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Effects of Coastal Circulation on the Distributional Patterns of Pelagic Juvenile Fishes and Otolith Chemistry, and on the Timing of Juvenile Reef Fish Settlement

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Author
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Effects of coastal circulation on the distributional patterns of pelagic juvenile fishes and otolith chemistry, and on the timing of juvenile reef fish settlement

A Dissertation submitted in partial satisfaction of the requirements for the degree Doctor of Philosophy in Marine Science

by

Mary Miyoko Nishimoto

Committee in charge:
Professor Libe Washburn, Chair
Professor Robert Warner
Professor Mark Carr
Doctor Milton Love
Doctor Stephen Ralston

March 2009
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Robert Warner

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Mark Carr

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Milton Love

____________________________________________
Stephen Ralston

____________________________________________
Libe Washburn, Committee Chair

March 2009
Effects of coastal circulation on the distributional patterns of pelagic juvenile fishes and otolith chemistry, and on the timing of juvenile reef fish settlement

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by

Mary Miyoko Nishimoto
ACKNOWLEDGEMENTS

I thank my exemplary advisor, Dr. Libe Washburn, for having as much time as needed to listen and work with me through the development and fruition of my studies. I thank Dr. Robert Warner for helpful conversations and insight. I thank Dr. Mark Carr and Dr. Stephen Ralston for their expert advice. I am indebted to Dr. Milton Love for encouraging me to achieve my doctoral degree while I worked on his projects. Heartfelt thanks to Donna Schroeder for friendship, intellectual exchanges, and support on projects over the years. I thank Dr. David Lea for his support providing the ICPMS laboratory and resources for otolith microchemistry. Thank you to Frank Donahue, owner and captain of the F/V Gus-D, whose good spirit, knowledge of coastal waters, and expert vessel and gear handling were critical to the success of the midwater trawl surveys. This research required the dedicated assistance of many professionals, technicians, students, and volunteers in the water, on the water, and in the laboratory. I also thank the researchers, postdocs, and graduate students who engaged in helpful discussion and reviewed drafts of my work. With so many to name, I extend my appreciation in the chapters. I am blessed with the huge amount of support from my extended family and friends through the years. I would not be writing these words of gratitude were it not for David Fedorko, my husband. I treasure his love, patience, understanding, and humor that have kept me going. To the other love of my life, Zoe, my daughter, I hope you always will be joyful and fascinated as you explore and seek answers to your questions about our world.
This dissertation is dedicated to

my mother, Dorothy

and the memory of

my father, Sunny
VITA OF MARY MIYOKO NISHIMOTO
March 2009

EDUCATION

Bachelor of Science in Psychology, University of California, Davis, June 1984
Graduate Certificate in Secondary Education, Biological Sciences, University of California, Santa Cruz, June 1987
Master of Science in Marine Science, Ichthyology, Moss Landing Marine Laboratories, California State University, Hayward, August 1996
Doctor of Philosophy in Marine Science, University of California, Santa Barbara, March 2009 (expected).

CREDENTIALS

California Teaching Credential, Single Subject, Life Science, September 1986.

PROFESSIONAL EMPLOYMENT

1988-1989: Shipboard Instructor, Marine Science Institute, Redwood City, CA
Fall 1990: Teaching Assistant, “Marine Ecology,” Moss Landing Marine Laboratories
1991: Laboratory Technician, Sediment trap study, Moss Landing Marine Laboratories
August 1991: Technician, Invertebrate Museum, Moss Landing Marine Laboratories
1995-2001: Staff Research Associate II, Biological Resources Division-Minerals Management Service Project, “The ecological role of natural reefs and oil and gas production platforms on rocky reef fishes in Southern California.” Marine Science Institute, University of California, Santa Barbara
May 1997 and March 1998: Consultant, Workshops on species identification of larval rockfish (Sebastes spp.). Diablo Canyon Power Plant Monitoring Study, Tenera Environmental, San Luis Obispo, CA
2001-2002: Staff Research Associate II, California Sea Grant College Program, “Linking early fish growth and transport to circulation using otolith
microstructure and microchemistry.” Marine Science Institute, University of California, Santa Barbara

2002-2004: Staff Research Associate II, Minerals Management Service Project, “The ecological role of natural reefs and oil and gas production platforms on rocky reef fishes in Southern California.” Marine Science Institute, University of California, Santa Barbara

2004-2006: Staff Research Associate II, Minerals Management Service Project, “Assessing the fate of juvenile rockfishes at offshore platforms and natural reefs in the Santa Barbara Channel.” Marine Science Institute, University of California, Santa Barbara

2006-Present: Staff Research Associate II, Minerals Management Service Project, “Reproductive Ecology and Body Burden of Resident Fish Prior to Decommissioning.” Marine Science Institute, University of California, Santa Barbara

October 2007 and October 2008: Associated Investigator, “IMPACT, A submersible survey program monitoring Marine Protected Areas in deep water off central California,” University of California Cooperative Extension Sea Grant Program and NOAA Southwest Fisheries Science Center, Santa Cruz, CA

PUBLICATIONS


Li, Z., M. M. Nishimoto, M. S. Love, A. J. Gharrett. 2006. Comparing the identification of Southern California juvenile rockfishes (genus *Sebastes*
spp.) by restriction site analysis of the mitochondrial ND3/ND4 region and by morphological characteristics. *Fishery Bulletin* 104:376-382


REPORTS


FIELD OF STUDY

Major field: Marine Ecology and Oceanography
Studies in interdisciplinary oceanography with Professor Libe Washburn
Studies in community ecology and otolith microchemistry
    with Professor Robert Warner
Studies in fish ecology with Dr. Milton Love
ABSTRACT

Effects of coastal circulation on the distributional patterns of pelagic juvenile fish and otolith chemistry, and on the timing of juvenile reef fish settlement

by

Mary Miyoko Nishimoto

In three studies, I examined water masses and ocean current variability to elucidate some effects of coastal circulation on the distributional patterns of pelagic juvenile fish and otolith chemistry, and on the timing of juvenile reef fish settlement. In the first study, I found a strong link between coastal mesoscale flows and the spatial abundance patterns of juvenile and late-stage larval fishes. Surface currents observed by high frequency radar and concurrent CTD sampling during midwater trawling surveys in the Santa Barbara Channel region suggest that interannual abundance variations were linked to circulation that produced significant retention of fishes in 1998, but not in 1999. Findings indicate that cyclonic eddy circulation, when persistent, retains small fishes within a local area. Such features may help offset large scale declines in populations. From an ecological perspective, these fishes are forage for seabirds, marine mammals, and piscivorous fishes. In the second study, I found that fish from distinct coastal water masses possessed unique otolith elemental signatures.
I used in situ temperature and salinity measured at the time pelagic juvenile fish were sampled to identify water masses. Chemistry of the most recent growth zone in the otolith not only differentiated fish collected in different water masses from distant areas spanning nearly 500 km within the California Current System, but also discriminated individuals that resided in different water mass environments associated with eddy circulation within the Santa Barbara Channel (first study). I discuss how phenomena associated with the 1997-1998 El Niño and eddy circulation may have affected coastal ocean conditions and variation in otolith chemistry. In the final study, I used water mass dynamics and ocean current variability observed during the settlement of juvenile fishes at oil platforms in the eastern Santa Barbara Channel to reconstruct recent transport pathways taken by the recruits. Results indicate that currents from the Southern California Bight, rather than from Central California, supplied recruits to settlement habitat. I concluded that remote sources, particularly from the Bight, subsidized local fish populations in the eastern Channel given the broad spatial scale of ocean currents over the course of the pelagic early life history.
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I. Patterns of coastal eddy circulation and abundance of pelagic juvenile fish in the Santa Barbara Channel, California

Mary M. Nishimoto¹, Libe Washburn²

¹Marine Science Institute and Interdepartmental Graduate Program in Marine Science
²Institute for Computational Earth System Science and Department of Geography
University of California
Santa Barbara, CA 93106

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ABSTRACT

Annual midwater trawling surveys (sampling at depths of 20 to 40 m) in early summer 1998 and 1999 revealed strong interannual variability in the patterns of abundance of late-stage larval and juvenile fishes in the Santa Barbara Channel. In June 1998, sampling revealed high concentrations of fishes in the center of a cyclonic eddy in the western Channel corresponding to the lowest dynamic height in the study area. In contrast, eddy circulation was not consistent during the second survey in June 1999, and high concentrations of fishes were not observed. Patterns of evolving surface currents, observed by high frequency radar and concurrent CTD sampling during the trawling surveys, suggest that inter-annual variability in fish abundance within the Santa Barbara Channel resulted from local retention in 1998, but not in 1999. Time series of relative vorticity (a measure of eddy rotation) computed from surface current fields indicates that the cyclonic eddy observed during the 1998 survey was a stable, persistent feature developing about 6 wk before the trawling surveys. We speculate that the closed circulation of the eddy in 1998 retained larval and juvenile fishes from about late April until late June. In 1999, trains of smaller eddies propagated across the region beginning in mid-May, lasting through the survey period. Given their size and circulation strength, the propagating eddies probably disrupted the closed circulation in the western Channel. These observations indicate a strong link between coastal mesoscale flows and spatial abundance patterns of juvenile and late-stage larval fishes.
INTRODUCTION

Natural fluctuations in many marine populations often result from changes in recruitment, defined here as the addition of an incoming year-class. Many temperate and tropical nearshore fishes have planktonic phases lasting weeks or months in their early life histories (Brothers et al. 1983, Moser & Boehlert 1991). Mortality during this period is high and variable. Typically, less than one percent of the offspring survive through metamorphosis to settle in nursery or adult habitats (Cushing 1974, Chambers & Trippel 1997). Small changes in per capita mortality during early development can have a disproportionate effect on the size of the recruiting year-class. Because of this variability, juvenile abundance appears to be a better predictor of recruitment than larval abundance (Sissenwine 1984, Peterman et al. 1988, Bradford 1992, Ralston & Howard 1995).

Ocean dynamics directly and indirectly affect the spatial and temporal variability of egg and larval mortality. Storms, for example, disperse larvae and destroy food patches (Lasker 1981, Peterman & Bradford 1987), and persistent wind-induced upwelling or anomalous currents along a coast can advect larvae to unsuitable areas where growth and survivorship can be low or where returning to nearshore settlement habitat is unlikely (Hjort 1914, Parrish et al. 1981). At greater temporal and spatial scales, climatic events alter water mass distributions, water column structure, current patterns, and coastal upwelling of nutrient-rich water (McGowan et al. 1998). These environmental perturbations
affect movement, spawning, and recruitment patterns of fish populations (McFarlane et al. 2000). El Niño events are linked to delayed and reduced phytoplankton productivity, reduced zooplankton biomass, and increased mortality of coastal fishes during their planktonic larval phase (Lenarz et al. 1995, McGowan et al. 1998, Kahru & Mitchell 2000). A growing body of evidence suggests that large-scale physical processes producing mortality in the early pelagic phase of fishes and other marine organisms can be offset by smaller-scale mechanisms (Connolly & Roughgarden 1999, Mullin et al. 2000). For example, coastal eddies, mesoscale features inherent in temporally and spatially variable current fields, can retain fishes during their pelagic phase and may enhance recruitment (Owen 1980, Vastano et al. 1992, Hare & Cowen 1996, Sakuma & Ralston 1997, Sanchez & Gil 2000).

Few surveys have targeted the later pelagic stages due to sampling difficulties, such as the size and complexity of the gear required to sample the less abundant and patchily distributed juveniles (e.g. Berry & Perkins 1963). Fewer surveys have resolved coastal mesoscale physical processes in relation to the distribution of late-stage larvae and pelagic juvenile fishes (Dickey-Collas et al. 1997, Limouzy-Paris et al. 1997). Although they are not typically designed to resolve mesoscale physical processes, some large scale surveys have shown that increased spatial variability of late-stage larvae and pelagic juvenile catches is associated with eddy fields detected post hoc in physical oceanographic data and satellite imagery (Sakuma & Ralston 1995, 1997, Hare & Cowen 1996, Sanchez & Gil 2000, Logerwell & Smith 2001). In this study, we investigated the
relationship between populations of late-stage larval and juvenile fishes and the mesoscale flow field in and around the Santa Barbara Channel, a part of the larger California Current System.

The California Current System (CCS) is the eastern boundary current system of the North Pacific (Hickey 1998). Eddies, filaments, and meanders driven by variable winds and pressure gradients characterize the flow field over the shelf and offshore in the equatorward-flowing jet of the CCS (e.g. Strub et al. 1991). These mesoscale features result in part from headlands and bathymetry along the coast (Kelly 1985). Our study area, the Santa Barbara Channel, is a transition region between the strong coastal upwelling regime extending northward from Point Conception to Washington and the warmer waters of the Southern California Bight.

The circulation in the western Santa Barbara Channel consists primarily of a cyclonic flow that is strongest spring through fall and weakest or absent in winter (Dever et al. 1998, Harms & Winant 1998, Winant et al. 1999). A poleward, temperature-dependent pressure gradient tends to drive strong westward currents in the Channel. Opposing the pressure gradient are winds that tend to induce upwelling and drive eastward flow, especially in the southern Channel. When effects of wind and pressure gradients balance, the flow is cyclonic with westward flow along the northern boundary of the Channel and eastward flow along the Channel Islands, the southern boundary. Currents in the upper layers carry a diversity of fish species into the Santa Barbara Channel where many recruit to adult habitats (Love et al. 1999).
We found variations in abundance patterns of small pelagic fishes collected during midwater trawling surveys in early summer 1998 and 1999 consistent with differences in the evolving mesoscale flow field in the Santa Barbara Channel region. In this paper, we focus on the most abundant and ubiquitous fishes sampled: three midwater fish species, California smoothtongue *Leuroglossus stilbius* (family Bathylagidae), northern lampfish *Stenobrachius leucopsar*us (Myctophidae), Mexican lampfish *Triphoturus mexicanus* (Myctophidae); a cod-like species, Pacific hake *Merluccius productus* (Merlucciidae); and a species complex of rockfishes *Sebastes* spp. (Scorpaenidae). Of particular interest are the latter 2 taxa, which were represented by late-stage larvae and pelagic juveniles. From an ecological perspective, these small fishes of about 15 to 100 mm standard length (SL) in our surveys are important forage for seabirds, marine mammals, piscivorous fishes including salmon, and other marine life (Ainley et al. 1996). We examined the hypothesis that interannual abundance variations were linked to flow patterns that produced significant retention of fishes in 1998, but not in 1999. Our findings indicate that eddy circulation, when persistent, retains small fishes within a local area. While we could not conclusively prove a linkage between high abundance and this mechanism of retention, lines of evidence from several data sources were consistent with this interpretation.
MATERIALS AND METHODS

Shipboard surveys in 1998 and 1999 began in early June and included midwater trawling and vertical profiling of water properties at stations throughout the Santa Barbara Channel and adjacent waters to the north and south (sampling region shown in Fig. 1; survey maps in Figs. 3 & 5). Fishes were sampled at night to minimize net avoidance (Sakuma et al. 1999). We typically made 4 net hauls between 2100 and 0500 PST using a modified Cobb mid-water trawl with a nominal $12.2 \times 12.2$ m opening and a 9 mm mesh codend. During each haul, a fixed length of wire was payed out and the net was towed for 15 min at ~5 km h$^{-1}$ covering 1.4 $\pm$ 0.2 km. A time-depth recorder attached to the headrope (rope across the top of the net opening) provided trawling depth every minute. The histogram of Fig. 2 shows the distribution of headrope depth sampled every minute for all tows in 1998 ($n = 41$), and Fig. 3 shows the trawling stations. The modal depth bin was centered on 20 m. The mean headrope depth was $20 \pm 2$ m (SD). In 1999, net depth data were collected only during the first 2 survey nights; and mean headrope depth was $26 \pm 1$ m for 7 hauls. Acoustic measurements have shown that the area of the opening of a net changes with trawling depth, and based on the measurements by Lenarz et al. (1991), we estimate that the opening was 10 m wide and 14 m high when trawling at a headrope depth of 20 m, so the corresponding water volume sampled per haul was $\sim 2 \times 10^5$ m$^3$. 

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Vertical profiles of water properties were obtained using a conductivity-temperature-depth (CTD) profiler (SBE-19, SeaBird Electronics) immediately before or after each net haul so we could associate patterns of larval fish abundance with local hydrographic conditions. The CTD was lowered to 200 m, or to about 10 m above the bottom at shallow stations. Some casts were obtained at stations without net hauls to augment coverage of the study area. During casts, temperature, conductivity, and pressure were sampled at 2 Hz and then averaged into 1 m depth bins during subsequent processing. Salinity $S$, potential density anomaly $\sigma_\theta$, and dynamic height $\phi$ (at 5 dbar relative to a 200 dbar reference pressure) were computed from the 1 m averages of conductivity, temperature, and pressure.

We directed sampling for fishes and water properties based upon satellite sea surface temperature (SST) images and surface current maps from an array of three high frequency (HF) radars located along the mainland coast. Neither the satellite imagery nor the HF radar velocity could be accessed from the research vessel, but daily communication with shore-based personnel provided descriptions of sea surface currents and SST patterns based on images such as shown in Fig. 1.

Maps of surface currents in the western Santa Barbara Channel were produced hourly. The HF radars operated at frequencies around 12 MHz and were deployed at Point Conception, Refugio, and Coal Oil Point (triangles in Fig. 1B). HF radars measure coastal currents in the upper ~1 m of the water column using a Doppler radar technique (e.g. Barrick & Lipa 1998). Two or
more radars with overlapping coverage measure the total velocity vector field of surface currents in the overlap area. The radars were configured to have a range of 42 km, a radial resolution of 1.5 km, and azimuthal resolution of 5°. Surface velocity vectors were located on a square grid with points separated by 2 km. Every hour, all radial vectors within a 3 km radius of each grid point were fitted to north and east velocity components using the least-square technique of Gurgel (1994). The circle in the lower left hand corner of Fig. 1B shows the scale of this spatial averaging compared with the radar coverage area. Our processing of radial current vectors to form surface current maps is the same as that used by Paduan & Rosenfeld (1996). Emery et al. (2002) found significant correlation between radial currents measured with these HF radars and those measured by an array of moored current meters in the study area. Graber et al. (1997) and Shay et al. (1998) provide a comprehensive discussion of the errors and expected differences between moored current measurements and HF radars.

Generally, all fishes from each haul were sorted, identified, enumerated, and most were frozen. In the June 1998 survey, several hauls with extremely large catches of fishes and zooplankton required representative subsampling, and subsamples of known volume were sorted and abundances were estimated from the total volume of the haul. When a species or species complex was very abundant in a sorted sample, the fish were counted and 100 fish of one species or 1000 ml of a species complex were retained for inspection in the laboratory. However, all rockfishes (Sebastes spp.) sorted from a sample or subsample were retained. In the laboratory, fishes were identified to species level or to a higher
taxonomic level when species could not be determined based on meristics, morphology, and pigment pattern, or due to damage.

A number of rockfish species were collected during the surveys. Only 5 species of rockfishes present in the samples, shortbelly rockfish *Sebastes jordani*, bocaccio *S. paucispinis*, cowcod *S. levis*, chilipepper *S. goodei*, and blackgill rockfish *S. melanostomus*, could be identified with confidence as both late-stage larvae and pelagic juveniles. These species are described in Moser (1996), and all except for shortbelly rockfish were rare in the samples. Two species, squarespot rockfish *S. hopkinsi* and halfbanded rockfish *S. semicinctus* were abundant as pelagic juveniles; but identification of the late-stage larvae and transforming juveniles of these species was problematic. Given these limitations, we chose to group all rockfish species as a complex, *Sebastes* spp.

In post-survey analysis, the hauls were grouped according to the spatial distribution of $\phi$ and geographic position of the stations. Contour maps of $\phi$ and vertical cross-sections of $S$, $\theta$, and $\sigma_\theta$ were created using Surfer (Golden Software 1999) with a Kriging algorithm. We used SPSS for Windows to carry out statistical procedures (SPSS 1999). ANOVA was employed to test for differences in catches among defined groups of stations. Abundance data (fish haul$^{-1}$) was log $(x+1)$ transformed to reduce heteroscedacity. We used the Levene test to evaluate the equality of variances among groups ($p < 0.01$). If ANOVA determined that differences existed among the means, we used either the Tukey test or Tamhane T2 test to determine which means differed. The
Tamhane T2 test, a conservative pairwise comparisons test based on a $t$ test, is appropriate when the variances are unequal. The Tukey test is appropriate when variances are equal. The independent samples $t$ test, generating a $t$ statistic that is based on either equal or unequal variances, was used for between-year comparisons. A significance level $\alpha = 0.05$ was assigned for the ANOVA, pairwise comparison tests, and $t$ test.

RESULTS

Concentrated abundance of fishes in a persistent mesoscale eddy in June 1998

At the beginning of the juvenile fish survey on 2 June 1998 the surface circulation was strongly cyclonic (Fig. 1B), consistent with previous observations of the summer flow field in the western Santa Barbara Channel (e.g. Harms & Winant 1998), and water flow was dominated by an eddy centered at 120.1° W and 34.3° N with a diameter of about 30 km. The rotation of the eddy, quantified by its relative vorticity $\zeta$ (equal to twice the angular rotation rate), ranged from $0.2 \, f$ (rotation period of $\sim 9$ d) on the periphery to about $0.7 \, f$ (rotation period of $\sim 3$ d) in the center, where $f$ is the Coriolis parameter ($f^{-1} = 21.5$ h). We estimated $\zeta$ at each point by using a centered first difference, $\zeta = \Delta v / \Delta x - \Delta u / \Delta y$ where $\Delta u, \Delta v$ are the changes in the northward and eastward components of surface current velocity between 2 grid points, and $\Delta x, \Delta y$ are twice the 2 km grid spacing in the east and north directions. The
relatively uniform vorticity (red shading, Fig. 1B) in the center indicated that the core of the eddy was approximately in solid body rotation. Alternating warm and cool streaks wrapped around the eddy, revealed by satellite sea surface temperature (SST) imagery, also indicated strong rotary flow in the eddy (Fig. 1A).

The eddy circulation was not merely a surface flow, but extended well below the surface layer. The spatial pattern of $\phi$ had a minimum in the core of the eddy (Fig. 3A), consistent with the strong cyclonic circulation revealed by the HF radars. We defined the eddy by $\phi \leq 0.37$ m (shaded region, Fig. 3A). Isotherms along an east-west section across the eddy (section location shown in Fig. 3A) rose sharply in the eddy center consistent with the cyclonic rotation (Fig. 4A). For example, the 10°C isotherm rose about 80 m in the center of the section compared with its positions on the ends of the section. Isopleths of $S$ and $\sigma_0$ exhibited similar deflections across this section (Figs. 4B & C). The higher salinity in the eddy center extended almost to the surface while cooler water in the center was not evident above about 20 m, possibly due to local solar heating.

Horizontal density gradients in the eddy supported vertical shear in horizontal geostrophic currents: current speed increased by 0.2 m s$^{-1}$ over the 200 m from the reference level to the sea surface (Fig. 4D). Currents across the section revealed southward flow at depth west of the center and northward flow to the east, such that the deep flow was cyclonic. Deflections of the deepest isopleths in Fig. 4 indicate the cyclonic circulation of the eddy extended below
200 m. The nine CTD casts in the area where $\phi \leq 0.37$ m (Fig. 3A) were obtained during the nights of 2, 3, 4, and 9 June 1998 indicating that the eddy persisted at least a week, and time series of relative vorticity obtained from the HF radars showed that the eddy persisted for much longer (see below).

During the 2 wk sampling, 2–15 June 1998, net hauls were conducted in the eddy and surrounding waters to explore possible influences on juvenile fish abundance. Hauls were grouped into 7 geographic areas, including the eddy center (defined by $\phi \leq 0.37$ m). Mean abundances of 4 of the 5 dominant taxa in the eddy exceeded those found outside of the Channel north of Pt. Conception (Pts. Purisima and Arguello) and off Pt. Mugu by at least an order of magnitude (Fig. 3B), except for the catch of Mexican lampfish, which was about a third of that in the eddy center, reflecting its southerly distribution loosely bounded at Pt. Conception (Moser et al. 1993). Pacific hake and rockfishes were represented by late-stage larvae and pelagic juveniles. Pacific hake catches ranged from 142 to 11063 fish haul$^{-1}$ in the eddy center, 12 to 750 fish haul$^{-1}$ at the eddy periphery, and 0 to 146 fish haul$^{-1}$ in the east Channel and areas outside of the Channel combined. Rockfish catches in the same areas ranged from 39 to 2434 fish haul$^{-1}$, 1 to 197 fish haul$^{-1}$, 0 to 265 fish haul$^{-1}$, respectively. The midwater fishes, represented by specimens $\geq$ 1 yr old, were absent from some areas; none of the 3 midwater species (California smoothtongue, northern lampfish, Mexican lampfish) were collected off Pt. Purisima (Fig. 3B). Given this and the disproportionately large number of samples collected in the eddy center, we
combined areas and divided the midwater trawling stations into 3 groups for the ANOVA: eddy center (stations labeled L in Fig. 3A, n = 9); west and south of the eddy center (A, P, W, and S; n = 18); and north and east of the eddy center (N, E, and M; n = 14).

ANOVA determined that the catch of each of the 5 taxa differed among the groups of stations (Table 1). The pairwise multiple comparison tests showed that the 5 taxa were concentrated in the eddy center, and their abundances were significantly lower in the 2 areas outside of the eddy (p < 0.002). These 2 outer areas did not significantly differ from one another for any of the 5 taxa (p > 0.200).

Overall, the midwater species and Pacific hake dominated the survey catches in 1998. California smoothtongue, northern lampfish, and Mexican lampfish comprised 39.8, 24.3, and 4.2% of the mean total catch, respectively. Mostly fish older than 1 yr represented these midwater species. Pacific hake and rockfishes represented by late-stage larvae and pelagic juveniles comprised 25.2 and 4.0% of the mean total catch, respectively. These 5 taxa comprised 97.5% of the mean total catch. The remaining 2.5% was dominated by northern anchovy *Engraulis mordax*, and sanddabs *Citharichthys sordidus* and *C. stigmaeus*. 
Dispersed fish abundance patterns and variable mesoscale flows
in June 1999

Compared with 1998, conditions in the Channel and surrounding waters were much different in June 1999, when stronger winds and cooler water temperatures prevailed (Hayward et al. 1999). Because of the higher wind speeds, completion of the surveys in 1999 took all of June to complete, 2 wk longer than in 1998. In the post-survey analysis, we divided the hydrographic and trawl data into 2 sampling periods. Leg 1 included the first 7 survey nights from 6–21 June 1999 when samples were collected off Point Purisima, within the Channel, and off Point Mugu. We designated the 3 remaining nights from 24–30 June as leg 2 when the Channel was resampled and the area outside of the western entrance of the Channel was sampled for the first time. This allowed us to reconstruct and compare the hydrography and spatial distribution of fishes of 2 synoptic periods bearing in mind that the first leg was a protracted time interval, and that not all areas were re-sampled during leg 2.

Circulation in the Channel was more variable in 1999 compared with the stable cyclonic eddy flow pattern in 1998. During the 1999 surveys, the spatial pattern of $\phi$ rapidly evolved as indicated by repeated sampling in the western Channel. Shipboard sampling of leg 1 showed that $\phi$ was low in the Channel north of the San Miguel-Santa Rosa Islands passage (shaded area, Fig. 5A), corresponding to a cyclonic turning of currents observed by HF radar (data not shown). High winds terminated leg 1 sampling on 21 June. Resampling during
leg 2 revealed a region of low $\phi$ on the westernmost line, just outside the Channel (shaded area, Fig. 5B). At this time $\phi$ was higher in the Channel north of the San Miguel-Santa Rosa Islands passage than in leg 1.

In contrast to 1998, no consistent pattern of concentration among the dominant taxa was found in the areas of low $\phi$ for either leg (Fig. 5C; note difference in y-axis scale compared with Fig. 3B). During leg 1 inside the Channel, California smoothtongue, northern lampfish, and Pacific hake exhibited an increase in abundance in the low $\phi$ area; however, ANOVA and pairwise multiple comparison tests showed that all 5 taxa were most abundant outside of the Channel (Table 2). Late-larval stage and pelagic juvenile rockfishes and Pacific hake were most abundant north of the Channel. Rockfishes were collected at each of the 3 stations off Pt. Purisima and the catch ranged from 2 to 12 fish haul$^{-1}$. The largest rockfish catch was 13 fish collected at a station outside of the western entrance of the Channel northwest of San Miguel Island during leg 2. The remaining hauls contained only 1 or no rockfish. Pacific hake exhibited a spatial distribution similar to rockfishes. Largest Pacific hake catches were off Pt. Purisima and ranged from 141 to 1033 fish haul$^{-1}$. The remaining catches ranged from 0 to 7 fish haul$^{-1}$ typically with only 4 larger catches between 25 and 55 fish haul$^{-1}$. California smoothtongue and Mexican lampfish were most abundant off Pt. Mugu.

Overall, catch abundance in 1999 was lower by an order of magnitude compared to 1998 (Table 3A). The difference between years was striking for
pelagic young-of-year rockfishes. The average catch dropped from 128.1 fish haul\(^{-1}\) in 1998 to 0.9 fish haul\(^{-1}\) in 1999. The eddy where fishes were most abundant in 1998 was repeatedly sampled, so such a comparison is biased. The average catch is reduced four-fold between years if samples only collected outside of the eddy center in 1998 are considered, but this interannual difference remains significant (Table 3B).

The contribution of the principal taxa to the catch changed to some extent between years. Together, the 5 taxa comprised 97.5 and 95.7% of the total catch in 1998 and 1999, respectively (Table 3A). However, the rank order among the taxa and overall abundance changed. Although the mean catch of Mexican lampfish from all hauls decreased from 1998 to 1999, the contribution of this species to the assemblage increased from 4.2% in 1998 to 33.8% in 1999.

Young-of-year Pacific hake and rockfishes were less important in the fish assemblage in 1999. Pacific hake ranking fell from 2nd in 1998 to 4th in 1999. Rockfishes represented only 0.3% of the mean total catch in 1999, down from 4.0% in 1998. The abundance of Pacific sanddab *Citharichthys sordidus* surpassed that of rockfishes in 1999. The mean catch of late-larval stage and pelagic juvenile stage Pacific sanddab was nearly 8 times greater than that of rockfishes; however, the contribution of Pacific sanddab to the total fish assemblage in 1999 (2.6%) was less than that of rockfishes in 1998, underlining the decline in importance of rockfishes to the species assemblage between years.
DISCUSSION

Stable cyclonic eddy in 1998 and local retention

Over the 6-week period beginning 1 May 1998 (which included the trawling surveys), the pattern of mean surface currents observed by HF radar was consistent with a stable eddy circulation and closed streamlines (Fig. 6A). Vectors shown in Fig. 6 were obtained from the area of highest coverage by the radars; total vectors were available for at least 80% of the time over a 3-year record. The eddy was centered over the deepest part of the Santa Barbara Basin with higher flow speeds in the northwest portion of the eddy, possibly due to higher northwest winds in the western part of the Channel. Current direction approximately followed bathymetric contours around the basin.

To examine the stability of the eddy beyond just the mean flow pattern of Fig. 6A, we computed the time series of spatially averaged relative vorticity $\zeta$ over a large region of the western Channel. To form $\overline{\zeta}$, all values of $\zeta$ within the region outlined by the box in Fig. 7C were averaged together and plotted as a time series (blue dots, Fig. 7A). The 24-hour running mean of $\overline{\zeta}$ (red line, Fig. 7A) consistently indicated cyclonic rotation for about two months, from late April through late June with $\overline{\zeta}$ fluctuating in the range 0.2-0.4 $f$. Three representative images during May 1998 of the surface velocity and vorticity fields showed the cyclonic eddy over the Santa Barbara Basin (Figs. 7B, C, and D). During July and August the circulation was much more variable with large excursions in $\overline{\zeta}$ on time scales of a few days. The higher concentrations of
fishes observed during the trawling survey (indicated by green vertical lines, Fig. 7A) were consistent with retention by the eddy’s stable rotary flow and closed streamlines. It is unlikely, however, that eddy retention in the western Channel could have occurred before late April 1998.

The large scale dynamic height field observed during the CalCOFI survey of 2-23 April 1998 showed that strong equatorward (eastward) flow swept through the Channel during part of April 1998, a flow pattern inconsistent with retention. As discussed by Hayward et al. (1999), a low salinity region was positioned near shore during the spring 1998 CalCOFI survey. This jet-like feature is clearly seen by the crowding of lines of dynamic height anomalies north of Point Conception- (Fig. 8). Within the limited spatial resolution of the CalCOFI survey, the pattern of dynamic height anomalies indicated eastward, or equatorward transport through the Channel. Time series of near-surface currents at the western Channel entrance supported this conclusion.

Current meters at 5 m depth on mooring 'SMIN' (part of an array of recorders deployed by Scripps Institution of Oceanography; location shown in Fig. 10) recorded episodes of equatorward (eastward) currents occasionally exceeding 0.2 m s⁻¹ from 20 March to 24 April 1998 (Fig. 9A). Out of these 36 d, equatorward flow occurred at 5 m depth on 19 d (shaded areas, Fig. 9A). At 45 m, the pattern was similar but flow speeds were less (data not shown). Equatorward flow, especially during spring and summer, is unusual at 'SMIN' because alongshore pressure differences at a scale larger than the Channel typically force poleward (westward) flow there (Dever et al. 1998, Harms &
Winant 1998, Winant et al. 1999). For the 6 weeks preceding the 1999 survey, the current meter at 'SMIN' recorded only a few brief (~1 day or shorter) episodes of eastward currents (Fig. 9B).

During the equatorward flow episodes at 'SMIN' in 1998, the limited data available from the HF radars for April indicated a broader pattern of equatorward flow. (Hardware problems with the radars resulted in data loss for much of April, 1998). A 24 h average of surface currents obtained by the HF radars on 28 March during an equatorward flow episode at SMIN (dashed lines, Fig. 9A) showed equatorward flow spanning the Channel entrance. The flow meandered eastward through the western Channel (Fig. 10) around a small cyclonic eddy-like feature, centered at 120.03° W, 34.27° N. We speculate that the broad equatorward flow made retention in the western Channel unlikely before late April 1998.

**Strongly variable flow in 1999 and no eddy retention**

In contrast to the stable eddy circulation in 1998, highly variable flow prevailed in the weeks before and during the trawling surveys of 1999. The pattern of mean flow over the 6-week period beginning 1 May 1999 was not eddy-like, but rather was a cyclonic turning of a broad westward flow along the northern Santa Barbara Basin into a southeast flow toward the Channel Islands (Fig. 6B). The turning flow from westward to southward and then to
southeastward approximately followed isobaths. This flow pattern with its open streamlines was unlikely to have retained larvae prior to the trawling surveys.

Not only was the flow pattern more open in 1999, it was more variable. Time series showed $\zeta$ cycling from near zero to $\sim 0.5 \, f$ then back to near zero on timescales of 3 to 4 wk beginning in early May and continuing through August (Fig. 11). These cycles corresponded to strongly changing flow and vorticity patterns as seen in three representative examples from May 1999 (Fig. 11B, C & D). The patterns of Fig. 11D suggested the mechanism for strongly varying $\zeta$: two eddy-like features visualized as regions of fairly uniform, but opposite vorticity (red and blue regions, Fig. 11D). As reported by Beckenbach et al. (2000) and Washburn et al. (2000), these were propagating eddies, rotating in opposite directions and moving westward across the Channel at speeds of about 7 km day$^{-1}$. The propagating eddies occurred in groups or trains lasting up to 2 mo, most commonly in summer, but also in fall. Their passage through the Channel dominated variance in $\zeta$ over frequencies of 0.1 to 0.05 cycle d$^{-1}$ (periods of 10 to 20 d). Patterns of dynamic height obtained across the propagating eddies suggested they were not just surface features, but extended to at least 200 m (data not shown). We speculate that these eddies disrupted the larger scale cyclonic circulation in the Channel and prevented larval retention. The propagating eddies were also present in 1998, but did not begin strongly until after the trawling surveys. The prominent peak in $\zeta$ in early July 1998 of Fig. 7A coincided with their onset.
Cyclonic eddies and fish abundance

Cyclonic eddies modify their physical environment in a number of ways that may account for higher abundance of larval and juvenile (and some adult) fishes within them. Surface current drogues have demonstrated a pattern of cyclonic recirculation in the western Channel on time scales of several days (Dever et al. 1998, Winant et al. 1999). Typical azimuthal current speeds in the persistent eddy observed in 1998 were 0.2 to 0.3 m s\(^{-1}\), generally exceeding the sustainable swimming speed of larval and juvenile fishes (Stobutski & Bellwood 1997). If the fishes exhibited no directed swimming behavior to move radially outward, they would tend to remain in the eddy.

A simple explanation for the higher abundance of fishes in the eddy center is concentration due to uplift of water within the eddy. The cyclonic eddy in the Channel in 1998 was approximately in geostrophic balance (Rossby number \(\zeta/f\) \(\approx 0.3\) in May and June 1998 from Fig. 7A) such that colder, salty, high density water occupied the eddy center due to strong uplift of isopleths of \(\theta\), \(S\), and \(\sigma_\theta\) in the center (Fig. 4). Assuming for simplicity that fishes were initially distributed uniformly within a range of temperatures before the eddy developed, uplift associated with cyclonic circulation could have compressed isotherms in the eddy center and thus concentrated fishes by vertical advection. This mechanism would increase density proportionately with compression of isothermal surfaces.

As shown in Fig. 4A, temperatures in the eddy center within the trawling range of 20 to 35 m ranged from about 10 to 11°C. The vertical spacing of the 10 and
11°C isotherms was about 10 m in the high gradient region in the center and about 60 m on either end of the section, outside the eddy. This suggests that passive uplift in the eddy could have increased concentrations six-fold within the eddy center. This increase is comparable to the abundance increase found for California smoothtongue and northern lampfish (Fig. 3B). In contrast, densities of Pacific hake, rockfishes, and Mexican lampfish increased much more than six-fold in the eddy suggesting passive advection alone did not account for the increases.

We cannot discount the possibility that relatively high densities of fishes occurred at depths where we did not sample; however, concentrations of fish comparable to those found in the eddy feature are not likely in deeper water. Lenarz et al. (1991) and Sakuma & Ralston (1997) found that pelagic juvenile rockfishes and Pacific hake were most abundant at depths around 30 m and shallower, based on sampling at 10, 30, and 100 m depths. Our sampling was centered in the 20 to 35 m stratum (Fig. 2), but was roughly within the expected center of the distribution of these taxa. It is possible that large concentrations may have occurred near the surface where we did not sample. For example, Lenarz et al. reported the occurrence of large catches of Pacific hake at 10 m.

Fishes can actively maintain themselves in favorable environments and can be attracted to strong vertical temperature gradients. Uplift of isothermal surfaces due to geostrophic balance, such as we observed in the cyclonic eddy in 1998, has been associated with nutrient enrichment and heightened primary productivity in the euphotic zones of other cyclonic eddies (Hayward & Mantyla
Zooplankton are concentrated in the cold cores of eddies (Schwing et al. 1991, Huntley et al. 1995, Zimmerman & Biggs 1999, Kimura et al. 2000), and high densities of larval fish have been associated with the zooplankton concentrations (Kimura et al. 2000). In a cyclonic eddy off central California, euphausiids and copepods were found to be concentrated in the fluorescence maxima at the pycnocline (Huntley et al. 2000). Other studies show concentration of particles at or near the pycnocline (Malkiel et al. 1999). Many larval species are diel vertical migrants as indicated by surveys comparing the day and night vertical distribution patterns of larval fishes (Boehlert et al. 1985, Sakuma et al. 1999). Midwater fishes (California smoothtongue, northern lampfish, and Mexican lampfish), represented by juveniles and adults in the present study, are extensive vertical migrants ascending several 100s of meters to feed in surface waters nightly. These midwater fishes may have been attracted to prey concentrations at the thermocline within the eddy observed in 1998.

Laboratory studies demonstrate that fish can modify or eliminate diel vertical migration patterns in response to one or a combination of environmental factors (e.g. light, temperature, turbidity, food density, presence of predators) and intrinsic factors (e.g. stage of development, hunger, condition) (Neilson & Perry 1990, Olla et al. 1996). Pacific hake exhibit an ontogenetic shift in their vertical distribution; larvae are most abundant below the mixed layer and juveniles are most abundant in the upper mixed layer during the night off central California (Sakuma & Ralston 1997). Such a shift is not uncommon; comparable changes
with development in the depth distribution of shortbelly rockfish and other rockfishes have also been observed (Lenarz et al. 1991).

Late-stage larvae and pelagic juveniles exhibit considerable control over their speed, direction, and position in the water column (Olla et al. 1996; Leis & Carson-Ewart 1997, 1999). Leis & Carson-Ewart (1997) observed in situ tropical late-stage larvae frequently examining food particles, maneuvering around objects such as marine snow and jellies, and engaging in stop-go behavior, sometimes in the presence of predators. Furthermore, Stobutski & Bellwood (1997) showed that swimming ability of late pelagic stages of a variety of tropical reef fishes (ranging in size from about 15 mm to 30 mm total length) was related to morphology and developmental stage as well as size. Laboratory studies show that larval and juvenile fishes learn to aggregate when searching for food that is patchily distributed, and after encountering a patch of prey, they remain aggregated within the patch to feed (Olla et al. 1996).

Conversely, when food is dispersed, fish do not aggregate and forage more independently—this may account at least in part for the relatively low densities of fishes in areas outside of the eddy in 1998 and throughout the study region in 1999. Given the behavioral capabilities of late-stage larvae and pelagic juveniles, it is likely that many fishes do not passively concentrate in eddies but respond to some environmental factor(s) that characterize the features.

In a broader context, the very high abundance of pelagic juvenile fishes in the eddy observed in the Channel contrasts sharply with results from an oceanographic and midwater trawling survey conducted by NOAA in May-June
1998 in central California coastal waters. Pelagic juvenile catches off central California in 1998 were among the lowest since annual assessments began in 1985, a result attributed in part to the strong 1997-98 El Niño (Hayward 2000). Our sampling methods were similar to those employed by NOAA, allowing us roughly to compare our catch statistics. Our low rockfish catches north of the Channel (e.g. no rockfish were collected off Pt. Arguello and the average catch of rockfish off Pt. Purisima was 1.3 fish haul$^{-1}$) were similar to the average catch of 1.2 fish haul$^{-1}$ (n = 92) off central California (S. Ralston, pers. comm.). In contrast, the average rockfish catch within the Santa Barbara Channel eddy during our survey was 462 fish haul$^{-1}$ (SE = ± 259 fish haul$^{-1}$, n = 9 hauls). Similarly, the average catch of Pacific hake in the eddy was 3400 fish haul$^{-1}$ (SE = ± 1300 fish haul$^{-1}$, n = 9) compared to 7.3 fish haul$^{-1}$ (n = 92) from the central California survey. Such differences of at least two orders of magnitude between mean catches off central California and in the Santa Barbara Channel eddy suggests that persistent cyclonic eddies may be important mechanisms for locally offsetting large scale declines in marine populations.

**Sequential events and survivorship**

Strong year-classes, separated by several years of poor recruitment, are characteristic of some fisheries including Pacific hake and rockfishes. A goal in fisheries ecology is to identify mechanisms that produce these events of strong recruitment for a species. Mullin et al. (2000) suggest that a 'sequential alignment of favorable states in several components of the environment of larvae
and of juveniles' might be necessary to produce a strong year-class. These causal mechanisms, operating at spatial and temporal scales relevant to the ecology of developing fish, need not be the same from year to year, and can be ephemeral and in phase with only one of several cohorts from a spawning season.

We surmise that a particular sequence of events in 1998 led to the distributional pattern of late-larval and pelagic juvenile fishes that we observed. The spawning range of Pacific hake and many rockfishes is broad, encompassing the Channel and waters off central, northern, and southern California (Bailey et al. 1982, Moser & Boehlert 1991). Pacific hake spawn over the continental slope between January and March but the season can extend to May. All rockfishes are ovoviviparous and many species including the ones common to our survey (shortbelly rockfish, half-banded rockfish, and squarespot rockfish) have a protracted parturition season releasing larvae during the late winter through early spring and most likely in or near the habitat where they regularly reside (Moser & Boehlert 1991). Potentially, a number of cohorts separated in time and space can contribute to the same year-class. For the fish populations we observed, conditions may have been detrimental to early-stage larvae during early 1998. February and March 1998 was a period of exceptionally intense winter storm activity along the west coast (Sakuma et al. 2000). Such intense turbulence can destroy food patches and interfere with larval feeding (Peterman & Bradford 1987). During this time, strong downwelling was coupled with a strong countercurrent transporting warm, saline, low nutrient water northward along the
coast. Productivity in coastal waters was low at this time. Survivorship of the cohorts from early in the reproductive season may have been poor.

Circulation changed dramatically in April 1998 with unusually weak upwelling persisting through May off California and Baja California (Fig. 8) (Lynn et al. 1998). Offshore advection, which generally contributes to substantial offshore dispersal of coastal species, probably declined along central California due to the weak upwelling and a strong equatorward jet near shore. It is plausible that larvae in coastal waters that survived or were spawned after the detrimental storm conditions could have been transported from central California through the Santa Barbara Channel in the equatorward jet. The influx of central California coastal water may have contributed to an increase in primary production in the Channel (Hayward 2000). Data from two CalCOFI surveys (23 January–14 February and 2–23 April 1998) shows that coastal SST in the Santa Barbara Channel region dropped from about 15°C to 13°C, and 10 m chlorophyll increased from about 2 mg l⁻¹ to greater than 7 mg l⁻¹. Following this event was the establishment of closed, cyclonic circulation in the western Channel by late April. Nutrient upwelling in the cyclonic eddy may have sustained production trapped in surface waters during the protracted period of closed recirculation. The relatively high density of fishes in the eddy could then have been a consequence of high food availability and feeding success (Theilacker et al. 1996; McLaren et al. 1997). We hypothesize that fish growth was enhanced in the persistent eddy and survivorship was increased (Houde 1997, Sogard 1997).
amidst poor circumstances for the populations of pelagic early life history stages elsewhere in the region.

In contrast to 1998, in the spring 1999 CalCOFI survey (1–20 April), the equatorward jet was no longer near the coast. Upwelling anomalies were particularly strong along the entire California coast in April 1999 and were among the largest ever in the over-50-year record of the upwelling index (Schwing et al. 2000). Offshore advection may have contributed to larval loss in April producing a subsequent paucity of late-stage larvae and pelagic juvenile fishes along the coast. We suggest that retention was relatively weak or absent due to propagating eddies which characterized the Channel from May 1999 through much of the summer and that significant mixing and transport occurred between these unstable features and surrounding waters resulting in the dispersal of fishes and their prey.

CONCLUSIONS

The June 1998 midwater trawling survey revealed very high concentrations of fishes in the core of a cyclonic eddy, an area of lowest dynamic height, in the western Santa Barbara Channel. Concentrations of five dominant taxa were at least an order of magnitude higher in the eddy compared with outside the eddy. Based on time series of currents and vorticity from an array of HF radars, the eddy may have retained fishes for up to 6 wk before the June 1998 trawling survey. It is unlikely that the eddy retained the fishes longer than 6 wk because
strong equatorward flow swept through the Santa Barbara Channel during most of April 1998.

A second survey in June 1999 failed to show high concentrations of fishes in the western Channel and a persistent cyclonic eddy was not found. Instead, the flow in the weeks leading up to the June 1999 survey consisted of a cyclonic turning of a broad open flow pattern that was inconsistent with retention. Compared to 1998, the mesoscale flow pattern was much more variable in 1999, when small propagating eddies produced large variations in vorticity.

Our results suggest that very large interannual abundance variations in coastal populations of larval and juvenile fishes result from changing mesoscale flow patterns. In particular, persistent cyclonic eddies, with their closed streamlines and enhanced vertical temperature gradients, may concentrate fishes through a variety of physical and behavioral mechanisms. We surmise that the development of a cohort of larval fishes may serendipitously be in phase with some sequence of mesoscale phenomena, which in this case study included the cyclonic eddy that we observed in 1998. Consequently, survivorship would be promoted within spatially and temporally limited boundaries, and a local subpopulation could contribute substantially to the population at large.

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Schroeder provided logistics support during the trawling surveys and helpful discussion during the analysis. We also benefited from helpful discussion with E. Dever, C. Winant, and M. Hendershott. We thank M. Love, R. Warner, S. Ralston, D. Krause, and the anonymous reviewers for their useful comments on the manuscript. The support of L. Thorsteinson is greatly appreciated. Moored current data were provided by the Center for Coastal Studies at the Scripps Institution of Oceanography. M. Knope, E. Love, K. Mendiola, M. Moreti, M. Petueli, T. Ross, M. Simmons, E. Simons and others assisted with laboratory work. We thank E. Beckenbach and B. Emery for their analysis of the surface flow fields in 1998 and 1999. We thank S. Ralston for catch statistics from NOAA’s central California surveys (NMFS/SWFSC, Santa Cruz, CA). The California Department of Fish and Game provided the midwater trawl net. Funding for the trawling surveys was provided by the Biological Resources Division of the U.S. Geological Survey under cooperative agreement 1445-CA09-95-0836. The California Artificial Reef Enhancement Program provided additional support. The Minerals Management Service and the David and Lucile Packard Foundation funded operation of the HF radars and related data analysis. The radars were obtained with funding from the W. M. Keck Foundation. We thank the California Department of Parks and Recreation, UCSB, the U.S. Air Force, and the U.S. Coast Guard for allowing the installation of HF radar equipment at their facilities. The views and conclusions contained in this document are those of the authors and should not be interpreted as necessarily
representing the official policies, either express or implied, of the U.S. Government.
Table 1. ANOVA on 1998 log(x+1) transformed data divided into 3 groups: (1) stations to the west and south of the eddy center; (2) inside the eddy; and (3) to the east and north of the eddy center ($F_{0.05, 2, 38} = 4.08$). Taxa ordered by mean abundance in 1998. A multiple comparison test determined what groups differed as indicated by an inequality with type 1 error probability for individual pairs of groups.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Source of variation</th>
<th>SS</th>
<th>DF</th>
<th>MS</th>
<th>F</th>
<th>Tukey(^1) or Tamhane(^2)</th>
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<td>48.8</td>
<td>2</td>
<td>24.4</td>
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<td>$2 \neq 1, 3$ (p&lt;0.0001)(^1)</td>
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<tr>
<td></td>
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<td>38</td>
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</tr>
<tr>
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<td>Total</td>
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<td>33.4</td>
<td>2</td>
<td>16.7</td>
<td>23.4</td>
<td>$2 \neq 1, 3$ (p&lt;0.0001)(^1)</td>
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<td>12.3</td>
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<td>21.5</td>
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<td>20.1</td>
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<td>Total</td>
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<tr>
<td></td>
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Table 2. ANOVA on log(x+1) transformed data from 1999 leg 1 divided into 4 groups: (1) Pt. Purisima; (2) low dynamic height in the western Channel; (3) eastern Channel; and (4) Pt. Mugu areas ($F_{0.05, 2, 3, 3.26} = 3.67$). Taxa ordered by mean abundance in 1999 during leg 1. Tukey multiple comparison test determined what groups differed as indicated by an inequality with type 1 error probability for individual pair of groups.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Source of variation</th>
<th>SS</th>
<th>DF</th>
<th>MS</th>
<th>F</th>
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<td>$1 \neq 2, 3, 4$ (p&lt;0.0001)*</td>
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<td></td>
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<td>23</td>
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<td></td>
<td>Total</td>
<td>1.8</td>
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<td></td>
</tr>
<tr>
<td>Pacific hake</td>
<td>Groups</td>
<td>14.8</td>
<td>3</td>
<td>4.9</td>
<td>22.1</td>
<td>$1 \neq 2, 3, 4$ (p&lt;0.0001)</td>
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<tr>
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<tr>
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<td>0.3</td>
<td>0.4</td>
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<td>Total</td>
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<tr>
<td>Mexican lampfish</td>
<td>Groups</td>
<td>10.7</td>
<td>3</td>
<td>3.6</td>
<td>10.8</td>
<td>$4 \neq 1, 2, 3$ (p&lt;0.012)</td>
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<tr>
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<td>Error</td>
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</tr>
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<td>Total</td>
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<td></td>
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<tr>
<td>Other fishes</td>
<td>Groups</td>
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<td>13.2</td>
<td>$4 \neq 2, 3$ (p&lt;0.027)</td>
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<tr>
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<td>Error</td>
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<td>Total</td>
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<td>26</td>
<td></td>
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</table>

* Variances were not equal among groups. The Tamhane test did not detect differences between groups ($\alpha=0.05$). Results from the Tukey test are given.
Table 3. (A) Interannual comparison of fish abundance. Average number of fish per haul and standard deviation in the 1998 survey, in 1998 excluding 9 samples collected in the center of the eddy and in the 1999 survey. Taxa ordered by mean abundance in 1998. (B) Independent samples t-test comparison of fish abundance between years. Data was log (x+1) transformed. Taxa ordered by mean abundance in 1998.

(A)

<table>
<thead>
<tr>
<th>Taxon</th>
<th>1998 (N=41)</th>
<th>1998, eddy center excluded (N=32)</th>
<th>1999 (N=41)</th>
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<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
</tr>
<tr>
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<td>1265.2</td>
<td>4264.7</td>
<td>195.3</td>
</tr>
<tr>
<td>Pacific hake</td>
<td>801.9</td>
<td>2259.2</td>
<td>58.1</td>
</tr>
<tr>
<td>Northern lampfish</td>
<td>773.0</td>
<td>1739.3</td>
<td>258.3</td>
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<td>Mexican lampfish</td>
<td>132.1</td>
<td>397.2</td>
<td>28.4</td>
</tr>
<tr>
<td>Rockfishes</td>
<td>128.1</td>
<td>395.1</td>
<td>33.8</td>
</tr>
<tr>
<td>Other fishes</td>
<td>78.3</td>
<td>101.8</td>
<td>82.9</td>
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<tr>
<td>All fishes</td>
<td>3178.7</td>
<td>7238.8</td>
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(B)

<table>
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<tbody>
<tr>
<td></td>
<td>t</td>
<td>df</td>
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<tr>
<td>California smoothtongue</td>
<td>0.92 *</td>
<td>71.99</td>
</tr>
<tr>
<td>Pacific hake</td>
<td>3.81 *</td>
<td>67.56</td>
</tr>
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<td>Northern lampfish</td>
<td>2.92 *</td>
<td>61.25</td>
</tr>
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<td>Sebastes spp.</td>
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<td>80.00</td>
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*Levene's test determined unequal variances between groups, p<0.01
Figure 1. Eddy circulation in the study area. (A) Satellite sea surface temperature image at 0152 GMT on 3 June 1998 shows a cyclonic eddy visualized by curving temperatures features in the western Santa Barbara Channel. (B) Spatial pattern of surface currents at 1900 GMT on 2 June 1998 showing a strong cyclonic eddy. Color scale indicates magnitude of relative vorticity $\zeta$. The highest rotation rates occurred in the eddy center. Evolving surface currents were mapped with high frequency radars at Coal Oil Point (COP), Refugio (RFG), and Point Conception (PTC). Box indicates area over which $\zeta$ was averaged to produce the time series of Figs. 7 & 11. Scale for current speed is at lower left. Circle (radius = 3 km) at lower left is the area over which current vectors were averaged.
Figure 1.
Figure 2. Frequency distribution of headrope depths (position of the top of the net, sampled once per min) from all net tows of 1998 survey (n = 41). The net opening extended 14 m below the headrope depth.
Figure 3. (A) Distribution of dynamic height $\phi$ at 5 dbar computed with respect to a reference pressure level of 200 dbar. The center of the eddy is indicated by $\phi \leq 0.37$ m (shaded region). Letters indicate groups of trawling locations in the eddy and surrounding waters: L, eddy center; P, Point Purisima; A, Point Arguello; W, west Channel entrance; S, southern and western edge of eddy; N, northeastern edge of eddy; E, eastern edge of eddy and east Channel; and M, Point Mugu. Vertical profiles of water properties were obtained at all trawling locations. X, vertical profiles of water properties only. Dashed line: sections of T, S, and $\sigma_0$ of Figure 4. (B) Mean catch per haul ($\pm 1$ SE) of the 5 dominant fish taxa

A)
Figure 3 continued.

B)
Figure 4. East-west vertical sections of: (A) potential temperature $\theta$ (°C), (B) salinity, (C) potential density anomaly $\sigma_\theta$ (kg m$^{-3}$), and (D) geostrophic velocity (m s$^{-1}$) along the section indicated by the line in Fig. 3A. Vertical lines indicate profile locations identified by station numbers along the x-axis at the top. Stn 301 and 302 were in the eddy center, defined by dynamic height $\phi < 0.37$ m. The cyclonic flow of the eddy produced the large uplift of isotherms. Deep cyclonic flow of the eddy was indicated by southward flow (shaded region, panel D) west of the eddy center and northward flow east of the center.
Figure 4.
Figure 4 continued.
Figure 5. (A) Distribution of dynamic height as in Fig. 3A but for leg 1 (6–21 June 1999, 6 sampling nights) and (B) leg 2 (24 June–1 July 1999, 3 sampling nights). Areas of dynamic height with $\phi \leq 0.34$ m are shaded. (C) Mean catch per haul ($\pm 1$ SE) of 5 dominant fish taxa during 2 sampling legs in 1999. Letters indicate trawling locations (same abbreviations as in Fig. 3)
Figure 5.
Figure 5 continued.

C)

- California smoothtongue
  - Leg 1
  - Leg 2

- Northern lampfish

- Mexican lampfish

- Pacific hake

- Rockfishes

n = 3 4 16 4 2 7 5

Area
Figure 6. (A) Mean surface currents in western Santa Barbara Channel from 1 May to 15 June 1998. (B) As in (A), but for 1 May to 15 June 1999. These 6 wk periods included the 1998 and 1999 trawling surveys.
Figure 6 continued.
Figure 7. (A) Time series of spatially averaged relative vorticity $\bar{\zeta}$ normalized by the Coriolis parameter $f$, in the western Santa Barbara Channel from 1 December 1997 through 31 December 1998. $\zeta$ was computed from surface current data obtained by HF radar. The box of panel (C) shows the region over which spatial averages were computed. Blue dots indicate hourly values of $\bar{\zeta}/f$ and the red line is a 36 h running mean. Positive values indicate cyclonic (counter-clockwise) flow. Vertical green lines indicate the period of the trawling surveys. (B) Surface flow field in the western Channel at 1200 GMT on 1 May 1998. Arrows at lower right are the velocity scale. Color contours show relative vorticity $\zeta$ as indicated on the color scale. (C) As in (B), but for 17 May 1998 at 1600 GMT. (D) as in (B), but for 31 May 1998 at 1400 GMT.
Figure 7.
Figure 8. Dynamic height field from the CalCOFI survey of 2–23 April 1998 adapted from (Hayward et al. 1999). Crowding of dynamic height contours shows an equatorward jet near the coast. The pattern indicated strong equatorward (eastward) flow through the Santa Barbara Channel.
Figure 9. (A) Current time series at 5 m depth measured at mooring 'SMIN' from late March through June 1998. Heavy lines show eastward currents (u), and light lines show northward currents (v). Shaded areas show episodes of sustained strong equatorward flow in March and April. The location of mooring 'SMIN' is indicated by the circle in Figure 10. (B) As in (A), but for 1999; note absence of sustained eastward currents.
Figure 9.
Figure 10. Spatial distribution of surface currents in the western Santa Barbara Channel on 28 March 1998. Arrows show currents averaged over 24 h. Circle indicates position of mooring 'SMIN'. Time of this image is indicated by dashed line in current time series of Fig. 9A
Figure 11. As in Fig. 7A, but for period from 1 January 1999 through 31 January 2000. (B) As in Fig. 7B, but for 1 May 1999 at 0000 GMT. (C) As in Fig. 7B, but for 16 May 1999 at 0100 GMT. (D) As in Fig. 7B, but for 26 May 1999 at 0300
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II. Otolith elemental signatures reflect residency in coastal water masses

Mary M. Nishimoto\textsuperscript{1,2}, Libe Washburn\textsuperscript{3}, Robert Warner\textsuperscript{4}, and Milton Love\textsuperscript{1}

\textsuperscript{1}Marine Science Institute
\textsuperscript{2}Interdepartmental Graduate Program in Marine Science
\textsuperscript{3}Institute for Computational Earth System Science and Department of Geography
\textsuperscript{4}Ecology Evolution and Marine Biology

University of California
Santa Barbara, CA 93106
ABSTRACT

We examined variability in otolith chemistry of wild caught fish in relation to in situ temperature and salinity within the California Current System. Barium, magnesium, and iron from the most recent growth zone in otoliths differentiated pelagic juvenile shortbelly rockfish (Sebastes jordani) residing in water masses with distinct temperature and salinity properties from central and southern California spanning nearly 500 km of coastline. The 3-element signature also discriminated fish that resided in different water masses that were associated with mesoscale cyclonic eddy circulation in the Santa Barbara Channel.

Variability in otolith chemistry reflected the spatial patterns of both horizontal gradients and vertical gradients in water mass properties related to circulation. Although we found that the concentrations of particular elements in otoliths were correlated to ambient temperature or salinity, we suggest that these parameters are more useful as an identifying signature of distinct water masses associated with unique otolith signatures rather than as factors directly affecting otolith chemistry. Other factors varying among the water masses or among the fish populations residing in the water masses may also affect otolith chemistry.

We discuss how oceanographic phenomena associated with the 1997-1998 El Niño and the persistent, recirculating eddy in the Channel may have affected coastal ocean conditions and variation in otolith chemistry of fish in the study area.
INTRODUCTION

Elemental and isotopic assays of fish otoliths and invertebrate hard parts have been directed at questions concerning the tracking and mixing of marine and freshwater populations. The use of these structures as biogeochemical tags relies on the chemical composition reflecting to some degree the physicochemical characteristics of the ambient water. Particularly useful is the timekeeping property of the structures, otoliths and statoliths for example, that grow throughout the lifetime of the organism as material is deposited and preserved without resorption or chemical reworking. The spatial variability of the chemical composition of otoliths has been used successfully to discriminate individuals collected from different locations such as spawning stocks regions (Campana et al. 2000, Rooker et al. 2003), nursery areas (Thorrold et al. 1998, Secor et al. 2002), and natal origins (Warner et al. 2005). Inferences about fish homing behavior (Secor et al. 1995, Thorrold et al. 2001), connectivity estimates (Hamer et al. 2003, Miller and Shanks 2004, Standish et al. 2008), and larval dispersal histories (Swearer et al. 1999, FitzGerald et al. 2004, Hamilton et al. 2008) have been based on otolith chemistry as geographic tags. Typically, site discrimination using otolith chemistry is successful when the locations from which individuals are identified are physicochemically distinct areas such as estuaries or rivers (Thorrold et al. 1998, Gillanders 2002), sites along a pollution gradient (Hanson and Zdanowicz 1999), estuaries versus coastal marine habitats (Gillanders and Kingsford 1996, Yamashita et al. 2000, Forester and Swearer 2002, Brown 2006), and coastal or open ocean areas that likely are exposed to

These applications of otolith chemistry do not necessarily require the determination of how element concentrations, salinity, and temperature in the environment are related to element concentrations in the otolith; what is required is that the chemical assays of fish otoliths discriminate individuals from different locations. However, at least two important limitations in utilizing otolith chemistry to assess the movement of individuals and the mixing of populations among locations stem from not knowing how environmental variability relates to the spatial and temporal variability in otolith chemistry.

The first limitation is the reliability of site-specific otolith elemental signatures over time. Sufficient consistency in the spatial variability of otolith elemental signatures allows discrimination among habitat sites within a year; however, many studies that have compared otolith chemical composition among locations over two or more years have found significant interannual variability (Milton et al. 1997, Dove and Kingsford 1998, Patterson et al. 1999, Campana et al. 2000, Gillanders 2002, Brown 2006, Hamer et al. 2003; Miller and Shanks 2004). This temporal inconsistency is especially problematic if the goal, for example, is to examine a population over time to estimate connectivity via migration or larval dispersal among spatially distinct habitats.

The second limitation is that individuals of unknown residency can only be assigned to the set of sampled locations that define the spatial variability of the signatures. There is an unknown degree of error in assigning fish of unknown
residency to a specific site of a set of sampled locations, because fish residing in
unsampled locations might share the same elemental signature as fish from the
set of sampled locations. This can occur even if the spatial variability of the
otolith elemental signatures defined by a set of sampled locations is consistent
over time and the elemental signatures are good discriminators of the sites
sampled.

Presently, inferences are limited to the geographic scale of sampling, the
localities sampled, and the time of sampling within individual studies, because
of the uncertainty of changing environmental conditions that affect the
variability in otolith chemistry over time and space. We turn our attention from
the utility of using otolith chemistry as a location-based discriminator, and focus
on the prospect of utilizing otolith chemistry to identify water mass residency.
A motivation for this study is that if unique elemental signatures are associated
with distinct water masses, then a reference or atlas identifying these
relationships might be developed for widely using otolith chemistry and
oceanography to reconstruct the transport histories of individuals and estimate
the connectivity of populations across broad regions and over time.

The central goal of this study was to test the hypothesis that variability
among otolith trace element signatures of wild-caught fish was associated with
in situ water masses. An otolith grows incrementally as calcium carbonate
material is added onto its surface on a daily basis, and the elemental signature of
the outermost otolith material (i.e., edge of a sectioned otolith) reflects the most
recent conditions of the fish’s water environment. To identify distinct water
masses, we examined temperature and salinity measured during pelagic juvenile fish sampling off central California in May 1998 (Sakuma et al. 2000) and off the southern California coast in June 1998 (Nishimoto and Washburn 2002) spanning a distance of nearly 500 km (Fig. 1). The otolith signatures of shortbelly rockfish (*Sebastes jordani*) from these surveys were defined by a suite of elements assayed from otolith material grown in the recent days preceding capture. Otolith sampling included fish found concentrated in a persistent cyclonic eddy in the western Santa Barbara Channel (Nishimoto and Washburn 2002; Figs. 1 and 2). We examined the variability in otolith chemistry in relation to temperature and salinity across the study area and the three-dimensional circulation of the eddy.

**MATERIALS AND METHODS**

**Water mass sampling and otolith chemistry**

Similar methods were used in the central and southern California surveys (Nishimoto and Washburn 2002 (Chapter 1 of this dissertation), Wyllie Echeverria et al. 1990, Sakuma et al. 2000) to collect the otoliths and oceanographic data for this study. Fish were collected at night with a modified Cobb mid-water trawl with a 9 mm codend towed at depth for 15 minutes at ~5 km h\(^{-1}\) covering ~1.5 km (Nishimoto and Washburn 2002). The opening of the net used in both surveys was approximately 10m wide and 14 m high when trawling at a headrope depth of 20 m (Nishimoto and Washburn 2002). The
depth interval for each haul was estimated as the distance from the mean depth of the headrope (rope across the top of the net opening) to 14 m below \( d_0 \) (Table 1) where \( d_0 \) was measured with a pressure sensor mounted at the middle of the headrope. Vertical profiles of potential temperature \( T \) and salinity \( S \) (averaged into 1-m depth bins) were obtained either immediately before or after each haul to at least 200 m or a few meters above shallower bottom depths. Water masses where fish were sampled were defined by the profiles. Table 1 summarizes mean \( T \) and \( S \) within the trawling depth range at each sampling station.

Otoliths from 68 specimens of shortbelly rockfish sampled from the central and southern California collections were assayed using laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS) (Fig. 1, Table 1). The fish ranged from 12.8 mm to 47.2 mm SL. Shortbelly rockfish were the most abundant of the pelagic juvenile rockfishes collected in the survey. Fifty-seven specimens represent all areas defined by Nishimoto and Washburn (2002) where shortbelly rockfish were collected during 3-15 June 1998 in southern California (Fig. 1B, Table 1): 14 individuals from waters off Purisima Point located north of Point Conception (station numbers 11, 12, and 13), 9 from the western entrance of the Santa Barbara Channel (16, 17, 18), 21 from an eddy in the western Santa Barbara Channel defined by dynamic height \( \phi < 0.37 \) (at 5 dbar relative to a 200 dbar reference pressure) (Nishimoto and Washburn 2002; 7, 9, 14), 1 from the southwestern side of the eddy (8), 4 from the northeastern side of the eddy (10, 15), 5 from the east Channel (19, 20, 21), and 3 from Point Mugu at the eastern entrance of the channel (22, 23, 24). Eleven otolith samples from
central California were collected during 11-27 May 1998 from the Farallon Islands west of San Francisco to Cypress Point, Monterey (stations 1-6 in Fig. 1A and Table 1). The otoliths of one to four specimens per station were assayed (Table 1).

The otolith samples from the two surveys were handled somewhat differently. Specimens from the 1998 southern California survey were subsampled in 2000 from an ETOH-preserved archive, measured, and the sagittae extracted. The fish had been frozen at sea, and then thawed, identified, measured, and stored as separate hauls in undiluted, undenatured ETOH within several months after collection. The otoliths were rinsed in deionized water to remove visible organic matter, air dried in a covered plastic multiwelled tissue culturing tray, and stored in plastic bags for several months until the time when each otolith was affixed to a plastic slide using epoxy resin (Epo-Thin, Buehler). The fish collected in the central California survey were frozen at sea. Within several months, the specimens were thawed, measured, and the otoliths extracted. The central California otoliths were rinsed with tap water, dried and affixed to glass slides using a clear nail polish epoxy (Sally Hansen’s Hard-as-Nails brand).

All otoliths were polished down to about 15 µm above the center of otolith nucleus using a lapping wheel and 9, 3, and 1 µm 3M diamond polishing films. After polishing, decontamination steps described by Ruttenberg et al. (2005) and Warner et al. (2005) were performed in a clean laboratory. Polished otoliths were rinsed in ultra-pure water (N-pure, resistivity>18.1 MΩ) and soaked in a
15% semiconductor grade H₂O₂ buffered with Suprapur NaOH (0.05 N) for 30 minutes. Samples were sonicated in N-pure for 5 minutes and rinsed with N-pure. The sonification procedure was repeated three times. The otoliths were dried under a HEPA-filter class 100 laminar flow hood. Throughout the decontamination process, each individual otolith was isolated from other otoliths, and acid-leached plastic dishware and Teflon forceps were used to avoid trace element contamination.

Otolith material produced in recent days preceding capture was analyzed on a Finnigan MAT Element 2-sector field ICPMS as described in Warner et al. (2005) and Ruttenburg et al. (2005). A VG UV microprobe Nd:YAG (Neodymium-doped Yttrium Aluminum Garnet) 266 nm laser ablation system was outfitted with a helium aerosol carrier system to transfer the sample from the enclosed sample chamber to the ICPMS as described in Zacherl et al. (2003). The laser was used to ablate three sample spots in the same growth zone near the edge of the anterior rostrum of each otolith. A suite of seven element ratios: Sr/Ca, Ba/Ca, Pb/Ca, Mg/Ca, Mn/Ca, Fe/Ca, and Zn/Ca were measured from each of the three sampling spots. The Santa Barbara Channel otoliths were run in May 2002. The central California otoliths were run in September 2003.

The laser beam was directed as close to the edge of the sectioned otolith as possible, but care was taken to avoid epoxy that typically overlaid one or two outermost daily increments. Each ablation spot sampled otolith material from increments grown within one week preceding the time of collection. An imaging system was used to focus the laser on the surface of the otolith before...
sampling a targeted spot. For the southern California otoliths, the laser aperture was set to 1 µm which emitted a beam that ablated a pit diameter of about 20 µm. For the central California otoliths, the laser aperture was set to 2 µm which ablated a pit diameter of about 30 µm. The laser was set at 0.1 mJ at 3 Hz. Each targeted spot on the sectioned otolith was pre-ablated with two laser pulses as a precautionary cleaning measure. Two samples were collected at each spot to assay a suite of isotopes: Calcium 48 (\(^{48}\text{Ca}\)), Strontium 86 (\(^{86}\text{Sr}\)) Barium 138 (\(^{138}\text{Ba}\)) and Lead 208 (\(^{208}\text{Pb}\)) were determined by using low resolution mode (R=300); Magnesium 24 (\(^{24}\text{Mg}\)), Calcium 48 (\(^{48}\text{Ca}\)), Manganese 55 (\(^{55}\text{Mn}\)), Iron 56 (\(^{56}\text{Fe}\)), and Zinc 64 or Zn 66 (\(^{64}\text{Zn}\) for SBC samples and \(^{66}\text{Zn}\) for CC samples) were determined in medium resolution mode (R=4000). Eight laser pulses were emitted on the targeted spot to collect each sample. The isotope intensities of each sample were blank-corrected by subtracting isotope intensities of a 1% nitric acid (HNO\(_3\)) instrument blank preceding the sample sequence. The abundance of an element was expressed as a ratio relative to the amount of calcium to control for the amount of material analyzed per sample spot.

Average detection limits for each element per sequence (N=20 sequences), calculated as 3 x SD of the intensity of 1% HNO\(_3\) blanks and expressed as ratios of the isotope intensity and mean otolith Ca48 intensity, were 24 µmol/mol for Mg/Ca, 0.95 µmol/mol for Mn/Ca, 12.74 µmol/mol for Fe/Ca, 6.77 µmol/mol for Zn/Ca, 59 µmol/mol for Sr/Ca, 0.06 µmol/mol for Ba/Ca, 0.06 µmol/mol for Pb/Ca. We analyzed solid glass standard reference material (NIST 612) at the beginning and end of each workday to check instrument analytical precision or
repeatability; average percent relative standard deviation (N=10 workdays) were 21% for Mg/Ca, 13% for Mn/Ca, 26% for Fe/Ca, 37% for Zn/Ca, 39% for Sr/Ca, 10% for Ba/Ca, 10% for Pb/Ca.

We excluded negative blank-corrected intensity values from the sample spot dataset. This reduced the original dataset of three samples of seven isotopes per otolith to 0-3 samples of each isotope per otolith. The abundance of each element from the otolith edge was estimated from either a single sample spot or the mean of two or three sample spots after the molar ratio dataset was log-transformed (i.e., log[µmol element/mol Ca]). A specimen lacked an abundance estimate for a given element if the readings from all three sample spots at the otolith edge were excluded.

**Relating otolith chemistry to *in situ* water masses**

We examined the T-S distribution within the trawling depth ranges to resolve water mass groups. Principal component analysis (PCA) of T (15 1-m bin averaged variables, T _d=0, 1, 2, …, 14_) and S (15 variables, S _d=0, 1, 2, …, 14_) profile data over the depth interval of each haul was used to confirm the water mass groups. T and S values from each profile were normalized by subtracting the mean of all profiles and dividing by the standard deviation of all profiles. The PCA was run using PRIMER 6 software (Plymouth Routines In Multivariate Ecological Research, version 6).
Otoliths were assigned to the water mass groups by pairing hauls with vertical T-S profiles. Canonical discriminant function analysis (DFA) was used to test whether the elemental signature of otoliths identified water mass membership (SPSS Inc. 2002). Initially, the DFA was run stepwise to identify the elements that were the best discriminators of the water mass groupings. The stepwise DFA was run on a subset of otoliths with data for all seven elements. Otoliths with excluded data from all three sample spots for at least one of the seven elements were not included in the stepwise DFA. Next, we ran a DFA on an expanded subset of otoliths that had readings of the discriminating elements identified in the stepwise DFA regardless of whether other element abundances could be estimated. Thus, the second DFA accounted for more variance of the discriminating elements and permitted better testing of whether otolith chemistry identified water mass membership.

The classification accuracy of each DFA was evaluated by leave-one-out cross-validation, also called jack-knife reclassification (SPSS Inc. 2002, White and Ruttenberg 2007). The prior probabilities of group membership were assumed to be uniform. We used the randomization test of White and Ruttenberg (2007) to estimate the probability (p-value) that the observed jack-knife reclassification success rate was drawn from a null distribution of jack-knife values given no difference among groups of samples. This null distribution was generated from 5000 randomizations: for each randomization, otoliths were randomly assigned to water mass groups and the jack-knife reclassification success rate was estimated. The null expectation is that the
observed jack-knife reclassification success of otolith samples into assigned water mass groups is no better than that expected by chance.

To detect differences in the concentrations of particular elements among water masses, we performed one-way analysis of variance (ANOVA) to test for the effect of the water mass group on individual log-transformed element ratios in otoliths ($\alpha=0.05$) (SPSS, Inc. 2002). Although we would have preferred to use a nested ANOVA to account for within-group variability in individual elemental abundances due to station (i.e., water mass defined by the CTD cast data at an individual station) differences, the dataset was unsuitable because 10 of the 24 stations were represented by only one otolith, including all but one of the stations from central California. The Tukey’s honestly significant difference (HSD) test was used to detect a posteriori differences among means ($\alpha=0.05$).

We examined relationships between element abundances in the otolith and relationships between otolith elemental properties and T and S. We used the Pearson product-moment correlation coefficient, r, to determine whether otolith element abundances that were identified as the best discriminators of the water mass groupings co-varied (SPSS, Inc. 2002). We estimated the correlation between the average otolith element abundance at a station and the average T or S. If the correlation was significant, we used least squares regression to model the relationship between T or S, the environmental predictor, and otolith log[element/Ca], the dependent variable, by fitting a linear equation to the observed data (Systat Software Inc. 2006).
All ANOVA and regression analyses were performed on log-transformed otolith element ratio data. Prior to the analyses, we assessed the normality and homoscedadcity of the otolith data among water mass groups (SPSS, Inc. 2002). In addition to graphically evaluating observed and expected distributions, normality was tested using the Kolmogorov-Smirnov statistic with a Lilliefors significance level. We used the Constant Variance test to check that the variance of the dependent variable was constant regardless of the value of the independent variable. The Levene homogeneity of variance test was used to test for equal variances among groups.

We evaluated whether otolith element abundance was related to fish size. We estimated the correlation coefficient, \( r \), to determine the relationship between \( \log(\text{element/Ca}) \) and \( \log(\text{mm SL}) \). ANOVA was used to test for the effect of the water mass group on individual log-transformed body length (\( \alpha=0.05 \)) (SPSS, Inc. 2002). We performed the Tukey’s HSD test to detect \textit{a posteriori} differences among means (\( \alpha=0.05 \)).

**RESULTS**

**Water masses**

Based on the T-S observations, the assayed fish resided in a range of water masses across the study area (Fig. 3). We resolved four water mass groups: central California (CC), southern California (SC), uplifted deep water in the eddy (UE), and stratified shallow and deep water in the eddy (SE) (Fig. 3 and
Table 1). The CC samples (blue T-S curves) were cooler \((T<11.7^\circ C)\) than the SC water masses which were sampled outside of the eddy (green T-S curves). Both CC and SC water mass groups were less saline \((S<33.70\) psu) than the three water mass samples (stations 7 and 8, black curves; station 14, red curves) within the eddy in the Santa Barbara Channel defined by dynamic height \(\phi <0.37\) (Fig. 1B, Nishimoto and Washburn 2002) and one station at the southwestern boundary of the eddy (station 9, red curve).

The two water mass samples in the UE group (Fig. 3, black T-S curves, stations 7 and 8) have T and S properties within the trawling range of 19 m to 33 m that are consistent with deep water uplifted from 100 m within the eddy described by Nishimoto and Washburn 2002 (Fig. 2, \(T<11.7^\circ C\) and \(S>33.7\) psu). The water mass samples in the SE group (Fig. 3, red T-S curves, stations 9 and 14), share T-S properties of uplifted deep water (UE group) and the most saline SC samples found outside of the eddy within the Santa Barbara Channel (stations 10, 15, 19, 20).

The T-S properties of the central California samples are bounded by the characteristic T-S of two distinct end-members: San Francisco Bay Plume water (12.6, 32.85 psu, defined by Hurst and Bruland 2008) and subarctic water (mean temperature 10.6\(^\circ\) C, mean salinity 33.36 psu, defined by Warn-Varnas et al. 2007) transported by the equatorward California Current (Fig. 3). The intermediate T-S properties of our central California samples from waters 50 m and shallower (stations 2, 3, 5 and 6; \(d_0<36\) m) indicate advection and mixing of the two relatively fresh sources along the Central California coast. The two
deeper CC samples (stations 1 and 4; \(d_0=75 \text{ and } 77 \text{ m, respectively}\)) and UE group are different “deep” water masses; although similar in temperature, the two CC samples are less saline than the UE group.

PCA of the T-S profile data was consistent with the distribution of water masses (i.e., T-S curves in Fig 3). The first two principal components, PC1 and PC2, explained 97% of the variance among the water mass samples (data not shown). PC1 separated CC samples from the southern California samples (SC, UE, and SE). PC2 separated the eddy samples, UE and SE, from SC. PC 3, which explained 2% of the variance, separated SE from UE, SC, and CC.

**Relationships between otolith signatures and water masses**

The PCA run on a subset of 47 otoliths with all seven elements suggested that the distribution of the otolith signatures could be differentiated by the four water masses (Fig. 4). The first two principal components of the PCA explained 63% of the variance in elemental signatures among otoliths. Inspection of the plot suggested that fish residing in central California had otolith signatures that differed from that of fish in southern California, and that fish residing in the UE water mass were distinct from fish from the SC water mass (Fig 4). The separation of otolith signatures from CC and UE along PC1 are consistent with the lack of overlap in T and S properties of the water masses (Fig. 3). The lack of separation of otoliths from SE and SC (Fig. 4) is consistent with the intersection of the T-S properties of the two water masses for T>11.6\(^\circ\) C (Fig. 3).
The stepwise DFA identified three discriminating elements, Mg, Ba, and Fe, using 43 otoliths that had readings of all seven elements assigned to four water mass groups (data not shown). Cross-validation of the DF showed that 72% of the fish correctly grouped into the assigned water mass type based on the otolith signature of Mg/Ca, Ba/Ca, and Fe/Ca, significantly better than the reclassification success of 25.3% (SD=9.2%, upper 95% quartile of the null distribution=39.5%) expected by chance (p=0.0002). Four otoliths with extremely high abundances of one or more elements were excluded from the stepwise DFA. The PCA run on the seven-element otolith signature revealed the four outliers: two otoliths from the cold core of the eddy were outliers along PC1 (Fig. 4, PC1>1) because of extremely high values of Mg/Ca, Mn/Ca, and Zn/Ca; one otolith from northeast of the eddy was an outlier along PC2 (Fig. 4, PC2>1) because of very high Fe/Ca, Zn/Ca, and Pb/Ca; and one otolith from Purisima Point was an outlier along PC3 (data not shown) because of extremely low Mn/Ca.

We accounted for a greater amount of variance of the three discriminating elements by running a second DFA on 61 otoliths that had readings of Mg, Ba, and Fe, regardless of whether other element abundances could be estimated (Fig. 5). The four outliers that were excluded from the stepwise DFA were included. Cross-validation showed that 69% of the otoliths correctly grouped into one of the four assigned water mass types (Table 2), significantly better than 25.6% (SD=8.3% upper 95% quartile of the null distribution=39.3%) expected by chance (p=0.0002). The 3-element signature, Mg/Ca, Ba/Ca, and Fe/Ca,
correctly grouped 100% of the otoliths collected in CC, and 8 of 9 otoliths collected in UE corresponding with the distinct T-S properties of the two water masses. The 3-element signature poorly discriminated the residency of fish collected in SC and SE; however, none of the otoliths from these two groups were misclassified as CC otoliths. Fifty percent of the otoliths from SE were incorrectly reassigned to UE (3 of 12 otoliths) and SC (3 of 12 otoliths). The lack of a distinctive SE otolith signature and the similarity of otolith signatures of fish collected from SE to otolith signatures from UE and SC (Fig. 5) are consistent with the mixed water mass properties of SE (Fig. 3).

The strength in discriminating otoliths from the different water masses was associated with trends of decreasing otolith Ba and increasing otolith Mg with increasing S. Ba/Ca in the otoliths was negatively correlated with S (r = -0.77, P < 0.01, N=23), and the regression explained 60% of the variance in Ba/Ca (Fig. 6D). Ba concentration in the otoliths from the CC water mass was significantly higher than in otoliths from UE, SE, and SC water masses (P<0.001) (Fig. 7A; Table 3). The UE otoliths did not differ from SE and SC otoliths. In contrast, Mg/Ca was highest in otoliths from UE (P<0.001), and lowest in otoliths from CC (P<0.016) (Fig. 7B; Table 3). Mg concentration was significantly correlated with S (r = 0.49, P = 0.02, N=23), although the regression explained only 25% of the variance in Mg/Ca (Fig. 6E).

Mg and Ba concentrations in otoliths from UE and SE differed from those in otoliths from CC despite similar T between 10 and 12 C (Fig 6A and 6B). Mg/Ca was not significantly correlated with T (r = -0.13, P = 0.57, N=23).
Ba/Ca was negatively correlated with T (r = -0.45, P = 0.03, N=23); however, T was a weak predictor of Ba/Ca in otoliths explaining only 21% of the variance (Fig. 6A).

Fe concentrations in otoliths from central California were significantly lower than those from the water masses of the Santa Barbara Channel region (P<0.003) (Fig. 7C; Table 3). Fe/Ca was correlated with S (r = 0.45, P = 0.03) and T (r = 0.50, P = 0.02, N=23); however, S and T were weak predictors of Fe/Ca with each explaining less than 25% of the variance (Fig. 6C, F). The estimated Fe concentrations of 22 otoliths from 11 stations, including all otoliths from central California, were below our calculated detection limit (Figs. 6, 7). Fe/Ca is typically excluded from otolith microchemistry analyses, because uncertainty in element abundance estimates is assumed to be high for signals below detection limits (Campana et al. 1999). Ben-Tzvi et al. (2007) found that LA-ICPMS element/Ca measurements that would be discarded as noise using conventional DL standards (e.g., 3xSD) often formed sequences that were symmetrical about the otolith core (palindrome), and argued that these sub-DL signals can contain valuable information.

Estimated otolith elemental ratios were highly variable among otoliths included in the analyses ranging 76.82-24,890.3 µmol/mol for Mg/Ca (n=61 otoliths); 0.01-11.16 µmol/mol for Mn/Ca (n=47); 1.55-283.86 µmol/mol for Fe/Ca (n=61); 1.58-318.09 µmol/mol for Zn/Ca (n=47); 1404.12-5202.73 µmol/mol for Sr/Ca (n=47); 0.34-2.60 µmol/mol for Ba/Ca (n=61); and 0.02-1.66 µmol/mol for Pb/Ca (n=47). The average otolith element/Ca per station,
based on using all laser spot samples with positive blank-corrected isotope intensity readings to estimate the element/Ca ratio for each otolith, is presented in Table 4.

There was evidence of weak covariation between the water mass-discriminating elements in otoliths. Mg/Ca and Fe/Ca were slightly correlated (n=61, R=0.263, p= 0.041; rho=0.220, P=0.021, Fig. 8). Ba/Ca was not correlated with Mg/Ca or Fe/Ca.

Otolith Mg/Ca (R=0.272, n=60, P=.036) and Ba/Ca (R= -0.288, n=60, P=0.026) were weakly correlated with standard length (Fig. 9). Fish were significantly larger in UE than in CC (Tukey HSD test, P=0.0469) and SC (Tukey HSD test, P=0.0095) (ANOVA, n=60, F=4.665, d. f.=3, P=0.006, Fig. 10).

The differences in Ba/Ca among water mass groups do not correspond with fish size differences among water mass groups. Ba concentration in the otoliths from CC was significantly higher than in otoliths from the three southern California water masses (Fig. 7A); however, size of fish from CC did not differ from SE and SC (Fig. 10). Ba in UE otoliths did not differ from SC otoliths (Fig. 7B) of fish that were significantly smaller than UE fish (Fig. 10).

In contrast, otolith Mg was somewhat related to fish size differences among water masses. Mg/Ca was highest in otoliths from UE (Fig. 7B) where fish were larger than fish from CC or SC (Fig. 10). Mg/Ca was lowest in otoliths from CC (Fig. 7B), but these fish were not the smallest among water masses (Fig. 10).
DISCUSSION

Otolith element/Ca ratios varied among the sampled water masses in the California Current System. Examining the variability in otolith chemistry in relation to temperature and salinity allowed us to not only distinguish fish from geographically distant regions with contrasting oceanographic conditions but also to discriminate fish that resided in different water mass environments that were associated with a local, physical phenomenon — cyclonic eddy circulation in the Santa Barbara Channel. We found that Ba, Mg, and Fe varied significantly among the distinguishable water masses that we sampled. Fish from central California had elevated otolith Ba/Ca compared with fish from southern California. In contrast, otolith Fe/Ca was elevated in fish from southern California compared to fish from central California. Otolith Mg/Ca was highest in fish collected from deep water uplifted to shallow depths by cyclonic eddy circulation in the Santa Barbara Channel and lowest in fish from central California. The 3-element signature correctly predicted the residency of nearly 90% of the fish collected in the cold core of the eddy in the Santa Barbara Channel and separated 100% of the fish collected in the Channel region from fish collected from Central California. Two of the three elements, Ba/Ca and Mg/Ca, have been useful for distinguishing fish from different coastal and oceanic locations of other studies.

We found that otolith Ba/Ca was negatively correlated with salinity of the water mass occupied by the wild-caught fish. We did not measure elemental
concentrations in water mass samples; however, we surmise that ambient Ba/Ca was negatively associated with salinity and that otolith Ba/Ca reflected the availability of Ba/Ca. Laboratory and field studies have determined that otolith Ba/Ca correlates with ambient Ba/Ca (Bath et al. 2000, Elsdon and Gillanders 2003, Elsdon and Gillanders 2005b). Compared to the influence of ambient Ba/Ca, the effect of ambient temperature and salinity on otolith Ba/Ca has been shown to be minimal (Bath et al. 2000, Elsdon and Gillanders 2004, 2005b). Elsdon and Gillanders (2005a) attributed the inverse relationship between otolith Ba/Ca of black bream and ambient salinity in estuarine and coastal environments of southern Australia to the input of Ba from fluvial sediments in freshwater runoff. In the Southern California Bight, ambient Ba/Ca in estuarine waters (about 6 µmol/mol) were higher than coastal waters (about 3 to 5 µmol/mol) in several studies that were not conducted during our survey year (Forrester 2005, Warner et al. 2005, Lloyd et al. 2008). In a three-year study off central California, Brown (2006) found that whole otolith Ba/Ca of two flatfish species along central California was highest in 1998 (the year of our collections) and lowest in 1999, in correspondence with runoff levels.

River runoff is the major source of Ba to coastal waters (Chan et al. 1977) and may have contributed substantially to the Ba load off Central California during our study. Increased precipitation in California and coastal runoff are frequently associated with strong El Niño events, and the winter of 1997–1998, when an exceptionally strong El Niño was fully developed, was one of the wettest seasons on record. The impact of sediment and freshwater transport in
nearshore waters from coastal watersheds was spatially extensive in satellite imagery during the winter and spring of 1998 (Mertes and Warrick 2001). Oceanographic surveying with the collection of the central California specimens indicate that outflow from the San Francisco Bay, draining the largest watershed of California, generated a markedly low salinity signal that extended 100 km down the central California coast to Monterey Bay (Sakuma et al. 1999). High turbidity and elevated nutrient levels were correlated with low salinity in Monterey Bay providing evidence that low salinity in the upper 15-20 m was the result of local and remote runoff and river outflow in 1998 (Friederich et al. 2002). The concentrations of some trace elements (e.g., Cu and Cd; Ba was not among the elements measured) have been found to be higher in the San Francisco Bay plume than in coastal and upwelled waters (Hurst and Bruland 2008).

Elevated Ba/Ca in otoliths and invertebrate hard parts has been associated with upwelling (Lea et al. 1989, Patterson et al. 1999, Zacherl 2005, Brown 2006) and deep water (Zumholz et al. 2007). Dissolved Ba in oceanic waters shows a nutrient-like distribution with very low concentrations in surface waters and higher values in deep water (Chan et al. 1977). In the Santa Barbara Channel, upwelling within the cyclonic eddy is a mechanism that can draw up nutrient-rich waters from below the thermocline into shallower depths where the juvenile fish were sampled; however, otolith Ba/Ca within the cyclonic eddy was not significantly higher than that outside of the eddy (Fig. 7). Bograd and Lynn (2001) regarded the depth of the 12°C isotherm a reliable proxy for the
nutricline depth in the Southern California Bight and Santa Barbara Channel. Figure 3 suggests that the nutricline was uplifted within the core of the eddy; however, it is plausible that variation in ambient Ba did not significantly affect otolith Ba among the three water masses in southern California. Warner et al. (2005) found no correspondence between the concentrations of Ba in seawater and Ba in otoliths of adult or embryonic larval kelp rockfish (*Sebastes atrovirens*) from nearshore reefs within our study region.

An alternate, plausible mechanism that would limit otolith Ba/Ca in the fish from the core of the eddy is localized Ba depletion from rapid plankton production in the euphotic zone where the fish were residing. Lochte and Pfannkuche (1987) observed nutrient depletion in the upper 50 m within the center of a cyclonic eddy. They proposed that the physical isolation of eddy surface waters due to the formation of a shallow thermocline lead to rapid utilization of nutrients. Off the Baja California coast, the waning stages of an upwelling-induced phytoplankton bloom were associated with Ba depletion in surface waters (Esser and Volpe 2002). The relationship between Ba removal from surface seawater, uptake by different organisms, and biological productivity are poorly understood and beyond the scope of this discussion.

In contrast to otolith Ba/Ca, Mg/Ca was lowest in otoliths of fish from central California, where the waters were freshest in our study area, and highest in otoliths of fish residing in the core of the eddy, where waters were the most saline. Unlike Ba which has a nutrient-like vertical distribution in the ocean, Mg, like Ca, has generally a conservative distribution and is present at relatively
high concentration levels in constant proportion to salinity (Nozaki 1997). Ratios of conservative elements, Mg/Ca for example, are not expected to vary significantly in seawater (Lea et al. 1999). Rivers contribute Mg to coastal areas (Tipper et al. 2006); however, it is likely that the input of Mg from freshwater runoff would be swamped out by the concentration of Mg in seawater, which is about 5 times higher than Ca in seawater. Significant differences in ambient Mg/Ca among the water masses we sampled seem unlikely, so variation in otolith Mg/Ca probably is due to other factors.

A large body of studies shows that Mg/Ca is useful for discriminating fish from different open coastal and oceanic locations exposed to water masses. For example, in nearshore coastal waters along Washington and Oregon, Miller and Shanks (2004) found that Mg/Ca was the most important discriminator among a suite of elements for assigning juvenile rockfish to their collection locations. Mg is one of the most important elements in otoliths separating fish from deepwater areas. Swan et al. (2006) found that Mg along with Pb were important for differentiating deep water fish stocks of the European hake, *Merluccius merluccius*, in the northeastern Atlantic. The otolith chemistry results were consistent with the treatment of a northern stock west of Norway and a southern stock off Portugal that were separated by an oceanographic and bathymetric feature, the Bay of Biscay. Ashford et al. (2005) used Mg along with Ba, Mn, and Sr in otoliths of deep-water Patagonian toothfish to successfully distinguish fish collected off South America from fish collected
south of the subantarctic front in the Atlantic, Indian, and Pacific regions of the Southern Ocean.

The effects of ambient Mg/Ca on otolith Mg/Ca and the effects of salinity and temperature on Mg uptake are unclear. We found that otolith Mg/Ca was weakly correlated with S and not related to T. Most of the experimental studies have found no effect of salinity on otolith Mg/Ca (Fowler et al. 1995b, Hoff and Fuiman 1995, Martin and Thorrold 2005). Fowler et al. (1995a) found that Mg and Ca were more abundant in the whole otoliths of fish in low-temperature treatments. In contrast, in experimental manipulations of salinity and temperature, Martin and Thorrold (2005) observed that the uptake rate of Mg in otoliths increased with increasing temperature (although the relationship was not statistically significant) while ambient Mg/Ca did not vary among the treatments. With exception of Martin and Thorrold (2005), the limitation of most of the experimental studies was that dilution of a single natural water mass or artificial seawater was used to manipulate salinity, and neither ambient Mg/Ca nor the effect of dilution on ambient Mg/Ca were measured in the majority of studies. The effect of ambient Mg/Ca on otolith Mg/Ca and possible interactions with ambient temperature and salinity is yet to be rigorously tested.

It is arguable whether ambient Mg/Ca actually has an effect on otolith Mg/Ca, because Mg is under strict osmoregulatory control (Campana 1999). Elsdon and Gillanders (2002) found that Mg/Ca showed little or no effects due to temperature or salinity and varied considerably among individuals within temperature and salinity treatments. Endogenous controls would vary among
individuals due to genetics, ontogeny, condition, metabolism, and somatic growth. We found that otolith Mg was somewhat related to fish size differences among water masses. Mg/Ca was highest in otoliths from UE where fish were larger than fish from CC or SC; however, Mg/Ca was lowest in otoliths from CC where fish were not the smallest among water masses. Ontogenetic differences may account for some of the variance in Mg/Ca observed among water masses. Fowler et al (1995ab) found that Mg in whole otoliths varied with ontogeny. Martin and Thorrold (2005) showed that uptake rate of Mg in otoliths and otolith Mg/Ca was related to otolith precipitation and somatic growth, which is often highly correlated with temperature in the field. If endogenous control of otolith Mg/Ca is not measurably mediated by ambient Mg, temperature, and/or salinity from the environment, then otolith Mg/Ca may not be a reliable indicator of water mass residency, but rather a useful discriminator for the separation of populations that have unique physiological traits mediated by genetics, growth, and condition.

It is tempting to speculate that otolith Mg/Ca was a good discriminator of the fish residing in the different water masses that we sampled, because the population of young-of-year fish within each water mass possessed unique intrinsic characteristics. Oceanographic processes that determined circulation patterns along with behaviors such as swimming capability, temperature or depth preferences, and schooling may have contributed to the isolation of these pelagic juvenile fish populations.
CONCLUSIONS

We found that otolith chemistry was a good predictor of water mass residency. The chemistry of the most recent growth zone in the otolith not only differentiated fish collected in different water masses from distant geographic areas spanning nearly 500 km within the California Current System, but also discriminated fish that resided in different water mass environments that were associated with mesoscale cyclonic eddy circulation. Variability in otolith chemistry reflected the spatial patterns of both horizontal gradients and vertical gradients in water mass properties related to circulation.

Neither ambient temperature nor salinity must necessarily relate to otolith chemistry in order to be useful for discriminating fish from different water masses; rather, we suggest that temperature and salinity are useful as identifiers of distinct water masses that are associated with unique otolith elemental signature in the residing fish. We found it sufficient to use only temperature and salinity to discriminate among water masses; however, utilizing other parameters such as $O_2$ and nutrients (often measured in oceanographic surveys) will likely improve our ability to identify water masses and refine future investigations of this kind. If shown to be reliable (i.e., temporally consistent), then the development of a reference or atlas of water mass-specific otolith elemental signatures is promising. Potentially, the use of an atlas of water mass-specific otolith signatures with water mass monitoring and current mapping could greatly reduce the uncertainty surrounding reconstructions of larval and adult
movements and connectivity estimates among locations such as spawning and
nursery areas and marine reserves.

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for the Interdisciplinary Study of Coastal Oceans funded by the David and
Lucile Packard Foundation. We thank Dr. David Lea for providing the ICPMS
laboratory and resources for otolith microchemistry. We thank G. Paradis and
M. Sheehy for guidance and assistance with otolith microchemistry and LA-
ICPMS procedures. We thank K. Sakuma for otolith samples and the catch and
oceanographic data from NOAA’s central California surveys (NMFS/SWFSC,
Santa Cruz, CA). Funding for the southern California trawling survey was
provided by the Biological Resources Division of the U.S. Geological Survey
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Reef Enhancement Program provided additional support. The California
Department of Fish and Game provided the midwater trawl net. We thank F.
Donahue, captain of the F/V 'Gus-D', for skillful vessel operation during the
trawling survey in southern California and many others for their assistance in the
field and laboratory. We thank E. Cheng and A. Muto for their work in the
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Table 1. Station number, survey date, net headrope depth $d_0$ (m), average potential temperature $T$ ($^\circ$C) and salinity $S$ (psu) of the trawling depth range $d_0$ to $d_0+14$m, and the number of otoliths sampled by LA-ICPMS.

<table>
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<th>$T$</th>
<th>$S$</th>
<th>N</th>
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<td>33.57</td>
<td>1</td>
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<td>30</td>
<td>11.52</td>
<td>33.09</td>
<td>3</td>
</tr>
<tr>
<td>3</td>
<td>5/15/98</td>
<td>36</td>
<td>11.16</td>
<td>33.32</td>
<td>1</td>
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<tr>
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<td>33.47</td>
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<td>33.76</td>
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<td>33.72</td>
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<td>13.43</td>
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<td>21</td>
<td>12.92</td>
<td>33.44</td>
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Table 2. Cross-validated classification of otoliths (N=61) into the four water mass groups using Mg, Ba, and Fe in the canonical discriminant function.

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<th>SE</th>
<th>UE</th>
<th>SC</th>
<th>Total</th>
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<td>0</td>
<td>0</td>
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<td>0</td>
<td>9</td>
</tr>
<tr>
<td>SC</td>
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<td>12</td>
<td>0</td>
<td>22</td>
<td>34</td>
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Table 3. ANOVA test of the effect of water mass group on element ratios in otoliths.

<table>
<thead>
<tr>
<th>Element Concentration</th>
<th>Source of Variation</th>
<th>Sum of Squares</th>
<th>DF</th>
<th>Mean Square</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
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<td>log[Ba/Ca]</td>
<td>Groups</td>
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<td>3</td>
<td>0.39</td>
<td>13.39</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>1.66</td>
<td>57</td>
<td>0.03</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>2.84</td>
<td>60</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>log[Mg/Ca]</td>
<td>Groups</td>
<td>12.82</td>
<td>3</td>
<td>4.27</td>
<td>42.98</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>5.67</td>
<td>57</td>
<td>0.10</td>
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<tr>
<td></td>
<td>Total</td>
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<td></td>
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<td>log[Fe/Ca]</td>
<td>Groups</td>
<td>3.09</td>
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<td>1.03</td>
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<tr>
<td></td>
<td>Error</td>
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<td>57</td>
<td>0.11</td>
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<td>Total</td>
<td>9.11</td>
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</table>
Table 4. Station number, water mass group, average fish standard length ± SD mm SL (N specimens), and average element/Ca ± SD umol/mol (N otoliths with positive blank-corrected intensity readings for one to three sample spots) of Mg, Mn, Fe, Zn, Sr, Ba, and Pb.

<table>
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<tr>
<th>Station</th>
<th>Group</th>
<th>SL</th>
<th>[Mg/Ca]</th>
<th>[Mn/Ca]</th>
<th>[Fe/Ca]</th>
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<td>8.39(1)</td>
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<td>5.28 ± 5.28(2)</td>
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<td>2.03(1)</td>
<td>6.25(1)</td>
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<td>4.06(1)</td>
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<td>153(1)</td>
<td>0.73(1)</td>
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<td>1121 ± 1928(4)</td>
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<td>3.76(1)</td>
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<tr>
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<td>23.20 ± 14.12(8)</td>
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Figure 1. The study area. Midwater trawling and oceanographic surveys in late spring 1998 were conducted off (A) central California and (B) southern California. The central California specimens and temperature-salinity profiles were collected 11-27 May 1998 from stations numbered 1-6. The southern California specimens and profiles were collected 3-15 June 1998 at stations 7-24. The eddy (shaded gray area) in the western Santa Barbara Channel was defined by station dynamic height $\phi < 0.37$ (5 dbar/200 dbar) (Nishimoto and Washburn 2002). The closed circles mark stations where shortbelly rockfish were absent or no otoliths were sampled.
Figure 1 continued.
Figure 2. East-west vertical sections of: (A) potential temperature, $T^\circ C$, and (B) salinity, $S$ psu, along the section indicated by the line in Fig. 1. Vertical dotted lines in (A) indicate T-S profile locations. The cyclonic flow of the eddy produced the large uplift of isotherms and isohalines. Two horizontal dashed lines bound the 14-m trawling stratum. The average depth for all hauls in the Santa Barbara Channel survey was 20 m. Oceanographic details in Nishimoto and Washburn (2002).
Figure 3. Relationship of T-S profile data from the 14-m trawling stratum at stations where otoliths were sampled. The water mass samples were assigned to four groups: central California, CC, blue; uplifted deep water in the eddy, UE, black; stratified warm and cool water mass in the eddy, SE, red; southern California, SC, green. The water mass groups are separated by grey horizontal and vertical reference lines at 11.7°C and 33.7 psu. Each T-S plot is labeled with a station number (see Fig. 1). Markers, P and S, in the plot are reference T-S of San Francisco Bay Plume water (12.6, 32.85 psu, defined by Hurst and Bruland 2008) and subarctic water (10.6°C, 33.36 psu, defined by Warn-Varnas et al. 2007), respectively.
Figure 3 continued.
Figure 4. Principal components analysis for a subset of 47 otoliths using Mg, Mn, Fe, Zn, Sr, Ba, and Pb. Colors indicate the water mass groups from where otoliths were sampled as in Fig 3. Each otolith sample is labeled with a station number (see Fig. 1).
Figure 5. Canonical Discriminant Analysis (CDA) of 61 otoliths using Mg, Ba, and Fe. Colors indicate water mass groups from where otoliths were sampled as in Fig 3.
Figure 6. Least squares regression, \( y = (a \pm 95\% \text{ CI})x + (b \pm 95\% \text{ CI}) \), fit to the mean log otolith concentration of Ba, Mg, and Fe (Xs in plots A-E) v T (plots A, C, E) and S (plots B, D, F) at each station (n=23). Gray dashed lines are 95% confidence bands. The closed circles are log[element/Ca] per otolith color-coded to indicate the water masses from where otoliths were sampled as in Figure 3. The detection limit for Fe, the dotted horizontal line in plots C and F, was within the range of otolith Fe concentrations.
Figure 6.

A

\[ y = (-0.85 \pm 0.32)x + (28.47 \pm 10.61) \]

\[ r^2 = 0.60, P < 0.001 \]

B

Temperature (mean C, z+14m)

C

Temperature (mean C, z+14m)

D

Salinity (mean PSU, z+14m)

E

Salinity (mean PSU, z+14m)

F

Salinity (mean PSU, z+14m)
Figure 7. Average (A) Ba, (B) Mg (C) Fe (µmol element/mol Ca ± 1 SE) at edge of otoliths collected from the four water masses: CC, UE, SE, and SC (see Fig. 3 for definition of abbreviations). Total number of otoliths= 61 used in the CDA. The detection limit for Fe, the dotted horizontal line in plots C and F, was within the range of otolith Fe concentrations.
Figure 8. Otolith Mg v otolith Fe. Statistically significant but weak correlation between Log[Mg/Ca] and log[Fe/Ca]. Total number of otoliths= 61 used in the CDA. Circles are element/Ca (µmol/mol) per otolith color-coded to indicate the water mass designation as in Figure 3.
Figure 9. Otolith element concentration vs body length. Log(standard length, SL) was significantly but weakly correlated with (A) Log [Mg/Ca] and (B) log [Ba/Ca]. Circles are element/Ca (µmol/mol) per otolith color-coded to indicate the water mass designation as in Figure 3.
Figure 10. Average body length of fish (mm SL ± 1 SE) from the four water masses: CC, UE, SE, and SC (see Fig. 3 for definition of abbreviations).
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III. Timing of fish settlement coincides with water mass advection
into the Santa Barbara Channel, California, USA

Mary M. Nishimoto\textsuperscript{1,2}, Libe Washburn\textsuperscript{3,4}, Milton S. Love\textsuperscript{1}, Donna M. Schroeder\textsuperscript{5}, and Brian Emery\textsuperscript{1}

\textsuperscript{1}Marine Science Institute
\textsuperscript{2}Interdepartmental Graduate Program in Marine Science
\textsuperscript{3}Department of Geography
\textsuperscript{4}Institute for Computational Earth System Science
\textsuperscript{5}Minerals Management Service, Pacific OCS Region, University of California, Santa Barbara, 93106

770 Paseo Camarillo, Camarillo, CA 99010

The study presented in this chapter is included in the report:
ABSTRACT

Recent pathways taken by pelagic juvenile fishes to settlement habitat, oil and gas production platforms, in the eastern Santa Barbara Channel, California, USA, were reconstructed from water mass dynamics and ocean current variability observed during settlement of recruits. Onset of the recruitment season for juvenile rockfishes (genus *Sebastes*, Scorpaenidae) at the platforms coincided with the advection of a low salinity water mass into the Channel from the Southern California Bight. Before arrival of this water mass, water at the platforms resembled upwelled water around the Point Conception region at the western channel entrance. Settlement pulses of rockfishes and blacksmith (*Chromis punctipinnis*, Pomacentridae) were observed during advective events when salinity decreased in the upper 40 m and currents turned northwestward or intensified in that direction. Two abundant rockfish species (bocaccio (*Sebastes paucispinis*) and treefish (*Sebastes serriceps*)) showed synchronous patterns of juvenile settlement between platforms separated by 7 km. Our findings indicate that currents from the Bight, rather than from Central California, supplied recruits to settlement habitat in the eastern Channel and that the spatial scale of connectivity for some fish populations in the eastern Santa Barbara Channel is greater than the Channel itself.
INTRODUCTION

A wide variety of marine organisms are distributed as sedentary adult or reproductive populations occupying spatially distinct habitats (e.g., islands, coastal reefs, estuaries and bays, deep sea vents). Many of these species have a planktonic phase in their early life histories (e.g., egg, larval, and juvenile stages) lasting for days or months. During this time, oceanographic mechanisms influence dispersal away from or retention near their natal populations. Recruitment dynamics, rather than some kind of regulatory process after settlement, may control local population dynamics, particularly for long-lived species that occur at low densities and only occasionally produce large year-classes (Warner & Chesson 1985, Doherty & Williams 1988, Caley et al. 1996, Pineda 2000). The degree to which a population receives recruits (defined herein as the young that have left a pelagic existence and have newly settled into demersal habitat) from other populations or local sources is a major unanswered question in ecology and resource management (Warner & Cowen 2002, Sale et al. 2005, Carr & Syms 2006). Linking recruitment to oceanographic variability is critical for predicting regional and local marine population responses to evolving ocean conditions such as those due to climate change.

Numerical modeling studies suggest that the distribution and transport of pre-recruits in the pelagic environment to suitable settlement areas control to some extent the spatial and temporal variability of recruitment (Roughgarden et al. 1988, Siegel et al. 2003, Cowen et al. 2006, Byers & Pringle 2006). Such studies have motivated empirical research focused on identifying the origin of

Observational studies have shed light on the potential oceanographic processes leading to settlement of recruits to populations residing on open coasts (e.g., Paris & Cowen 2004, Sotka et al. 2004). However, few have directly linked hydrographic conditions and regional circulation to pathways of recruits during their pelagic phase (e.g., Schmitt & Holbrook 2002, Roughan et al. 2005, Shanks 2006). Broitman et al. (2005) documented a gradient in recruitment of intertidal barnacles and mussels spanning a sea surface temperature gradient along Santa Cruz Island bordering the Santa Barbara Channel, CA, and surmised that the increase in larval recruitment at eastern sites of the island was associated with advective currents. In this study, we directly examined water mass dynamics and ocean current variability to reconstruct a portion of the pelagic history of recently settled juvenile fishes in the eastern Santa Barbara Channel—the probable pathways taken by the recruits during the days to weeks before settlement.

Fish surveys and oceanographic observations were carried out on two oil and gas production platforms (Fig. 1). Such structures are similar to seamounts where juvenile fishes commonly are abundant (Carr et al. 2003, Love et al. 2003); the platforms extend vertically through the water column and provide shallow water substrate in the offshore environment with the platform legs serving as structure leading to bottom habitat. Because habitat, created by the
platform structure and encrusting biota, is similar among platforms, the temporal
and spatial variability of the recruitment process can be examined without the
confounding effect of variable habitat complexity (e.g., low vs. high relief
substrate, presence vs. absence of kelp) that can be problematic in natural reef
studies (Pineda 2000, Carr & Syms 2006). Furthermore, shallow water currents
in offshore areas can be observed with minimal boundary effects, such as strong
vertical shear and near-bottom turbulence caused by interactions with
bathymetry that varies among nearshore areas (Shanks 2006).

Juvenile fishes commonly observed at platforms are rockfishes (genus
Sebastes) and blacksmith (Chromis punctipinnis (Pomacentridae)) (Carr et al.
2003, Love et al. 2003). Recruitment of these taxa tends to be relatively higher
at platforms than at natural reefs in the Santa Barbara Channel and off Point
Conception. Rockfishes are the most abundant fishes at the 27 oil and gas
platforms off central and southern California. About 35 of 65 species of
rockfishes that live off the Pacific coast of North America dominate three
distinct assemblages found around platforms: the bottom, shell mound, and
midwater assemblages. A number of species of adult and subadult rockfishes
dominate the bottom and shell mound. The midwater assemblage is composed
almost entirely of juvenile fishes. Carr et al. (2003) found that the vertical
distribution of young-of-year fishes in the midwater varied among species. For
example, blacksmith juveniles, along with adults, occurred strictly in the upper
portion of the water column above depths where rockfishes settle. Juvenile
rockfish typically recruited shallower than depths occupied by adults of the same species.

Rockfishes and blacksmith have contrasting life histories. All rockfish species are viviparous, and many species are slow-growing and long-lived (Love et al. 2002). They mature relatively late to reproduce annually during the rest of their lifespans, and have extremely variable juvenile recruitment success (Laidig et al. 2007). Recruitment usually occurs after a 3-6 month pelagic phase when the juveniles are about 3-9 cm in length (Love et al. 2002). Most rockfishes settle at nearshore rocky reefs and platforms off California during May-July, although the timing for a particular species varies among years (Carr 1991, Love et al. 2003). Most species settle in relatively shallow water habitat and eventually move to the deeper habitats of adults (Love et al. 1991). In comparison, blacksmith are benthic spawners; males guard eggs and the larvae and juveniles are pelagic (Limbaugh 1955, Turner and Ebert 1962). Blacksmith are mature at about 14 cm TL and 2 years of age. Spawning occurs in rocky areas about 4 to 26 m deep in the summer, and 2 cm young-of-year typically are observed in the late-summer and fall. By June of the following year, the juveniles are 4-6 cm. Adult and juvenile blacksmith commonly school together (Carr et al. 2003).

Within a recruitment season, species composition and densities of juvenile fishes can vary tremendously among platforms and reefs separated by less than 10 km (Carr et al. 2003, Love et al. 2003, Love et al. 2005). We surmise that this spatial variability is influenced by the distribution of the pre-recruits among...
different water masses, and the advection of the pelagic juveniles to settlement areas by ocean current patterns. The specific objectives of this study were to: (1) describe the spatial and temporal variability of settlement of young-of-year fishes within a recruitment season at two offshore platforms in the eastern Santa Barbara Channel, (2) determine if the timing of recruitment is related to oceanographic variability, and (3) identify the transport pathway(s) that delivered recruits to settlement habitat.

MATERIALS AND METHODS

Fish surveys and oceanographic observations were carried out at two platforms, Gail and Gilda, in the eastern Santa Barbara Channel from 1 May through 30 August 2004 (Fig 1A). This period corresponds with the season of much of the fish recruitment in this area (Limbaugh 1955, Love et al. 2002). Gail (34° 10’N, 119° 25’W; 225 m depth) and Gilda (34° 10’N, 119° 25’W; 62 m depth), separated by 7 km, are in an area where ocean currents vary strongly over a scale of several days and where fronts and eddies are observed (Winant et al. 1999). Both platforms harbor high densities of young-of-year rockfishes (Love et al. 2003; Love et al. 2006).

Study area

The Santa Barbara Channel is a biogeographic transition zone for marine flora and fauna, separating the strong coastal upwelling regime extending from
Point Conception to Washington from the warmer subtropical waters of the Southern California Bight (Horn & Allen 1978, Horn et al. 2006, Lynn & Simpson 1987, Blanchette et al. 2006). The Southern California Bight is the region east of the Santa Rosa Ridge and includes the Santa Barbara Channel (Fig. 1B) (Bray et al. 1999). Circulation in the Channel, which we distinguish from the remaining Bight, is complex and variable where a number of distinct water masses of the California Current System converge (Hickey 1993, Harms & Winant 1998, Winant et al. 1999, Winant et al. 2003, Dever 2004, Nishimoto 2000). The circulation in the Channel consists primarily of a cyclonic flow that varies in strength through the year: It is strongest spring through fall and weakest or absent in winter. The cyclonic flow tends to drive westward flow along the northern boundary of the Channel and eastward flow along the Channel Islands, the southern boundary. Unidirectional flows toward the east or west occur mostly in the winter, but also intermittently throughout the year. Currents carry a diversity of larval and juvenile fish species into the Channel that can recruit to adult habitats (Moser and Watson 2006).

**Estimating the abundance of recently settled juvenile fishes**

Fish surveys were conducted at both platforms every 3-4 days to estimate the density and size distribution of species following the sampling design and protocols developed to assess fish populations at platforms (Love et al. 2003). Observers used scuba to survey three depths: 5 m at both platforms (herein
referred to as the shallow levels), cross members at 11 m at Gilda and 12 m at Gail (middle levels), and cross members at 26 m at Gilda and 31 m at Gail (deep levels). Scuba divers visually surveyed fishes along rectangular belt transects (2m width x 2m height) that coursed along the perimeter and crossed through the structure bounding a third of the area of the platform at each depth. Scuba divers identified, counted, and estimated the sizes of all fishes observed with the aid of a ruler on the data recording slate. Observers were trained to estimate the total length of fishes to the nearest centimeter. Our analysis focused on the most abundant young-of-year fishes observed.

The abundance of recently settled juvenile fish (herein referred to as recruits) for a given period and platform is defined as the increase in number of fish observed within 2-cm TL size classes from one survey to the next at a platform. For a given taxon, the number of recruits, $R_t$, per survey at time $t$, is

$$R_t = \sum_{i}^{m} (N_i(t) - N_i(t-1))$$

where $N_i$ is the number of fish observed in a 2-cm size class interval $i$, $s$ is the index identifying the upper limit of a size class (e.g., $s=4$ for 2-4cm TL, $s=6$ for 4-6 cm TL,…) and $m$ is the maximum size class index of the fish we defined to be recent settlers. If $(N_{it} - N_{it-1}) < 0$, then this difference is set equal to 0.

We used this approach to distinguish recently settled juveniles from individuals that may have settled during the previous survey. We devised this estimate because we observed a broad size distribution among individuals on the
first day of settlement at either platform, and we did not want to limit our approximation of recruits to a single size class of only small individuals. For example, the first settlement event of bocaccio was comprised of young-of-year 6-12 cm TL. Rockfishes grow about 0.2 to 0.3 mm day$^{-1}$ with the notable exception of bocaccio (0.72 mm day$^{-1}$) (Love et al. 1991). An individual bocaccio grows 1 cm in about two weeks; thus, it is a reasonable assumption that fish would remain in a given size class for the few days between observations and that an increase in abundance from one survey to the next was the arrival of new settlers. Mortality and emigration to deeper, unsurveyed portions of the platform are not factored into the estimate.

Two measures were used to determine the degree of synchrony in settlement patterns at the two platforms (SPSS for Windows, Release 11.5.0, 2002-2005). Kendall’s correlation coefficient, $\tau_b$, was used to measure the tendency of concordant changes (i.e., corresponding increases and decreases) in recruit abundance at the two platforms from one paired survey to the next. The value, $\tau_b$, ranges from 1 (perfect concordance or synchrony between the two platforms) to -1 (perfect discordance or negative correspondence). Cohen’s Kappa, $\kappa$, was used as a measure of agreement in the presence and absence of recruits between platforms. The value, $\kappa$, is the proportion of agreements after chance agreement has been excluded. If agreement between two nominal variables is at a chance level, then $\kappa = 0$; if there is perfect agreement, then $\kappa = 1$. The values, $\tau_b$ and $\kappa$, divided by the standard error are each roughly equivalent to a t-test.
Oceanographic observations

Various oceanographic data collected by us and others were examined to determine if patterns of settlement were related to ocean circulation. An ADCP (600 KHz Workhorse Sentinel by RD Instruments) and a moored conductivity, temperature, depth instrument (herein called a moored CTD; SBE37-SMP Microcat by Sea-Bird Electronics, Inc.) were mounted as a package to the southeast leg of each platform: Gilda at 23 m and Gail at 26 m depth. Scuba diving logistics limited the depth of the packages which were deployed a few meters above the deepest level surveyed at the platforms. Approximately every 4 weeks, the ADCP and moored CTD were retrieved to upload data, and the instruments were redeployed the following day. The ADCP logged vertical profiles of horizontal currents every 6 minutes, the moored CTD logged conductivity, temperature, and pressure every 3 minutes. The ADCP was upward-looking and tilted away from the platform to avoid physical interference by the structure. Processing of the ADCP data accounted for the tilt of the instrument. The depth range profiled was 17.2 - 24.9 m at Gail (19 bins) and 10.2 - 22 m at Gilda (29 bins). The bin interval was ~0.4 m in the vertical.

We used a SBE 19 CTD with pump (Sea-Bird Electronics, Inc.) to profile the water column within 100 m of the platform on survey dates starting on 10 June. Conductivity, temperature, and pressure were measured to at least 100 m at Gail and to about 60 m (2 meters from the bottom) at Gilda. CTD cast and moored
CTD data were processed for salinity and potential temperature using the software provided by the manufacturer.

Regional water mass data were obtained from a cruise during 13-28 July 2004 as part of the California Cooperative Oceanic Fisheries Investigations (http://www.calcofi.org/newhome/data/data_archives.htm). We used potential temperature and salinity data from the CalCOFI survey and descriptions of large-scale circulation patterns off Southern California (Bray et al. 1999) to define regional hydrographic signatures and to identify the source of the water masses that occupied the platform habitat during our study.

Hourly high-frequency (HF) radar surface current observations provided maps of the surface current field around the platforms and most of the Santa Barbara Channel. Currents in the upper ~1 m of the water column in the western Channel have been continuously mapped since 1998; however, mapping of the eastern Channel was initiated for this study with the addition of a radar site at Summerland, California (Fig. 1). Operational details and data processing for the HF radar array are discussed further by Emery et al. (2004).

The time series of surface current patterns from the HF radar and subsurface currents from the ADCP were used to interpret the near-field flow at the platforms. Time series data from the ADCP, moored CTD, and surface current mapping were low-pass filtered with a 1/36 hr\(^{-1}\) cutoff frequency to suppress tidal variations.
RESULTS

Time series of juvenile fish recruitment

Some synchrony in settlement occurred between platforms and among the four most commonly observed taxa of juvenile rockfishes (family Sebastidae): bocaccio (*Sebastes paucispinis*); treefish (*Sebastes serriceps*); the copper, kelp, gopher, black-and-yellow complex of rockfishes (*Sebastes caurinus, Sebastes atrovirens, Sebastes carnatus, Sebastes chrysomelas*) are grouped together because of the difficulty in distinguishing recently settled juveniles of the species; and squarespot rockfish (*Sebastes hopkinsi*). Time series of the number of fish observed (○) and the estimated number of recruits (*) per survey are shown for each taxon in Fig. 2A-F. Because the two platforms differed in size and the lengths of the survey transects at each depth differed between platforms, the number of fish per survey is not an estimate of absolute density (i.e., number of fish per m3) that is comparable between the platforms. However, the temporal pattern of abundance can be compared between platforms. All four rockfish taxa showed a settlement pulse within one week from 28 June to 6 July which we identify as the beginning of the rockfish recruitment season. After this time, settlement for all taxa continued for the rest of the study, herein called the recruitment period, as sequences of settlement pulses. Blacksmith, the most abundant non-rockfish species recruiting to the platform, had a settlement pattern that differed spatially and temporally from the rockfishes (Fig. 2G, H).
The timing of settlement was synchronized between the two platforms for at least two rockfish species. Bocaccio and treefish occurred at both Gail and Gilda and clearly exhibited two temporal patterns: the seasonality of recruitment and episodic pulses of settlement within the recruitment period (Fig. 2A-D). The abundances of the copper rockfish complex and squarespot rockfish were too low at Gail to make a comparison.

The bocaccio recruitment period began on or just before 1 July when hundreds of recruits, 10 cm TL or less, were found at Gail and Gilda (Fig. 2A, B). Before this date, relatively low levels of settlement occurred between 24 May and 21 June at Gail and on one occasion at Gilda, 1 June. The time series of recruit abundance at the two platforms were significantly correlated ($\tau_b=0.363$, SE=0.127, $t=2.843$, $\alpha=0.004$, N=31). Recruits were present during 24 surveys at Gail and 15 surveys at Gilda and occurred at both platforms on 14 occasions. The synchrony in the presence and absence of recruits at both platforms (20 of 31 surveys) exceeded chance expectations (chance agreement=15.2 surveys, $\kappa=0.303$, SE=0.139, $t=2.052$, $\alpha=0.040$, N=31). Nearly all juvenile bocaccio occurred at the deep levels: only one of 1046 juveniles counted at Gilda and 0.2% of 4851 juveniles counted at Gail occurred at the middle levels; no bocaccio were observed at the shallow level at either platform.

As with bocaccio, synchronous settlement patterns of treefish recruits, 10 cm TL or less, were observed at the platforms. Aside from an occasional sighting of a single recruit, the first pulse of recruits, occurred at Gail on 21 June (Fig. 2D). The first recruits at Gilda arrived on 28 June and coincided with a second pulse.
at Gail (Fig. 2C, D). The time series of recruit abundance at the two platforms were significantly correlated ($\tau_b = 0.596$, SE=0.106, t=5.438, $\alpha < 0.0005$, N=31). Recruits were present during 21 surveys at Gail and 16 surveys at Gilda and occurred at both platforms on 15 occasions. The synchrony in the presence and absence of recruits at both platforms (24 of 31 surveys) exceeded chance expectations (chance agreement=15.6 surveys, $\kappa=0.303$, SE=0.143, t=3.199, $\alpha=0.001$, N=31). All treefish were 14 cm TL or less; 94% at Gail and 99% at Gilda were 10 cm TL or less. Most of the juveniles, 10 cm or less, were counted at the two deeper levels: 7% and 92% of 500 juveniles were observed at the middle and deep levels, respectively, at Gail; 15% and 84% of 156 were observed at Gilda.

The copper rockfish complex and squarespot rockfish recruited in substantial numbers to Gilda (Figure 2E, F) but not at Gail where only three juveniles of the copper rockfish complex recruited during July and August and three juvenile squarespot rockfish recruited in late July (data not shown). Like bocaccio and treefish, recruitment of both taxa occurred primarily at the deep level. Of the 479 juveniles of the copper rockfish complex counted at Gilda (6 cm TL or less), 449 (94%) were counted at the deep level. Among the four rockfish taxa, squarespot rockfish tended to settle latest in the recruitment period, in late August. All squarespot rockfish at Gilda occurred at the deep level and ranged in size from 3 to 14 cm TL. Juveniles (10 cm TL or less) comprised 76% of these fish. While the first occurrence of juvenile squarespot rockfish was on 21
May, recruits were not observed again until 14 June followed by a pulse on 1 July.

Juvenile blacksmith (6cm TL or less) recruited to both platforms when the surveys started at the beginning of May (Fig. 2G, H) In contrast, rockfish recruits were absent until the second week in May. Blacksmith recruits were present during 16 surveys at Gail and 14 surveys at Gilda and occurred at both platforms on 9 occasions. Although there was some synchrony in the presence and absence of blacksmith recruits at both platforms (19 of 31 surveys), this did not exceed chance expectations (chance agreement=15.5 surveys, \( \kappa = 0.228 \), SE=0.173, \( t = 1.281 \), \( \alpha = 0.200 \), N=31). The settlement patterns of the recruits at the two platforms were not significantly correlated (\( \tau_b = 0.161 \), SE=0.162, \( t = 0.986 \), \( \alpha = 0.324 \), N=31). Unlike the juvenile rockfishes, blacksmith occurred in the upper water column: at Gail, 51% and 39% of all juvenile blacksmith occurred at the shallow and middle levels, respectively; while at Gilda, these values were 19% and 77%, respectively. Juveniles comprised 11% and adults (\( \geq 15 \) cm TL) comprised 50% of all blacksmith observed. Unlike rockfishes, juvenile blacksmith were not closely associated with the substrate and were typically observed schooling with adult blacksmith.

**Water mass advection and juvenile fish recruitment**

The juvenile rockfish recruitment period was preceded by the arrival of a low salinity water mass to the study area. Time series of salinity, measured near
the deep level at both platforms where most of the juvenile rockfishes settled, declined from 33.6 to less than 33.45 during 1-14 June (Fig. 3, black lines). The salinity from the CTD casts at the depth of the moored CTDs also exhibits this change (Fig. 3, solid circles). Time series of the vertical profiles of salinity and potential temperature from CTD casts (Fig. 4) show that the low salinity values were associated with a mid-depth water mass centered between 15 and 40 m from the surface. Advection of the low salinity water mass is evident in the salinity depth-time contours at both platforms during 10-17 June (Fig. 4A, B). At this time, rockfish recruits were absent, but blacksmith settled in substantial numbers at both platforms. The appearance of salinities less than 33.4 at both platforms around 27 June-7 July coincided with the beginning of the rockfish recruitment period and another settlement pulse of blacksmith.

During the recruitment period, water near the deep level where most juvenile rockfish settled resembled water from the inshore and offshore regions of the Southern California Bight (Fig. 1B, red and green stations) as shown by moored temperature and salinity (TS) from 23 m at Gilda (●) and 26 m at Gail (♦), and TS profiles, 0 to 100 m, from CalCOFI (red and green lines) (Fig. 5). Before the recruitment period, water properties (Fig. 5, Gilda (●), Gail (+)) resembled upwelled water characteristic of the Pt. Conception region at the western entrance of the Channel (Fig 1B, blue stations; Fig. 5, blue TS lines) and an offshore band extending southwestward from Point Conception along the Santa Rosa Ridge, the boundary of the Southern California Bight (Fig 1B, cyan stations; Fig. 5, cyan TS lines.) Time series of subsurface currents indicate that
the low salinity water mass advected into the Channel from the Bight when currents switched from generally SE to NW beginning around 15 June (Fig. 6). These currents had a westward component typically near 10 cm s$^{-1}$ with a maximum of about 20 cm s$^{-1}$; the northward component was somewhat weaker at both platforms.

The switch in surface current direction was part of an evolving large scale pattern (Fig. 7). The HF radar maps show strong eastward surface current flow throughout the offshore area of the eastern Channel on 10 June. The flow weakened and cyclonic flow was evident south of Gilda and Gail on 12 June. The surface currents turned predominately poleward by 14 June and the surface current flowed through the eastern entrance and through the gap between Santa Cruz Island and Anacapa Island from the Southern California Bight into the Channel. The surface currents continued westward along the isobaths of the mainland coast of the Channel.

Advective events corresponded with settlement pulses. Salinity decreased in the upper 40 m (Figs. 3 and 4) and currents turned northwestward or intensified in that direction (Fig. 6) on four occasions: 13-22 June, 26 June-6 July, 18-25 July, and 15-31 August. Settlement pulses of blacksmith were associated with all four events (Fig. 2). Copper-complex settlement peaked during the second event. Settlement pulses were observed among all taxa except squarespot rockfish during the third event. During the second week of August, currents turned strongly eastward in opposition to the westward flow that characterized the four events, salinity abruptly increased in the upper 40 m, and relatively few
recruits, aside from treefish, settled at the platforms. After westward currents resumed during the fourth event, salinity declined to the lowest values observed during the study, and all taxa settled at the platforms in relatively high numbers.

**DISCUSSION**

Some level of larval import from outside an area may be required to sustain local populations, and the importance of these remote subsidies versus local recruitment is expected to vary among biophysical systems (review by Sponaugle et al. 2002, Carr & Syms 2006). Shanks et al. (2003) show that dispersal distance typically increases with pelagic larval duration (PLD); coastal species with relatively long PLD (e.g., 30 days and greater) are expected to disperse on the scale of 100 km. Long-distance dispersers are more likely to subsidize remote sources than species with PLD on the order of several days. Cowen et al. (2006) cautions that dispersal distance can be substantially reduced by retention and used a biophysical model that resolved eddy circulation to show that typical larval dispersal distance were on the scale of 10 to 100 km for a variety of reef fish species in the Caribbean. We infer from our study that the scale of connectivity is at the upper end of this range for at least some rockfish species in the Santa Barbara Channel.

The water mass change preceding the recruitment period at the platforms was consistent with the seasonal transition from spring to summer oceanographic conditions in the Southern California Bight. Seasonal variations
have been observed on the regional scale of the Bight (Lynn & Simpson 1987, Bray et al. 1999) as well as in the Channel (Harms & Winant 1998, Otero & Siegel 2004). In the spring, equatorward flow predominates throughout the Bight at all depths to 500 m. We observed this flow as an eastward current at the platforms during the first portion of our study (Fig 6). Poleward (i.e., northwestward) alongshore flow develops in the summer and persists through the fall and winter throughout the Bight except for the western part of the Channel where cyclonic circulation predominates (Bray et al. 1999). The core of the poleward flow shoals through the late summer from about 100 m in July to the surface in early October. The low salinity water mass that delivered recruits to the platforms from the Bight, may have been associated with this phenomenon since the timing and flow direction are consistent.

Various lines of evidence suggest that populations from the Southern California Bight provide greater contributions than from Central California to some fish populations in the Santa Barbara Channel. Blacksmith, a subtropical nearshore species ranging from central Baja to Monterey Bay, is rare north of Point Conception (Love et al. 2005). Matala et al. (2004) found that bocaccio populations in the Channel were genetically indistinguishable from coastal populations in the Bight (Santa Monica Bay) and off Northern Baja California. Furthermore, these three coastal populations south of Point Conception formed a group that genetically differed from populations north of Point Conception and from Tanner Bank, an offshore ridge south of the Channel, that is in the path of the California Current. The genetic structure of some species of Pteropodus, a
subgenus of *Sebastes* that typically resides in shallower areas than adult bocaccio and includes the copper rockfish complex (Li et al. 2006), also are consistent with the division of central and southern California oceanographic regimes (e.g., grass rockfish (*Sebastes rastrelliger*), Buonaccorsi et al. 2004; brown rockfish (*Sebastes auriculatus*), Buonaccorsi et al. 2005; but see kelp rockfish, Gilbert-Horvath et al. 2006). Larval dispersal of nearshore and offshore species may be similarly affected by large-scale (100+ kilometers) currents.

The delivery of young fishes from coastal areas north of Point Conception into the Channel may be restricted by persistent upwelling at the headland that functions as a hydrographic barrier to dispersal along the coast. The mean current along the California coast is equatorward during spring and early summer when larvae and juveniles are in the pelagic environment. However, upwelling at Point Conception would advect larvae from central California offshore (Winant et al. 2003, Dever 2004). Real and simulated surface drifter trajectories starting off Point Conception indicate that transport in offshore waters is southward with advection into the Channel unlikely (Emery et al. 2006). Pelagic stages of nearshore demersal invertebrates and fishes, including larval and juvenile rockfishes, are rare in newly upwelled water (Nishimoto 2000, Wing et al. 1998).

Studies from other areas indicate that larval retention can affect local population abundance (e.g., Swearer et al. 1999, Jones et al. 2005). Because the fish species in our study have a long planktonic period, and we could not
reconstruct transport pathways from natal origin to juvenile settlement habitat, we cannot eliminate the possibility that larval sources from the channel contributed significantly to recruitment. However, our results indicate that most juvenile rockfish recruits were transported into the Channel by currents from the Bight. Previous circulation studies suggest short retention times within the Channel compared with the pelagic larval and juvenile duration of rockfishes and blacksmith. In general, the residence time for drifters in the Channel was on the order of one to three weeks; however, a third of the drifters released ran aground on the Channel mainland or islands (Dever et al. 1998, Winant et al 1999). During the spring and early summer, the drifters exited the Channel through the passes separating the islands. If larvae are dispersed (but see Fisher (2005) and Leis et al. (2006)) by the typical mean current speeds observed in the Channel of 0.2 m s$^{-1}$ (Dever et al 1998, Winant et al 2003), then they would move 100 km in 12 days, a scale comparable to the length of the Channel. Therefore, some combination of behavioral and physical mechanisms would have to operate throughout the pelagic phase to retain the recruits or return them to the Channel.

Eddies occur year-round throughout the Southern California Bight and in the Santa Barbara Channel (DiGiacomo & Holt 2001), and may be important in the connectivity scheme linking local and remote populations. Larvae can be carried away from a local population by coastal currents and subsequently entrained and mixed in eddies with larvae from other sources. Dispersal is extensive, as far as 400 km offshore, during December through April when
larval rockfish are abundant (Moser et al. 2000). However, 80% of the larvae occur within 100 km of the mainland or near offshore islands and shallow ridges of the Southern California Bight (Moser et al. 2000) where eddies occur frequently (DiGiacomo & Holt 2001). Taylor et al. (2004) found more early-stage larvae within eddies than outside eddies in the Bight. Nishimoto & Washburn (2002) observed much higher densities of pelagic juvenile rockfish in a persistent cyclonic eddy in the western Channel than in surrounding waters. In the present study, settlement was synchronous between the two platforms separated by 7 km and the rate of settlement typically increased and then decreased over two or three surveys. Based on recruitment pulses persisting 1-6 days and the transport of recruits in a current speed of 0.1 m s⁻¹ (8 km d⁻¹), we estimate that the patch size of pelagic juveniles is roughly 8-48 km. DiGiacomo & Holt (2001) observed that all eddy diameters in the Southern California Bight were less than 50 km and 50% ranged 5-20 km. The synchrony in settlement pulses at the two platforms separated by 7km may reflect the scale of patch size of the pre-settlers, a remnant effect of eddy retention during the pelagic early life history of the recruits. The likelihood of larvae dispersing from natal habitat and encountering eddies may be high for species such as rockfishes with their long planktonic durations; however, the degree to which recruits return to suitable habitat after retention in offshore eddies, and whether eddies substantially affect abundance in local populations are unknown (Sponaugle & Pinkard 2004).

Shanks and Eckert (2005) hypothesize that coastal fish species have evolved a long planktonic period in combination with other life history traits, particularly
the timing of spawning or the release of larvae, to exploit the spatial and
temporal variability of the oceanographic setting and improve the odds of
offspring returning to settle, “not necessarily near their parents, but in the
parental population.” An important consideration is the spatial scale of the
parent population in question. We argue that the scale of the parental
populations of the recruits observed in this study extend beyond the Santa
Barbara Channel. Our study provides empirical evidence that ocean circulation
directly influences recruitment: an advecting water mass from the Southern
California Bight supplied juvenile recruits to settlement habitat in the eastern
Santa Barbara Channel. We conclude that remote sources, particularly from the
Southern California Bight, subsidize local fish populations in the eastern Santa
Barbara Channel given the broad spatial scale of ocean currents over the course
of the pelagic early life history of species.

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Figure 1. Bathymetric maps of the Santa Barbara Channel and the Southern California Bight with CalCOFI water mass reference areas. (A) The Channel: triangles show high frequency radar locations; squares show locations of oil and gas production platforms; Platforms Gail and Gilda, the study sites, are circled. (B) Six water mass regions of geographically distinct locations (see inset color code) are designated in the standard station grid (partially mapped) of triennial CalCOFI surveys. Water mass data (potential temperature and salinity (TS) from 0-100 m) from the six areas were used as references to identify the sources of water masses observed at the platforms (see Fig. 5).
Figure 1 continued.
Figure 2. Number of fish observed (○) and the estimated number of recruits (*) per survey from 3 May through 31 August, 2004, of bocaccio rockfish (size range denoted) at (A) Platform Gail and (B) Platform Gilda; treefish rockfish at (C) Platform Gail and (D) Platform Gilda; (E) copper-complex rockfishes from Platform Gilda; (F) squarespot rockfish at Platform Gilda; and blacksmith at (G) Platform Gail and (H) Platform Gilda. Four periods when salinity decreased in the upper 40 m and currents turned northwestward (NW above blocks) or intensified in that direction are blocked in the time series. A period in the second week of August is blocked when salinity increased and currents turned eastward (E). Blocks designate these five time periods in Figs. 3, 4, and 6.
<table>
<thead>
<tr>
<th>Number per survey</th>
<th>Date, 2004</th>
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<tbody>
<tr>
<td><strong>A)</strong> Gail: Bocaccio (&lt;10cm TL)</td>
<td>NW NW NW E NW</td>
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<tr>
<td><strong>B)</strong> Gilda: Bocaccio (&lt;10cm TL)</td>
<td>05/02 05/09 05/16 05/23 05/30 06/06 06/13 06/20 06/27 07/04 07/11 07/18 07/25 08/01 08/08 08/15 08/22 08/29 09/05</td>
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<td><strong>C)</strong> Gail: Treefish (&lt;10cm TL)</td>
<td>05/02 05/09 05/16 05/23 05/30 06/06 06/13 06/20 06/27 07/04 07/11 07/18 07/25 08/01 08/08 08/15 08/22 08/29 09/05</td>
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<td><strong>D)</strong> Gilda: Treefish (&lt;10cm TL)</td>
<td>05/02 05/09 05/16 05/23 05/30 06/06 06/13 06/20 06/27 07/04 07/11 07/18 07/25 08/01 08/08 08/15 08/22 08/29 09/05</td>
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<tr>
<td><strong>E)</strong> Gilda: Copper complex (&lt;6 cm TL)</td>
<td>05/02 05/09 05/16 05/23 05/30 06/06 06/13 06/20 06/27 07/04 07/11 07/18 07/25 08/01 08/08 08/15 08/22 08/29 09/05</td>
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<tr>
<td><strong>F)</strong> Gilda: Squarespot rockfish (&lt;10cm TL)</td>
<td>05/02 05/09 05/16 05/23 05/30 06/06 06/13 06/20 06/27 07/04 07/11 07/18 07/25 08/01 08/08 08/15 08/22 08/29 09/05</td>
</tr>
<tr>
<td><strong>G)</strong> Gail: Blacksmith (&lt;6 cm TL)</td>
<td>05/02 05/09 05/16 05/23 05/30 06/06 06/13 06/20 06/27 07/04 07/11 07/18 07/25 08/01 08/08 08/15 08/22 08/29 09/05</td>
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<tr>
<td><strong>H)</strong> Gilda: Blacksmith (&lt;6 cm TL)</td>
<td>05/02 05/09 05/16 05/23 05/30 06/06 06/13 06/20 06/27 07/04 07/11 07/18 07/25 08/01 08/08 08/15 08/22 08/29 09/05</td>
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Figure 3. 36-hour filtered time series of salinity (black line) from a moored CTD deployed at (A) 26 m depth at Platform Gail and (B) 23 m depth at Platform Gilda. Closed circles are salinity from the CTD casts at the same depths as the moored CTD at each platform. See Figure 2 legend for description of blocked time periods.
Figure 3.
Figure 4. Contoured time series of the vertical profiles of salinity at (A) Platform Gail and (B) Platform Gilda; and (C) potential temperature at Platform Gilda. Black horizontal lines at 30 m and 26 m on the Gail and Gilda plots, respectively, indicate the deepest level surveyed where the majority of the juvenile rockfish recruits were observed. See Figure 2 legend for description of blocked time periods.
Figure 4.
Figure 5. Identification of water mass signatures at the platforms. TS plots from the six CalCOFI reference regions mapped in Figure 1B (TS lines and regions have corresponding color codes) are laid over the mean TS from 24 hours preceding each survey at Platforms Gilda and Gail before (indicated by x and +, respectively) and after (indicated by ● and ♦, respectively) the nominal onset of the rockfish recruitment season, 28 June 2004.
Figure 5.
Figure 6. Time series of 36-hour filtered surface and subsurface currents at the platforms. (A) U component (eastward is positive) and (B) V component (northward is positive) of radar-derived surface currents (indicated by black line) and subsurface currents (each blue line represents the mean current within a depth interval with the red line representing the shallowest bin depth interval) from the ADCP deployed at Platform Gilda. (C and D) Same at Platform Gail. The surface current measurements are from the nearest radar mapping grid point to the southeast of each platform. The effective current profile range was 10.2 - 22 m at Platform Gilda (29 bins) and 17.2 - 24.9 m from the surface at Platform Gail (19 bins). The bin interval was 0.4 m. See Figure 2 legend for description of blocked time periods.
Figure 7. High-frequency radar maps of 25-hour mean surface currents from 10 June, 12 June, 14 June, and 16 June 2004 show abrupt transition from eastward currents to northwestward currents in the eastern Santa Barbara Channel.
Figure 7 continued.

C)

D)
LITERATURE CITED


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