with a lower AIC by a margin >2 , with the exception of Port Susan (table 2). For Port Susan as well as several other sites and regions, the difference in the AIC between the linear and quadratic models was <2 , which indicates that the second-best model cannot be excluded from consideration (Burnham and Anderson 2002). In these cases, we selected the linear model after considering

the strength of the other statistics (e.g., R^2 values; tables 2, 4, figs. 3–4). All regions in British Columbia had significant quadratic change in biomass over time, and interestingly, the curve for Haida Gwaii differed from the others since biomass there increased slightly since 2000 (fig. 3). When we summed all Washington data as a region, it also showed a curvilinear decline in biomass (table 2, fig. 3). Hood Canal had non-significant results for both regression models (table 2).

PCA of the 1980 to 2013 biomass data across sites and regions revealed one dominant mode (PC1) that explained about 45% of the variability in herring biomass in the CCE (table 3); with the exceptions of San Francisco Bay and the Strait of Georgia, all sites and regions loaded on PC1 similarly strongly. PC2 explained about 14% of the variability and had an eigenvalue <2 , indicating this is not a dominant mode of variability. PC1 demonstrated an overall decline in herring biomass across the ecosystem from 1980 to 2013, in support of our hypothesis, and suggesting that the decline was more substantial from ~ 1990 to 2013 than from 1980 to 1990 (fig. 5). PC2 reflects the pattern of variability in the Strait of Georgia (table 3, figs. 3, 6) and also shows a decline later in the time period, 2000–13.

TABLE 2
 Results of linear and quadratic regression on herring spawning stock biomass by region and Washington primary sites for 1980–2013. Also given is the AIC statistic and the calculated percent change in biomass per year (λ ; linear models only). Bold figures show significant p-values ($p < 0.1$). Shaded lines show the best selected models. In most cases this was the model with the lowest AIC, but we chose the linear model with a higher AIC for Port Susan (see Results for further details).

Regions	Model	N	F	p>F	R ²	Term	% change per year	t	p> t	AIC
San Francisco Bay, CA	linear	32	3.38	0.076	0.101	year	-2.25	-1.84	0.076	67.22
	quadratic	32	1.94	0.161	0.118	year		-1.16	0.254	68.61
Yaquina Bay, OR	linear	30	8.39	0.007	0.231	year	-6.54	-2.9	0.007	98.56
	quadratic	30	4.39	0.022	0.246	year		0.03	0.973	99.97
	year ²							-0.73	0.469	
South Puget Sound, WA	linear	14	22.97	<0.001	0.657	year	-12.01	-4.79	<0.001	16.11
	quadratic	14	17.8	<0.001	0.764	year		1.87	0.088	12.87
	year ²							-2.23	0.047	
Hood Canal, WA	linear	20	1.28	0.274	0.066	year	1.21	1.13	0.274	10.53
	quadratic	20	1.02	0.381	0.108	year		1.03	0.317	11.62
	year ²							-0.89	0.388	
Olympic, WA	linear	17	24.23	<0.001	0.618	year	-10.67	-4.92	<0.001	36.6
	quadratic	17	13.25	<0.001	0.654	year		-0.37	0.719	36.88
	year ²							-1.22	0.242	
Whidbey, WA	linear	18	0.35	0.563	0.021	year	-1.21	-0.59	0.563	24.52
	quadratic	18	5.26	0.019	0.412	year		3.08	0.008	17.35
	year ²							-3.16	0.007	
Anacortes, WA	linear	16	18.47	<0.001	0.569	year	-7.04	-4.3	0.001	12.82
	quadratic	16	9.68	0.003	0.598	year		-1.38	0.19	13.69
	year ²							0.97	0.348	
Whatcom, WA	linear	32	48.66	<0.001	0.738	year	-4.96	-9.2	<0.001	15.03
	quadratic	32	41.68	<0.001	0.742	year		-2.74	0.01	16.59
	year ²							0.63	0.534	
Washington	linear	34	219.83	<0.001	0.873	year	-5.99	-14.83	<0.001	0.9
	quadratic	34	159.71	<0.001	0.912	year		2.02	0.052	-9.42
	year ²							-3.68	0.001	
Strait of Georgia, BC	linear	33	0.48	0.494	0.015	year	0.37	0.69	0.494	14.22
	quadratic	33	8.48	0.001	0.361	year		4.12	<0.001	1.93
	year ²							-4.03	<0.001	
WC Vancouver Island, BC	linear	33	53.02	<0.001	0.631	year	-6.44	-7.28	<0.001	49.89
	quadratic	33	58.58	<0.001	0.796	year		2.44	0.021	32.31
	year ²							-4.93	<0.001	
Central Coast, BC	linear	33	55.58	<0.001	0.642	year	-4.46	-7.46	<0.001	23.36
	quadratic	33	47.72	<0.001	0.761	year		1.57	0.127	12.04
	year ²							-3.86	0.001	
Haida Gwaii, BC	linear	33	103.54	<0.001	0.77	year	-6.2	-10.18	<0.001	25.21
	quadratic	33	87.04	<0.001	0.853	year		-7.04	<0.001	12.38
	year ²							4.13	<0.001	
Prince Rupert District, BC	linear	33	7.02	0.013	0.185	year	-1.16	-2.65	0.013	1.67
	quadratic	33	7.12	0.003	0.322	year		1.7	0.1	-2.41
	year ²							-2.46	0.02	
WA Primary Sites										
Quartermaster Harbor, S. Puget Sound	linear	34	26.06	<0.001	0.449	year	-5.08	-5.1	<0.001	61.92
	quadratic	34	20.84	<0.001	0.574	year		1.53	0.136	55.21
	year ²							-3.01	0.005	
Port Gamble, Hood Canal	linear	34	31.36	<0.001	0.495	year	-4.62	-5.6	<0.001	49.04
	quadratic	34	29.73	<0.001	0.657	year		2.09	0.045	37.85
	year ²							-3.83	0.001	
Discovery Bay, Olympic	linear	34	39.27	<0.001	0.551	year	-15.06	-6.27	<0.001	125.56
	quadratic	34	19.24	<0.001	0.554	year		-1.07	0.291	127.34
	year ²							-0.44	0.662	
Port Susan, Whidbey	linear	32	23.73	<0.001	0.442	year	-6.76	-4.87	<0.001	74.41
	quadratic	32	13.56	<0.001	0.483	year		0.41	0.686	73.93
	year ²							-1.53	0.137	
Fidalgo Bay, Anacortes	linear	31	12.42	0.001	0.3	year	-5.52	-3.52	0.001	83
	quadratic	31	45.65	<0.001	0.765	year		5.73	<0.001	51.12
	year ²							-7.45	<0.001	
Cherry Point, Whatcom	linear	34	103.62	<0.001	0.764	year	-6.23	-10.18	<0.001	29.2
	quadratic	34	51.78	<0.001	0.77	year		-3.3	0.002	30.38
	year ²							0.87	0.393	

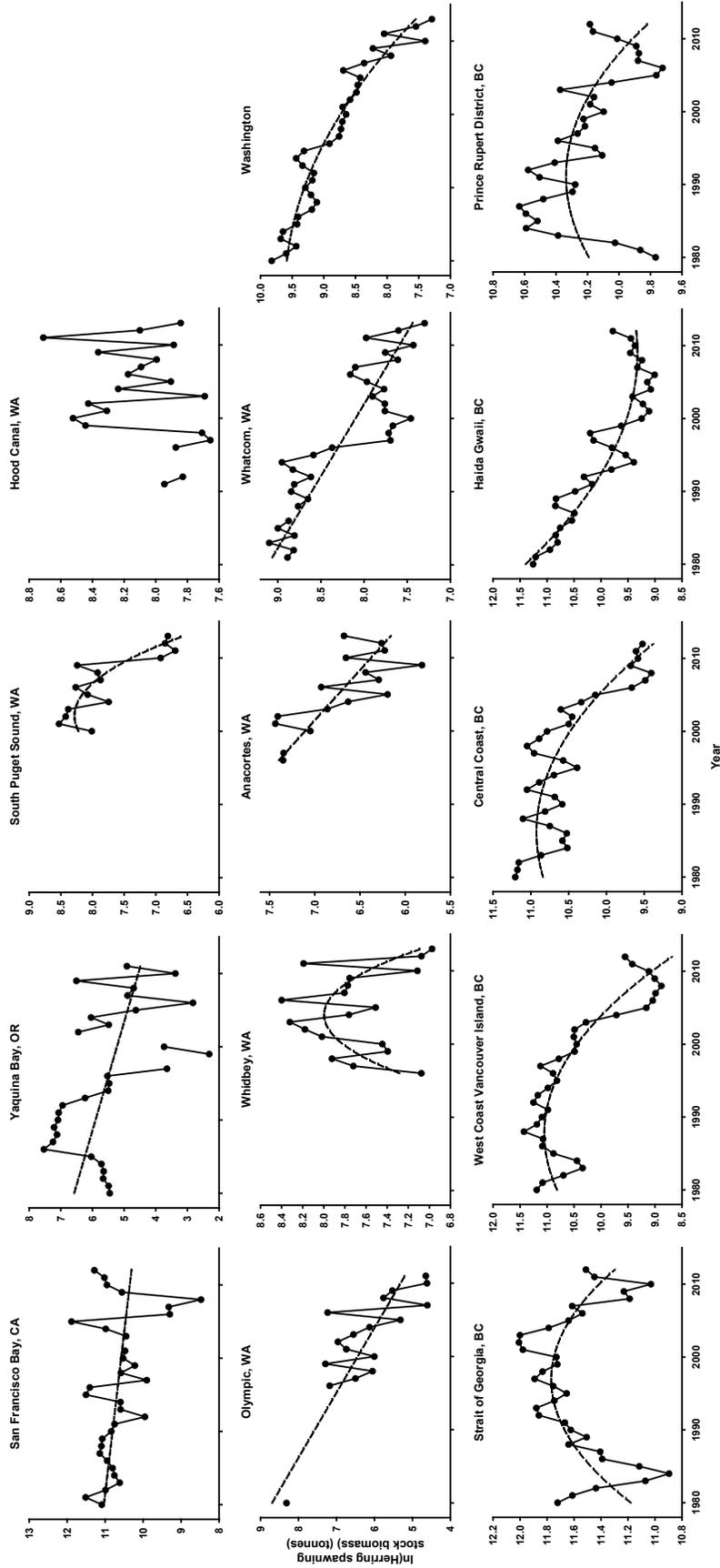


Figure 3. Trends in herring spawning stock biomass by region for the period 1980-2013. Trend lines (dashed) are shown corresponding to the best regression model (linear or quadratic), determined by lowest AIC (see table 2). Hood Canal has no regression line since neither model was significant.

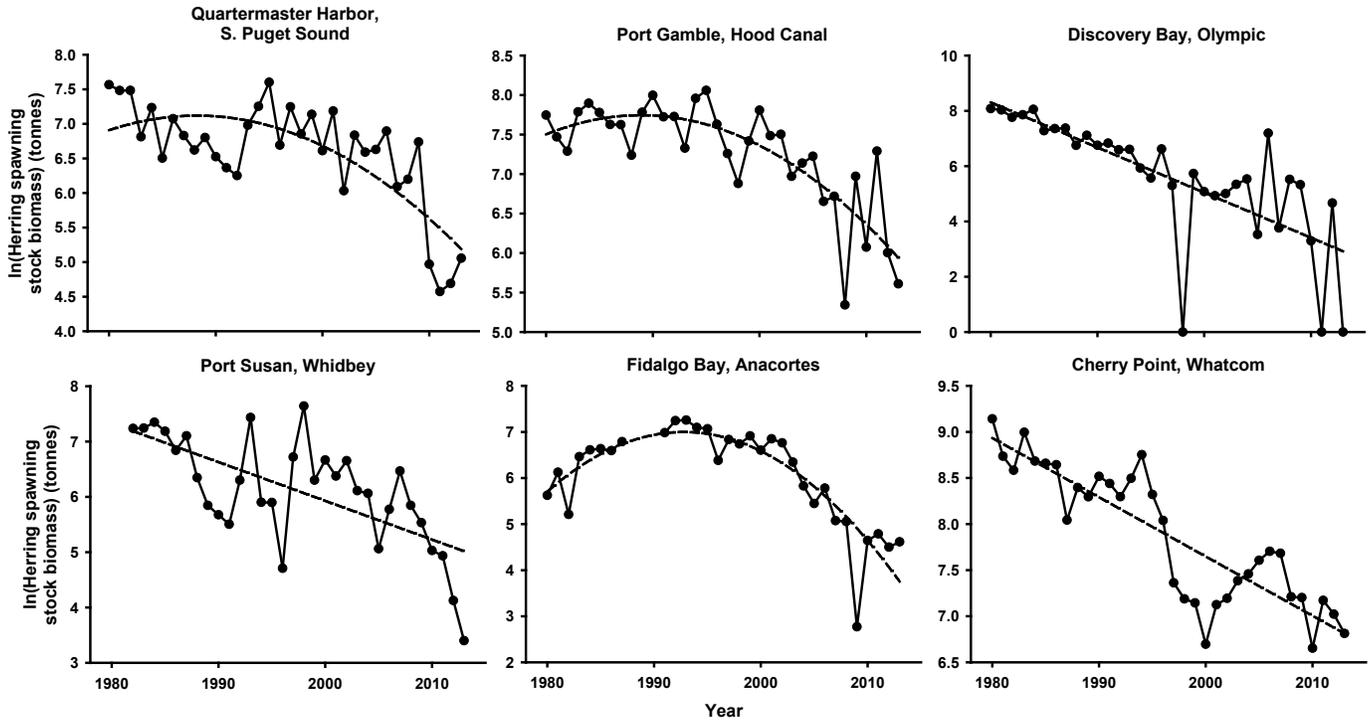


Figure 4. Trends in herring spawning stock biomass for Washington primary sites for the period 1980–2013. Trend lines (dashed) are shown corresponding to the best regression model (linear or quadratic), determined by lowest AIC (see table 2).

TABLE 3
 Results of principal component analysis (PCA) for regions and Washington primary sites for 1980–2013.
 (A) eigenvalues and proportion variance explained,
 (B) site/region loadings on PC1, PC2, and PC3.
 Loadings > |0.2| are shaded.

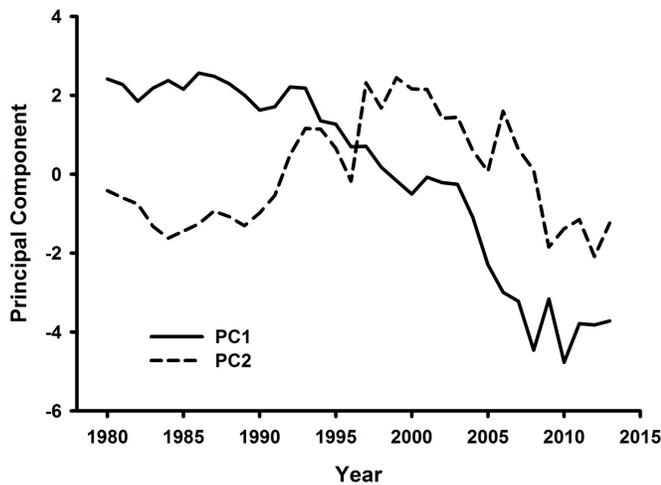


Figure 5. Scores for the first (solid line) and second (dashed line) principal components for 1980–2013. See Table 4 for site/region loadings.

(A)			
Component	Eigenvalue	Proportion	Cumulative
1	5.8466	0.4497	0.4497
2	1.8460	0.1420	0.5917
3	1.6107	0.1239	0.7156

(B)			
Site	Eigenvectors		
	1	2	3
San Francisco Bay, CA	0.1366	-0.2970	0.3856
Yaquina Bay, OR	0.2142	-0.3582	0.2557
Quartermaster Harbor, WA	0.2855	0.2619	-0.3391
Port Gamble, WA	0.3332	0.0703	0.0282
Discovery Bay, WA	0.2771	-0.1044	-0.4039
Port Susan, WA	0.2544	0.2152	-0.3290
Fidalgo Bay, WA	0.2961	0.3761	0.1053
Cherry Point, WA	0.3293	-0.2315	-0.2250
Strait of Georgia, BC	0.0592	0.5279	0.4001
WC Vancouver Island, BC	0.3682	0.0456	0.2594
Central Coast, BC	0.3520	0.1452	0.1444
Haida Gwaii, BC	0.2924	-0.3698	-0.0701
Prince Rupert District, BC	0.2382	-0.1382	0.2895

TABLE 4

Results of linear and quadratic regression on herring spawning stock biomass for full time series of British Columbia regions. Also given is the AIC statistic and the calculated percent change in biomass per year (λ ; linear models only). Bold figures show significant p-values ($p < 0.1$). Shaded lines show the best selected models.

Regions	Model	N	F	p>F	R ²	Term	% change per year	t	p> t	AIC
Strait of Georgia, BC	linear	62	13.82	<0.001	0.187	year	1.29	3.72	<0.001	88.03
	quadratic	62	7.04	0.002	0.193	year		0.3	0.766	89.62
						year ²		0.63	0.53	
WC Vancouver Island, BC	linear	62	1.16	0.286	0.019	year	-0.57	-1.08	0.286	141.09
	quadratic	62	22.01	<0.001	0.427	year		5.94	<0.001	109.72
						year ²		-6.49	<0.001	
Central Coast, BC	linear	62	0.56	0.459	0.009	year	0.31	0.75	0.459	109.8
	quadratic	62	5.88	0.005	0.166	year		3.43	0.001	101.1
						year ²		-3.33	0.001	
Haida Gwaii, BC	linear	62	0.04	0.844	0.001	year	-0.11	-0.2	0.844	152.51
	quadratic	62	5.75	0.005	0.163	year		3.23	0.002	143.52
						year ²		-3.38	0.001	
Prince Rupert District, BC	linear	62	0.14	0.707	0.002	year	-0.14	-0.38	0.707	101.46
	quadratic	62	0.56	0.586	0.018	year		-1.03	0.307	102.48
						year ²		0.97	0.337	

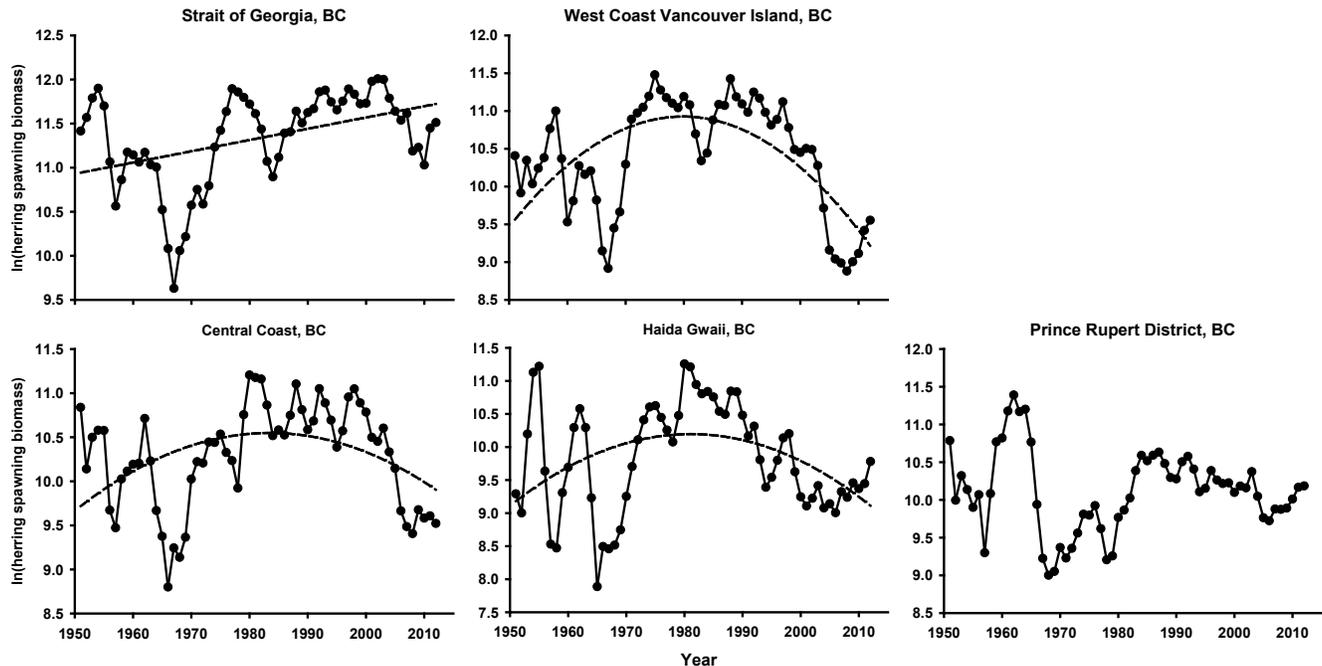


Figure 6. Trends in herring spawning stock biomass (tonnes) by region for the full time periods in the British Columbia regions. Trend lines (dashed) are shown corresponding to the best regression model (linear or quadratic), determined by lowest AIC (see table 4). Graphs show best timeline and biomass scale for each data set; note differing scales on each axis.

Trends in Biomass, 1950 to Present, British Columbia

One region, the Strait of Georgia, had an increase in herring spawning biomass since 1951 ($\lambda = 1.29\%/year$; table 4, fig. 6). No linear decreases were found, and instead spawning biomass for the West Coast Vancouver Island, Central Coast, and Haida Gwaii demonstrated cyclical (quadratic) patterns of change over time (table 4, fig. 6). Lastly, Prince Rupert District had insignificant trends in both the linear and quadratic models (table 4).

Trends in Variance

Five of the Washington regions had time series that were too short in order to be included in this analysis. All other regions, and the Washington primary sites, had at least three decades of data. In the south, San Francisco Bay and Yaquina Bay showed significantly increasing variance in biomass through time (table 5). In Washington, the overall numbers as well as three primary sites had significant increases in variance while the Whatcom region and the three other primary sites had nonsignificant change in variance. In contrast, to

TABLE 5
Spearman rank correlation on changes in variance in herring biomass over time. Only one region in Washington, Whatcom, had a time series long enough for this analysis. Shown are the sample size (N), Spearman Rho, and the associated p-value.

Regions	N	Rho	P-value
San Francisco Bay, CA	3	1.00	0.000
Yaquina Bay, OR	3	1.00	0.000
Whatcom, WA	3	-0.50	0.667
Washington	3	1.00	0.000
Strait of Georgia, BC	6	-0.03	0.957
WC Vancouver Island, BC	6	-0.60	0.208
Central Coast, BC	6	-0.26	0.623
Haida Gwaii, BC	6	-0.83	0.042
Prince Rupert District, BC	6	-0.83	0.042
WA Primary Sites			
Quartermaster Harbor, S. Puget Sound	3	1.00	0.000
Port Gamble, Hood Canal	3	1.00	0.000
Discovery Bay, Olympic	3	0.50	0.667
Port Susan, Whidbey	3	1.00	0.000
Fidalgo Bay, Anacortes	3	0.50	0.667
Cherry Point, Whatcom	4	0.80	0.200

the north, the Prince Rupert District and Haida Gwaii showed significantly decreasing variance.

DISCUSSION

Population Trends

Using a comprehensive data set for herring spawning stock biomass at sites and regions from California, Oregon, Washington, and British Columbia, we tested the hypothesis that herring biomass in the CCE has declined over the past three decades. To test this hypothesis, we used geographic classifications previously established by others conducting syntheses of herring population statistics in British Columbia (e.g., Hay et al. 2009), along with new site groupings in Puget Sound. For this period, we evaluated herring spawning stock biomass data for monotonic linear and curvilinear trends and changes in variance over time. The results from our study support our hypothesis of overall ecosystem-scale decline from the mid to late 1980s to the present (fig. 5), but even within this period, a few spawning populations showed no change or increased.

At two locations, Hood Canal and Strait of Georgia (using the full time series), herring biomass had an increasing trend. In both cases it is plausible that these increases reflect distributional shifts in local populations. The Strait of Georgia region is very close to Cherry Point, Washington, and while Strait of Georgia herring biomass has been increasing, biomass at Cherry Point has had a strong decline in the same time period. Similarly, though the Hood Canal region shows increasing

biomass, most sites near it have been decreasing (including Port Gamble, the primary site that we identified in that region in terms of time series completeness). The increasing herring biomass there is probably a product of emigration from other areas, not intrinsic growth of the Hood Canal population (Siple and Francis 2016).

Perhaps more significantly, when we examined the full time series (n = 62 years) from British Columbia, cyclic population fluctuations were evident, suggesting that the decline since ~1990 may reflect only the declining period of a low-frequency cycle. Cyclically fluctuating herring populations in other regions of the CCE may also occur; we found some curvilinear population trends at several sites in Washington. Though these other populations may also cycle, at present we do not have long enough time series at the other sites to conclusively describe this pattern. Cyclical patterns of herring abundance and other population characteristics such as growth have been related to climate indicators such as the Pacific Decadal Oscillation (Siple and Francis 2016), as well as specific ocean conditions such as sea surface temperature and salinity (Rose et al. 2008; Ito et al. 2015).

Independent of the longest modes of variability, biomass declined significantly across the ecosystem since the mid to late 1980s including in all five British Columbia coastal regions, except the Strait of Georgia (though see above note about Cherry Point). This interpretation of general decline is complicated by regional variation; abundance in the most recent years in San Francisco Bay, Yaquina Bay, Hood Canal, and Haida Gwaii (in addition to Prince Rupert District) was not exceptionally high nor low, though South Puget Sound, Olympic, Whidbey, and Whatcom all experienced very low biomass. Relatedly, in the last several years, herring biomass was at historically low values at all six of the Washington primary sites that we examined (Siple and Francis 2016) and we found a strong declining trend for Washington as a whole region since 1980. Continued monitoring and evaluation of herring population trends will provide a better understanding of the details of these individual population trends, relative to the entire CCE metapopulation.

Changes in Variance

For the longest time series available in our data set, we also examined changes in the variance in herring biomass by calculating the coefficients of variation by decade. Though the sample size is admittedly very low (n = 5 decades), some interesting patterns of population variability are evident. Most notably, the southernmost sites in the CCE, San Francisco Bay and Yaquina Bay, showed increasing variability in biomass, as did the Washington region when summed. The northernmost regions, Haida Gwaii and Prince Rupert District,

showed decreasing variability through time, and spawning populations in the center of the herring range in the CCE, as we defined it, showed no change in variance. Such changes in population variance could be attributed to a variety of factors. For one, it is predicted that climate change may increase variability in both physical and biological properties of marine ecosystems (IPCC 2013); these changes may be most apparent in the southern portions of species' ranges (Poloczanska et al. 2013; Pinsky et al. 2013). San Francisco Bay is near the southern end of herring range in the Northeast Pacific (Miller and Lea 1972), and variance in a variety of ecosystem properties in this region appears to be increasing (Sydeman et al. 2013; Black et al. 2014). A corresponding decrease in variability in the northern portion of species' ranges, such as we observed here, is also plausible relative to climate change, but has not been predicted by theory. Alternatively, the decreasing variability in the Prince Rupert District and Haida Gwaii may relate to the fact that these regions are located in an oceanographic transition zone between the CCE and Gulf of Alaska. Differences in population variability between the southern population of San Francisco Bay, and to a lesser extent Yaquina Bay, and northern British Columbia may also be related to the inverse production regime hypothesis (Hare et al. 1999), which indicates that ecosystem productivity in the CCE and Gulf of Alaska covary out of phase (i.e., are negatively correlated). However, Teo et al. (2009) showed similar variability in salmonid survival rates between the CCE and the Gulf of Alaska in similar periods, so this hypothesis is equivocal. Furthermore, the age structure of the northern populations do not show the same age structure changes as those to the south, but size at age has been decreasing (Therriault et al. 2009; Hay et al. 2012), and there is some evidence that recruitment is becoming more variable (Therriault et al. 2009). Understanding the variability of herring populations throughout the CCE will take more dedicated effort to examine age structure and size at age in relation to environmental conditions and other impacts.

Herring and the Forage Fish Community

The CCE is not a wasp-waist system (*sensu* Cury et al. 2000) in that many species make up the mid trophic levels responsible for energy transfer from primary producers to secondary and tertiary consumers (Miller et al. 2010). Along with northern anchovy, Pacific sardine, juvenile (age-0) rockfish and hake, smelts of various species, and mesozooplankton, notably euphausiid crustaceans, herring is one of the primary forage species (Brodeur et al. 2014; Szoboszlai et al. 2015). Lately, the CCE forage community has received considerable attention (Kaplan et al. 2013), mainly due to the decline of sardine, which constitutes an important fishery resource. A persistent decline in

sardine abundance from about 2005 to 2015 (Zwolinski and Demer 2012; Zwolinski et al. 2014) resulted in closure of that fishery across the CCE in 2016; as of the writing of this paper, the fishery is still closed, with estimated biomass in the entire ecosystem approximately 100,000 MT (Hill et al. 2016). The northern anchovy population has also shown a major decline in the heart of its range off south-central California (Koslow and Davison 2015; Sydeman et al. 2015a), with a current estimated biomass of <100,000 MT (MacCall et al. 2016; Thayer et al. in press). The precipitous decline of the central subpopulation of anchovy began in 2007–08 after a substantial spike in abundance in 2005–06, and there is little evidence of recovery by 2015–16 (Thayer et al. in press). Patterns of change in age-0 forage fish (juvenile rockfish and hake) are less clear. Juvenile rockfish catch per unit effort (CPUE) in the central CCE declined from the late 1980s to late 1990s before rebounding in the early 2000s, then declining to its lowest levels in 2005–07 before increasing again in recent years (Leising et al. 2015). Based on stock assessment models, the production of juvenile hake declined through the 1980s and 1990s, but has also recently rebounded (Grandin et al. 2016). Trends in euphausiid abundance have been variable, with some species showing low-frequency decreases (*Nyctiphanes simplex*, Di Lorenzo and Ohman 2013), while others are increasing (*Thysanoessa spinifera*, Sydeman et al. 2015a), or are stable (*Euphausia pacifica*, Brinton and Townsend 2003; Lavaniegos and Ohman 2007). The structure of the euphausiid community, however, has certainly shifted through time.

We may now add the CCE Pacific herring metapopulation to the list of recently declining forage fish, but with inconsistencies in subpopulation trends and uncertainty in whether patterns of change are unidirectional or part of a low-frequency cycle. Herring are more important to predators in the northern CCE (Szoboszlai et al. 2015), where they are also generally more abundant (this study). Fortunately, in the largest center of herring abundance in British Columbia, trends have not been negative (e.g., Strait of Georgia), though since the 1980s, most populations in British Columbia have also been in decline. The stronghold in the south, the San Francisco Bay population, shows weak evidence of decline, but its numbers have been volatile and this population cannot be considered stable. The pronounced decline in many species of the forage community, including herring, since the mid to late 1980s (fig. 5) may be related to the “biotic regime shift” of 1989–90 (Hare and Mantua 2000), coupled with increasing “marine climate” variability (e.g., Sydeman et al. 2013; Black et al. 2014). It is well known that herring recruitment is influenced by environmental conditions, such as water temperature and upwelling (Zebdi and

Collie 1995). Considering the late 1990s and 2000s, environmental conditions have been notably variable, including a major and rapid shift between extreme El Niño to La Niña conditions from 1998–99 (Chavez et al. 1999), highly delayed upwelling in 2005 (Schwing et al. 2006), record upwelling in 2013 (Leising et al. 2014) followed by an unprecedented marine heat wave (“The Blob”) in 2014–15 (Bond et al. 2015; Gentemann et al. 2017), and a severe El Niño in 2015–16 (Jacox et al. 2016). These conditions affected different regions of the CCE differently and produced a variety of ecosystem consequences, and this spatial variability may explain some of the differences observed in this study between populations.

Mechanistically, herring populations in the CCE are likely to be affected trophically through the availability of zooplankton prey, by changes in the abundance and distribution of major herring predators such as hake (Ware and MacFarlane 1995) and whales (Rice et al. 2011), or by water temperature and metabolic factors (Portner et al. 2008; Sydeman et al. 2015b). Indeed, humpback whales are significant predators of herring in the Northeast Pacific and their steadily increasing abundance means that they will have increased predatory influence on populations of herring and other forage fish species (Rice et al. 2011). Overall though, if the cause of declining trends were simply a trophic mechanism, we would expect to see similar trends in all populations that migrate and feed in offshore oceanic areas. What we observed, however, is that the subpopulations with a more lengthy “inshore” residence (Strait of Georgia and Puget Sound) have somewhat different trends than those that spend more time on the continental shelf areas. The different temporal trajectories between the Strait of Georgia and Puget Sound versus the West Coast of Vancouver Island and coastal populations to the south that may have the same summer feeding areas point to non-trophic factors, such as changes in habitat quality, as a parsimonious explanation for these differences in population trends between regions. We hypothesize that herring fisheries are unlikely to have been the cause of decline in most subpopulations. However, it has been suggested that fishing, on top of natural variability, may contribute to population fluctuations by altering the structure of populations (Essington et al. 2015). The coincidental recent decline in the central subpopulation of northern anchovy is thought to be almost exclusively environmentally driven (MacCall et al. 2016; Thayer et al. in press), whereas the decline in sardine has been ascribed to fishing during a period of poor recruitment (Zwolinski and Demer 2012; Hill et al. 2016). On a positive note, while the overall herring population biomass trend is negative, the largest regional populations, San

Francisco Bay and those in British Columbia, have shown cyclical patterns, some stability, and even slight increases since 2010. However, this pattern may reverse depending on the response of these populations to the recent ocean warming of 2014–16 (Bond et al. 2015; Jacox et al. 2016).

The northeast Pacific is a complex ecosystem in which herring are a vital part of pelagic food webs and important traditional and commercial fisheries. We do not understand the drivers of changes occurring in the herring metapopulation, nor have the consequences to upper trophic levels in this marine ecosystem been investigated comprehensively. Expansion of current monitoring and new directed research on relationships between herring and the environment and higher level consumers is therefore warranted and essential.

ACKNOWLEDGEMENTS

We thank the Pew Charitable Trusts and Marisla Foundation for financial support for this analysis.

LITERATURE CITED

- Akaike, H. 1974. New look at statistical model identification. *IEEE Trans. Auto. Cont.* AC19:716–723.
- Black, B. A., W. J. Sydeman, D. C. Frank, D. Griffin, D. W. Stahle, M. Garcia-Reyes, R. R. Rykaczewski, and S. J. Bograd. 2014. Six centuries of variability and extremes in a couple marine-terrestrial ecosystem. *Science* 345:1498–1502.
- Bond, N. A., M. F. Cronin, H. Freeland, and N. Mantua. 2015. Causes and impacts of the 2014 warm anomaly in the NE Pacific. *Geophys. Res. Lett.* 42:3414–3420.
- Boxberger, D. L. 2000. *To fish in common: The ethnohistory of Lummi Indian salmon fishing*. University of Washington Press, Seattle, Washington.
- Brinton, E., and A. Townsend. 2003. Decadal variability in abundances of the dominant euphausiid species in southern sectors of the California Current. *Deep-Sea Res. Pt. II* 50:2449–2472.
- Brodeur, R. D., J. C. Buchanan, and R. L. Emmett. 2014. Pelagic and demersal fish predators on juvenile and adult forage fishes in the Northern California Current: spatial and temporal variations. *Calif. Coop. Oceanic Fish. Invest. Rep.* 55:96–116.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: A practical information-theoretic approach*. Springer-Verlag New York, Inc. 488 pp.
- CDFW. 2014. Pacific herring commercial fishing regulations. Final Supplemental Environmental Document, SCH No. 98052052. California Department of Fish and Wildlife.
- CDFW. 2015. Pacific herring commercial fishing regulations. Draft Supplemental Environmental Document, SCH No. 98052052. California Department of Fish and Wildlife.
- Chavez, F. P., P. G. Strutton, G. E. Friederich, R. A. Feely, G. C. Feldman, D. G. Foley, and M. J. McPhaden. 1999. Biological and chemical response of the Equatorial Pacific Ocean to the 1997–98 El Niño. *Science* 286:2126–2131.
- Checkley, D. M., and J. A. Barth. 2009. Patterns and processes in the California Current System. *Prog. Oceanogr.* 83:49–64.
- Cury, P. A., B. Bakun, R. J. M. Crawford, A. Jarre, R. A. Quinones, L. J. Shannon, and H. M. Verheye. 2000. Small pelagics in upwelling systems: Patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES J. Mar. Sci.* 57:603–618.
- DFO. 2015. Stock assessment and management advice for British Columbia Pacific herring: 2014 status and 2015 forecast. DFO Canadian Science Advisory Secretariat Science Advisory Report 2014/060.
- Di Lorenzo, E., and M. D. Ohman. 2013. A double-integration hypothesis to explain ocean ecosystem response to climate forcing. *Proc. Nat. Acad. Sci.* 110:2496–2499.

- Essington, T. E., P. E. Moriarty, H. E. Froehlich, E. E. Hodgson, L. E. Koehn, K. L. Oken, M. C. Siple, and C. C. Stawitz. 2015. Fishing amplifies forage fish population collapses. *Proc. Nat. Acad. Sci.* 112:6648–6652.
- Gentemann, C. L., M. R. Fewings, and M. Garcia-Reyes. 2017. Satellite sea surface temperatures along the West Coast of the United States during the 2014–16 northeast Pacific marine heat wave. *Geophys. Res. Lett.* 44:312–319.
- Grandin, C. J., A. C. Hicks, A. M. Berger, A. M. Edwards, N. Taylor, I. G. Taylor, and S. Cox. 2016. Status of the Pacific hake (whiting) stock in U.S. and Canadian waters in 2016. Joint Technical Committee of the U.S. and Canada Pacific Hake/Whiting Agreement. National Marine Fisheries Service and Fisheries and Oceans Canada. 165 pp.
- Hare, S. R., and N. J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Prog. Oceanogr.* 47:103–145.
- Hare, S. R., N. J. Mantua, and R. C. Francis. 1999. Inverse production regimes: Alaska and West Coast Pacific salmon. *Fisheries* 24:6–14.
- Hay, D. E. 1985. Reproductive biology of Pacific herring (*Clupea harengus pallasii*). *Can. J. Fish. Aquat. Sci.* 42:111–126.
- Hay, D. E., and P. B. McCarter. 1999. Distribution and timing of herring spawning in British Columbia. Canadian Stock Assessment Secretariat Research Document 99/14. Fisheries and Oceans Canada, Biological Sciences Branch. 44 pp.
- Hay, D. E., P. B. McCarter, K. S. Daniel, and J. F. Schweigert. 2009. Spatial diversity of Pacific herring (*Clupea pallasii*) spawning areas. *ICES J. Mar. Sci.* 66:1662–1666.
- Hay, D. J., J. Schweigert, J. Boldt, J. Cleary, T. A. Greiner, and K. Hebert. 2012. Decrease in herring size-at-age: a climate change connection? *In: State of the physical, biological, and selected fishery resources of Pacific Canadian marine ecosystems in 2011*. J. R. Irvine and W. R. Crawford, eds. DFO Canadian Science Advisory Secretariat Research Document 2012/072. pp. 142.
- Hill, K. T., P. R. Crone, E. Dorval, and B. J. Macewicz. 2016. Assessment of the Pacific sardine resource in 2016 for U.S.A. management in 2016–17. NOAA Tech. Memo. NOAA-TM-NMFS-SWFSC-562. NOAA NMFS Southwest Fisheries Science Center.
- IPCC. 2013. Climate change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Stocker, T. F., et al. (Eds.) Cambridge University Press. Cambridge, U.K., and New York, N.Y., USA.
- Ito, S., K. A. Rose, B. A. Megrey, J. Schweigert, D. Hay, F. E. Werner, and M. N. Aita. 2015. Geographic variation in Pacific herring growth in response to regime shifts in the North Pacific Ocean. *Prog. Oceanogr.* 138:331–347.
- Jacox, M. G., E. L. Hazen, K. D. Zaba, D. L. Rudnick, C. A. Edwards, A. M. Moore, and S. J. Bograd. 2016. Impacts of the 2015–16 El Niño on the California Current System: Early assessment and comparison to past events. *Geophys. Res. Lett.* 43:7072–7080.
- Jolliffe, I. T. 2002. Principal Component Analysis. Springer-Verlag New York, Inc., New York.
- Kaplan, I. C., C. J. Brown, E. A. Fulton, I. A. Gray, J. C. Field, and A. D. M. Smith. 2013. Impacts of depleting forage species in the California Current. *Env. Cons.* 40:380–393.
- Koehn, L. E., T. E. Essington, K. N. Marshall, I. C. Kaplan, W. J. Sydeman, A. I. Szoboszlai, and J. A. Thayer. 2016. Developing a high taxonomic resolution food web model to assess the functional role of forage fish in the California Current ecosystem. *Ecol. Mod.* 335:87–100.
- Koslow, J. A., and P. C. Davison. 2015. Productivity and biomass of fishes in the California Current Large Marine Ecosystem: Comparison of fishery-dependent and -independent time series. *Env. Dev.* 17:23–32.
- Lavanigos, B. E., and M. D. Ohman. 2007. Coherence of long-term variations of zooplankton in two sectors of the California Current System. *Prog. Oceanogr.* 75:42–69.
- Leal, D. R. 2008. A fishermen's agreement and co-op in Yaquina Bay roe herring. *FAO Fisheries Technical Paper* 504. Food and Agriculture Organization of the United Nations. pp. 415–423.
- Leising, A. W., I. D. Schroeder, S. J. Bograd, E. Bjorkstedt, J. Field, K. Sakuma, J. Abell, R. R. Robertson, J. Tyburczy, W. T. Peterson, R. D. Brodeur, C. Barcelo, T. D. Auth, E. A. Daly, G. S. Campbell, J. A. Hildebrand, R. M. Suryan, A. J. Gladics, C. A. Horton, M. Kahru, M. Manzano-Sarabia, S. McClatchie, E. D. Weber, W. Watson, J. A. Santora, W. J. Sydeman, S. R. Melin, R. L. DeLong, J. Largier, S. Y. Kim, F. P. Chavez, R. T. Golightly, S. R. Schneider, P. Warzybok, R. Bradley, J. Jahncke, J. Fisher, and J. Peterson. 2014. State of the California Current 2013–14: El Niño looming. *Calif. Coop. Oceanic Fish. Invest. Rep.* 55:51–87.
- Leising, A. W., I. D. Schroeder, S. J. Bograd, J. Abell, R. Durazo, G. Gaxiola-Castro, E. Bjorkstedt, J. Field, K. Sakuma, R. R. Robertson, R. Goericke, W. T. Peterson, R. D. Brodeur, C. Barcelo, T. D. Auth, E. A. Daly, R. M. Suryan, A. J. Gladics, J. M. Porquez, S. McClatchie, E. D. Weber, W. Watson, J. A. Santora, W. J. Sydeman, S. R. Melin, F. P. Chavez, R. T. Golightly, S. R. Schneider, J. Fisher, C. Morgan, R. Bradley, and P. Warzybok. 2015. State of the California Current 2014–15: Impacts of the warm-water “Blob.” *Calif. Coop. Oceanic Fish. Invest. Rep.* 56:31–68.
- MacCall, A. D., W. J. Sydeman, P. C. Davison, and J. A. Thayer. 2016. Recent collapse of northern anchovy biomass off California. *Fish. Res.* 175:87–94.
- McKechnie, I., D. Lepofsky, M. L. Moss, V. L. Butler, T. J. Orchard, G. Coupland, F. Foster, M. Caldwell, and K. Lertzman. 2014. Archaeological data provide alternative hypotheses on Pacific herring (*Clupea pallasii*) distribution, abundance, and variability. *Proc. Nat. Acad. Sci.* 111:E809–E816.
- Miller, D. J., and R. N. Lea. 1972. Guide to the Coastal Marine Fishes of California. Fish Bulletin 157, California Department of Fish and Game. 235 pp.
- Miller, D. J., and J. Schmidtke. 1956. Report on the distribution and abundance of Pacific herring (*Clupea pallasii*) along the coast of central and southern California. *California Fish and Game* 42:163–187.
- Miller, T. W., R. D. Brodeur, G. Rau, and K. Omori. 2010. Prey dominance shapes trophic structure of the northern California Current pelagic food web: evidence from stable isotopes and diet analysis. *Mar. Ecol. Prog. Ser.* 420:15–26.
- Outram, D. N., and R. D. Humphreys. 1974. The Pacific herring in British Columbia waters. Fisheries and Marine Service, Pacific Biological Station, Nanaimo, B.C., Canada.
- Pinsky, M. L., B. Worm, M. J. Fogarty, J. L. Sarmiento, and S. A. Levin. 2013. Marine taxa track local climate velocities. *Science* 341:1239–1242.
- Poloczanska, E. S., C. J. Brown, W. J. Sydeman, W. Kiessling, D. S. Schoeman, P. J. Moore, K. Brander, J. F. Bruno, L. B. Buckley, M. T. Burrows, C. M. Duarte, B. S. Halpern, J. Holding, C. V. Kappel, M. I. O’Connor, J. M. Pandolfi, C. Parmesan, F. Schwing, S. A. Thompson, and A. J. Richardson. Global imprint of climate change on marine life. *Nature Clim. Change* 3:919–925.
- Portner, H. O., and A. P. Farrell. 2008. Physiology and climate change. *Science* 322:690–692.
- Rice, S. D., J. R. Moran, J. M. Straley, K. M. Boswell, and R. A. Heintz. 2010. Significance of whale predation on natural mortality rate of Pacific herring in Prince William Sound. *Exxon Valdez Oil Spill Restoration Project Final Report*. 123 pp.
- Rice, S. D., J. R. Moran, J. M. Straley, K. M. Boswell, and R. A. Heintz. 2011. Significance of whale predation on natural mortality rate of Pacific herring in Prince William Sound. *Exxon Valdez Oil Spill Restoration Project Final Report* (Restoration Project: 100804). National Marine Fisheries Service, Juneau, Alaska. 25 pp.
- Rose, K. A., B. A. Megrey, D. Hay, F. Werner, and J. Schweigert. 2008. Climate regime effects on Pacific herring growth using coupled nutrient-phytoplankton-zooplankton and bioenergetics models. *Trans. Amer. Fish. Soc.* 137:278–297.
- Schweigert, J. F., J. L. Boldt, L. Flostrand, and J. S. Cleary. 2010. A review of factors limiting recovery of Pacific herring stocks in Canada. *ICES J. Mar. Sci.* 67:1903–1913.
- Schwing, F. B., N. A. Bond, S. J. Bograd, T. Mitchell, M. A. Alexander, and N. Mantua. 2006. Delayed coastal upwelling along the US West Coast in 2005: A historical perspective. *Geophys. Res. Lett.* 33:L22S01.
- Siple, M. C., and T. B. Francis. 2016. Population diversity in Pacific herring of the Puget Sound, USA. *Oecologia* 180:111–125.
- Stick, K. C., and A. Lindquist. 2009. 2008 Washington State herring stock status report. Stock Status Report No. FPA 09–05. Washington Department of Fish and Wildlife, Fish Program, Fish Management Division.
- Stick, K. C., A. Lindquist, and D. Lowry. 2014. 2012 Washington State herring stock status report. Fish Program Technical Report No. FPA 14–09. Washington Department of Fish and Wildlife, Fish Program, Fish Management Division.
- Sydeman, W. J., S. A. Thompson, J. C. Field, W. T. Peterson, R. Tanasichuk, H. Freeland, S. J. Bograd, and R. R. Rykaczewski. 2011. Does positioning of the North Pacific Current affect downstream ecosystem productivity? *Geophys. Res. Lett.* 38:L12606.
- Sydeman, W. J., J. A. Santora, S. A. Thompson, B. Marinovic, and E. Di Lorenzo. 2013. Increasing variance in North Pacific climate relates to unprecedented ecosystem variability off California. *Glob. Change Biol.* 19:1662–1675.

- Sydeman, W. J., S. A. Thompson, J. A. Santora, J. A. Koslow, R. Goericke, and M. D. Ohman. 2015a. Climate-ecosystem change off southern California: Time-dependent seabird predator-prey numerical responses. *Deep-Sea Res. Pt. II* 112:158–170.
- Sydeman, W. J., E. Poloczanska, T. E. Reed, and S. A. Thompson. 2015b. Climate change and marine vertebrates. *Science* 350:772–777.
- Szoboszlai, A. I., J. A. Thayer, S. A. Wood, W. J. Sydeman, and L. E. Koehn. 2015. Forage species in predator diets: Synthesis of data from the California Current. *Ecol. Inform.* 29:45–56.
- Teo, S. L. H., L. W. Botsford, and A. Hastings. 2009. Spatio-temporal covariability in coho salmon (*Oncorhynchus kisutch*) survival, from California to southeast Alaska. *Deep-Sea Res. Pt. II* 56:2570–2578.
- Thayer, J. A., A. D. MacCall, P. C. Davison, and W. J. Sydeman. California anchovy population remains low, 2012–16. *Cal. Coop. Oceanic Fish. Invest. Rep.*, in press.
- Therriault, T. W., D. E. Hay, and J. F. Schweigert. 2009. Biological overview and trends in pelagic forage fish abundance in the Salish Sea (Strait of Georgia, British Columbia). *Mar. Ornithol.* 37:3–8.
- Thornton, T. F., M. L. Moss, V. L. Butler, J. Herbert, and F. Funk. 2010. Local and traditional knowledge and the historical ecology of Pacific herring in Alaska. *J. Ecol. Anthropol.* 14:81–88.
- Ware, D. M., and G. A. McFarlane. 1995. Climate-induced changes in Pacific hake (*Merluccius productus*) abundance and pelagic community interactions in the Vancouver Island upwelling system. *Can. Spec. Pub. Fish. Aquat. Sci.* 121:509–521.
- Womble, J., and M. Sigler. 2006. Seasonal availability of abundant, energy-rich prey influences the abundance and diet of a marine predator, the Steller sea lion *Eumetopias jubatus*. *Mar. Ecol. Prog. Ser.* 325:281–293.
- Zebdi, A., and J. S. Collie. 1995. Effect of climate on herring (*Clupea pallasii*) population dynamics in the Northeast Pacific Ocean. *Can. Spec. Pub. Fish. Aquat. Sci.* 121:277–290.
- Zwolinski, J. P., and D. A. Demer. 2012. A cold oceanographic regime with high exploitation rates in the Northeast Pacific forecasts a collapse of the sardine stock. *Proc. Nat. Acad. Sci.* 109:4175–4180.
- Zwolinski, J. P., D. A. Demer, G. R. Cutter, K. Stierhoff, and B. J. Macewicz. 2014. Building on fisheries acoustics for marine ecosystem surveys. *Oceanography* 27:68–79.

SUPPLEMENTARY SURVEY METHODS

DETAILS OF FIELD METHODS

A combination of spawning biomass survey methods was used by agencies across the geographic area of interest, and methods varied over the course of the time series for most stocks. The two primary survey methods were spawn deposition surveys, which measure egg deposition, and acoustic/trawl surveys measuring fish abundance (Stick et al. 2014). In British Columbia, surveys initially were shore or vessel based, concentrating on measuring the lengths of spawn deposition along the shore. Beginning in the 1980s, SCUBA surveys were used to estimate the width of spawn deposition (the distance between the highest intertidal and the deepest subtidal occurrence of eggs), and make in situ estimates of the number of egg layers. This approach became routine by the 1990s for the major stocks (Hay and McCarter 1999). In Washington, prior to 1996, the 10–12 larger stocks were assessed by both spawn deposition surveys and acoustic/trawl surveys while the 6–8 smaller stocks were only measured with spawn deposition surveys on a three-year rotation. From 1996 to 2009, one or both of these methods were used. Since 2010, only spawn

deposition surveys have been conducted, with the exception of an acoustic/trawl survey of the Cherry Point stock in 2011 (Stick et al. 2014). In Oregon, the number of spawning adults from the previous year was used to estimate spawning biomass (Dauble 2014). In San Francisco Bay, California, spawn deposition surveys were used from 1973 to 1990 and from 2003 to present. From 1991–2002, a combination of spawn deposition and hydroacoustic surveys were used (CDFW 2014).

REFERENCES

- California Department of Fish and Wildlife (CDFW). 2014. Pacific herring commercial fishing regulations: Final supplement and environmental document, SCH No. 98052052. State of California Department of Fish and Wildlife.
- Dauble, A. 2014. R & E grant application: Pacific herring assessment methodology. Accessed from http://www.dfw.state.or.us/fish/RE/projects/cycle_6_applications/13-100%20app%20w%20attachments%20for%20web.pdf.
- Hay, D. E., and P. B. McCarter. 1999. Distribution and timing of herring spawning in British Columbia. Canadian Stock Assessment Secretariat Research Document 99/14. Fisheries and Oceans Canada. Nanaimo, British Columbia. 44 pp.
- Stick, K. C., D. Lowry, and A. Lindquist. 2014. 2012 Washington State herring stock status report. Fish Program Technical Report No. FPA 14-09. 97 pp.

SUPPLEMENTARY TABLE 1

Herring spawning stock biomass data (unit: tonnes)
 for San Francisco Bay, CA, 1979–2012. Data were provided
 by the California Department of Fish and Wildlife.

Year	San Francisco Bay
1979	53,000
1980	65,400
1981	99,900
1982	59,200
1983	40,800
1984	46,900
1985	49,100
1986	56,800
1987	68,900
1988	66,000
1989	64,500
1990	51,000
1991	46,600
1992	21,000
1993	39,900
1994	40,000
1995	99,100
1996	89,600
1997	20,000
1998	39,500
1999	27,400
2000	37,300
2001	35,400
2002	
2003	34,400
2004	58,900
2005	145,100
2006	10,900
2007	11,200
2008	4,800
2009	38,400
2010	57,100
2011	61,000
2012	79,500

SUPPLEMENTARY TABLE 2

Herring spawning stock biomass data (unit: pounds,
 unlike all other sites for which biomass was given in
 tonnes) for Yaquina Bay, OR, 1979–2011. Data were
 provided by the Oregon Department of Fish and Wildlife,
 and converted to tonnes for analysis.

Year	Yaquina Bay ¹
1979	610,000
1980	512,000
1981	531,000
1982	631,000
1983	621,000
1984	667,000
1985	920,000
1986	4,120,000
1987	3,090,000
1988*	2,720,000
1989*	2,980,000
1990*	2,640,000
1991*	2,580,000
1992*	2,280,000
1993*	1,120,000
1994**	537,000
1995**	521,000
1996**	550,000
1997**	82,000
1998	“trace”
1999	20,000
2000	90,000
2001	“trace”
2002 ²	1,386,000
2003	528,080
2004	925,000
2005	223,178
2006	34,941
2007	290,962
2008	239,125
2009	1,473,070
2010	62,506
2011	296,624

*Values estimated from ODFW unpublished data.

**Values estimated, based on the following year's harvest and an assumed 20% harvest rate.

¹ Biomass is determined from observed spawning egg deposition.

² ODFW egg deposition survey estimate. BioSonics, Inc. survey of lower Yaquina Bay indicated 766,000 lbs.

SUPPLEMENTARY TABLE 3
Herring spawning stock biomass data (unit: tonnes) for primary sites in Washington, 1973–2013.
 Data were provided by the Washington Department of Fish and Wildlife.

Year	Quartermaster Harbor	Port Gamble	Port Susan	Discovery Bay	Fidalgo Bay	Cherry Point
1973						14998
1974						13963
1975						10337
1976	1357	1142		697		11844
1977	1413	2525		1488		11097
1978	1860	1984		1305		10973
1979	1941	1790		882		9957
1980	1930	2309		3220	276	9329
1981	1777	1753		3070	456	6219
1982	1778	1463	1391	2356	182	5342
1983	909	2407	1398	2578	640	8063
1984	1386	2685	1555	3144	742	5901
1985	667	2387	1321	1447	761	5760
1986	1181	2050	934	1566	731	5671
1987	924	2046	1216	1593	887	3108
1988	750	1390	570	853		4428
1989	898	2395	345	1225		4003
1990	681	2969	291	855		4998
1991	580	2259	245	925	1079	4624
1992	518	2270	545	727	1399	4009
1993	1075	1521	1693	737	1417	4894
1994	1412	2857	365	375	1207	6324
1995	2001	3158	363	261	1173	4105
1996	805	2058	110	747	590	3095
1997	1402	1419	828	199	929	1574
1998	947	971	2084	0	844	1322
1999	1257	1664	545	307	1005	1266
2000	743	2459	785	159	737	808
2001	1320	1779	587	137	944	1241
2002	416	1812	775	148	865	1330
2003	930	1064	450	207	569	1611
2004	727	1257	429	252	339	1734
2005	756	1372	157	33	231	2010
2006	987	774	321	1325	323	2216
2007	441	826	643	42	159	2169
2008	491	208	345	248	156	1352
2009	843	1064	252	205	15	1341
2010	143	433	152	26	103	774
2011	96	1464	138	0	119	1301
2012	108	404	61	105	89	1120
2013	157	273	29	0	100	908

SUPPLEMENTARY TABLE 4

Herring spawning stock biomass data (unit: tonnes) for regions in Washington, 1975–2013. Data were provided by the Washington Department of Fish and Wildlife. See the Methods section for information about data calculation by region.

Year	S. Puget Sound	Hood Canal	Whidbey	Olympic	Anacortes	Whatcom
1975						11109
1976		1913				12165
1977		3201				11731
1978						
1979						
1980				4075		
1981						7227
1982						6731
1983						8937
1984						6673
1985						8085
1986						7135
1987						
1988						6393
1989						5704
1990						6928
1991		2820				6685
1992		2511				5510
1993						6796
1994						7713
1995						5350
1996		2625	1182	1307	1556	4314
1997		2110	2251	664	1547	2195
1998		2224	2757	423		2241
1999		4644	1625	1461		2134
2000	3012	5025	1712	404	1151	1734
2001	5057	4057	3032	842	1695	2339
2002	4550	4563	3563	1053	1650	2342
2003	4368	2187	4111	699	953	2698
2004	2307	3775	2347	458	757	2363
2005	3217	2707	1824	203	490	2880
2006	3881	3548	4444	1379	1020	3493
2007	2622	3268	2451	100	540	3293
2008	2747	2962	2373	317	625	2014
2009	3795	4284	2333	251	335	2331
2010	1014	2659	1227	101	776	1683
2011	805	6063	3610	104	506	2906
2012	945	3294	1182		524	1999
2013	905	2544	1068		793	1477

SUPPLEMENTARY TABLE 5
Herring spawning stock biomass data (unit: tonnes) for regions in British Columbia, 1951–2012.
 Data were provided by Fisheries and Oceans Canada.

Year	Haida Gwaii	Prince Rupert District	Central Coast	Strait of Georgia	WC Vancouver Island
1951	10841	48293	50954	90733	33145
1952	8117	21909	25341	105691	20268
1953	26801	30342	36296	131767	31171
1954	68157	25223	39291	147164	22852
1955	74668	19911	39194	120527	28048
1956	15285	23587	15876	63864	32282
1957	5065	10926	12998	38700	47409
1958	4779	23908	22616	52186	59915
1959	11035	47489	24714	71259	31887
1960	16196	50010	26698	69162	13786
1961	29537	71520	27011	63689	18205
1962	39261	88347	44924	71178	29046
1963	29549	70880	27734	61891	25869
1964	10208	73193	15795	60161	27126
1965	2663	47359	11793	37142	18425
1966	4886	20710	6636	23895	9404
1967	4716	10144	10344	15217	7461
1968	4992	8107	9297	23336	12716
1969	6285	8530	11679	27340	15734
1970	10425	11713	22589	39084	29567
1971	16380	10179	27515	46709	53741
1972	24557	11587	27101	39565	58393
1973	33164	14178	34382	48749	62937
1974	40334	18213	34196	75551	72884
1975	41134	17976	37615	91236	96723
1976	34425	20407	30540	113016	79083
1977	28440	15035	27846	146412	71430
1978	23744	9950	20399	141195	66386
1979	35460	10468	46890	132722	62554
1980	77441	17446	73534	123166	72475
1981	73952	19219	71476	110357	64956
1982	56702	22571	70250	92685	44207
1983	49227	32415	52281	64253	30986
1984	50974	39701	36949	53901	34344
1985	46928	36943	39433	67234	53152
1986	37777	39782	37233	88473	65346
1987	36088	41458	46577	89814	64425
1988	51225	35608	66396	113537	91749
1989	50706	29586	49603	99382	72256
1990	35590	29077	39525	111746	65795
1991	25985	36465	43657	116767	58897
1992	30208	39194	62990	141442	76888
1993	18167	33115	53532	144148	70911
1994	11980	24490	44090	126162	58815
1995	13918	25649	32444	115151	49797
1996	18010	32454	39020	127192	53573
1997	25262	28650	57294	146026	67636
1998	26931	27330	62871	137674	48054
1999	15145	27595	53609	123416	35982
2000	10373	24278	48269	124287	34590
2001	9024	26440	36265	159240	36461
2002	10136	25813	34654	163978	35963
2003	12271	31986	40249	162735	29090
2004	8755	23085	30738	131553	16578
2005	9337	17367	25516	113517	9507
2006	8145	16696	15750	102563	8447
2007	11213	19513	13172	110549	8006
2008	10292	19408	12164	72217	7194
2009	12803	19735	15949	75331	8138
2010	11727	22267	14506	61659	9085
2011	12659	25979	14886	93731	12341
2012	17681	26495	13662	99835	14111

COMPOSITION AND INTERANNUAL VARIABILITY IN TRACE ELEMENT PROFILES OF PACIFIC SARDINE OTOLITHS

BARBARA J. JAVOR, EMMANIS DORVAL

Ocean Associates Inc., under contract to Southwest Fisheries Science Center
National Oceanographic and Atmospheric Administration
8901 La Jolla Shores Drive
La Jolla, CA 92037
ph: (858) 546-5679
barbara.javor@noaa.gov

ABSTRACT

Temperature is a primary factor separating Pacific sardine *Sardinops sagax* into cold and temperate stocks in the California Current Ecosystem. We collected otoliths of age-1 sardine captured in the spring off central California (1996–97) and in the Southern California Bight (SCB; 1991–92 and 1995–2004) where the cold and temperate stocks presumably overlap during seasonal migrations. To assess whether the sardine had distinguishing chemical characteristics, we compared trace element profiles of otoliths with seawater temperatures to evaluate composition and interannual variability. Ca, Mg, P, Sr, Mn, and Ba in dissolved whole otoliths were analyzed by inductively coupled plasma mass spectrometry. Cohorts from central and southern California differed by collection site in Mg/Ca and P/Ca ratios. Mg/Ca and P/Ca ratios covaried and correlated with seawater temperature in the SCB in most years. High interannual variability in some trace element ratios within sites made it difficult to characterize site-specific otolith profiles. Otolith composition was likely influenced by temperature and local conditions. Stock mixing in the SCB may have contributed to interannual variability as well.

INTRODUCTION

Cooperation between Canada, the United States (US), and Mexico in management of Pacific sardine *Sardinops sagax* (Jenyns 1842) fisheries along the North American coast would be facilitated by knowledge of the distribution of regional stocks of mature and immature sardine along with their spawning habits and migration patterns. The range of Pacific sardine encompasses much of the California Current Ecosystem (CCE, fig. 1). Three stocks are believed to exist with seasonally synchronous, north-south migrations: a cold, northern stock along the California coast that migrates to the Pacific Northwest in the summer as adults to feed; a temperate, southern stock along the Pacific coast of Baja California, Mexico, that migrates to southern California; and a warm, gulf stock within the Gulf of California that migrates to the Pacific coast as far as Bahía Magdalena, Mexico (Félix-Uraga et al. 2004, 2005; Smith 2005).

The biological and environmental factors that divide Pacific sardine into regional stocks are not definitive. Unique genetic profiles within stocks have not been identified (Hedgecock et al. 1989; Grant and Bowen 1998; Pereyra et al. 2004; García-Rodríguez et al. 2011). Other methods that have offered clues to describing regional stocks and migration patterns include: egg, larval, and adult surveys (Lo et al. 2005, 2010, 2011); vertebral counts and tags (Smith 2005); temperature at catch (Félix-Uraga et al. 2004, 2005; Demer et al. 2012; Demer and Zwolinski 2014); analysis of spawning habitats (Reiss et al. 2008; Zwolinski and Demer 2013); fish and otolith morphometric analysis and aging (Javor et al. 2011; Javor 2013; Vergara-Solana et al. 2013); and otolith stable isotope measurements (Valle and Herzka 2008; Dorval et al. 2011; Javor and Dorval 2014).

Trace element composition in immature sardine otoliths could reflect chemical and temperature differences in spawning regions. In US waters, sardine spawn primarily in the spring off central and southern California (Lo et al. 2005, 2010). They spawn in the late fall and winter in the Gulf of California, and in the summer in Bahía Magdalena off southern Baja California (Smith 2005). Seawater temperature of sardine habitats ranges from less than 10°C in the Pacific Northwest (Emmett et al. 2005) to over 25°C in their southern distribution in Mexico (Mitchell et al. 2002; Félix-Uraga et al. 2004, 2005). Temperature is believed to be the primary physical driver of sardine population and individual growth rates, abundance, and large-scale migrations along the North American Pacific coast (Demer et al. 2012; Hill et al. 2014; Dorval et al. 2015).

Fisheries biologists often use otolith trace element composition to identify fish stocks. Factors that influence elemental partitioning into otoliths include temperature, salinity (Hoff and Fuiman 1993; Fowler et al. 1995; Elsdon and Gillanders 2002; Bath Martin and Wuenschel 2006), age, and ontogeny (Begg et al. 1998; Rooper et al. 2001; Brophy et al. 2003; Ruttenberg et al. 2005). Using several experimental approaches to influence trace element chemistry of otoliths in a companion study of juvenile Pacific sardine, Javor and Dorval (2016) demonstrated Mg and P were metastable in the

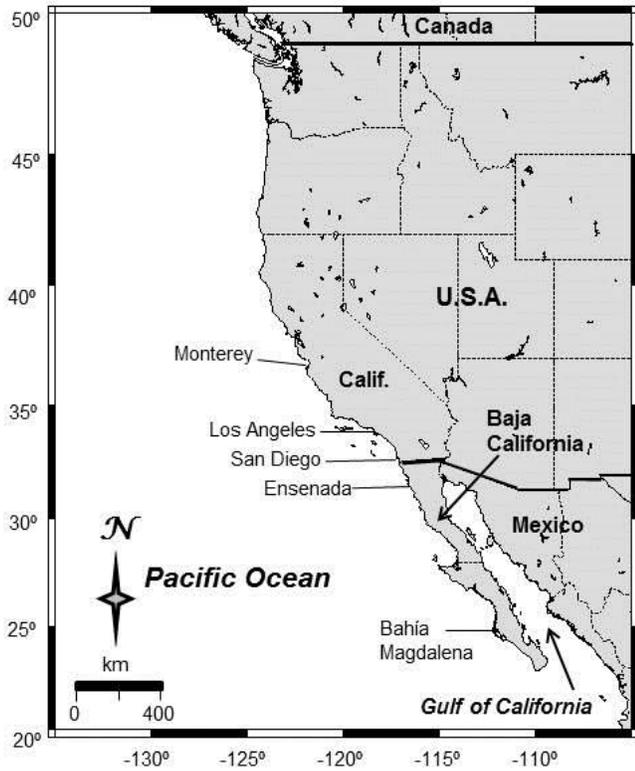


Figure 1. Map of collection sites of *S. sagax*.

otoliths of juveniles over time as they grew, and these two elements covaried in cultured sardine. Mg/Ca and P/Ca ratios decreased with growth in age-0 sardine at 16°–19°C, and Mn/Ca ratios increased.

The overall goal of this study was to use otolith trace element composition to identify and compare cohorts of age-1 Pacific sardine fished off central California (Monterey Bay) and in the Southern California Bight (SCB). The central California sardine belong to the cold stock, while the SCB sardine consist of seasonally influenced, migrating populations from cold and temperate stocks (Félix-Uraga et al. 2005). We approached the broad problem by addressing three specific issues: 1) How similar are trace element profiles of sardine otoliths within and between collection sites in the SCB? 2) How do otoliths of sardine cohorts in the SCB compare to each other and with seawater temperature over multiple years? 3) How do trace element profiles in otoliths of cohorts compare in age-1 sardine captured off central and southern California?

This investigation is a companion report to comparative surveys of oxygen stable isotopes in sardine otoliths (Dorval et al. 2011; Javor and Dorval 2014) and an experimental study of trace element behavior in otoliths of laboratory-reared, juvenile sardine (Javor and Dorval

TABLE 1
 Collection sites, dates, and number of otoliths used in this study.
 Mn/Ca and Ba/Ca ratios (both $\mu\text{mol mol}^{-1}$) are noted for each collection.

Site	Date	<i>n</i>	Mn/Ca Avg \pm S.E.	Ba/Ca Avg \pm S.E.
Monterey Bay	1996	30	2.286 \pm 0.105	3.224 \pm 0.175
	1997	26	2.353 \pm 0.144	4.095 \pm 0.211
SCB (Los Angeles)	1995–2003	122		
	1995	17	2.558 \pm 0.113	3.701 \pm 0.359
	1996	18	2.535 \pm 0.177	3.425 \pm 0.469
	1997	14	2.797 \pm 0.220	4.981 \pm 0.449
	1998	14	2.567 \pm 0.150	4.333 \pm 0.294
	1999	14	2.581 \pm 0.181	2.932 \pm 0.226
	2000	17	2.475 \pm 0.141	3.520 \pm 0.269
	2001	12	2.349 \pm 0.139	4.012 \pm 0.219
	2002	6	2.307 \pm 0.157	4.213 \pm 0.595
	2003	10	1.842 \pm 0.142	3.019 \pm 0.475
SCB (San Diego)	2004	10	2.187 \pm 0.212	1.919 \pm 0.186
Ensenada	1991	30		
	Apr	9	1.587 \pm 0.099	0.876 \pm 0.116
	Jun	6	2.014 \pm 0.135	2.255 \pm 1.037
	Oct	8	2.736 \pm 0.438	3.151 \pm 0.335
	Nov–Dec	7	2.710 \pm 0.323	4.179 \pm 0.810
	1992	30		
	Apr–May	11	2.338 \pm 0.128	5.216 \pm 0.755
	Jun	4	2.362 \pm 0.292	4.907 \pm 0.953
	Aug	5	2.630 \pm 0.323	7.338 \pm 1.134
	Sep	10	1.947 \pm 0.130	6.419 \pm 0.673

2016). The present study surveyed trace element composition in otoliths of wild-caught sardine to determine whether this method might be useful for differentiating stocks. It also addressed whether *in vivo* losses of Mg and P observed in otoliths of cultured juveniles could be detected in otoliths of wild sardine.

MATERIALS AND METHODS

Sources of Pacific Sardine

Fish were sampled each spring, coinciding with their presumed one-year birth date. During winter and spring, Pacific sardine migrate south when the SCB population is believed to consist of cold stock with some temperate stock influence (Félix-Uraga et al. 2005). Sardine otoliths were collected from port samples of commercial fisheries in central California (Monterey Bay) and the SCB (off Los Angeles, San Diego, and Ensenada) by Southwest Fisheries Science Center, California Fish and Wildlife, or Mexican affiliates (Javor and Dorval 2014) (fig. 1 and table 1). The SCB, 34.5° to 31.7°N, is considered here to include Ensenada, which is on the Baja California Peninsula (termed Baja California in this report), Mexico. One otolith of each pair was used for oxygen stable isotope analysis (Dorval et al. 2011; Javor and Dorval 2014), and the other was used for the trace element investigation.

Temperature

We compared otolith trace element ratios with published yearly sea surface temperatures (January–December averages at 5–15 m) for the SCB in US waters, determined from CalCOFI survey data as reported by Hill et al. (2014). The average measured temperature during 1995–2003 was 16.0°C, with annual values ranging from 14.9° to 16.7°C. However, based on oxygen stable isotopes determined in the study of Dorval et al. (2011), the average calculated temperature recorded in the whole otoliths of the 1995–2003 survey was 15.1°C, with the warmest years recorded in the 1996 and 1998 collections (both 16.6°C), and the coldest years recorded in the 1997 and 2002 collections (14.0° and 12.7°C, respectively). Temperatures calculated from oxygen stable isotopes in the otoliths were colder than the sea surface temperatures recorded in CalCOFI surveys of the SCB (Dorval et al. 2011). We did not include the temperature comparison with the 1991–92 Ensenada samples because we did not have data collected and averaged by the same methods for northern Baja California waters where currents and water masses are influenced by the Ensenada Front (McClatchie 2014).

Otolith Preparation

Otoliths were removed primarily from fresh fish with the remainder extracted from frozen fish.

After initially cleaning in deionized water (MilliQ™, MQ-H₂O), the otoliths were dried, weighed on a Cahn C-33 microbalance (0.005 mg accuracy), and stored in plastic microfuge tubes. They were further prepared in a Class 100 clean room using acid-cleaned implements. Following the procedure of Javor and Dorval (2016), the fragile otoliths were soaked in 2% sodium dodecyl sulfate for 30 min, washed at least 4 times with MQ-H₂O, soaked 3–5 min in 30% H₂O₂, and washed again with at least 4 final MQ-H₂O changes. Primarily left sagittal otoliths were analyzed. Preliminary measurements showed no difference in trace element composition between left and right otoliths (Javor and Dorval 2016).

There are significant linear and nonlinear relationships between otolith weight and trace element ratios in juvenile sardine, indicating strong ontogenetic effects on elements such as Mg and P (Javor and Dorval 2016). That study showed these effects were not significant when otolith weight was greater than 0.6 mg in age-0 sardine. To minimize size and age effects while comparing trace element ratios among groups of fish, we only used age-1 otoliths. The average weight of otoliths in this study was 1.0 mg (range = 0.8–1.4 mg) except for the 2004 collection off San Diego that had an average weight of 0.7 mg.

Inductively Coupled Plasma Mass Spectrometry (ICPMS)

Otoliths were dissolved in 2% HNO₃ with 2 ppb In as an internal standard for trace element analysis by solution-based ICPMS on a Finnegan MAT Element 2 instrument at Old Dominion University (Norfolk, Virginia). Samples were randomized in sets of 8 between a blank (to determine minimum detection limits and baseline) and a repeating standard (to determine drift). Average detection limits were: ²⁴Mg, 0.01 ppb; ³¹P, 0.22 ppb; ⁴⁸Ca, 0.01 ppm; ⁵⁵Mn, <0.01 ppb; ⁸⁸Sr, 0.01 ppb; and ¹³⁷Ba, <0.01 ppb. Mean RSD(%) were: Mg, 6.16%; Ca, 5.27%; Sr, 2.85%; and Ba, 3.68%. RSD values for P and Mn were not provided by the analytical laboratory. Trace element ratios are reported as mmol mol⁻¹ for Mg/Ca, P/Ca, and Sr/Ca; and μmol mol⁻¹ for Mn/Ca and Ba/Ca.

Standards, reagents, and their sources were reported by Javor and Dorval (2016) and are briefly summarized here. Standards for solution-based ICPMS were diluted from a master solution to bracket similar element ratios and concentrations as sardine otoliths: 200 ppm Ca, 30 ppb Mg, 300 ppb P, 2 ppb Mn, 300 ppb Sr, 8 ppb Ba, and 2 ppb In as internal standard. Element ratios in the standard mixture were: Mg/Ca, 0.247 mmol mol⁻¹; P/Ca, 1.935 mmol mol⁻¹; Sr/Ca, 0.685 mmol mol⁻¹; Mn/Ca, 7.280 μmol mol⁻¹; and Ba/Ca, 11.660 μmol mol⁻¹.

Data Analysis

Several statistical approaches were used to evaluate the data sets collected from different sites and sampling years. To compare otolith composition of sardine captured across the SCB, we used a nonparametric discriminant analysis, the k -nearest neighbor method with $k = 3$. This method evaluated the accuracy of classifying individual otolith samples to their site and year of collection in the SCB based on five trace element ratios (Hand 1981; Souza et al. 2003; Dorval et al. 2005). Classification rates of otolith samples within site-year were predicted for fish collected in the SCB off southern California from 1995 to 2004 and Ensenada in 1991 and 1992. Contrary to many other methods, and particularly for explanatory analyses, the k -NN approach also provides classification rates for an “Other group” that is assigned to individual samples that have a low probability of belonging to the groups explicitly specified in the analysis. The k -NN method is suitable for the kind of survey we conducted. A jackknife (leave one out) method was used to estimate final classification accuracy within site-year. Because the years of capture of the Ensenada samples did not overlap with the capture dates of the California collections, our main objective was to determine whether trace element profiles from these southernmost samples (with the highest likelihood of influence by temperate stock) had characteristics that could discriminate fish caught in Mexican waters from those collected over multiple years from US waters. We present the results as the percent of otoliths from each annual collection that self-identified.

We also evaluated how temperature may have influenced the temporal variability of otolith trace element composition within the US waters of the SCB over multiple years (1995–2003) for spring-caught sardine. We used a nonmetric, weighted, multidimensional scaling analysis based on Euclidian distance (Kruskal and Wish 1978; Schiffman et al. 1981). We used six variables (Mg/Ca, P/Ca, Mn/Ca, Sr/Ca, and Ba/Ca ratios, plus sea surface temperature) to compute Euclidian distances. Both the nearest neighbor and the multidimensional scaling analyses were performed using SAS software (version 9.4). In addition to the multidimensional analysis, we compared temporal trends of otolith element ratios and temperature with Spearman correlation coefficients. We considered correlation coefficients of 0.5 or less to be insignificant.

We also used 2 X 2 ANOVA tests to compare trace element ratios for the 1996 and 1997 cohorts that were born during the same annual spring spawning events off California and sampled as age-1 fish from central and southern California waters. Based on Hartley’s (1950) F_{max} -test described by Sokal and Rohlf (1995), these ratios showed homogeneity of variance within year and site of collection after log transformation. In the log

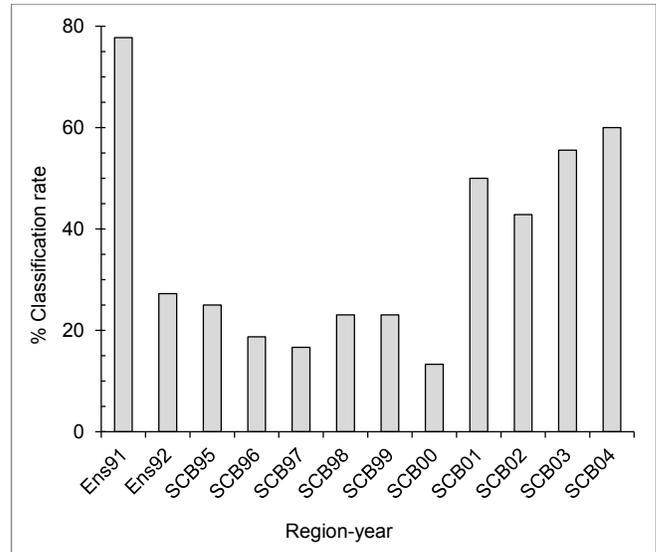


Figure 2. Classification rates using nearest neighbor analysis to compare otolith trace element profiles of *S. sagax*. Abbreviations: Ens = Ensenada 1991, 1992; SC = southern California 1995–2004.

scale, ratios were normally distributed within year and site based on the Kolmogorov–Smirnov test, except for Ba/Ca and Mn/Ca measured in 1996 from southern California otoliths. Mg/Ca ratios did not meet either the normality or the homogeneity of variance assumption. We performed simple 2-way ANOVA on P/Ca and Sr/Ca ratios using the Type III sum of squares method, and robust 2-way ANOVA on Mg/Ca, Mn/Ca, and Ba/Ca ratios. The R function *raov* from the *Rfit* package (*R* version 3.2.5) was used to conduct the robust test for main effects and interaction based on the algorithm developed by Hocking (1985).

RESULTS

Predictability of Trace Element Profiles Within and Between Sites

We compared otolith composition of samples collected off southern California and Ensenada using nearest neighbor classification methods to evaluate site-specific homogeneity calculated as rates of self-classification. Greater self-identity percentages indicated uniqueness of those sampled fish from trace element profiles of sardine otoliths in the SCB over the course of years surveyed. Self-classification rates were high (nearly 80%) for sardine collected off Ensenada in the spring of 1991, but they were less than 30% for sardine captured off Ensenada in 1992 and Los Angeles in 1995–2000 (fig. 2). The SCB samples were relatively distinctive in the 2001–04 collections (40%–60% rates). Among the sardine analyzed by the k -NN method, less than 4% could not be assigned to any region-year group. Overall, trace element composition of sardine otoliths gener-

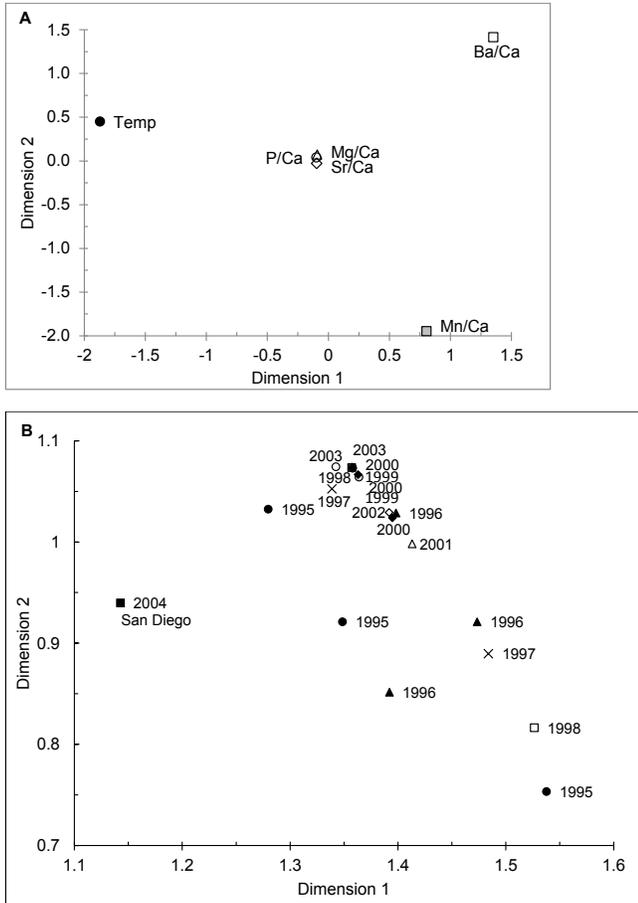


Figure 3. Multidimensional discriminant analysis of *S. sagax* otoliths from the SCB separated by trace element ratios (A) and by year (B).

ally followed regional patterns in some years in the SCB, but in other years they had relatively distinctive profiles.

We also evaluated the distinguishing factors of the spring, 1991 sardine from Ensenada by comparing Mn/Ca and Ba/Ca ratios in otoliths (table 1). All the otoliths from that collection had low Mn/Ca ratios (average $1.587 \mu\text{mol mol}^{-1}$) together with very low Ba/Ca ratios (average $0.876 \mu\text{mol mol}^{-1}$). Although some individual otoliths in this study had similarly low Mn/Ca ratios, otoliths having both low Mn/Ca and Ba/Ca ratios together were rare except in the Ensenada samples from spring 1991. This feature did not persist in subsequent samples from Ensenada. By the end of 1991 and through 1992, Mn/Ca ratios in Ensenada sardine resembled those measured in the SCB in the 1995–2003 samples while Ba/Ca ratios equaled and surpassed the averages measured in the 9-year survey. These observations on Mn/Ca and Ba/Ca trends were not further evaluated because the sample sizes were small and only two years were compared.

The predictability of assigning sardine to collection area was also analyzed with a multidimensional scale

model that evaluated the annual seawater temperature and trace element ratios of otoliths sampled in the SCB from 1995 to 2004. If otolith composition profiles had been similar over the collection years, the cluster patterns would have been simple. However, the results were complex. The configuration of temperature and trace elements based on Dimension 2 against Dimension 1 showed a tripod shape with Mg/Ca, Sr/Ca and P/Ca ratios forming a cluster at the center (fig. 3A). Dimension 1 separated this cluster from temperature, Ba/Ca, and Sr/Ca. In contrast, Dimension 2 showed the cluster was more related to temperature than to Ba/Ca (at the top, positive) and Mn/Ca (at the bottom, negative).

The plot of coefficients for annual samples in the SCB exhibited three distinct groups when depicted as Dimension 2 versus Dimension 1 (fig. 3B). Dimension 2 mainly separated years with low annual mean temperature (2001–03, with coefficients between 0 and 1.1) and low concentration in Mg/Ca and P/Ca from samples that were collected in years of warmer water conditions. Some fish collected in 1995–98 grouped with the 2001–03 collections, but others formed a wide range grouping along Dimension 2 (from 0.75 to 0.95). Fish collected in 2004 off San Diego in the SCB formed a unique cluster along Dimension 1, and thus they were not similar to any groups of fish collected off Los Angeles in 1995–2003. Multidimensional scale analysis of trace element ratios in the multiyear survey of cohorts from the SCB did not clearly depict sardine otoliths as having distinct trace element profiles that clustered as a single stock nor did they exhibit characteristics that varied every year that would suggest stock mixing.

Temporal and Spatial Trends in Samples from the SCB

The data for the 1995–2003 collections (corresponding to spawning years 1994–2002) from off Los Angeles were evaluated to assess trends over time and to compare them with sardine from other collection sites in the SCB. Otoliths from the 1995–2003 collections had average Mg/Ca, P/Ca, and Sr/Ca ratios of less than 1 mmol mol^{-1} , and average Mn/Ca and Ba/Ca ratios of $2\text{--}4 \mu\text{mol mol}^{-1}$ (table 2A). Over this 9-year period, average Mg/Ca ratios generally decreased as did mean temperature (fig. 4) although overall there was poor correlation between the two variables when all the years were considered (Spearman $\rho = 0.43$, $p = 0.25$). P/Ca and Mg/Ca ratios covaried over the 9-year period ($\rho = 0.990$; table 2B). There was no significant correlation between mean temperature and the other element ratios over the 9 years ($\rho \leq 0.4$; data not shown).

Sardine collected off San Diego in 2004 had some distinct characteristics from sardine captured about 150 km to the north off Los Angeles in 1995–2003. Mg/Ca ratios

TABLE 2
 Trace element ratios in age-1 *S. sagax* juveniles from the SCB off Los Angeles, 1995–2003, $n = 122$.
 A: Molar trace element ratios, average \pm S.E. B: Spearman correlations between trace element ratios.

A				
Mg/Ca	P/Ca	Sr/Ca	Mn/Ca	Ba/Ca
mmol mol ⁻¹	mmol mol ⁻¹	mmol mol ⁻¹	μmol mol ⁻¹	μmol mol ⁻¹
0.106 \pm 0.005	0.824 \pm 0.048	0.511 \pm 0.007	2.481 \pm 0.058	3.770 \pm 0.135
B				
	Mg/Ca	P/Ca	Mn/Ca	Sr/Ca
P/Ca	0.990			
Mn/Ca	0.702	0.674		
Sr/Ca	-0.006	-0.047	-0.096	
Ba/Ca	0.488	0.424	0.469	-0.001

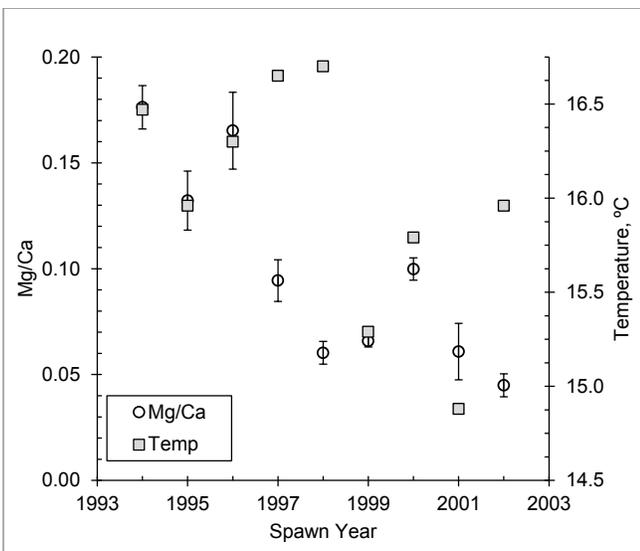


Figure 4. Temporal trends in average sea surface temperatures in the SCB, otolith Mg/Ca ratios (mmol mol⁻¹), and ranges of ratios (\pm S.E.) in age-1 *S. sagax* collected between 1995 and 2003 in the SCB off Los Angeles. Because the sardine spawned in the spring and spent the first ~8–9 months of their lives in the calendar year prior to their collection, the data are plotted according to the year of spawn.

averaged 0.276 ± 0.036 (\pm S.E.) mmol mol⁻¹, which were higher than most of the samples collected off Los Angeles (fig. 4). The 2004 otoliths were generally smaller (0.693 ± 0.018 mg) than the average size of age-1 otoliths which might have influenced the results for correlations and for the multidimensional analyses described above.

Because P/Ca and Mg/Ca ratios covaried in sardine otoliths, we compared P/Mg ratios in the collections to evaluate possible trends for both trace elements together. P/Mg ratios of sardine otoliths collected in 1991 and 1992 off Ensenada (9.071 ± 0.498 [S.E.]) differed little from ratios in otoliths of similar sized sardine caught off Monterey in 1996–97 (8.167 ± 0.401) and Los Angeles in 1995–2003 (7.816 ± 0.147). Lower P/Mg ratios were found in otoliths from sardine captured near San Diego in 2004 (4.498 ± 0.445).

Comparing Cohorts from Southern and Central California

We further assessed whether the Mg/Ca and P/Ca relationships in otoliths might be useful for differentiating and identifying sardine in neighboring regions and over time by comparing cohorts from 1996 and 1997 collected from Monterey Bay and off Los Angeles. The interaction between sites and years was significant for both P/Ca and Mg/Ca ratios (table 3). Although there were no significant differences between years, the Monterey sardine had significantly lower Mg/Ca ratios (fig. 5) and P/Ca ratios than southern California sardine. Comparisons of 1996 and 1997 results at the two sampling sites showed no significant site or year differences between other element ratios except for Ba/Ca ratios in Monterey that differed between the two years.

DISCUSSION

The overall picture of trace element profiles of age-1 otoliths of Pacific sardine captured in the SCB and Monterey is one of complex interactions between collection sites, year of capture, and seawater temperature. Of the five trace elements monitored, Mg, P, Mn, and Ba provided useful data for assessing profile similarities and differences. Sr/Ca ratios were largely similar in all the samples and were not useful for differentiating collections.

Predictability of Trace Element Profiles Within and Between Sites and Over Time

Trace element ratios in otoliths in our study were similar to those reported in a number of fish (Campana 1999), including Pacific sardine from the SCB grown in the laboratory (Javor and Dorval 2016) and *S. sagax* from Australia (Edmonds et al. 1995). By limiting the samples to age-1 and >0.6 mg, our study minimized ontogenetic effects on trace element composition (Javor and Dorval 2016). This stringency should have improved the predictability if otolith composition followed regu-

TABLE 3
 Results of two-way ANOVA performed on trace element ratios in sardine otoliths collected in 1996 and 1997 from central (Monterey Bay) and southern (Los Angeles) California waters. $n = 84$ with $df = 1$ (see Methods).
 A: Parametric model. B: Nonparametric model.

A. Parametric model				
Element ratio	Source	MS	F	$\bar{\eta}$
P/Ca	Site	19.51	137.85	0.0000
	Year	0.30	2.12	0.1490
	Site*Year	1.08	7.83	0.0071
	Error	0.14		
Sr/Ca	Site	0.00	0.03	0.8720
	Year	0.00	0.03	0.8564
	Site*Year	0.02	1.40	0.2397
	Error	0.02		
B. Nonparametric model				
Element ratio	Source	RD	F	$\bar{\eta}$
Mg/Ca	Site	1.54	117.51	0.0000
	Year	0.08	5.99	0.1648
	Site*Year	0.07	5.25	0.0244
	Error	0.01		
Mn/Ca	Site	1.12	3.98	0.0493
	Year	0.35	1.26	0.2643
	Site*Year	0.16	0.58	0.4499
	Error	0.28		
Ba/Ca	Site	0.59	1.25	0.2665
	Year	15.97	33.96	0.0000
	Site*Year	1.01	2.39	0.1494
	Error	0.42		

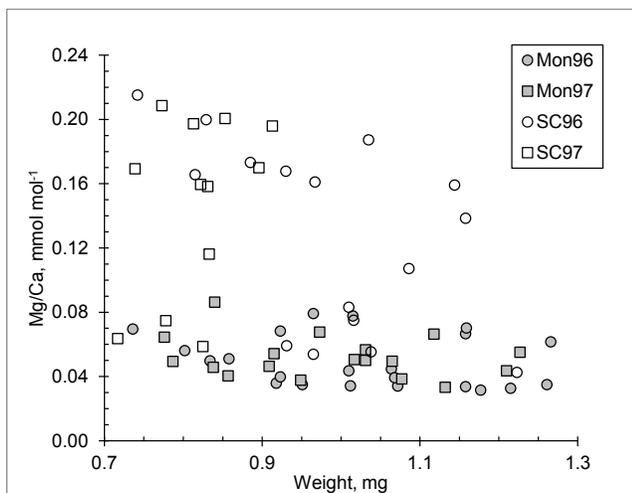


Figure 5. Relationships between molar ratios of Mg/Ca in age-1 *S. sagax* otoliths from cohorts collected near Monterey and in the SCB off Los Angeles, 1996 and 1997.

lar geographic and annual patterns. Our results showed similarities with studies of otolith trace element profiles in other fish species that compared sites and times of capture in that consistent profile patterns were often not detected (Gillanders 2002; Standish et al. 2011).

The annual self-classification rates in sardine were generally lower and more homogeneous in 1995–2000

than in 2001–04. Spring samples from Ensenada in 1992 resembled the 1995–2000 SCB samples, but the spring 1991 sardine from Ensenada had a largely unique profile. Mn/Ca and Ba/Ca ratios were both low only in the spring 1991 collection. To address whether those Ensenada sardine might have resembled a different stock, we compared the spring 1991 Ensenada samples with four monthly samples taken in 2004 from sardine captured in Bahía Magdalena farther south in Baja California. Those otoliths from presumably temperate and/or warm stocks did not share the low Mn/Ca–Ba/Ca feature (unpublished data). With limited sampling that lacked an overlap of dates, it is not possible to conjecture if and how low Mn–Ba trace element composition in sardine otoliths might be interpreted as an indicative population or stock feature.

The annual trends in self-classification in the SCB could have resulted from temporal changes in Pacific sardine stock size and composition. After the US stock collapsed in the 1940s and 1950s, the sardine population in US waters began to recover in the 1980s presumably by expansion of the population that had contracted into Mexican waters where the southern, temperate stock dominated. The US population biomass (northern or cold stock) was about 0.73 mmt in 1995, reached a peak biomass of about 0.91 mmt in

1999, and declined to 0.35 mmt by 2003 (Hill et al. 2014). During the period of the US sardine recovery in the 1980s and 1990s, the population in the SCB was likely influenced by the influx of temperate stock from Mexico and increasing local recruitment from the growing biomass of cold stock spawned in US waters. Shifts in sardine population sizes in the SCB, northern and southern sources of migrating stock, and environmental factors during this period could have altered trace element profiles recorded in age-1 sardine otoliths in 2001–04 following a period of relatively homogeneous trace element profiles in 1992–2000 when the US population was generally increasing.

Temporal Trends in Samples from the SCB

Although Mg/Ca ratios showed only modest overall correlations with temperature in the 9-year survey of sardine captured off Los Angeles, in 6 of the 9 years Mg/Ca ratios and temperature did correlate well (fig. 4, 1994–96 and 1999–2001, $\rho = 0.9$). These results indicate temperature could have played a significant role in otolith Mg incorporation during the first year of growth. Other variables that may have influenced trace element composition include overall stock composition (discussed above), local and regional stock mixing during seasonal migrations, variations in birth dates (and hence ontogeny), and physiological state (Sturrock et al. 2014, 2015).

Variations in temperatures actually experienced by the fish sampled in the collections as a result of depth preferences may have played a role as well. Otolith $\delta^{18}\text{O}$ composition indicates sardine in the SCB recorded temperatures colder than sea surface temperature which likely reflected their time spent in deeper water during daylight hours (Dorval et al. 2011; Javor and Dorval 2014). Sardine can avoid warm temperatures during El Niño events by remaining deeper for longer periods, but they cannot escape cold water during La Niña periods.

We did not assess seasonal trends in regional populations in this study. However, our preliminary unpublished data from a limited sample of sardine otoliths collected in summer and autumn months of 2004 from Bahía Magdalena in southern Baja California indicated trace element profiles in the November collection differed from summer collections, coinciding with expected seasonal migrations of temperate and warm stocks (Félix-Uraga 2004, 2005). Expanded annual surveys in different seasons from the SCB, Bahía Magdalena, and the Gulf of California might improve the resolution of regional identification of stocks of age-1 sardine. Used in combination with temperature and relevant morphometric criteria that might indicate stock identity (Javor et al. 2011; Javor 2013), otolith trace element profiles could

prove to be a useful tool to monitor stocks of subadult sardine throughout the California Current Ecosystem before they are large enough to undertake long-distance migrations.

Comparing Cohorts from Central and Southern California

The investigation comparing age-1 cohorts from central and southern California detected significant differences in Mg/Ca and P/Ca ratios between the two sites, but not the other trace elements measured. Salinity was similar at the two locations (Javor and Dorval 2014), hence differences in the composition of these trace elements might be attributable to temperatures during the first year of life. Based on oxygen stable isotopes in otoliths, sardine experienced an estimated average of 12°–14°C near Monterey (Javor and Dorval 2014), and 14°–17°C off Los Angeles in the SCB (Dorval et al. 2011).

Temperatures between 13° and 21°C affected the incorporation of Mg, P, Mn, Sr, and Ba in otoliths of juvenile sardine maintained in aquaria (Javor and Dorval 2016). That study showed negligible variation in Mg/Ca ratios of age-1 sardine grown at 13° and 17°C, two temperatures that juveniles likely experienced between central and southern California, respectively, where significant differences in Mg/Ca ratios were determined in this study. To reconcile these contradictory findings on temperature-Mg/Ca relationships in experimental and wild-caught sardine, we hypothesize incorporation and retention of Mg in sardine otoliths might respond to thermal influences differently during early life stages which were not assayed in this survey that analyzed dissolved whole otoliths of age-1 fish. Based on mass calculations, experiments showed Mg and P incorporated into juvenile sardine otoliths were metastable and partially lost during subsequent growth at 16°–19°C (Javor and Dorval 2016). We suggest the low Mg/Ca and P/Ca ratios in age-1 sardine captured in Monterey Bay may have resulted from greater losses of Mg and P from otoliths at cooler temperatures early in juvenile life relative to the sardine that presumably spent their first year in the SCB. Establishing geographic variations in the loss of entrapped or poorly bound Mg and P in juvenile sardine otoliths would be a novel application of addressing trace element ratios in biogenic carbonates. It might provide a key to differentiating populations in regions (i.e., between central California and the SCB) and in local sardine habitats (i.e., between Ensenada and San Diego where seasonal currents affect temperatures) (McClatchie 2014). This theory could be tested by time-course sampling of age-0 cohorts in growth series (e.g., monthly) from different sites.

CONCLUSIONS

Trace element composition in age-1 Pacific sardine otoliths off central California and in the SCB showed predictable profiles in some years and relatively distinctive profiles in others. Mg/Ca and P/Ca ratios were important for defining trace element profiles in cohorts between central and southern California, and were consistent with the possible loss of these trace elements from juvenile otoliths as the fish grew. Seawater temperature was a factor in Mg and P composition in most years. Interannual variations in trace element composition within collection sites of the SCB made identification of cold stock characteristics challenging. Our analyses showed that more frequent sampling within and between sites would be required for assessing population characteristics from trace element profiles in sardine otoliths.

ACKNOWLEDGMENTS

We thank Russ Vetter, John Hyde, Brian Wells, and anonymous reviewers for their suggestions. This study was supported by NOAA, the NOAA Fisheries and the Environment (FATE) Program, and a NRC Postdoctoral fellowship to E. Dorval.

LITERATURE CITED

- Bath Martin, G., and M. J. Wuenschel. 2006. Effect of temperature and salinity on otolith element incorporation in juvenile gray snapper *Lutjanus griseus*. *Mar. Ecol. Prog. Ser.* 324:229–239.
- Begg, G. A., M. Cappel, D. S. Cameron, S. Boyle, and M. Sellin. 1998. Stock discrimination of school mackerel, *Scomberomorus queenslandicus*, and spotted mackerel, *Scomberomorus munroi*, in coastal waters of eastern Australia by analysis of minor and trace elements in whole otoliths. *Fish. Bull.* 96:653–666.
- Brophy, D., B. S. Danilowicz, and T. E. Jeffries. 2003. The detection of elements in larval otoliths from Atlantic herring using laser ablation ICP-MS. *J. Fish. Biol.* 63:990–1007.
- Campana, S. E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. *Mar. Ecol. Prog. Ser.* 188:263–297.
- Demer, D. A., J. P. Zwolinski, K. Byers, G. R. Cutter Jr., J. S. Renfree, S. T. Sessions, and B. J. Macewicz. 2012. Seasonal migration of Pacific sardine (*Sardinops sagax*) in the California Current ecosystem: prediction and empirical confirmation. *Fish. Bull.* 110:52–70.
- Demer, D. A., and J. P. Zwolinski. 2014. Corroboration and refinement of a method for differentiating landings from two stocks of Pacific sardine (*Sardinops sagax*) in the California Current. *ICES J. Mar. Sci.* 71:328–335.
- Dorval, E., C. M. Jones, and R. Hannigan. 2005. Chemistry of surface waters: Distinguishing fine-scale differences in sea grass habitats of Chesapeake Bay. *Limnol. Oceanogr.* 50:1073–1083.
- Dorval, E., K. Piner, L. Robertson, C. S. Reiss, B. Javor, and R. Vetter. 2011. Temperature record in the oxygen stables of Pacific sardine otoliths: experimental vs. wild stocks from the Southern California Bight. *J. Exper. Mar. Biol. Ecol.* 397:136–143.
- Dorval, E., J. D. McDaniel, B. J. Macewicz, and D. L. Porzio. 2015. Changes in growth and maturation parameters of Pacific sardine *Sardinops sagax* collected off California during a period of stock recovery from 1994 to 2010. *J. Fish. Biol.* 87:286–310.
- Edmonds, J. S., N. Caputi, M. J. Moran, W. J. Fletcher, and M. Morita. 1995. Population discrimination by variation in concentrations of minor and trace elements in sagittae of two Western Australian teleosts. *In: Secor, D. H., J. M. Dean, and S. E. Campana (Eds.), Recent developments in fish otolith research. The Belle W Baruch Library in Marine Science 19.* Belle W Baruch Institute for Marine Biology and Coastal Research. University of South Carolina Press, Columbia, pp. 655–670.
- Eldson, T. S., and B. M. Gillanders. 2002. Interactive effects of temperature and salinity on otolith chemistry: challenges for determining environmental histories of fish. *Can. J. Fish. Aquat. Sci.* 59:1796–1808.
- Emmett, R. L., R. D. Brodeur, T. W. Miller, S. S. Pool, P. J. Bentley, G. K. Krutzikowsky, and J. McCrae. 2005. Pacific sardine (*Sardinops sagax*) abundance, distribution, and ecological relationships in the Pacific Northwest. *Calif. Coop. Oceanic Fish. Invest. Rep.* 46:122–143.
- Félix-Uraga, R., V. M. Gómez-Muñoz, C. Quiñónez-Velázquez, F. N. Melo-Barrera, and W. García-Franco. 2004. On the existence of Pacific sardine groups off the west coast of the Baja California Peninsula and southern California. *Calif. Coop. Oceanic Fish. Invest. Rep.* 45:146–151.
- Félix-Uraga, R., C. Quiñónez-Velázquez, K. T. Hill, V. M. Gómez-Muñoz, F. N. Melo-Barrera, and W. García-Franco. 2005. Pacific sardine (*Sardinops sagax*) stock discrimination off the west coast of Baja California and southern California using otolith morphometry. *Calif. Coop. Oceanic Fish. Invest. Rep.* 46:113–121.
- Fowler, A. J., S. E. Campana, C. M. Jones, and S. R. Thorrold. 1995. Experimental assessment of the effect of temperature and salinity on elemental composition of otoliths using solution-based ICPMS. *Can. J. Fish. Aquat. Sci.* 52:1421–1430.
- García-Rodríguez, F. J., S. A. García-Gasca, J. De La Cruz-Agüero, and V. M. Cota-Gómez. 2011. A study of the population structure of the Pacific sardine *Sardinops sagax* (Jenyns 1842) in Mexico based on morphometric and genetic analyses. *Fish. Res.* 107:169–176.
- Gillanders, B. M. 2002. Temporal and spatial variability in elemental composition of otoliths: implications for determining stock identity and connectivity of populations. *Can. J. Fish. Aquat. Sci.* 59:669–679.
- Grant, W. S., and B. W. Bowen. 1998. Shallow population histories in deep evolutionary lineages of marine fishes: Insights from sardines and anchovies and lessons for conservation. *J. Heredity* 89:415–426.
- Hand, D. J. 1981. Discrimination and classification. Wiley, 218 pp.
- Hedgecock, D., E. S. Hutchinson, G. Li, F. L. Sly, and K. Nelson, K. 1989. Genetic and morphometric variations in the Pacific sardine *Sardinops sagax caerulea*: comparisons and contrasts with historical data and with variability in northern anchovy *Engraulis mordax*. *Fish. Bull. U.S.* 87:653–671.
- Hill, K. T., P. R. Crone, D. A. Demer, J. Zwolinski, E. Dorval, and B. J. Macewicz. 2014. Assessment of the Pacific sardine resource in 2014 for U.S.A. management in 2014–15. NOAA-TM-NMFS-SWFSC-531.
- Hocking, R. R., 1985. The analysis of linear models. Brooks/Cole, Monterey, 369 p.
- Hoff, G. R., and L. A. Fuiman. 1993. Morphology and composition of red drum otoliths: changes associated with temperature, somatic growth rate, and age. *Comp. Biochem. Physiol.* 106A:209–219.
- Javor, B. J. 2013. Do shifts in otolith morphology of young Pacific sardine (*Sardinops sagax*) reflect changing recruitment contributions from northern and southern stocks? *Calif. Coop. Oceanic Fish. Invest. Rep.* 54:85–96.
- Javor, B., N. Lo, and R. Vetter. 2011. Otolith morphometrics and population structure of Pacific sardine (*Sardinops sagax*) along the west coast of North America. *Fish. Bull.* 109:402–415.
- Javor, B., and E. Dorval. 2014. Geography and ontogeny influence the oxygen and carbon stable isotopes of otoliths of Pacific sardine in the California Current. *Fish. Res.* 154:1–10.
- Javor, B., and E. Dorval. 2016. Stability of trace elements in otoliths of juvenile Pacific sardine *Sardinops sagax*. *Calif. Coop. Oceanic Fish. Invest. Rep.* 57:109–123.
- Kruskal, J. B., and M. Wish. 1978. Multidimensional scaling. Sage Publications.
- Lo, N. C. H., B. J. Macewicz, and D. A. Griffith. 2005. Spawning biomass of Pacific sardine (*Sardinops sagax*), from 1994–2004 off California. *Calif. Coop. Oceanic Fish. Invest. Rep.* 46:93–112.
- Lo, N. C. H., B. J. Macewicz, and D. A. Griffith. 2010. Biomass and reproduction of Pacific sardine (*Sardinops sagax*) off the Pacific northwestern United States, 2003–05. *Fish. Bull.* 108:174–192.
- Lo, N. C. H., B. J. Macewicz, and D. A. Griffith. 2011. Migration of Pacific sardine (*Sardinops sagax*) off the west coast of the United States. *Bull. Mar. Sci.* 87:395–412.
- McClatchie, S. 2014. Regional fisheries oceanography of the California Current System. The CalCOFI program. Springer, New York. 235 p.
- Mitchell, D. L., D. Ivanova, R. Rabin, T. J. Brown, and K. Redmond. 2002. Gulf of California sea surface temperatures and the North American Monsoon: mechanistic implications from observations. *J. Climate* 15:2261–2291.
- Pereyra, R. T., E. Saillant, C. L. Pruett, C. E. Rexroad, A. Rocha-Olivares, and A. R. Gold. 2004. Characterization of polymorphic microsatellites in the Pacific sardine *Sardinops sagax* (Clupeidae). *Molec. Ecol. Notes* 4:739–741.

- Reiss, C., D. M. Checkley Jr., S. J. Bograd. 2008. Remotely sensed spawning habitat of Pacific sardine (*Sardinops sagax*) and Northern anchovy (*Engraulis mordax*) within the California Current. *Fish. Oceanogr.* 17:126–136.
- Rooker, J. R., V. S. Zdanowicz, and D. H. Secor. 2001. Chemistry of tuna otoliths: assessment of base composition and postmortem handling effects. *Mar. Biol.* 139:35–43.
- Ruttenberg, B. I., S. L. Hamilton, M. J. H. Hickford, G. L. Paradis, M. S. Sheehy, J. D. Standish, O. Ben-Tzvi, and R. R. Warner. 2005. Elevated levels of trace elements in cores of otoliths and their potential for use as natural tags. *Mar. Ecol. Prog. Ser.* 297:273–281.
- Schiffman, S. S., M. L. Reynolds, and F. W. Young. 1981. Introduction to multidimensional scaling: Theory, methods, and applications. Academic.
- Smith, P. E. 2005. A history of proposals for subpopulation structure in the Pacific sardine (*Sardinops sagax*) population off western North America. *Calif. Coop. Oceanic Fish. Invest. Rep.* 46:75–82.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry: the principles and practice of statistics in biological research*. H. Freeman, New York.
- Souza, J., Jr., R. H. De Almeida Santos, M. M. C. Ferreira, F. A. Molfetta, A. J. Camargo, K. M. Honório, and A. B. F. Da Silva. 2003. A quantum chemical and statistical study of flavonoid compounds (flavones) with anti-HIV activity. *Eur. J. Med. Chem.* 38:929–938.
- Standish, J. D., J. W. White, and R. R. Warner. 2011. Spatial pattern of natal signatures in the otoliths of juvenile kelp rockfish along the Californian coast. *Mar. Ecol. Prog. Ser.* 437:279–290.
- Sturrock, A. M., C. N. Trueman, J. A. Milton, C. P. Waring, M. J. Cooper, and E. Hunter. 2014. Physiological influences can outweigh environmental signals in otolith microchemistry research. *Mar. Ecol. Prog. Ser.* 500:245–264.
- Sturrock, A. M., E. Hunter, J. A. Milton, EIMF, R. C. Johnson, C. P. Waring, and C. N. Trueman. 2015. Quantifying physiological influences on otolith microchemistry. *Methods Ecol. Evol.* 6:806–8016.
- Valle, R. S., and S. Z. Herzka. 2008. Natural variability in $\delta^{18}\text{O}$ values of otoliths of young Pacific sardine captured in Mexican waters indicates subpopulation mixing within the first year of life. *ICES J. Mar. Sci.* 65:174–190.
- Vergara-Solana, F. J., F. J. García-Rodríguez, and J. De La Cruz-Agüero. 2013. Comparing body and otolith shape for stock discrimination of Pacific sardine *Sardinops sagax* Jenyns, 1842. *J. Appl. Ichthyol.* 29:1241–1246.
- Zwolinski, J. P., and D. A. Demer. 2013. Environmental and parental control of Pacific sardine (*Sardinops sagax*) recruitment. *ICES J. Mar. Sci.* doi:10.1093/icesjms/fst173

BIOLOGICAL INDICATOR OF 2014–15 WARMING CONDITIONS: PRESENCE OF THE MEXICAN LOOKDOWN (*SELENE BREVOORTII*), PACIFIC TRIPLETAIL (*LOBOTES PACIFICUS*) AND CORTEZ BONEFISH (*ALBULA GILBERTI*) IN THE TEMPERATE EASTERN PACIFIC OF MEXICO

JORGE A. ROSALES-CASIÁN

División de Oceanología, Departamento de Ecología Marina
Centro de Investigación Científica y de Educación Superior de Ensenada, B.C. (CICESE)
Carretera Ensenada-Tijuana, No. 3918, C.P. 22860, Ensenada, B.C., México
ph: 52 (646) 175-0500
fax: 52 (646) 175-0545
jrosales@cicese.mx

ABSTRACT

Two Panamic fish species and one species from the Cortez–San Diegan Provinces were recorded for the first time in and near Bahía de San Quintín, Baja California, Mexico, during 2014 and 2015. The area is normally cold because of locally intense upwelling. However, during 2014 and 2015, warm water prevailed, which appears to have led to the presence of these fish species within and outside of the bay. Five specimens of *Selene brevoortii* (Mexican lookdown) were recorded, one individual in October 2014, and three more individuals during July 2015; another specimen, completely dry, was provided by a fisherman as evidence of their presence at an intermediate date within this period. Also in 2015, seven individuals of fish were captured with a commercial gill net set just outside of the bay; five of these were identified as *Lobotes pacificus* (Pacific tripletail) and the other two individuals as *Albula gilberti* (Cortez bonefish). Captures of these tropical species, in an usually cold-water environment are evidence of a substantial fish movement from the tropical Pacific toward the temperate waters of Baja California and California, USA, during warming conditions.

INTRODUCTION

In the coastal area of the eastern Pacific Ocean, climatic and oceanographic changes have occurred during El Niño events, and this has favored the presence of tropical fish species in the temperate zone extending their distribution to the north; this has been documented in California during warm events with the presence of carangid fishes (Lea and Walker 1995; Love et al. 2015), and many other Panamic fish species (Lea and Rosenblatt 2000).

In the temperate coastal zone of northern Baja California, the presence of tropical species associated with warm events, such as the white grunt (*Haemulon leuciscus*; Rosales-Casián and Ruiz-Campos 1999), the bigscale goatfish (*Pseudupeneus grandisquamis*), the bullseye puffer (*Sphoeroides annulatus*), the Paloma pompano (*Trachinotus paitensis*; Rosales-Casián 2004b), and the roosterfish (Rosales-Casián 2013) have also been documented.

A large patch of anomalously warm water appeared off Alaska and subsequently stretched south to Baja California during 2013–14, and was named “The Blob” (Bond et al. 2015). In February 2014, the El Niño Southern Oscillation (ENSO) Alert system of the National Oceanic and Atmospheric Administration (NOAA) reported positive subsurface temperature anomalies across the east-central Pacific, although neutral conditions remained for the Northern Hemisphere in spring 2014; the alert status changed from ENSO non-active to El Niño Watch in March 2014 (NOAA 2014); this condition continued until September, when it showed a weak El Niño, and in April 2015 reflected a strong El Niño episode; after dominating the Pacific for more than a year, El Niño ended in May 2016 (NOAA 2016).

These two anomaly events kept the temperate environment warm for a long period and favored the northward movements of fishes. The present work documents the presence of the fish species caught by coastal commercial fishing and sportfishing in the area of San Quintín, Baja California, Mexico: the Mexican lookdown (*Selene brevoortii*; Gill 1863), the Pacific tripletail (*Lobotes pacificus*; Gilbert 1898) and the Cortez bonefish (*Albula gilberti*; Pfeiler and van der Heiden 2011). Also, the previous records of first time occurrence are presented for two fish species in California waters (*S. brevoortii* by Lea and Walker 1995; *Lobotes pacificus* by Rounds and Feeney 1993), and a brief discussion of *Albula gilberti* (Pfeiler et al. 2011).

METHODS

To document both sportfishing and artisanal commercial fishing, monthly surveys were conducted from 2014–16 in Bahía de San Quintín (fig. 1), an embayment over 300 km south of the US–Mexico border. During this time, vessels returning from outside of the bay were monitored at the Old Mill site. Identification for temperate fishes from the San Quintín coastal area is usually done with the Miller and Lea (1972) guide as well as with the rockfishes work by Love et al. (2002), but in the case of those considered warm fish species I used the work of Allen and Robertson (1998), and Humann and Deloach (2004).

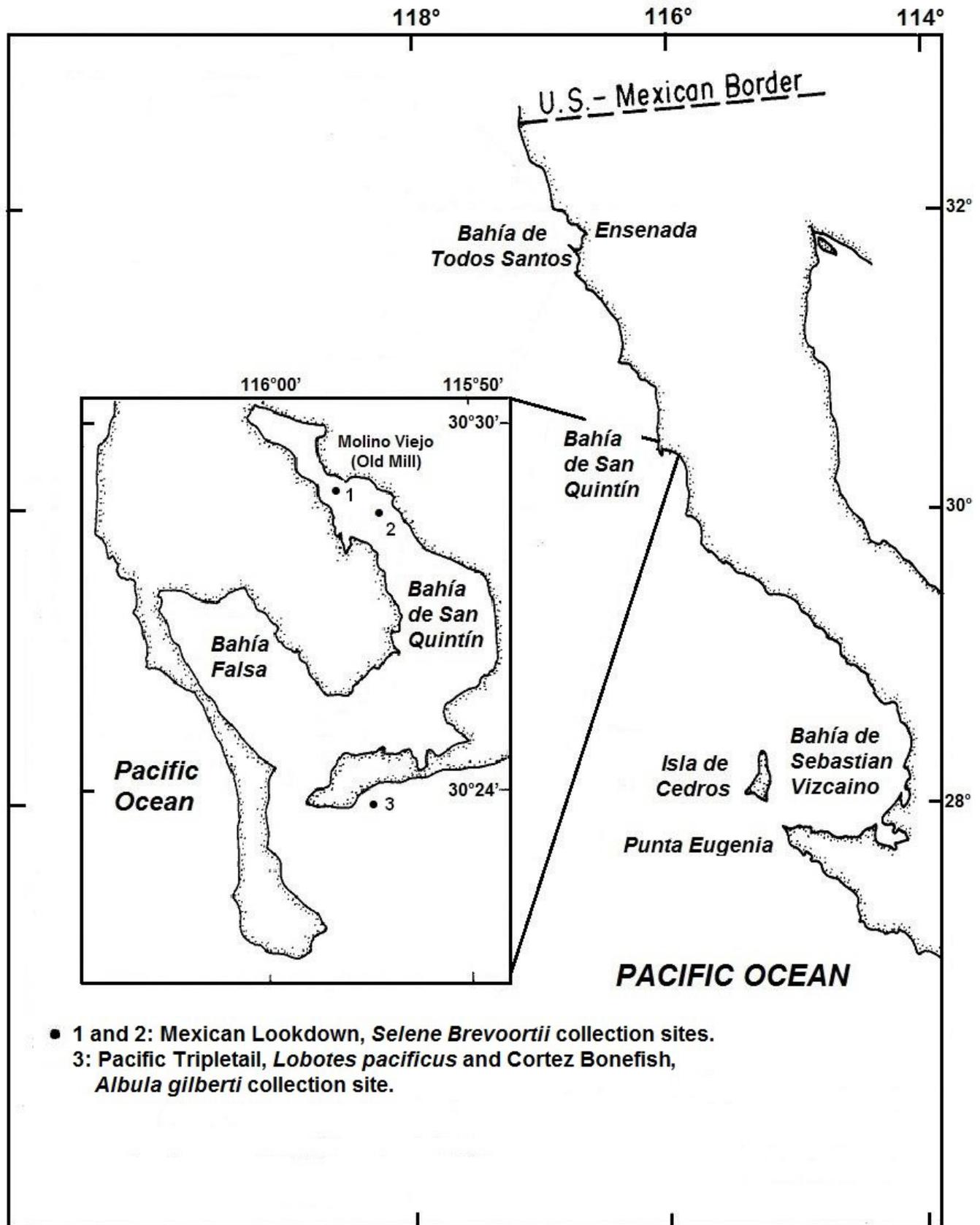


Figure 1. Catch sites of Mexican lookdown, Pacific tripletail and Cortez bonefish in the area of San Quintin, Baja California, Mexico.



Figure 2. Individuals of Mexican lookdown, *Selene brevoortii*, captured in Bahia de San Quintin, Baja California, Mexico.

TABLE 1
 Lengths (mm), weights (g), sites, surface temperature (°C) and dates of tropical fish species captured in the area of San Quintin, Baja California, Mexico.

Fish species	Length Total	(mm) Standard	Weight (g)	Site	Temp. °C	Date
<i>Selene brevoortii</i>	225	160	120	San Quintin Bay	20.9	23 Oct. 2014
	165	130	63		28.9	11 July 2015
	176	135	69		11 July 2015	
	184	140	79		11 July 2015	
Dry	136	98	10			2015
<i>Lobotes pacificus</i>	500	415	1803	San Quintin Coast	16.7	28 March 2015
	610	535	3564			28 March 2015
	480	420	1802			28 March 2015
	490	425	1962			28 March 2015
	550	480	2809			28 March 2015
<i>Albula gilberti</i>	380	210	369	San Quintin Coast	16.7	28 March 2015
	360	300	357			28 March 2015

RESULTS

Selene brevoortii

During 2014 and 2015, there were two separate collections of living *Selene brevoortii* (Mexican lookdown, family Carangidae) (Spanish: *jorobado mexicano*; Page et al. 2013) inside of Bahia de San Quintin, Baja California, Mexico. The first individual was captured in the main channel (fig. 2; table 1), against the piling remnants of an old pier, on 23 October 2014 (30.4649 N, 115.9099 W). Three more individuals were captured in the same chan-

nel but close to an old rocky jetty and the Old Mill boat ramp on 11 July 2015 (table 1). Both collections were made with small lures (Sabiki rigs) by the sportfishing anglers trying to catch live bait (Pacific mackerel, *Scomber japonicus*). In addition, another individual of *S. brevoortii*, this one dried, was provided to me on 13 February 2016 from Bahia de San Quintin, an evidence that it was captured at an unknown date within the bay, but certainly during 2015 (fig. 3, table 1).

These individuals were identified based on the following characteristics: body strongly compressed, pen-



Figure 3. Dry individual of Mexican lookdown, *Selene brevoortii*, from Bahía de San Quintín, Baja California, Mexico.

tagonal-shaped strongly, a depth up to 60% of standard length; the entire body of fresh specimens was silvery color with a deep head and a steep concave forehead and snout profile; caudal fin is deeply forked, and curved pectoral and anal fins (Jarvis et al. 2009). The body is scaleless, and lateral line scutes are poorly differentiated (Smith-Vaniz et al. 2010). The specimens presented: dorsal fin: VIII+1, 21–23; pectoral fin: 18–19; anal fin: I, 18; gill rakers: 8 + 31–32. Fresh individuals of *S. brevoortii* measured from 165 to 225 mm total length LT (table 1).

Lobotes pacificus* and *Albula gilberti

On 28 March, 2015, a commercial fishing trip captured seven tropical fish individuals with a 100 m long gillnet (6 inches mesh light). The individuals were caught in the nearshore off Bahía de San Quintín (fig. 1), on sandy bottom, 8–10 m depth, and close to the Punta Azufre sandbar, east side of the bay's mouth, 30.2924 N,

115.9737 W (fig. 1). When fish were measured, all were without viscera.

After reviewing the fishes, five individuals were identified as *Lobotes pacificus*, the Pacific tripletail (Spanish: *dormilona del Pacífico*; Page et al. 2013). These specimens were olive in color; robust, deep and moderately compressed body (fig. 4); the dorsal, anal, and caudal fins resemble three tails or a rounded caudal fin; preopercle was visibly serrated and covered with scales; the specimens had a continuous dorsal fin with 12 spines and 15 rays, and anal fin with three spines and 11 rays. All the characteristics agree with *L. pacificus*, family Lobotidae (Froese and Pauly 2016). Tripletails captured in San Quintín presented sizes from 480 to 610 mm LT (table 1).

In the same gill net set, two captured fish were identified as bonefish, *Albula* sp. (fig. 5). Both specimens exhibited an elongated and fusiform body, with a coni-



Figure 4. Individual of Pacific tripletail, *Lobotes pacificus*, captured off Bahia de San Quintin, Baja California, Mexico.



Figure 5. Individuals of Cortez bonefish, *Albula gilberti*, captured off Bahia de San Quintin, Baja California, Mexico.

cal snout extending slightly beyond the lower mouth; a silver body with yellow pectoral fins; region of the head without scales. Dorsal fin with 15 soft rays, anal fin with seven soft rays. These characteristics coincide with the genus *Albula* (Froese and Pauly 2016), and Pfeiler et al. (2011) separated all of the bonefish distributed on the outer coast of Baja California and off southern

California as the Cortez bonefish (*Albula gilberti*, family Albulidae; Spanish: *macabí de Cortes*). The two individuals measured 360 mm and 380 mm LT (table 1).

Temperatures within the bay measured between 20.9°C in October 2014 and 28.9°C in July 2015, and in the coastal zone registered 16.7°C in March 2015 (table 1).

DISCUSSION

In the eastern North Pacific, anomalous warm conditions started at the end of 2013 and this surface water remained significantly warmer from 2014 to 2015 (Bond et al. 2015; Dewey 2015). The temperature increases along the North American Pacific coast allowed a range of tropical fish species to move north as the bigeye scad, *Selar crumenophthalmus* (Carangidae), found in California waters during 2015 (Love et al. 2015). Further north in waters of British Columbia, Canada, the warm-temperate affinity species, finescale triggerfish (*B. polyepis*), was found during 2014 (Brooks et al. 2016).

All three species, the Mexican lookdown, the Pacific tripletail, and the Cortez bonefish reported in the present study are known, from rare occurrences, off southern California, north of our study site (Lea and Walker 1995; Rounds and Feeney 1993; Pfeiler et al. 2011). However, what is particularly noteworthy is that in the 30 years of sampling along the Pacific coast of northern Baja California this was the first time that these three tropical fish species were observed; fish studies include the *Macrocystis pyrifera* beds of Bahia de Todos Santos (Diaz-Diaz and Hammann 1987) and south of the bay at Kennedy's Camp (Moreno-Mendoza 2016); the soft-bottom of Bahia de Todos Santos (Rosales-Casián 1997a) and Bahia El Rosario, Punta Baja (Rosales-Casián 2011); the coastal lagoons as Punta Banda estuary (Rosales-Casián 1997b) and Bahia de San Quintin (Rosales-Casián 1996, 2004a,b), the catch of artisanal fishing in commercial fishing camps along Pacific coast (Rosales-Casián and Gonzalez-Camacho 2003), unpublished data of the Bahia de Santa Rosalilita (28°40'N, 114°15'W) at 650 km from California border (Rosales-Casián), USA, and the last study about the fishes of Ojo de Liebre (Scamoon) lagoon (Civico-Collados 2017). Of particular importance, Bahia de San Quintin is one of the most important lagoons in the Pacific coast of Baja California due to its high productivity of phytoplankton, seagrasses, and by the presence of a permanent upwelling near the mouth (Lara-Lara and Alvarez-Borrego 1975; Poumian-Tapia 1995; Rosales-Casián 1996; Gracia-Escobar et al. 2015). The lagoon is considered a cold site (11.2° to 18.6°C) because upwelling water is transported to the interior by tidal currents (Rosales-Casián 1997b; 2011).

Mexican lookdown, the Pacific tripletail, and the Cortez bonefish are considered tropical or subtropical species (Robertson and Allen 2015) with a Pacific distribution (Page et al. 2013), however their presence in temperate environments of northern Baja California coasts is possibly attributed to the anomalous higher temperatures that impacted the epipelagic ecosystem of the California current from the end of 2013 and during 2014–15 (Gómez-Ocampo et al. 2017). Those anomalous condi-

tions were significantly warmer than the last few decades and impacted the entire west coast of North America (Bond et al. 2015; Dewey 2015).

The Mexican lookdown is a Panamic species (Carangidae) that was recorded before the 1990s as far north as Bahia Magdalena, Baja California Sur, Mexico, including the lower half of the Gulf of California (Robertson and Allen 2015). Much further north, one individual of this species was captured for the first time in San Diego Bay, California (USA), on 4 February 1993, and was considered a northward movement related to the warm-water oceanographic conditions that prevailed during 1992–93 (Lea and Walker 1995). On 18 November 2008, two juvenile Mexican lookdowns (62 and 63 mm standard length) were collected with beach seine hauls in Seal Beach, California (north of San Diego Bay), close to the warm water effluent of a power generation station; both juveniles had a characteristic long filamentous ray in their anterior dorsal spine and larger pelvic fins (Jarvis et al. 2009; Smith-Vaniz 1995; Humann and Deloach 2004).

The Carangidae family is distributed in Canada, the United States, and Mexico, and is composed of 55 species with 16 genera, and are named pompanos, jacks, and lookdowns (Page et al. 2013). Mexican lookdown shares its distribution with two other species in the sandy bottoms of the Mexican Pacific (nearshore and estuaries), including the Gulf of California: *Selene orstedii* and *S. peruviana* (Lea and Walker 1995; Snow 2016). No individuals of *S. brevoortii* were collected before in temperate nearshore sites in the Northern Pacific Baja California (Rosales-Casián 1997a, b, 2004a, b, 2011), but were recorded in California waters during warm periods in 1993, and 1997–98 (Lea and Walker 1995; Lea and Rosenblatt 2000; Jarvis et al. 2009).

Pacific tripletail, *L. pacificus* (Lobotidae), is distributed in tropical areas in the eastern Pacific from the Gulf of California to Peru (Froese and Pauly 2016). The name in Spanish, “*dormilona*” (sleepyhead) is because individuals can remain sideways on the surface and look like a dark leaf (Allen and Robertson 1998). A first record of tripletail was reported in California waters during the strong 1992–93 El Niño, however was identified as *Lobotes surinamensis* (Rounds and Feeney 1993). In the warming event of the present study, three individuals were captured by sportfishing anglers in San Diego Bay (www.sportfishingmag.com 27 August 2014), and another from the Ocean Beach pier (<http://sdfish.com/forums/> 28 August 2014). It is a species rarely seen, although, when caught, it is usually during the warmest summer months (Snow 2016).

With respect to bonefish, previously genetically distinct species from the eastern Pacific were grouped in the *Albula vulpes* complex or *Albula* species (Nelson

et al. 2004). However, Pfeiler et al. (2011) made a formal description, genetic characterization, and comparisons with several relatives, and separated it as Cortez bonefish (*Albula gilberti*, Pfeiler and van der Heiden 2011) the species that is distributed throughout the Gulf of California and up to Morro Bay, California, USA (Page et al. 2013). Previous records of bonefish in the San Diego Bay were named as *Albula vulpes*, during the warm years of 1998 (Allen 1999) and 2008 (Pondella et al. 2009).

The occurrence of the Panamic fish species inside and outside of the Bahía de San Quintín is important as a biological indicator of northward fish movement, and coincident with warm water oceanographic conditions (Bond et al. 2015; Dewey 2015). These fish increase the list of species with tropical affinity that have been registered in the San Quintín area during El Niño 1997–98 event as the bigscale goatfish (*Pseudupeneus grandisquamis*), the white grunt (*Haemulopsis leuciscus*), the bullseye puffer (*Sphoeroides annulatus*), and the Paloma pompano, *Trachinotus paitensis* (Rosales-Casián 2004b), and in the coastal area, the tropical-warm-temperate species such as the finescale triggerfish (*B. polylepis*) captured during warm conditions of 2011 (Rosales-Casián 2013).

ACKNOWLEDGEMENTS

I appreciate the revision to this manuscript by Milton Love (University of California, Santa Barbara), and Dan Pondella (Vantuna Research Group, Occidental College), and one anonymous reviewer, which substantially improved the manuscript with their comments. Thanks to Mr. Alberto Flores (*Tiburón* sportfishing boats) from Old Mill, Bahía de San Quintín, Baja California (Mexico), for providing all fish species specimens, and the catch information. This research was financed by the Centro de Investigación Científica y Educación Superior de Ensenada, B.C. (CICESE).

LITERATURE CITED

- Allen, G. R., and D. R. Robertson. 1998. Peces del Pacífico Oriental Mexicano. CONABIO, Ciudad de México, 327 pp.
- Allen, L. G. 1999. Fisheries inventory and utilization of San Diego Bay, San Diego, California. Final report for contract to the U.S. Navy Naval Engineering Naval Command Southwest Division and the San Diego Unified Port District, 138 pp.
- Bond, N. A., M. F. Cronin, H. Freeland, and N. Mantua. 2015. Causes and impacts of the 2014 warm anomaly in the NE Pacific. *Geophys. Res. Lett.* 42:3414–3420.
- Brooks, A., G. Hanke, C. Foote, G. Gillespie, and J. Bedard. 2016. First Records of Finescale Triggerfish (*Balistes polylepis*) and Louvar (*Luvarus imperialis*) in British Columbia, Canada. *Northwestern Naturalist*, 97(1):7–12.
- Cívico-Collados, L. 2016. Estructura de la comunidad de peces y captura comercial estacional en la Laguna Ojo de Liebre, B.C.S., México durante 2015–16. M.Sc. Dissertation. Centro de Investigación Científica y de Educación Superior de Ensenada, B.C. México, 78 pp.
- Dewey, R. 2015. Warm North East Pacific Ocean conditions continue into 2015. *Ocean Networks Canada*—Newsletter. Available at: <http://www.ocean-networks.ca/warm-north-east-pacific-ocean-conditions-continue-2015/>.
- Díaz-Díaz, M. E., and M. G. Hammann. 1987. Relaciones tróficas de los peces asociados a un manto de *Macrocystis pyrifera* en la Bahía de Todos Santos, Baja California, México. *Ciencias Marinas* 13:81–96.
- Froese, R., and D. Pauly 2016. Fishbase. World Wide Web electronic publication www.fishbase.org, version (10/2016).
- Gómez-Ocampo, E., G. Gaxiola-Castro, R. Durazo, and E. Beier. 2017. Effects of the 2013–16 warm anomalies on the California Current phytoplankton. Deep-Sea Research II <http://dx.doi.org/10.1016/j.dsr2.2017.01.005>.
- Gracia-Escobar, M. F., R. Millán-Núñez, E. Valenzuela-Espinoza, A. González-Silvera, and E. Santamaría-del-Ángel. 2015. Changes in the Composition and Abundance of Phytoplankton in a Coastal Lagoon of Baja California, México, during 2011. *Open J. Mar. Sci.* 5: 69–181.
- Humann, P., and N. Deloach. 2004. Reef fish identification, Baja to Panama. New World Pub. Inc. Jacksonville, 343 pp.
- Jarvis, E. T., H. Glianik, O. Horning, and C. Linardich. 2009. Occurrence of juvenile Mexican lookdown, *Selene brevoortii* (Gill, 1863), in Seal Beach, California. *Calif. Fish and Game* 95(4):188–192.
- Lara-Lara, J. R., and S. Álvarez-Borrego. 1975. Ciclo anual de clorofilas y producción orgánica primaria en Bahía San Quintín, B.C. *Ciencias Marinas* 2(1):77–97.
- Lea, R. N., and R. H. Rosenblatt. 2000. Observations on fishes associated with the 1997–98 El Niño off California. *Calif. Coop. Oceanic. Fish. Invest. Rep.* 41:117–129.
- Lea, R. N., and H. Walker. 1995. Record of the bigeye trevally, *Caranx sexfasciatus*, and Mexican lookdown *Selene brevoortii*, with notes on other carangids from California. *Calif. Fish and Game*. 81(3): 89–95.
- Love, M. S., M. Yoklavich, and L. Thorsteinson. 2002. The rockfishes of the Northeast Pacific. University of California Press, Los Angeles. 405 pp.
- Love, M., S. J. K. Passarelli, C. Okamoto, and D. W. Diehl. 2015. The bigeye Scad, *Selar crumenophthalmus* (Bloch, 1793) (Family Carangidae), new to the California marine fauna, with a list to and keys for all California Carangids. *Bull. South. Calif. Acad. Sci.* 114(3):141–148.
- Miller, D. J., and R. N. Lea. 1972. Guide to the coastal marine fishes of California. *Calif. Dept. Fish Game, Fish Bull.* 157. 235 pp.
- Moreno-Mendoza, R. J. 2016. Estructura comunitaria de los peces asociados a bosques de macroalgas en Campo Kennedy, Ensenada, Baja California, México. M.Sc. Dissertation. Centro de Investigación Científica y de Educación Superior de Ensenada, B.C. México. 48 pp.
- Nelson, J. S., E. J. Crossman, H. Espinosa-Pérez, L. T. Findley, C. R. Gilbert, R. N. Lea, and J. D. Williams. 2004. Common and scientific names of fishes from the United States, Canada, and Mexico. Sixth edition. American Fisheries Society, Special Publication 29, Bethesda, Maryland. 386 pp.
- NOAA 2014. El Niño/Southern Oscillation (ENSO) Diagnostic Discussion. Available at http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/enso_disc_mar2014/.
- NOAA 2016. El Niño/Southern Oscillation (ENSO) Diagnostic Discussion. Available at http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/enso_disc_jun2016/ensodisc.pdf.
- Page, L. M., H. Espinosa-Pérez, L. T. Findley, C. R. Gilbert, R. N. Lea, N. E. Mandrak, R. L. Mayden, and J. S. Nelson. 2013. Common and scientific names of Fishes from the United States, Canada, and Mexico, 7th ed. American Fisheries Society, Special Publication 34, Bethesda. 384 pp.
- Pfeiler, E., A. M. van der Heiden, R. S. Ruboyanes, and T. Watts. 2011. *Albula gilberti*, a new species of bonefish (Albuliformes: Albulidae) from the eastern Pacific, and a description of adults of the parapatric *A. esuncula*. *Zootaxa* 3088:1–14.
- Pondella, D. J., and J. P. Williams. 2009. Fishery inventory and utilization of San Diego Bay, San Diego, California for surveys conducted in April and July 2008. Vantuna Research Group, Moore Laboratory of Zoology, Occidental College 1600 Campus Rd., Los Angeles, CA 90041, February 2009.
- Poumian-Tapia, M. 1995. Sobre la cuantificación de la biomasa de *Zostera marina* L. en Bahía San Quintín BC, durante un ciclo anual. M.Sc. Dissertation. Centro de Investigación Científica y de Educación Superior de Ensenada, B.C. México. 152 pp.
- Robertson, D. R., and G. R. Allen. 2015. Shorefishes of the tropical eastern Pacific online information system. Version 2.0 Smithsonian Tropical Research Institute, Balboa, Panama. <http://biogeodb.stri.si.edu/fstep/en/pages>. Accessed 11 April 2016.
- Rosales-Casián, J. A. 1996. Ichthyofauna of Bahía de San Quintín, Baja California, México, and its adjacent coast. *Ciencias Marinas* 22(4):443–458.
- Rosales-Casián, J. A. 1997a. Estructura de la comunidad de peces y el uso de los ambientes de bahías, lagunas y costa abierta en el Pacífico Norte de Baja California. Ph.D. Dissertation. Centro de Investigación Científica y de Educación Superior de Ensenada, B.C. México. 201 p.

- Rosales-Casián, J. A. 1997b. Inshore soft-bottom fishes of two coastal lagoons on the northern Pacific coast of Baja California. Calif. Coop. Oceanic. Fish. Invest. Rep. 38:180–192.
- Rosales-Casián, J. A. 2004a. Composition, importance and movement from San Quintin Bay, Baja California, México. Ciencias Marinas 30(1A):109–117.
- Rosales-Casián, J. A. 2004b. Tropical fish species as indicator of 1997–98 El Niño in Bahía de San Quintín, Baja California, México. Bull. South. Calif. Acad. Sci. 103(1):20–23.
- Rosales-Casián, J. A. 2011. The fish assemblages from the nearshore area of Punta Baja, B.C., México, the southern limit of the Southern California Bight. Calif. Coop. Oceanic. Fish. Invest. Rep. 52: 162–181.
- Rosales-Casián, J. A. 2013. Finescale Triggerfish (*Balistes polylepis*) and Roosterfish (*Nematistius pectoralis*) Presence in Temperate Waters off Baja California, México: Evidence of El Niño Conditions. Calif. Coop. Oceanic. Fish. Invest. Rep. 54:81–84.
- Rosales-Casián, J. A., and J. R. Gonzalez-Camacho. 2003. Abundance and importance of fish species from the artisanal fishery on the Pacific coast on Northern Baja California. Bull. South. Calif. Acad. Sci. 102(2):51–65.
- Rosales-Casián, J. A. and G. Ruiz-Campos. 1999. Northern range extension of the white grunt, *Haemulopsis leuciscus*. Calif. Fish and Game. 85(3):135–138.
- Rounds, J. M. and R. F. Feeney. 1993. First record of the tripletail (*Lobotes surinamensis*, family Lobotidae) in California waters. Calif. Fish and Game. 79:167–168.
- Smith-Vaniz, W. F. 1995. Carangidae. Jureles, pámpanos, cojinúas, zapateros, cocineros, casabes, macarelas, chicharros, jorobados, medregales, pez pilota. In Guia FAO para Identificación de Especies para los Fines de la Pesca. Pacífico Centro-Oriental, W. Fischer, F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter and V. Niem, eds. Rome: FAO, pp. 940–986.
- Smith-Vaniz, B., R. Robertson, A. Dominici-Arosemena and H. Molina. 2010. *Selene brevoortii*. The IUCN Red List of Threatened Species 2010: e.T183636A8148902. Available at <http://dx.doi.org/10.2305/IUCN.UK.2010-3.RLTS.T183636A8148902.en>.
- Snow, J. 2016. Mexico, fish, flora and fauna: Photos and species information of Baja California. Mexican lookdown, *Selene brevoortii*. <http://www.mexfish.com/mexico/mexican-lookdown/>. Accessed 07 March 2017.

CORRECTING FOR BIAS IN CALCOFI ICHTHYOPLANKTON ABUNDANCE ESTIMATES ASSOCIATED WITH THE 1977 TRANSITION FROM RING TO BONGO NET SAMPLING

ANDREW R. THOMPSON, SAM MCCLATCHIE,
EDWARD D. WEBER, AND WILLIAM WATSON

NOAA Fisheries Service
Southwest Fisheries Science Center
8901 La Jolla Shores Drive
La Jolla, CA 92037-1509
ph: (855) 546-7132
andrew.thompson@noaa.gov

CLERIDY E. LENNERT-CODY
Inter-American Tropical Tuna Commission
8901 La Jolla Shores Drive
La Jolla, CA, 92037-1509

ABSTRACT

To correctly interpret trends in species' abundance in long time series it is essential to account and correct for biases that may arise in association with changes in sampling methodology. We assess how gear changes for oblique plankton net tows (from 1 m diameter ring to 0.71 m diameter bongo net in 1977) affected ichthyoplankton abundance estimates from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program. Paired ring and bongo net samples were analyzed from 133 stations sampled in 1977–78. To quantitatively correct for net-associated bias, we first modeled abundance in bongo nets as a function of abundance in ring nets for larvae and eggs summed across all taxa during day and night with generalized linear models (GLM; identity link with gamma error structure). Models suggest that greater visual avoidance for ring than bongo nets induces bias in abundance estimates as slope estimates were greater than 1 for combined larvae during the day but did not differ significantly from 1 for combined larvae at night, or eggs during day or night. Ratios of summed abundances between bongo and ring nets for the 15 most common taxa indicated that there were significantly higher abundances for 4 taxa in the bongo than the ring net during the day but values did not differ at night between net types. To make data collected in ring nets before 1978 more comparable to data from bongo nets our results suggest it is necessary to adjust abundance estimates during the day from ring nets by a factor of 2 for *Cyclothone* spp., 2.17 for *Diogenichthys* spp., 2.06 for *Engraulis mordax*, and 1.53 for *Vinciguerria* spp. It may also be necessary to reevaluate results from past studies that utilize the CalCOFI larval time series that did not correct for net bias. More data are needed to ascertain the effect of net change on species such as *Sardinops sagax* or *Tarletonbeania crenularis* that were uncommon in the late 1970s but have been encountered frequently in recent years.

INTRODUCTION

Long time series are essential for truly understanding the mechanisms governing variability in the dynamics of populations and communities in all ecosystems

(Krebs et al. 2001; McClatchie 2014). Short-term fluctuations are often nested within long-period dynamics and attempts to discern the causes of species variability over short time periods may produce erroneous conclusions (McClatchie et al. 2017). This is particularly true in an era of rapid climate change as the effect of changes in environmental conditions on ecosystems can be conceptualized only when placed in the context of a long time series. Therefore, it is extremely important for species management and conservation programs to maintain and build upon long time series over upcoming years and decades.

Equally important as maintaining long time series is ensuring that samples collected over time are comparable to one another. Bias can arise if systematic differences in collection methods that affect the probability of capturing an organism are imposed upon the time series (MacKenzie et al. 2002). For example, trends from fishery-dependent data may not reflect true population dynamics of a fished species if the fleet introduced more effective gear for catching the targeted species at some point in the time series. Accounting for methodological differences in data collection is imperative to properly interpret potential changes in species abundances for time series analysis (MacKenzie et al. 2005).

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) program provides some of the most complete marine ecosystem monitoring data in the world. CalCOFI has continuously sampled biological (plankton tows) and oceanographic conditions (CTD and water collections) from the same 66 core stations off southern California since 1951 (McClatchie 2014). From a biological perspective, the resultant data give information on variability in the distribution and abundance of zooplankton (McGowan and Walker 1985; McGowan et al. 1998; Lavaniegos and Ohman 2007) and ichthyoplankton (Hsieh et al. 2005; Hsieh et al. 2006; Hsieh et al. 2009; Lindegren et al. 2016) over more than six decades.

At several points in the time series CalCOFI plankton sampling was changed to introduce methodological improvements. In all years, samples were obtained by lowering a net to a set depth and towing it obliquely (at a 45° angle) to the surface at a constant speed. However,

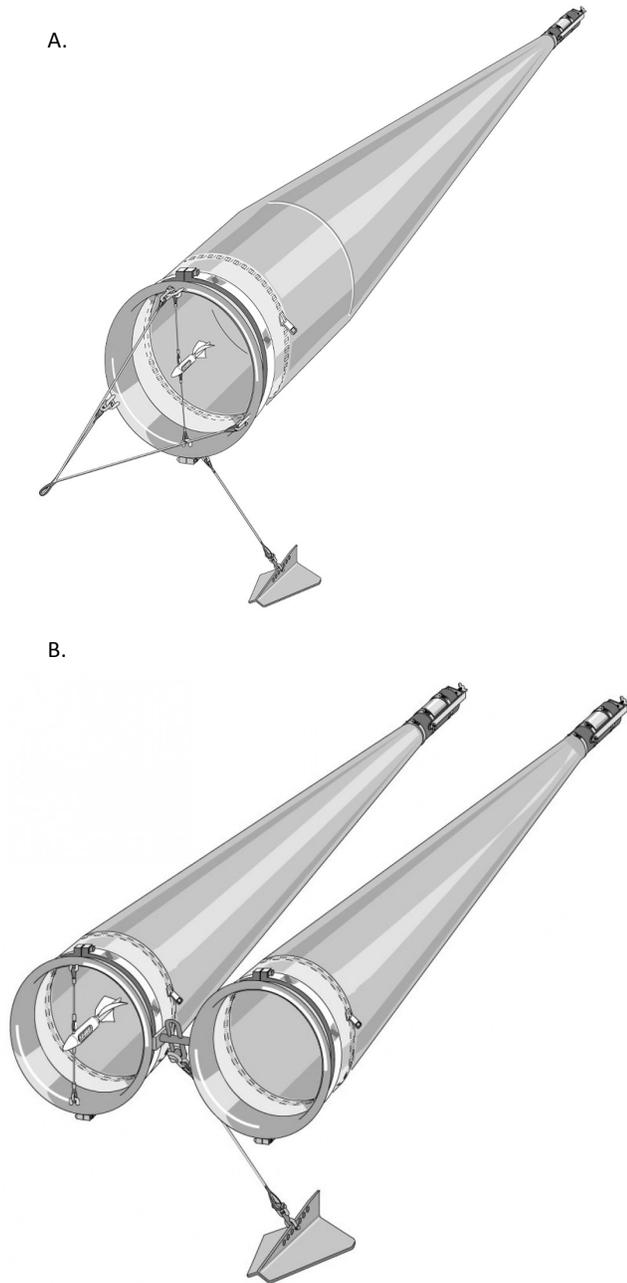


Figure 1. Illustrations of A. ring and B. bongo nets. Note that the bridle is directly in front of the mouth of the ring net but connects to the frame between the twin nets of the bongo, leaving the net mouths unobstructed (samples analyzed here were taken from the starboard net). Illustrations kindly provided by Hydro-Bios (<http://www.hydrobios.de>).

different types of nets were used at various time periods. From 1951 to fall 1977 plankton were collected using a ring net with a 1 m diameter mouth (fig. 1). Due to concern that the ring net bridle (fig. 1A) diminished zooplankton sampling efficiency, bongo nets that have an offset bridle (fig. 1B) (McGowan and Brown 1966) were introduced in the winter of 1977. To deduce how these two nets affected collection efficiency, samples were col-

lected using both nets at the same 160 stations during seven CalCOFI cruises between winter 1977 and summer 1978. At present, net effects on sampling efficiency have been thoroughly vetted for zooplankton (Smith 1974; Brinton and Townsend 1981; Ohman and Smith 1995; Rebstock 2001; Ohman and Lavaniegos 2002). However, with the exception of an investigation on northern anchovy, *Engraulis mordax* (Hewitt 1980), comparable analyses have not been published for ichthyoplankton. Here we evaluate if larval abundance estimates are biased by gear type and test the hypothesis that bias will be greater during the day when larvae would be able to better see and avoid the ring than the bongo net.

METHODS

Collection

One hundred and sixty paired ring and bongo samples were taken during seven CalCOFI cruises (7712, 7801, 7803, 7804, 7805, 7807, and 7808) in 1977 and 1978. The sampling area varied somewhat by cruise but overall ranged from just north of Monterey Bay, California, to offshore of Bahia de Magdalena, Baja California Sur (fig. 2). The majority of samples were collected at CalCOFI station 60, which is located over the continental slope. Additional sample sites were closer inshore between CalCOFI station 30 and 40 (mostly at 30) and further offshore at station 90.

Ring and bongo nets had 1 and 0.71 m diameter mouth openings, respectively, and 0.505 mm mesh. Both were towed obliquely (approximately 45°) from 210 m to the surface following standard CalCOFI methodology (Kramer et al. 1972; McClatchie 2014). Samples were collected during both night and day and paired samples were typically obtained within 30 minutes of each other. Plankton from the starboard side of the bongo (samples were not collected on the port side as there wasn't a cod end attached to the port net) and from the ring net were preserved in sodium borate-buffered 2% formaldehyde at sea. We included samples collected less than half an hour before sunrise or after sunset in the day samples because there is still typically some light during this period.

Fish eggs and larvae were sorted from the plankton and identified to the lowest practical taxon at the NOAA Southwest Fisheries Science Center ichthyoplankton laboratory. Larval identification was conducted for 133 of the 160 stations where paired samples were collected from cruises 7712, 7801, 7803, 7804, 7805, and 7807 (fig. 2). Subsampling (usually 50%) was done prior to sorting if zooplankton abundances were excessively high. Most taxa were identified to species, but some were characterized to genus (bristlemouths, *Cyclothone*; sanddabs, *Citharichthys*; lampfishes, *Nannobranchium*; rockfishes, *Sebastes*; and lightfishes, *Vinciguerria*). To standard-

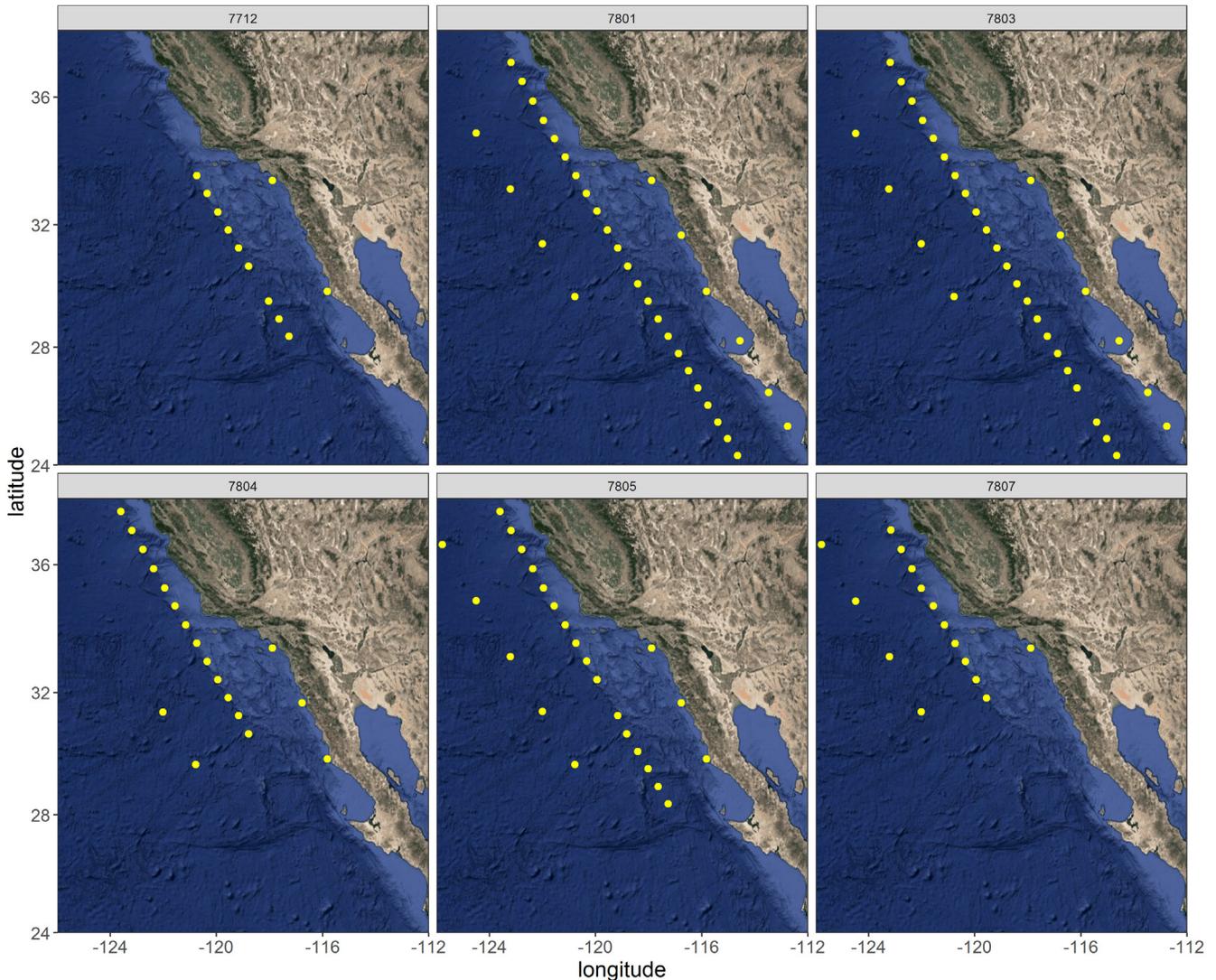


Figure 2. Sampling locations in each of 6 cruises. The first two digits of the cruise name is the year (i.e., 1977 and 1978) and the last two digits are the month.

ize differences in the amount of water filtered or tow depths, raw larval counts were divided by the proportion of the sample that was sorted and multiplied by a standard haul factor based on flowmeter data (Kramer et al. 1972; McClatchie 2014) such that final abundances were expressed as individuals under 10 m² of sea surface.

Analysis

We began by modeling the pooled abundance of all larval taxa in bongo nets as a function of the pooled abundance of all larval taxa in ring nets for paired samples to determine if there was evidence for differences in the efficiency of larval capture between net types. Our working hypothesis was that larvae may visually avoid the bridle in front of the ring net and that this effect would manifest during the day but not at night. We therefore tested bongo~ring relationships separately

for samples collected during day and night. We further assessed the potential for visual avoidance by modeling fish eggs in the bongo versus ring nets. Because eggs are passive particles we hypothesized that there would be no difference in egg abundance between nets, for both day and night collections.

We modeled the relationship between paired bongo and ring abundances for each species group and day/night category using generalized linear models (GLMs). Preliminary exploration of the data indicated that the variability in bongo abundance increased with increasing abundance, and model residuals using several distributions and link functions suggested that model assumptions were best met using a gamma distribution with an identity link function.

If the slope of the bongo~ring relationship did not differ from 1, then there would be no difference in

TABLE 1
 Estimated species-specific ratios of summed abundances and 95% confidence for the 15 most abundance species, for daytime and nighttime samples. “No. stations” refers to the number of stations where the species was present (out of 133 stations). Confidence intervals that do not overlap with 1 are shown in bold font.

species	no. stations	day/night	bongo/ring ratio	2.5% CI bound	97.5% CI bound
<i>Bathylagoides wesethi</i>	22	day	1.23	0.66	1.80
<i>Citharichthys</i> spp.	20	day	1.29	0.63	1.94
<i>Cyclothone</i> spp.	31	day	2.00	1.21	2.79
<i>Diogenichthys</i> spp.	32	day	2.17	1.42	2.92
<i>Engraulis mordax</i>	17	day	2.06	1.57	2.56
<i>Leuroglossus stilbius</i>	11	day	1.66	-0.52	3.83
<i>Lipolagus ochotensis</i>	37	day	1.55	0.87	2.23
<i>Merluccius productus</i>	21	day	2.04	0.42	3.66
<i>Nannobranchium</i> spp.	40	day	1.48	0.88	2.08
<i>Protomyctophum crockeri</i>	39	day	1.45	0.75	2.14
<i>Sebastes</i> spp.	30	day	1.18	0.81	1.55
<i>Stenobranchius leucopsarus</i>	28	day	1.79	1.01	2.57
<i>Trachurus symmetricus</i>	19	day	1.38	0.84	1.91
<i>Triphoturus mexicanus</i>	24	day	2.53	0.95	4.11
<i>Vinciguerria</i> spp.	32	day	1.53	1.01	2.04
<i>Bathylagoides wesethi</i>	22	night	0.82	0.60	1.04
<i>Citharichthys</i> spp.	36	night	1.36	0.82	1.89
<i>Cyclothone</i> spp.	21	night	1.44	0.80	2.08
<i>Diogenichthys</i> spp.	26	night	0.98	0.55	1.42
<i>Engraulis mordax</i>	28	night	1.16	0.98	1.35
<i>Leuroglossus stilbius</i>	23	night	1.14	0.87	1.42
<i>Lipolagus ochotensis</i>	35	night	0.98	0.65	1.31
<i>Merluccius productus</i>	24	night	1.16	1.01	1.32
<i>Nannobranchium</i> spp.	31	night	1.00	0.46	1.55
<i>Protomyctophum crockeri</i>	37	night	0.94	0.61	1.27
<i>Sebastes</i> spp.	29	night	0.96	0.64	1.28
<i>Stenobranchius leucopsarus</i>	29	night	1.40	0.99	1.82
<i>Trachurus symmetricus</i>	19	night	1.47	0.57	2.37
<i>Triphoturus mexicanus</i>	13	night	0.82	0.55	1.08
<i>Vinciguerria</i> spp.	22	night	0.85	0.59	1.11

abundance estimates between the two nets and hence no need to make adjustments to abundance estimates. Therefore, we evaluated whether estimated slopes from daytime and nighttime data differed significantly from 1 using t-tests: (t-statistic = (slope estimate-1)/(slope standard error) with the degrees of freedom equal to the number of observations - 2, and measuring significance based on a one-tail t-distribution (Zar 1996).

We next explored how net bias affected individual taxa as model results revealed that summed larval abundances, pooled over taxa, were greater in the bongo than ring nets during the day. We limited taxa-specific analyses to the 15 taxa that were found in at least 10 stations during both day and night (table 1). Model diagnostics indicated that GLMs fitted to the individual species data performed poorly, even when using hurdle and zero-inflated models. Hence, we examined the ratio of the sum of abundance from the bongo net to the sum of abundance from the ring net, for each of the 15 taxa, day and night, where the sums were computed across all stations. We calculated approximate 95% confidence intervals (CI) analytically for each of these ratios using the methods outlined in Levy and Lemeshow (2008) and considered ratios significantly different from 1.0 if

the CI did not contain the value 1. Ratios of sums have the potential to be unduly influenced by small number of samples with high abundances. Therefore, to test the sensitivity of the species-specific ratio estimates to a relatively few number of samples with very high abundances, we sorted all pairs by samples based on abundance in the bongo net and sequentially trimmed the lowest and highest abundance stations, from 1% to 10%, and calculated ratios and 95% CI at each level of trimmed data.

If active avoidance was the cause of net bias, then smaller, weaker swimming larvae would be less likely to exhibit net bias than larger, relatively well developed individuals. Larval sizes were available for northern anchovy, *Engraulis mordax*, and Pacific hake, *Merluccius productus*. We created size bins for anchovy that were similar to Hewitt (1980) who also evaluated differences in catch ratio between ring and bongo nets. Because the number of larvae was sparse at larger sizes we grouped sizes between 7.25 and 31 mm so that abundances exceeded 100 individuals for each bin during day and night. For hake, bin size classes were created so that at least 100 individuals fell within each bin. We then calculated ratios of sums and 95% CIs for each bin and determined if the CI overlapped 1.

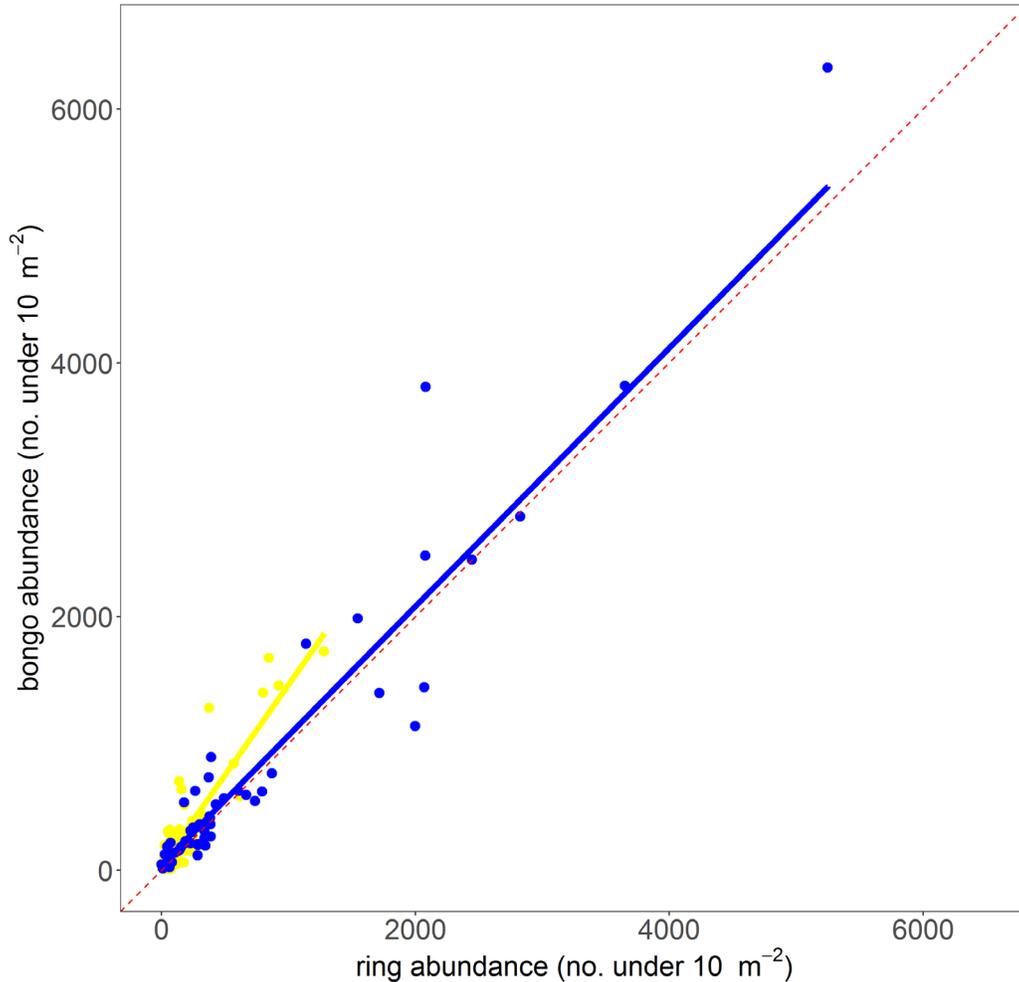


Figure 3. Scatter plot of paired abundances (all taxa) from ring and bongo nets at each station. Blue depicts samples taken at night while yellow characterizes samples collected during the day. Solid lines show the estimated linear relationships from the gamma models.

All analyses were conducted using the R statistical software. GLMs were fitted using the “glm” function in the R software environment version 3.2.3 (R Core Team 2015). The R package StreamMetabolism version 1.1.1 (Sefick Jr. 2015) determined whether it was day or night based on the date, time, latitude and longitude of a station. We used the package survey version 3.31–2 (Lumley 2016) to calculate 95% CI around ratios of summed abundances. All plots were created using ggplot2 version 2.1.0 (Wickham 2009) and/or ggmap version 2.6.1 (Kahle and Wickham 2013).

RESULTS

The estimated slope of the relationship between ring and bongo abundances of pooled larval taxa was significantly different from 1 for daytime samples (fig. 3; $\text{bongo.abundance} = 1.42 \cdot \text{ring.abundance} + 39.7$; intercept s.e. = 12.6, slope s.e. = 0.19; test of H_0 : slope = 1: $t = -2.27$, $p = 0.026$). Estimated slopes did not differ from

1 for pooled larval taxa from nighttime samples (fig. 3; $\text{bongo.abundance} = 1.02 \cdot \text{ring.abundance} + 45.2$ slope s.e.=0.087, test of H_0 : slope = 1: $t = -.21$, $p = .83$) or for eggs from either daytime ($\text{bongo.abundance} = 0.89 \cdot \text{ring.abundance} + 20.3$; intercept s.e. = 9.51, slope s.e. = 0.19; test of H_0 : slope = 1: $t = 1.1$, $p = 0.26$) or nighttime samples ($\text{bongo.abundance} = 1.02 \cdot \text{ring.abundance} + 13.2$; intercept s.e. = 13.3, slope s.e. = 0.11; test of H_0 : slope = 1: $t = -.15$, $p = 0.88$).

Species-specific estimated ratios of summed abundances (bongo/ring) from daytime samples were significantly greater than 1 for one-third of the most common taxa: *Cyclothone* spp., *Diogenichthys* spp., *Engraulis mordax*, *Stenobranchius leucopsarus*, and *Vinciguerria* spp. (table 1, fig. 4). For 4 of these 5 taxa, sensitivity analyses suggested that there was no strong evidence that the ratio estimates were unduly affected by outliers; ratio estimates were significantly greater than 1 on most or all of the trimmed data sets (fig. 5). *Stenobranchius leucopsarus*

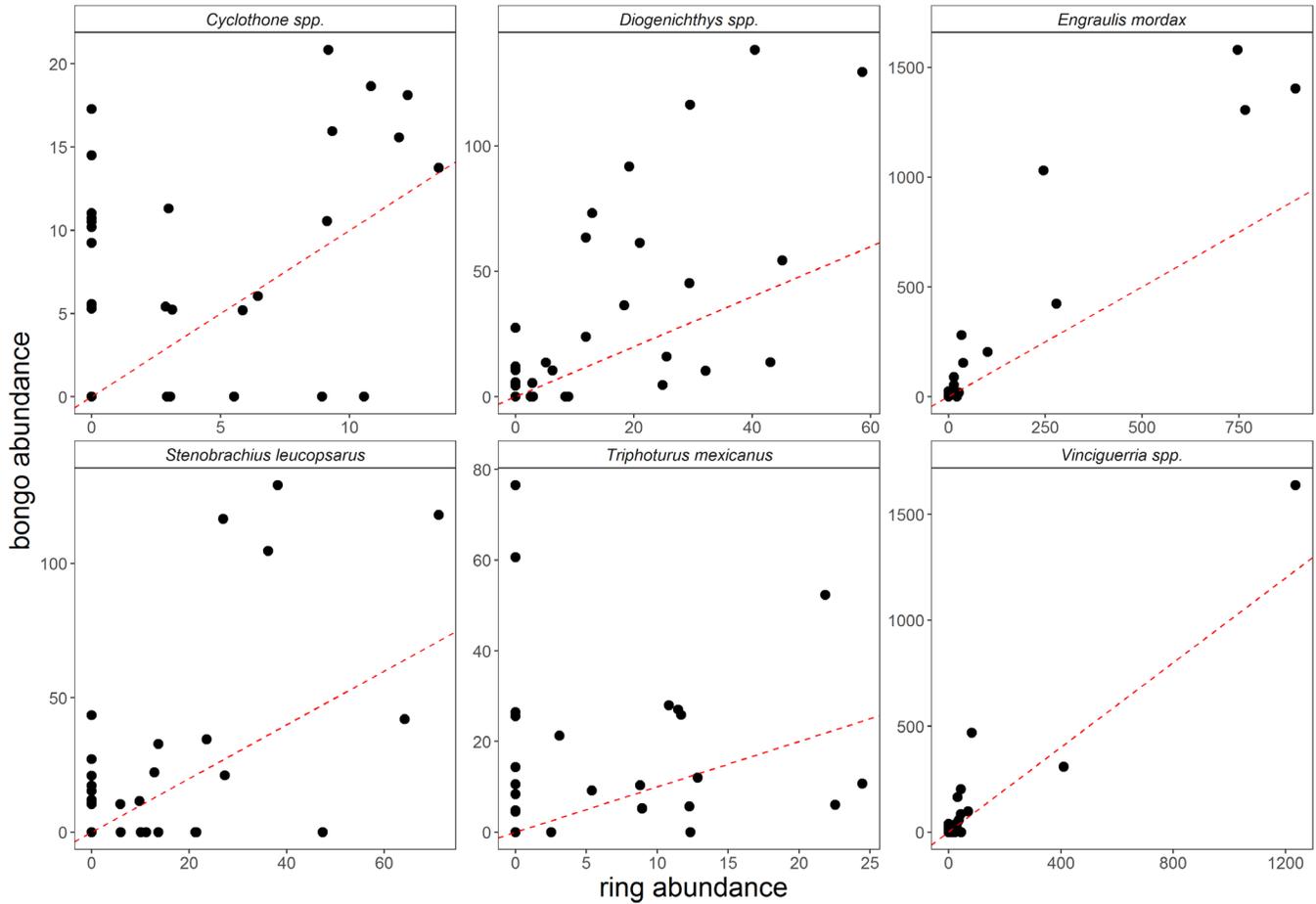


Figure 4. Scatter plots of species-specific abundances from paired ring and bongo daytime samples for the five species with estimated ratios of summed abundances significantly greater than 1. Diagonal red, dashed lines depict 1:1 relationships. Note that scales differ on x and y axes.

rus, however, was affected by trimming as removal of the lowest and highest 1% and 6%–10% resulted in confidence intervals that overlapped 1. Similarly, for most of the ten taxa with ratio estimates not differing significantly from 1, trimming did not lead to estimates that were consistently different from 1. The one exception was *Triphoturus mexicanus* where the trimmed data sets at 1%–4% and 6%–8% had estimated slopes greater than 1.

In contrast to the daytime results, 95% confidence intervals for the species-specific ratios of summed abundances overlapped 1 for all taxa except *Merluccius productus* (table 1). The ratio estimate for *Merluccius productus*, however, was sensitive to data trimming as ratios from only half of the trimmed data sets were significantly greater than 1.

Estimated bongo/ring ratios were significantly greater than 1 for *Engraulis mordax* at all but the smallest size bin for daytime samples (fig. 6). Nonetheless, there was a tendency for variance about the ratio estimates to increase with size, and the 95% CI for the largest size

bin completely contained the 95% CIs for two of the three smaller size bins suggesting that there was no significant difference in the ratio as a function of size. For nighttime samples, CIs of the estimated ratios for 3 of the 4 size bins overlapped 1. Ratios did not differ significantly from 1 for *Merluccius productus* at any size bin for daytime samples and there was no indication that the daytime ratio changed with size. At night, the 95% CI around the ratio for *Merluccius productus* were below 1 for the smallest size class but did not differ from 1 for the other size classes.

DISCUSSION

Our results indicated that the slope of bongo~ring abundance relationship was significantly greater than 1 for combined larval taxa from daytime samples but not from nighttime samples. Estimated species-specific bongo to ring ratios also were significantly greater than 1 and resilient to sensitivity analyses for 4 of the 15 most common taxa. These results indicate that adjustments need to be made to abundance estimates for *Cyclothone*

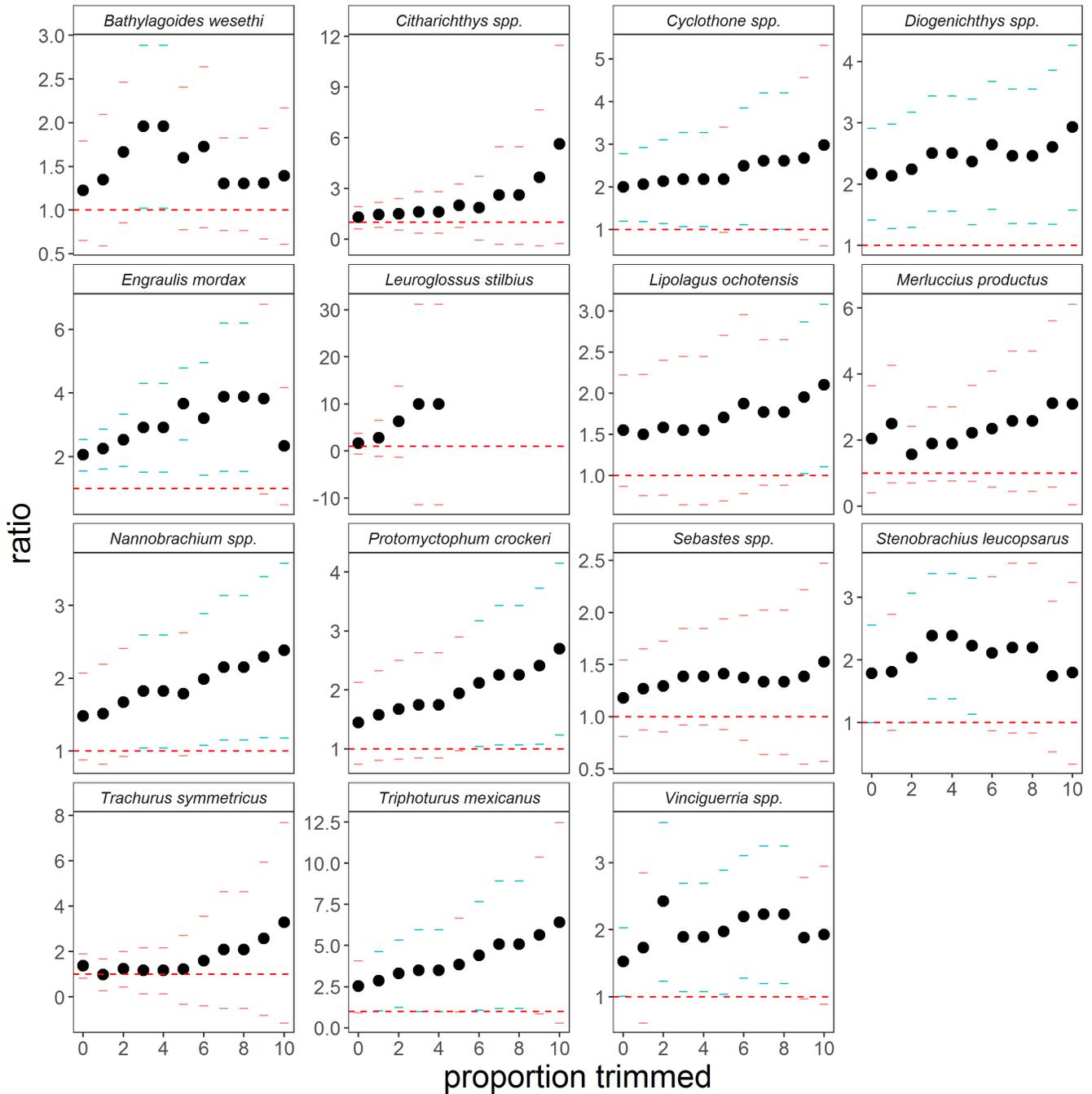


Figure 5. Estimated species-specific ratios of summed abundance and approximate 95% CIs for trimmed data sets. Horizontal, red, dashed lines depict ratios of 1. Dashes around points are 95% confidence intervals (CI). Dashes are blue if the CI does not overlap 1 and red if the CI does overlap 1.

spp., *Diogenichthys* spp., *Engraulis mordax*, and *Vinciguerria* spp. collected in ring nets prior to 1978 to ensure that the CalCOFI time series is more comparable before and after the implementation of bongo net sampling.

This is the first comprehensive analysis evaluating how changing gear affected abundance estimates of ichthyoplankton for multiple species in the CalCOFI program. Hewitt (1980), however, used these same data to

examine the relationship between bongo and ring net catches on *Engraulis mordax* larva and concluded that there was very little difference in catchability between net types. Specifically, Hewitt (1980) calculated the ratio of *E. mordax* larvae abundance at night divided by abundance at day for 15 size bins from ring and bongo nets. He concluded that there was not a large (twice as many) difference in night/day ratios between ring and bongo

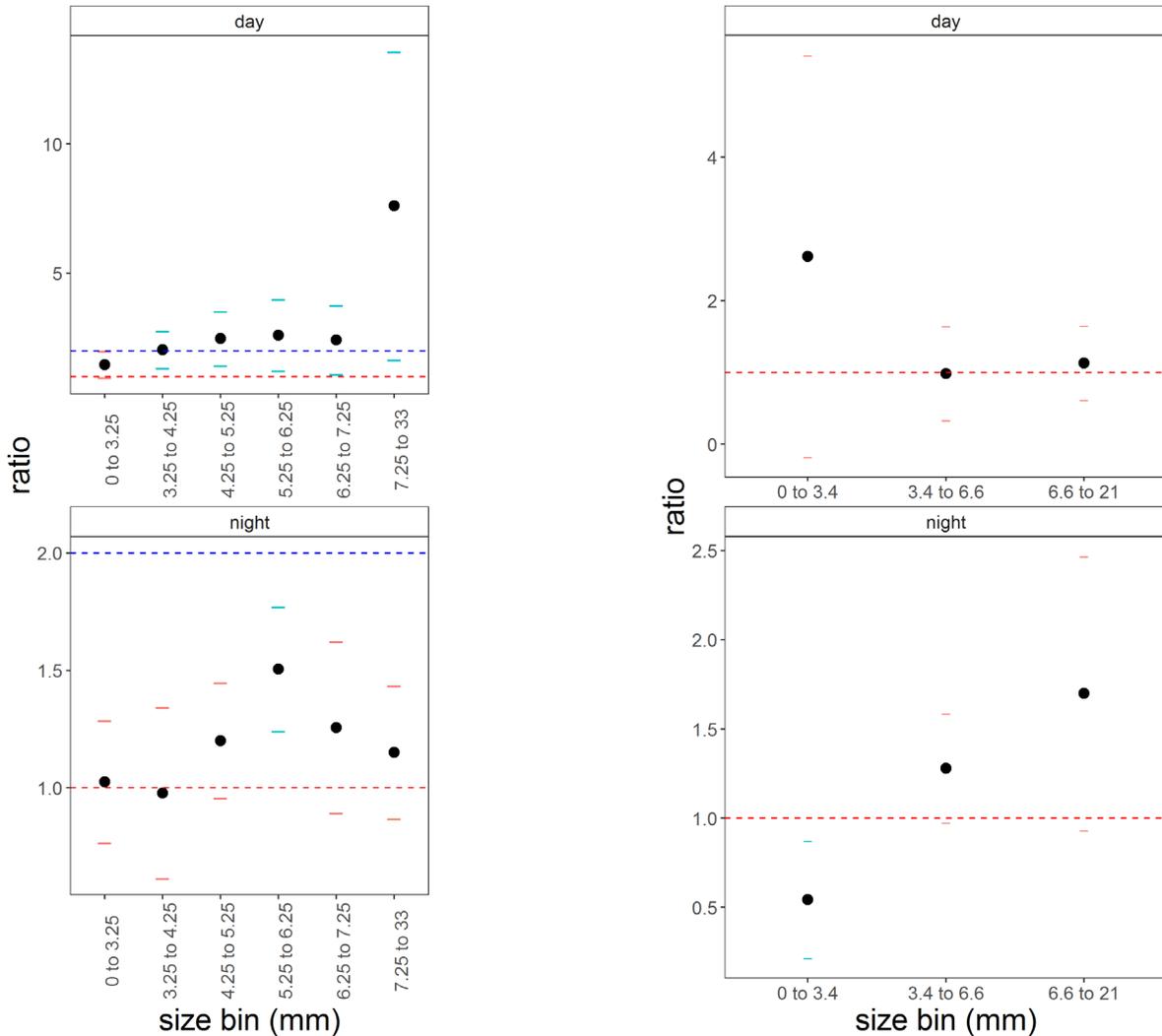


Figure 6. Estimated ratios of summed abundance by size category, and approximate 95% CIs, from daytime and nighttime samples for anchovy (*Engraulis mordax*) (top two panels) and hake (*Merluccius productus*) (bottom two panels). Bin boundaries were created so that the number of larvae were similar between bins. Dashes around points are 95% CI. Blue and red CI are those that do not and do overlap with 1, respectively. Red dashed lines are at 1 and the blue dashed line is at 2.

nets until larvae were larger than 6.75 mm and that because larvae > 6.75 mm comprised only 10% of the catch, there was no reason to correct for net bias.

Our conclusion that there is a significant difference in catchability of *E. mordax* between nets during the day likely differs from Hewitt (1980) for at least two non-mutually exclusive reasons. First, the data used in both studies was designed to test for ring/bongo rather than day/night differences. Whereas both ring and bongo samples were collected at the same stations, day and night samples were taken from different stations. Therefore, the analysis of pooled daytime *versus* nighttime samples of Hewitt (1980) would not have as effectively controlled for any overall differences in size composition among stations, as compared to the approach presented herein, where the ratios summed abundances were compared

to the value 1, for daytime and nighttime samples, separately. Second, Hewitt states that the night/day catch ratio wasn't much different between ring and bongo nets until larvae are larger than 6.75 mm. However, his interpretation of a significant difference is qualitative, and rather liberal as corrections may be necessary even if difference in ratios are less than 2. It is evident from Figure 1 in Hewitt (1980) that although the magnitude of night/day ratios between nets was reduced for larvae that were smaller than 6.75 mm, the ratio was still higher in ring nets at the smaller size classes. As Hewitt (1980) does not statistically evaluate whether the ratios differ at any size class and does not report variance associated with ratio estimates, it is possible that differences were statistically significant at smaller size classes. Indeed, we found that bongo/ring 95% confidence intervals did not

overlap with 1 during the day for all except the 0–3.25 mm size bin. Further, the confidence intervals for all except the smallest size bin overlapped Hewitt's threshold of 2. Given that 67% of anchovy larvae examined in this study (combined ring and bongo) were larger than 3 mm, it is necessary to adjust anchovy abundances collected in ring nets to make abundance estimates directly comparable before and after 1977.

Our results indicate that net avoidance is affected by whether samples were collected during the day or night. This finding, coupled with a lack of day/night effect on passive eggs and no significant ratios above 1 for any taxa at night, suggests that larvae are using visual cues to better avoid the ring than the bongo net. The importance of sample time was also shown by Hewitt (1980) as night/day catch ratios of northern anchovy larvae were close to 1 for small larvae but around to 20:1 for larger individuals. Similarly, we detected an increase in ratio with *E. mordax* size, suggesting that larger larvae that are competent swimmers are better at net avoidance than smaller individuals. Our analysis, however, showed that even small *E. mordax* avoid the ring net at a higher rate than the bongo net.

Sakuma et al. (2007) provide further evidence that larval fishes can use visual cues to avoid plankton nets. They conducted bongo net sampling from a fixed location in central California every 2 hours over consecutive days and found that larval *Sebastes* spp. were much more abundant during the night than day. Sakuma et al. (2007) ascribed this discrepancy to visual avoidance during the day as *Sebastes* spp. larvae do not undergo diel vertical migration (Sakuma et al. 1999). Although we also observed that *Sebastes* spp. summed abundances were 1.8 times higher during the night than day, the ratio of summed abundances was not significantly different from 1 for either daytime or nighttime samples (this analysis was not reported in the Results). It is possible that the visual cues generated by the two net types were too subtle to evoke a degrees of avoidance behavior for *Sebastes* spp. that we could detect with our data.

An important finding of our work is that net avoidance capabilities differed among taxa. Sakuma et al. (2007) also echoed this conclusion as they found differences in catch rates between day and night for *Sebastes* spp. but not *M. productus* in central California. One explanation for the differences in avoidance behavior among taxa may be that different taxa have inherent differences in swimming ability. There are no obvious morphological characteristics, however, that can predict which taxa may be stronger swimmers. For example, *Sebastes* spp. and *M. productus* are morphologically similar as larvae and can be mistaken for one another. Similarly, *B. wesethi* and *E. mordax* larvae both have long, slender bodies but bongo/ring ratios were very different for the

two species. More research on larval swimming behavior will need to be conducted to determine if this factor can explain variability in net avoidance. Another explanation for the differences in ratio estimates among taxa may simply be that the taxa with higher bongo/net ratios in our study had proportionally greater numbers of large individuals in the samples. Although individual sizes were only available for *E. mordax* and *M. productus* flexion stage (preflexion, flexion, and postflexion) for other taxa were recorded on data sheets. However, perusal of the raw data sheets did not indicate any systematic differences in flexion stage among taxa. A third possibility is that vertical distributions differ between taxa during the day. If some taxa reside primarily in deeper water then light will be more limited even during the day, thus impeding capacity to visually detect the net. Further research is needed to discern the precise mechanism governing the apparent variation in net avoidance capabilities among taxa.

The correction factors presented in our research are intended to be applied to abundance estimates over an entire cruise rather than at any specific station. Making corrections to individual stations is more difficult because in any given cruise a majority of stations will have 0 individuals for a given taxa. To estimate whether individuals are likely to be present when not detected will require spatial modeling of abundance or modeling of abundances as a function of environmental covariates. Most of the past studies that explored dynamics of CalCOFI ichthyoplankton (Moser et al. 2000; Moser et al. 2001; Hsieh et al. 2005; Hsieh et al. 2006; Anderson et al. 2008; Hsieh et al. 2009) evaluated abundances at an annual scale (pooled over space) and are thus directly amenable to our corrections.

Previous work comparing zooplankton from the same samples analyzed here also detected significant differences between bongo and ring nets. Analysis of 12 euphausiid species revealed that larvae were more abundant in ring nets, that juveniles and adults were more abundant in bongo nets, and that total numbers were similar between nets (Brinton and Townsend 1981). Ohman and Smith (1995) found that overall zooplankton biomass was 1.36 times higher in bongo than ring nets. A follow up to this study showed that zooplankton differences among nets were driven primarily by salps (2.68 times more abundant in bongo nets) and secondarily by pteropods (1.09 times more abundant in bongo nets) while 15 other categories of zooplankton did not differ between net types (Ohman and Lavaniegos 2002). It thus appears that fish larvae abundance estimates were more affected by the transition from ring to bongo sampling than most zooplankton species.

Optimizing plankton sampling is a methodological challenge to fisheries science, and studies from around the globe have documented how gear affects ichthyo-

plankton abundance estimates. For example, bongo nets were found to more effectively catch small larvae but not large larvae relative to ring nets in an arctic fjord off Greenland (Swalethorp et al. 2014) and relative to Tucker trawls in eastern Canada (Pepin and Shears 1997). Similarly, a comparison of four types of sampling gear found significant differences in larval walleye pollock, *Theragra chalcogramma*, catch in the Gulf of Alaska (Shima and Bailey 1994). Habtes et al. (2014) also demonstrated that three net types strongly affected larval fish catch in the Gulf of Mexico. These studies and ours exhibit the need to evaluate and correct for differences in sampling efficiency when comparing larval fish abundances.

In addition to transitioning from ring to bongo nets in 1978, another major methodological change to CalCOFI sampling occurred in 1969. In this year the depth of net tows was changed from 140 to 210 m and silk nets with 0.55 mm mesh were replaced with nylon, 0.505 mm mesh nets. To evaluate the effects of these changes 42 tows were conducted in summer 1968 at station 93.3 30.0 (10 miles west of La Jolla, CA) (Smith 1974). Analysis of those data showed that zooplankton density was 1.37 times higher in the 210 m than 140 m tows. Interestingly, the zooplankton density was also 1.37 times greater in bongo versus ring net, thus making comparisons of zooplankton collected between 1951 and 1969 directly comparable to samples from 1979 to the present without correcting for sampling effects (Ohman and Smith 1995). At present, larval fish data from these samples is not available, and it is unknown if sampling biases for larval fishes cancel out between the earliest and current periods. Enumeration of larval abundances from the 1968 samples should be conducted to evaluate potential effects of transitioning from 140 to 210 m sampling depths and from silk to nylon mesh.

Our results demonstrated that there is systematic bias to estimates of larval fish abundance associated with the transition from ring to bongo nets in 1978. To ensure accuracy of larval fish time series analyses, corrections should be applied to *Cyclothone* spp., *Dio-genichthys* spp., *Engraulis mordax*, and *Vinciguerria* spp. Further, additional paired samples should be collected to improve sample sizes for other commercially and ecologically important species such as Pacific sardine (*Sardinops sagax*) and blue lanternfish (*Tarletonbeania crenularis*) that were mostly absent 1977–78 but have become more common at present. In addition, 1968 samples that evaluated the effect of changing net types, mesh size and tow depth should be sorted and analyzed to elucidate further potential effects on larval fish abundance estimation. Finally, studies on ichthyoplankton dynamics that utilized data pre and post implementation of bongo nets should be reanalyzed to ensure that the conclusions are robust to the net effects.

ACKNOWLEDGEMENTS

We greatly appreciate the effort of staff who collected the samples and those who sorted and identified the larvae in the laboratory. We thank Marc Fischer from Hydro-Bios for allowing us to use the illustrations in Figure 1. Discussion with Rasmus Swalethorp helped improve the manuscript. We thank two anonymous reviewers for helpful comments that improved this manuscript.

LITERATURE CITED

- Anderson, C. N. K., C. Hsieh, S. A. Sandin, R. Hewitt, A. Hollowed, J. Beddington, R. M. May, and G. Sugihara. 2008. Why fishing magnifies fluctuations in fish abundance. *Nature Climate Change* 452:835–839.
- Baumgartner T. R., A. Soutar, and V. Ferreira-Bartrina. 1992. Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara Basin, California. *California Cooperative Oceanic Fisheries Investigations Reports* 33:24–40.
- Brinton, E., and A. W. Townsend. 1981. A comparison of euphausiid abundances from bongo and 1-m CalCOFI nets. *California Cooperative Oceanic Fisheries Investigations Reports* 22:111–125.
- Habtes, S., F. E. Muller-Karger, M. A. Roffer, J. T. Lamkin, and B. A. Muhling. 2014. A comparison of sampling methods for larvae of medium and large epipelagic fish species during spring SEAMAP ichthyoplankton surveys in the Gulf of Mexico. *Limnology and Oceanography: Methods* 12:86–101.
- Hewitt, R. 1980. Distributional atlas of fish larvae in the California Current region: northern anchovy, *Engraulis mordax* (Girard), 1966–79. *California Cooperative Oceanic Fisheries Investigations Atlas* 28:1–101.
- Hsieh, C., H. J. Kim, W. Watson, E. Di Lorenzo, and G. Sugihara. 2009. Climate-driven changes in abundance and distribution of larvae of oceanic fishes in the southern California region. *Global Change Biology* 15:2137–2152.
- Hsieh, C., C. Reiss, W. Watson, M. J. Allen, J. R. Hunter, R. N. Lea, R. H. Rosenblatt, P. E. Smith, and G. Sugihara. 2005. A comparison of long-term trends and variability in populations of larvae of exploited and unexploited fishes in the Southern California region: A community approach. *Progress in Oceanography* 67:160–185.
- Hsieh, C., C. S. Reiss, J. R. Hunter, J. R. Beddington, R. M. May, and G. Sugihara. 2006. Fishing elevates variability in the abundance of exploited species. *Nature* 443:859–862.
- Kahle, D., and H. Wickham. 2013. ggmap: Spatial Visualization with ggplot2. *The R Journal* 5:144–161.
- Kramer, D., M. J. Kalin, E. G. Stevens, J. R. Thrailkill, and J. R. Zweifel. 1972. Collecting and processing data on fish eggs and larvae in the California Current region. NOAA Technical Report NMFS, Book CIRC-370.
- Krebs, C., R. Boonstra, S. Boutin, and A. Sinclair. 2001. What drives the 10-year cycle of snowshoe hares? *Bioscience* 51:25–35.
- Lavanigos, B., and M. Ohman. 2007. Coherence of long-term fluctuation of zooplankton in tow sectors of the California Current System. *Progress in Oceanography* 75:42–69.
- Levy, P. S., and S. Lemeshow. 2008. *Sampling of Populations Methods and Applications*. 4th edition. John Wiley & Sons, Hoboken, New Jersey.
- Lindgren, M., D. M. Checkley Jr., M. Ohman, J. Koslow, and R. Boericke. 2016. Resilience and stability of a pelagic marine ecosystem. *Proceedings of the Royal Society B* 283:2015931.
- Lumley, T. 2016. survey: analysis of complex survey samples. Rpackage version 3.31–5.
- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2005. *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrences*. Elsevier, San Diego, California, USA.
- McClatchie, S., I. L. Hendy, A. R. Thompson, and W. Watson. 2017. Collapse and recovery of forage fish populations prior to commercial exploitation. *Geophysical Research Letters* 44:1877–1882.

- McClatchie, S. 2014. Regional fisheries oceanography of the California Current System: the CalCOFI program. Springer. 235pp. ISBN 978-94-007-7222-9.
- McGowan J. A., and D. M. Brown. 1966. A new opening-closed paired zooplankton net. University of California Scripps Institute of Oceanography 66-23:1-56.
- McGowan J. A., D. R. Cayan, and L. M. Dorman. 1998. Climate-ocean variability and ecosystem response in the Northeast Pacific. *Science* 281: 210-217.
- McGowan J. A., and P. W. Walker. 1985. Dominance and diversity maintenance in an oceanic ecosystem. *Ecological Monographs* 55:103-118.
- Moser, H. G., R. L. Charter, W. Watson, D. A. Ambrose, J. L. Butler, S. R. Charter, and E. M. Sandknop. 2000. Abundance and distribution of rockfish (*Sebastes*) larvae in the Southern California Bight in relation to environmental conditions and fishery exploitation. *California Cooperative Oceanic Fisheries Investigations Reports* 41:132-147.
- Moser, H. G., R. L. Charter, W. Watson, D. A. Ambrose, K. T. Hill, P. E. Smith, J. L. Butler, E. M. Sandknop, and S. R. Charter. 2001. The CalCOFI ichthyoplankton time series: Potential contributions to the management of rocky-shore fishes. *California Cooperative Oceanic Fisheries Investigations Reports* 42:112-128.
- Nelson, G. A. 2015. fishmethods: Fishery Science Methods and Models in R. R package version 1.9-0. <https://CRAN.R-project.org/package=fishmethods>.
- Ohman, M. D., and B. E. Lavaniegos. 2002. Comparative zooplankton sampling efficiency of a ring net and bongo net with comments on pooling of subsamples. *California Cooperative Oceanic Fisheries Investigations Reports* 43:162-173.
- Ohman, M. D., and P. E. Smith. 1995. A comparison of zooplankton sampling methods in the CalCOFI time series. *California Cooperative Oceanic Fisheries Investigations Reports* 36:153-158.
- Pepin, P., and T. H. Shears. 1997. Variability and capture efficiency of bongo and Tucker trawl samplers in the collection of ichthyoplankton and other macrozooplankton. *Canadian Journal of Fisheries and Aquatic Science* 54:765-773.
- R_Core_Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Rebstock, G. 2001. Long-term changes in the species composition of calanoid copepods off Southern California. University of California, San Diego.
- Sakuma, K. M., S. Ralson, and D.A. Roberts. 1999. Diel vertical distribution of postflexion larval *Citharichthys* spp. and *Sebastes* spp. off central California. *Fisheries Oceanography* 8:68-76.
- Sakuma, K. M., S. Ralston, and D. A. Roberts. 2007. High-frequency patterns in abundance of larval Pacific hake, *Merluccius productus*, and rockfish, *Sebastes* spp., at a single fixed station off central California. *Fisheries Oceanography* 16:383-394.
- Sefick Jr., S. 2015. Stream Metabolism-A package for calculating single station metabolism from diurnal Oxygen curves. R package version 1.1.1.
- Shima, M., and K. M. Bailey. 1994. Comparative analysis of ichthyoplankton sampling gear for early life stages of walleye Pollock (*Theragra chalcogramma*). *Fisheries Oceanography* 3:50-59.
- Smith P. E. 1974. Distribution of zooplankton volumes in the California Current region, 1969. *California Cooperative Oceanic Fisheries Investigations Atlas* 20:118-125.
- Swalethorp R., E. Malanski, M. D. Agersted, T. G. Nielsen, and P. Munk. 2015. Structuring of zooplankton and fish larvae assemblages in a freshwater-influenced Greenlandic fjord: influence from hydrography and prey availability. *Journal of Plankton Research* 37:102-119.
- Wickham, H. 2009. ggplot2: elegant graphics for data analysis. Springer New York.
- Zar, J. H. 1996. Biostatistical Analysis. Prentice Hall New Jersey.

INSTRUCTIONS TO AUTHORS

CalCOFI Reports is a peer-reviewed journal. Papers submitted for publication in the “Scientific Contributions” section are read by two or more referees and by arbiters when necessary; “Symposium” papers are invited by the convener of the annual symposium and are reviewed and edited at the convener’s discretion. The “Reports, Review, and Publications” section contains newsworthy information on the status of stocks and environmental conditions; the papers in this section are not peer reviewed; the CalCOFI Editorial Board will not consider unsolicited review papers.

The CalCOFI Editorial Board will consider for publication in the “Scientific Contributions” section manuscripts not previously published elsewhere that address the following in relation to the North Pacific, the California Current, and the Gulf of California: marine organisms; marine chemistry, fertility, and food chains; marine fishery modeling, prediction, policy, and management; marine climatology, paleoclimatology, ecology, and paleoecology; marine pollution; physical, chemical, and biological oceanography; and new marine instrumentation and methods.

Submission Guidelines

Submissions are open year-round. Please submit manuscripts as MS word documents in electronic format via email to: calcofi_coordinator@coast.ucsd.edu. (use Word; see “Manuscript Guidelines” below for more details on preparing tables and figures). Include one complete file with all tables and figures for reviewers.

The manuscript should contain the following parts:

1. A title page containing the manuscript’s title, your name, your institutional affiliation and contact information (address, telephone and fax numbers, e-mail address), and a word count
2. An abstract of no more than 150 words that succinctly expresses only the manuscript’s most central points, using the active voice
3. Body of the text, including any footnotes
4. Literature cited, in alphabetical order
5. Acknowledgments, if any
6. Tables
7. Figures and captions

Manuscript Guidelines

Length. Unless previously approved by the Scientific Editor, manuscripts should not exceed 6,000 words, including title page, abstract, text body, footnotes, acknowledgments, and literature cited but excluding figures and tables.

Text. Double-space all elements of the text, allow margins of at least 1 inch on all sides, and use a standard font (such as Times or Times New Roman) no smaller than 12 points. Number the pages consecutively. Eliminate all nonessential formatting. Indi-

cate subordination of heads consistently; for example, use all caps for the main heads, boldface for the next level, and italics for the third level. To indent paragraphs, use the tab key, not the space bar or a “style” feature of any sort. Never use letters for numbers or vice versa; in other words, do not type the lowercase “el” for the number “one” or the capital letter “oh” for zero. Use your word-processor’s automatic footnoting feature to insert footnotes. Acknowledgments, if included, should be placed at the end of the text and may include funding sources. Place the entire text (title page, abstract, text body, footnotes, acknowledgments, and literature cited) in one document file, and label it with your name—for example, “Smith text.doc.”

Tables. Use your word-processor’s *Table* feature, rather than spaces or tabs, to create the columns and rows. Use *minimal* formatting, and do not insert vertical or horizontal rules. Double-space the tables and use a standard font, such as Times or Times New Roman. Number the tables consecutively, and provide a brief title for each. Place explanatory material and sources in a note beneath the table. Be sure each table is specifically referred to in the text.

Figures. Figures should be in black and white or color. Submit figures—whether drawings, graphs, or photographs—as separate, high-resolution electronic files (preferably 300 ppi for better printing purposes). Label the files, for example, “Smith fig 1” and “Smith fig 2.” If you are submitting as a PDF, please embed all fonts. If your figures are embedded in your Word docs, please create separate high-resolution PDF files of each figure from the original art file. Please review your files after saving them as PDFs, to make sure all your figures translated correctly. Contributors are advised to make a trial reduction of complex figures to ensure that patterns, shading, and letters will remain distinct when reduced. Include a north arrow and latitude and longitude lines on maps. Use consistent labels and abbreviations and the same style of lettering for all figures if possible. Number figures consecutively, and specifically refer to each in the text. Provide a caption for each figure. Gather the captions together, and place them at the end of the electronic text file, following the “Literature Cited” section.

Editorial Style

For matters of editorial style, contributors should consult recent editions of *CalCOFI Reports*. Contributors may also refer to *The Chicago Manual of Style*, 15th ed. Whenever possible, write in the first person, and use active verbs. Use the full name of a person, organization, program, or agency when mentioning it for the first time in your manuscript. Double-check the spelling of non-English words, and include special characters such as accents and umlauts. Use correct SI symbols for *units of measure* in figures, tables, and text (other units may be given in parentheses). Prepare *equations* in accordance with similar expressions in the printed literature.

Cite *sources* in the text as Smith (1999) or Smith and Jones (2000) or (Gabriel et al. 1998; Smith and Jones 2000) (the latter when there are three or more authors). There should be no comma between author and date. References should be cited in chronological order from the oldest to the most recent.

In the "Literature Cited" section, show sources alphabetically by the first author's surname, and secondarily in chronological order with earliest dates first. Provide surnames and first initials of all authors; do not use "et al." for multi-authored works. No source should appear in the "Literature Cited" section unless it is specifically cited in the text, tables, or figure captions. *Personal communications* and *unpublished documents* should not be included in the "Literature Cited" section but may be cited in the text in parentheses; use footnotes only when parentheses will not suffice. Abbreviate journal titles to match BIOSYS usage. Each source must be complete according to the following guidelines. Please note that initials follow the primary author's surname, but for secondary authors initials come before the surnames:

ARTICLE IN A JOURNAL:

Barnes, J. T., L. D. Jacobson, A. D. MacCall, and P. Wolf. 1992. Recent population trends and abundance estimates for the Pacific sardine (*Sardinops sagax*). Calif. Coop. Oceanic Fish. Invest. Rep. 33:60–75.

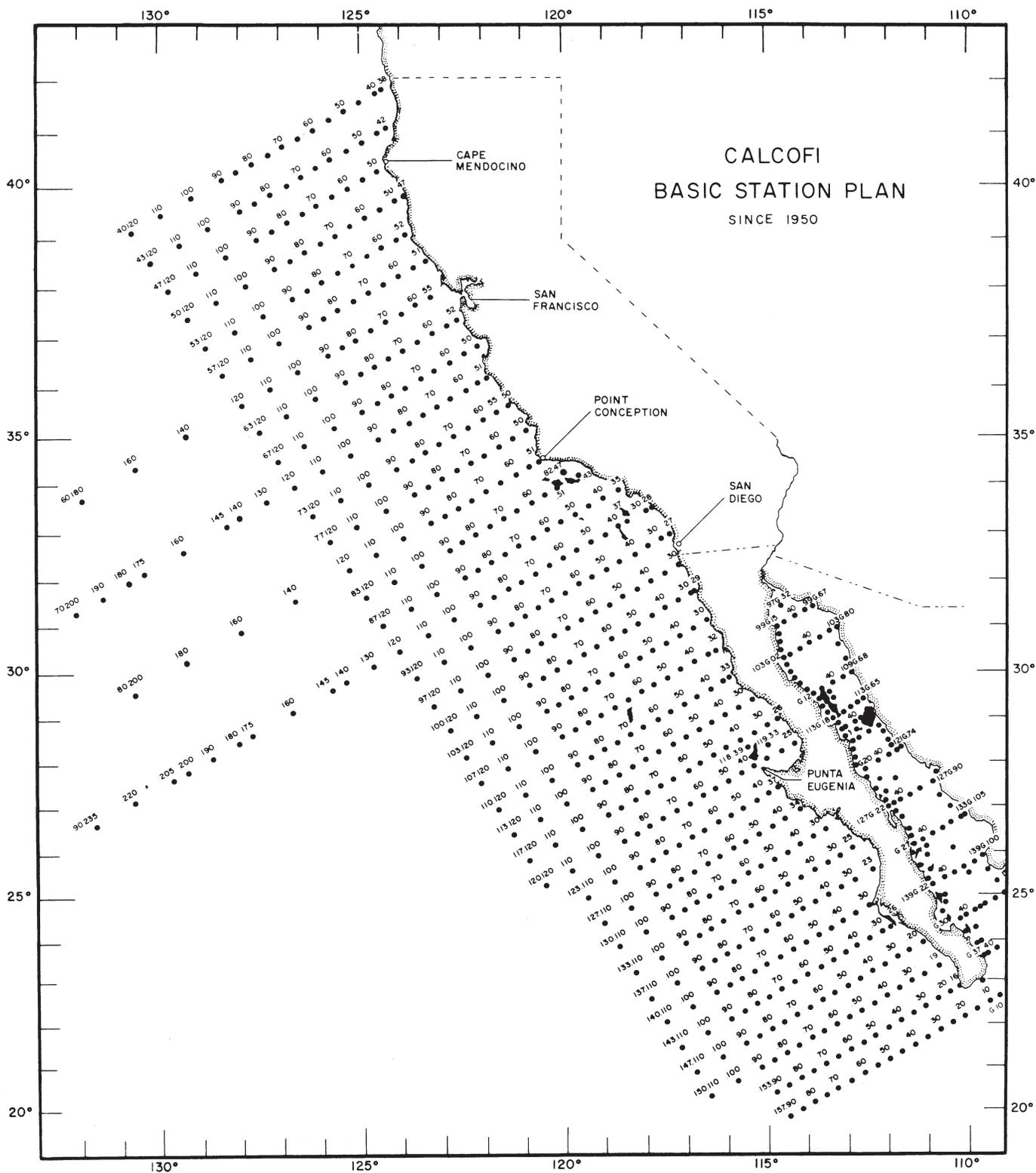
BOOK:

Odum, E. P. 1959. Fundamentals of ecology. 2nd ed. Philadelphia: Saunders. 546 pp.

CHAPTER IN A BOOK:

Wooster, W. S., and J. L. Reid Jr. 1963. Eastern boundary currents. *In* The sea, M. N. Hill, ed. New York: Interscience Pub., pp. 253–280.

If your manuscript is accepted for publication, we will provide further guidance regarding preparing it for editing.



CALCOFI

BASIC STATION PLAN
SINCE 1950