# IMPORTANCE OF FAR-OFFSHORE SAMPLING IN EVALUATING THE ICHTHYOPLANKTON COMMUNITY IN THE NORTHERN CALIFORNIA CURRENT 

TOBY D. AUTH<br>Cooperative Institute for Marine Resources Studies Oregon State University, Hatfield Marine Science Center 2030 Marine Science Drive<br>Newport, Oregon 97365, USA<br>toby.auth@noaa.gov


#### Abstract

The distribution and concentration of ichthyoplankton were examined from stations extending $2-364 \mathrm{~km}$ offshore at $7-53 \mathrm{~km}$ intervals along the Newport Hydrographic (NH) and Crescent City (CC) (July 2008 only) lines in the northern California Current (NCC) during March, April, and October 2007, and March, June, and July 2008. A total of 2372 fish larvae representing 36 taxa from 22 families were collected in 72 bongo samples from 30 stations: 15 stations were "shelf" (<2000 m depth), 15 were "far-offshore" (>2000 m depth). Four dominant taxa accounted for $90 \%$ of the total larval fish concentration: Stenobrachius leucopsarus (47\%), Sebastes spp. (25\%), Engraulis mordax (12\%), and Tarletonbeania crenularis (6\%). Mean study-wide concentrations of the dominant taxa were significantly greater in the far-offshore region than in the shelf region. Weighted mean length was significantly greater only for larval Sebastes spp. collected at the far-offshore compared with the shelf stations, while E. mordax larvae were only collected at far-offshore stations in June and July 2008. Larval distributions and concentrations were also examined in relation to variable local environmental factors (i.e. temperature, salinity, dissolved oxygen, fluorescence, and east-west Ekman transport) and basin-scale indices (i.e. MEI and PDO). Historic and ongoing survey designs used to characterize the plankton community in the NCC have usually incorporated only coastal and shelf ( $<\sim 100 \mathrm{~km}$ offshore) stations extending out to the continental slope ( $\sim 2000 \mathrm{~m}$ depth). Increased sampling effort at far-offshore stations will be required to adequately characterize the ichthyoplankton community of the NCC in the future.


## INTRODUCTION

Ichthyoplankton surveys have long been recognized as cost-effective proxies to identify spawning locations, success, environmental requirements, essential fish habitat, and recruitment potential of marine fish stocks (Hunter et al. 1993; Houde 1997; Lyczkowski-Shultz 2006), as well as providing ecosystem indicators of environmental change (Brodeur et al. 2008) and an understanding of trophic interactions between zooplankton
and important piscivores (Hunter and Kimbrell 1980). However, by focusing their sampling efforts almost exclusively on near-shore and shelf waters while neglecting to sample far-offshore waters beyond the continental slope, these surveys may not adequately sample the entire, or even primary, cross-shelf range of the dominant larval taxa of interest.

During the past 40 years, most ichthyoplankton studies conducted in the northern California Current (NCC) have focused on fish eggs and larvae collected inshore of the continental slope (Richardson and Pearcy 1977; Richardson et al. 1980; Mundy 1984; Boehlert et al. 1985; Brodeur et al. 1985; Auth and Brodeur 2006; Auth et al. 2007; Auth 2008; Brodeur et al. 2008; Parnel et al. 2008). Only three NCC studies have hitherto incorporated far-offshore ichthyoplankton samples: Waldron 1972, Richardson 1973, and Doyle 1992. However, Waldron 1972 only sampled during two months (April and May) in 1967, whereas Richardson 1973 only sampled from May to October in 1969 and only differentiated sampling effort between near-shore ( $<37 \mathrm{~km}$ from shore, $\sim 150 \mathrm{~m}$ in depth) and broadly-defined offshore (37-425 km from shore, $\sim 150-3000 \mathrm{~m}$ in depth) stations. Doyle 1992 reported on general ichthyoplankton densities from the NCC in 1980-87, but did not conduct any testable statistical analyses of cross-shelf distributions and concentrations.

During the two decades since the completion of Doyle's 1992 work, the NCC has experienced extreme and variable climate-induced environmental fluctuations, including multiple shifts between warm and cold regimes, El Niño and La Niña events, variability in seasonal upwelling intensity, and change in biological communities (Schwing and Moore 2000; Peterson and Schwing 2003; Brodeur et al. 2006; Hooff and Peterson 2006) that may have altered the cross-shelf distribution of the ichthyoplankton community in the region. However, all studies during that time, including the on-going National Marine Fisheries Service (NMFS) Stock Assessment Improvement Plan (SAIP), U.S. Global Ocean Ecosystem Dynamics Program (GLOBEC), and Pacific Coast Ocean Observing System (PaCOOS) monitoring projects, have focused on collecting plankton samples primarily from
coastal and shelf stations, largely neglecting far-offshore waters beyond the continental slope.

The present study is the first in 20 years to examine the cross-shelf variability in distribution and concentration of ichthyoplankton collected in the NCC at regular spatial intervals from near-shore out to far beyond the continental slope during multiple seasons in two consecutive years, and the first to date to do so using testable statistical techniques. Through this, I hope to (1) compare the ichthyoplankton concentrations in the heav-ily-sampled coastal and shelf region to those in the undersampled far-offshore region in the NCC; (2) relate these concentration data to local (i.e. temperature, salinity, dissolved oxygen [DO], fluorescence, and eastward Ekman transport [EET]) and basin-scale (i.e. Multivariate El Niño-Southern Oscillation Index [MEI] and Pacific Decadal Oscillation [PDO]) environmental variables and indices; (3) compare and contrast these results to those of previous studies; and (4) provide a recommendation of the extent of cross-shelf sampling that is needed to adequately characterize the ichthyoplankton community of the NCC in ongoing and future sampling efforts.

## METHODS

## Sampling procedures

A total of 72 ichthyoplankton samples were collected during the study. Samples ( $n=8-9$ per cruise) were collected from 13 stations extending 2-238 km offshore at $7-53 \mathrm{~km}$ intervals along the NH line $\left(44.65^{\circ} \mathrm{N}\right)$ off the central Oregon coast in the NCC during March, April, and October 2007, and March, June, and July 2008 (fig. 1). Not all stations were sampled during all cruises. An additional 17 stations were sampled in July 2008 extending 274-364 km offshore along the NH line ( $n=$ 3 ) and $7-276 \mathrm{~km}$ offshore along the Crescent City (CC) line $\left(41.9^{\circ} \mathrm{N}\right)(n=14)$ off the northern California coast at $7-46 \mathrm{~km}$ intervals (fig. 1). Stations were sampled at different times during both day ( $n=32$ ) and night ( $n=$ 40). No significant diel differences in larval concentration were found ( $p>0.05$ ), therefore all samples were used in theses analyses regardless of time of sampling. Samples were collected using a bongo net with a 70 cm ( 60 cm in June and July 2008) diameter mouth opening and $335 \mu \mathrm{~m}$ mesh nets. The bongo was fished as a continuous oblique tow from $\sim 45 \mathrm{~m}$ to the surface at a retrieval rate of $28 \mathrm{~m} / \mathrm{min}$ and a ship speed of 1.0-1.5 $\mathrm{m} / \mathrm{s}$. In June and July 2008, the bongo was fished from $\sim 100 \mathrm{~m}$ (or within 5 m of the bottom at stations $<100$ $\mathrm{m})$ to the surface at the same retrieval rate and ship speed. A depth recorder and flowmeter were placed in the net during each tow to determine tow depth and volume of water filtered. The mean water-volume filtered was $132.5 \mathrm{~m}^{3}$ (standard error $[\mathrm{SE}]=5.7$ ). Temperature $\left({ }^{\circ} \mathrm{C}\right)$,


Figure 1. Locations of stations sampled in March, April, and October 2007, and March, June, and July 2008 (circles). Not all stations were sampled during each cruise. Stations indicated by triangles were only sampled during July 2008. Depth contours of 200,500, 1000, and 2000 m (continental slope) are shown. The 2000 m isobath represents the separation between normallysampled coastal and shelf stations and normally-unsampled slope and open ocean stations.
salinity, DO ( $\mathrm{ml} / \mathrm{L}$ ), and fluorescence (volts) (an indicator of primary productivity) were measured throughout the water column using a Seabird SBE 911 (SBE 25 in June 2008) CTD.

Because sampling was conducted as part of multiple unrelated projects, station locations, sampling depth, and mouth opening of the sampling gear were not uniform throughout the study. However, the same relative number of shelf and far-offshore stations were sampled during each cruise, and the sampling depth and gear were identical for all stations within each cruise. Since the study was designed to test for differences in larval fish concentrations between two cross-shelf regions and not between, but within, different months or years, it is not likely that the variability in sampling design over the course of the study biases the results and interpretation of any cross-shelf differences that were found.
Ichthyoplankton samples were preserved at sea in a $10 \%$ buffered-formalin seawater solution. Fish larvae from each sample were completely sorted, counted, and identified to the lowest taxonomic level possible in the laboratory using a dissecting microscope. The majority of larval Citharichthys spp., Osmeridae, Sebastes spp., and Sebastolobus spp. collected were not identifiable below the generic or family level based on meristics and pigmentation patterns, so no species-specific inferences are intended for these taxa in this study. However, the majority of those individuals classified as Citharichthys


Figure 2. Cross-section of the Newport Hydrographic $(\mathrm{NH})$ line showing $(A)$ temperature $\left({ }^{\circ} \mathrm{C}\right)$ and $(B)$ salinity contours from the surface to 100 m in June and July 2008.
spp. most likely are either C. sordidus or C. stigmaeus based on the larger, identifiable individuals collected and the dominance of these paralichthyid taxa in the NCC ichthyoplankton (Matarese et al. 1989). The lesser of either all larvae or a random sub-sample of 30 individuals from each taxon in each sample was measured to the nearest 0.1 mm standard length (SL) (or notochord length for preflexon larvae) using UTHSCSA Image Tool Version 3.0 image processing and analysis software (http://ddsdx.uthscsa.edu/dig/itdesc.html 2009).

## Data analyses

Along the NH line the continental slope abruptly descends from the shelf (<900 m depth) onto the abyssal plain ( $\sim 3000 \mathrm{~m}$ depth) between 84 and 102 km offshore. To facilitate cross-shelf distributional analyses, stations were classified as either shelf (station depth $<900 \mathrm{~m}$ ) or far-offshore (station depth $>2800 \mathrm{~m}$ ) based on the location and depth of the continental slope. Larval fish concentrations were expressed as the number of individuals per $1000 \mathrm{~m}^{3}$. An ANOVA and $t$-test were applied to the $\log _{\mathrm{e}}(n+0.1)$-transformed larval concentration data to test for significant differences between shelf and far-offshore stations. Weighted mean (based on concentration) lengths of the dominant and total larval taxa were also calculated for each station, and were similarly tested for significant differences between cross-shelf classifications.

Pair-wise correlation analyses were also conducted to assess the relationship between concentrations of several dominant taxa (Engraulis mordax, Sebastes spp., Stenobrachius leucopsarus, and Tarletonbeania crenularis) and total fish larvae, and the following environmental variables: temperature, salinity, DO, and fluorescence all measured at both 3 m and 20 m depths. The environmental variables from 3 m represent near-surface conditions, while those from

20 m represent conditions near the pycnocline and the depth stratum with the highest Sebastes spp., S. leucopsarus, and T. crenularis larval concentrations as reported by Auth and Brodeur 2006. Prior to inclusion in the analyses, larval concentrations were $\log _{\mathrm{e}}(n+0.1)$-transformed which normalized the data and homogenized residual variances. Statistical significance was determined at $\alpha=0.05$. All ANOVA and correlation analyses were performed using the statistical software JMP Version 7 (SAS Institute 2007).

## RESULTS

## Hydrography

Temperature, salinity, DO, and fluorescence sections (not shown) showed little cross-shelf variability in March, April, and October 2007, and March 2008 (and in June and July 2008 for DO and fluorescence). Near-surface temperatures generally increased and near-surface salinities generally decreased with distance offshore. In June and July 2008, however, pronounced upwelling-induced cross-shelf variability in temperature and salinity was observed, with cold, saline water rising to the surface from depth nearshore ( $<50 \mathrm{~km}$ ), while warmer, less-saline water was pushed along the surface offshore (fig. 2). The presence of Columbia River plume waters along the NH line was apparent by a patch of warm, less-saline nearsurface water 100-160 km offshore in June (mean 3 m temperature $=12.3^{\circ} \mathrm{C}$; mean 3 m salinity $=30.4$ ) and $120-275 \mathrm{~km}$ offshore in July (mean 3 m temperature $=$ $15.1^{\circ} \mathrm{C}$; mean 3 m salinity $=31.4$ ) 2008. Temperature at 3 m depth along the NH line varied between $9.3^{\circ}-10.0^{\circ} \mathrm{C}$ in March, $9.8^{\circ}-10.8^{\circ} \mathrm{C}$ in April, and $11.2^{\circ}-13.6^{\circ} \mathrm{C}$ in October 2007 , and $8.7^{\circ}-9.1^{\circ} \mathrm{C}$ in March, $11.5^{\circ}-13.0^{\circ} \mathrm{C}$ in June, and $7.5^{\circ}-15.5^{\circ} \mathrm{C}$ in July 2008.

TABLE 1
Composition, frequency of occurrence, mean concentration (no. $/ 1000 \mathrm{~m}^{3}$ ), and percent of total concentration for all larval fish collected off the Oregon coast at stations along the Newport Hydrographic (NH) line ( $44.65^{\circ} \mathrm{N}$ ) in March, April, and October 2007, and March, June, and July 2008, as well as off the northern California coast at stations along the Crescent City (CC) line ( $41.9^{\circ} \mathrm{N}$ ) in July 2008.

|  | Common name | Frequency occurrence | Mean concentration (no. $/ 1000 \mathrm{~m}^{3}$ ) | Total concentration (\%) |
| :---: | :---: | :---: | :---: | :---: |
| Clupeidae |  |  |  |  |
| Sardinops sagax | Pacific sardine | 0.01 | 0.07 | 0.03 |
| Engraulidae |  |  |  |  |
| Engraulis mordax | Northern anchovy | 0.10 | 29.97 | 12.24 |
| Bathylagidae |  |  |  |  |
| Bathylagus pacificus | Pacific blacksmelt | 0.01 | 0.10 | 0.04 |
| Lipolagus ochotensis | Eared blacksmelt | 0.08 | 1.48 | 0.60 |
| Osmeridae |  |  |  |  |
| Undetermined spp. | Smelts | 0.03 | 1.30 | 0.53 |
| Stomiidae |  |  |  |  |
| Chauliodus macouni | Pacific viperfish | 0.03 | 0.19 | 0.08 |
| Tactostoma macropus | Longfin dragonfish | 0.01 | 0.14 | 0.06 |
| Paralepididae |  |  |  |  |
| Lestidiops ringens | Slender barracudina | 0.01 | 0.16 | 0.07 |
| Myctophidae |  |  |  |  |
| Protomyctophum crockeri | California flashlightfish | 0.06 | 0.40 | 0.16 |
| Protomyctophum thompsoni | Bigeye lanternfish | 0.04 | 0.34 | 0.14 |
| Tarletonbeania crenularis | Blue lanternfish | 0.49 | 13.80 | 5.64 |
| Nannobrachium regale | Pinpoint lampfish | 0.21 | 2.39 | 0.98 |
| Stenobrachius leucopsarus | Northern lampfish | 0.68 | 113.91 | 46.53 |
| Diaphus theta | California headlightfish | 0.04 | 0.62 | 0.25 |
| Gadidae |  |  |  |  |
| Microgadus proximus | Pacific tomcod | 0.01 | 1.73 | 0.71 |
| Bythitidae |  |  |  |  |
| Cataetyx rubrirostris | Rubynose brotula | 0.01 | 0.09 | 0.04 |
| Trachipteridae |  |  |  |  |
| Trachipterus altivelis | King-of-the-salmon | 0.01 | 0.09 | 0.04 |
| Scorpaenidae |  |  |  |  |
| Sebastes spp. | Rockfishes | 0.63 | 61.80 | 25.25 |
| Sebastolobus spp. | Thornyheads | 0.13 | 2.04 | 0.83 |
| Anoplopomatidae |  |  |  |  |
| Anoplopoma fimbria | Sablefish | 0.01 | 0.18 | 0.08 |
| Cottidae |  |  |  |  |
| Artedius fenestralis | Padded sculpin | 0.01 | 0.19 | 0.08 |
| Agonidae |  |  |  |  |
| Bathyagonus pentacanthus | Bigeye poacher | 0.01 | 0.06 | 0.03 |
| Liparidae |  |  |  |  |
| Liparis fucensis | Slipskin snailfish | 0.06 | 0.70 | 0.29 |
| Liparis mucosus | Slimy snailfish | 0.01 | 0.34 | 0.14 |
| Cryptacanthodidae |  |  |  |  |
| Cryptacanthodes aleutensis | Dwarf wrymouth | 0.01 | 0.18 | 0.07 |
| Icosteidae |  |  |  |  |
| Icosteus aenigmaticus | Ragfish | 0.04 | 0.42 | 0.17 |
| Ammodytidae |  |  |  |  |
| Ammodytes hexapterus | Pacific sand lance | 0.01 | 0.19 | 0.08 |
| Centrolophidae |  |  |  |  |
| Icichthys lockingtoni | Medusafish | 0.07 | 0.37 | 0.15 |
| Tetragonuridae |  |  |  |  |
| Tetragonurus cuvieri | Smalleye squaretail | 0.03 | 0.20 | 0.08 |
| Paralichthyidae |  |  |  |  |
| Citharichthys sordidus or stigmaeus | Pacific or speckled sanddab | 0.04 | 0.65 | 0.27 |
| Pleuronectidae |  |  |  |  |
| Embassichthys bathybius | Deepsea sole | 0.01 | 0.11 | 0.04 |
| Glyptocephalus zachirus | Rex sole | 0.11 | 2.45 | 1.00 |
| Isopsetta isolepis | Butter sole | 0.03 | 0.84 | 0.34 |
| Lyopsetta exilis | Slender sole | 0.18 | 3.04 | 1.24 |
| Microstomus pacificus | Dover sole | 0.08 | 1.21 | 0.49 |
| Parophrys vetulus | English sole | 0.06 | 2.65 | 1.08 |
| Undetermined |  | 0.01 | 0.14 | 0.06 |



Figure 3. Cross-shelf concentrations (number/1000 $\mathrm{m}^{3}$ ) of the dominant larval fish taxa collected off the Oregon coast at stations along the Newport Hydrographic (NH) line (44.65 N ) in March, April, and October 2007, and March, June, and July 2008, as well as off the northern California coast at stations along the Crescent City (CC) line ( $41.9^{\circ} \mathrm{N}$ ) in July 2008. Vertical dotted lines indicate the separation between normally-sampled coastal and shelf stations and normallyunsampled far-offshore stations. * $=$ station not sampled.


Figure 3 (continued). Cross-shelf concentrations (number/1000 m³) of the dominant larval fish taxa collected off the Oregon coast at stations along the Newport Hydrographic (NH) line ( $44.65^{\circ} \mathrm{N}$ ) in March, April, and October 2007, and March, June, and July 2008, as well as off the northern California coast at stations along the Crescent City (CC) line ( $41.9^{\circ} \mathrm{N}$ ) in July 2008. Vertical dotted lines indicate the separation between normally-sampled coastal and shelf stations and normallyunsampled far-offshore stations. * $=$ station not sampled.


Figure 3 (continued). Cross-shelf concentrations (number/ $1000 \mathrm{~m}^{3}$ ) of the dominant larval fish taxa collected off the Oregon coast at stations along the Newport Hydrographic (NH) line ( $44.65^{\circ} \mathrm{N}$ ) in March, April, and October 2007, and March, June, and July 2008, as well as off the northern California coast at stations along the Crescent City (CC) line ( $41.9^{\circ} \mathrm{N}$ ) in July 2008. Vertical dotted lines indicate the separation between normally-sampled coastal and shelf stations and normallyunsampled far-offshore stations. ${ }^{*}=$ station not sampled.

## Larval concentrations and distributions

A total of 2372 fish larvae representing 36 taxa from 22 families were collected throughout the study (tab. 1). Four dominant taxa accounted for $90 \%$ of the total larval concentration: S. leucopsarus (47\%), Sebastes spp. (25\%), E. mordax (12\%), and T. crenularis (6\%). Several other taxa occurred at relatively high frequencies $(>0.10)$ but at lower mean concentrations: Nannobrachium regale, Lyopsetta exilis, Sebastolobus spp., and Glyptocephalus zachirus.

Mean study-wide concentrations of all dominant taxa (excluding an anomalously high Sebastes spp. value at the 38 km station on the CC line in July 2008) and total larvae were significantly higher in the normally-unsampled far-offshore region than the normally-sampled coastal and shelf region (fig. 3). This was particularly true for E. mordax larvae, which were exclusively found in the warmer Columbia River plume waters in the far-offshore region in June and July 2008. Mean study-wide concentration of Sebastes spp. larvae was 2.6 times higher at far-offshore than at shelf stations, with a monthly maximum of 33 times higher in March 2007. Larval S. leucopsarus were five times more concentrated overall at far-offshore than shelf stations, and as much as 15 times more in March 2007. Tarletonbeania crenularis larvae were six times more concentrated throughout the study at faroffshore than shelf stations, and were exclusively collected at far-offshore stations in half of the months sampled (March and October 2007, and March 2008). A high concentration (442.4/1000 $\mathrm{m}^{3}$ ) of diverse, nearshore, non-dominant larval taxa (i.e. Ammodytes hexapterus, Artedius fenestralis, Citharichthys spp., Isopsetta isolepis, Liparis fucensis, Microgadus proximus, Osmeridae, and Parophrys vetulus) were also collected along the NH line
in March 2008 at a station 9 km from shore, and comprised $25 \%$ of all non-dominant larvae collected throughout the study.

Study-wide weighted mean length was significantly greater for larval Sebastes spp. collected at far-offshore (mean $=6.1 \mathrm{~mm}, \mathrm{SE}=0.2$ ) than at shelf (mean $=4.3$ $\mathrm{mm}, \mathrm{SE}=0.2$ ) stations ( $p<0.0001$ ). However, no significant cross-shelf differences in weighted mean lengths were found for either S. leucopsarus or T. crenularis larvae.

## Environmental relationships

Pair-wise correlation analyses revealed that larval fish concentrations were generally positively correlated with temperature and negatively correlated with salinity (tab. 2). Concentration of larval E. mordax was significantly positively correlated with 3 and 20 m temperature, and negatively correlated with 3 m salinity and 3 m and 20 m fluorescence ( $p<0.05$ ). S. leucopsarus larvae were significantly positively correlated with 3 m and 20 m temperature and 20 m DO, and negatively correlated with 3 m and 20 m salinity $(p<0.05)$. T. crenularis larval concentration was significantly positively correlated with 3 m and 20 m temperature, and negatively correlated with 20 m salinity $(p<0.05)$. However, there were no significant correlations between any of the measured environmental variables and larval Sebastes spp. concentration ( $p>0.05$ ).

## DISCUSSION

The four dominant larval taxa found in this study were among the dominant taxa reported by other crossshelf studies conducted in the last 40 years in the NCC during spring and summer (Waldron 1972; Richardson

TABLE 2
Correlation coefficients for 13 variables sampled off the Oregon coast at stations along the Newport Hydrographic (NH) line ( $44.65^{\circ}$ N) in March, April, and October 2007, and March, June, and July 2008, as well as off the northern California coast at stations along the Crescent City (CC) line ( $41.9^{\circ} \mathrm{N}$ ) in July 2008: 3 m and 20 m temperature ( ${ }^{\circ} \mathrm{C}$ ) ( $n=67$ ), salinity ( $n=67$ ), dissolved oxygen (DO) ( $\mathrm{ml} / \mathrm{L}$ ) ( $n=67$ ), fluorescence $(n=54)$, and $\log _{\mathrm{e}}(n+0.1)$-transformed concentrations (no. $1000 \mathrm{~m}^{3}$ ) of Engraulis mordax, Sebastes spp., Stenobrachius leucopsarus, Tarletonbeania crenularis, and total larvae. $\star=p<0.05$.

|  | Engraulis mordax | Sebastes spp. | Stenobrachius <br> leucopsarus | Tarletonbeania <br> crenularis |
| :--- | :---: | :---: | :---: | :---: |
| Temperature 3 m | $0.50^{\star}$ | -0.06 | $0.30^{\star}$ | $0.40^{\star}$ |
| Salinity 3 m | $-0.31^{\star}$ | -0.17 | $-0.26^{\star}$ | -0.19 |
| DO 3 m | 0.11 | 0.01 | -0.09 | 0.13 |
| Fluorescence 3 m | $-0.29 \star$ | -0.04 | -0.09 | -0.20 |
| Temperature 20 m | $0.47 \star$ | -0.11 | $-0.34^{\star}$ | -0.02 |
| Salinity 20 m | -0.22 | -0.12 | $-0.33^{\star}$ | -0.09 |
| DO 20 m | -0.02 | 0.20 | $0.39^{\star}$ | $-0.31^{\star}$ |
| Fluorescence 20 m | $-0.29^{\star}$ | -0.03 | -0.07 | -0.24 |

1973; Richardson and Pearcy 1977; Richardson et al. 1980; Brodeur et al. 1985; Doyle 1992; Auth and Brodeur 2006; Auth et al. 2007; Auth 2008). A single Sardinops sagax larva ( 4.3 mm notochord length) was also collected at a station 320 km offshore along the NH line in July 2008, while several S. sagax eggs were collected at the furthest offshore stations ( 320 and 364 km offshore) along the NH line and the furthest offshore station ( 276 km offshore) along the CC line in July 2008. This species has only been known to spawn in the study area since the mid-1990s after an absence of nearly 40 years (Emmett et al. 2005), and would not have been detected during this study under a normal shelf-sampling-only regime.

The cross-shelf distributions of the dominant larval taxa found in this study differed in some cases from those reported by previous studies conducted in the California Current region. Engraulis mordax larvae were found in high concentrations and exclusively in the warm, offshore Columbia River plume waters as reported previously (Richardson 1973; Shenker 1988; Auth and Brodeur 2006). However, because the Columbia River plume was located far offshore during June and July (when peak E. mordax spawning occurs) 2008, these larvae would not have been detected along this transect had sampling only occurred at normally-sampled coastal and shelf stations. The myctophid larvae were much more prevalent at faroffshore than shelf stations during the present study. In the NCC region, Waldron 1972 reported more zero catches of S. leucopsarus and T. crenularis larvae in shelf than far-offshore waters, while Doyle's 1992 meandistribution maps for 1980-87 showed marginally higher concentrations of these two taxa offshore of the continental slope. In the southern California Current (SCC) region, the 1951-98 California Cooperative Oceanic Fisheries Investigation (CalCOFI) surveys showed that S. leucopsarus larvae were distributed in higher concentrations inshore of the continental slope than farther offshore, while T. crenularis larvae were more evenly distributed (Moser et al. 2001).

Previous studies also identified variable cross-shelf distributions of Sebastes spp. larvae. In the NCC region, Waldron 1972 found higher concentrations of larval Sebastes spp. inshore of the continental slope, and Richardson 1973 reported a similar distribution between stations inshore and offshore of 37 km , while Doyle 1992 reported the highest concentrations along the continental slope. In the SCC region, the CalCOFI surveys showed that Sebastes spp. larvae were almost exclusively distributed inshore of the continental slope (Moser et al. 2001). Although mean concentrations of larval Sebastes spp. in the present study were higher in the far-offshore than the shelf region, these larvae were distributed on both sides of the slope. In fact, an anomalously high number of Sebastes spp. larvae $(n=164)$, around four times greater than the number found at any other station during the study, were collected at a mid-shelf station located 38 km offshore along the CC line in July 2008. However, since all of those larvae were relatively small and similar in size (mean $=4.2 \mathrm{~mm}$, standard deviation $[\mathrm{SD}]=0.6$ ), this was determined to be an outlier resulting from smallscale spatial patchiness which can be a common confounding factor in any large-scale ichthyoplankton survey (Gray 1996).

Variations in local and basin-scale environmental factors and indices did not appear to explain the consistently higher concentrations of the dominant larval fish taxa in far-offshore than shelf and coastal waters during this study. Although E. mordax, S. leucopsarus, and T. crenularis larval concentrations were positively correlated with temperature and negatively correlated with salinity as previously reported (Auth and Brodeur 2006), the magnitude and direction of cross-shelf variability in these environmental factors were not consistent between the different months in which sampling occurred. In addition, MEI, PDO, and EET index values all varied between positive, neutral, and negative during the different sampling periods (fig. 4), while mean concentrations of the dominant and total larval fish taxa remained consis-


Figure 4. Monthly-averaged multivariate El Niño-southern oscillation index (MEI), Pacific decadal oscillation (PDO), and eastward Ekman transport (EET) (kg/m) from $45^{\circ} \mathrm{N}, 125^{\circ} \mathrm{W}$.
tently higher at far-offshore than more-nearshore stations. Variations in seasonal or annual cross-shelf zooplankton prey concentrations and assemblages may help explain the high far-offshore larval fish concentrations observed in this study, which will be examined in a future study (W. Peterson ${ }^{1}$ ).

It is important to note that the four dominant taxa found in this study are all commercially or ecologically significant to the northeast Pacific Ocean fishery and ecosystem. Adult Sebastes spp. and E. mordax are widely harvested throughout the NCC region (Brodeur et al. 2003), while myctophids such as S. leucopsarus and T. crenularis are the dominant component of the micronekton community and represent a vital trophic link between zooplankton and piscivorous organisms in the north Pacific Ocean (Beamish et al. 1999; Brodeur and

[^0]Yamamura 2005; Suntsov and Brodeur 2008, Phillips et al. 2009). With such high concentrations of the larvae of these dominant taxa being found far offshore beyond the continental slope, it would be unreasonable to assume that these individuals are lost from the system or will not recruit to the more nearshore adult community. Active or passive advection of far-offshore larvae back onto the shelf may occur as a result of larvae and juveniles regulating their position in the water column through diel vertical migrations to take advantage of selective Ekman transport and varying tidal currents (Norcross and Shaw 1984; Auth et al. 2007). If such advection does occur, then the numerous larvae found far offshore may substantially contribute to the overall recruitment of more inshore stocks, and must be considered as part of any stock assessment program incorporating an ichthyoplankton component.

Stock assessments for many of the $\sim 40$ species of Sebastes occurring in the NCC region are regularly con-
ducted as part of the fisheries management plans for the important commercial stocks within this genus. Although Sebastes spp. larvae could not be identified to species in this study based on meristic and pigmentation patterns, future studies may result in identification of specimens to species using molecular genetics techniques (Gray et al. 2006). This could eventually lead to the incorporation of larval abundance data in stock assessments. Variability in cross-shelf location and seasonal timing of spawning may occur for different species of Sebastes within the NCC region (Love et al. 2002). This may contribute to the cross-shelf and seasonal variability in concentration and length of Sebastes spp. larvae found in this study. The more numerous, larger larvae found far offshore may be different species than the less numerous, smaller larvae collected over the shelf, or could represent an advection of recently-spawned larvae of similar species composition from more-nearshore to farther-offshore waters through ontogeny. If the species composition and spawning time is similar in the two cross-shelf regions, then the larger size of the far-offshore larvae could be due to an increased growth rate resulting from increased prey quantity and/or quality in the far-offshore region. In any case, with a pelagic larval-stage duration of one to two months and a juvenile stage lasting weeks to months before demersal settlement (Love et al. 2002; Matarese et al. 2003), early-life stages of Sebastes spp. could accomplish cross-shelf migrations in search of optimal environmental conditions and prey availability before finally settling in coastal and shelf waters.

Evidence for Sebastes spp. surviving into the juvenile stage in far-offshore waters was found in June 2008, when the highest concentration $\left(4.4 / 1000 \mathrm{~m}^{3}\right)$ of Sebastes spp. juveniles (mean SL $=23.9 \mathrm{~mm}, \mathrm{SD}=2.4$ ) ever recorded out of all 176 mid-water trawl samples containing at least one Sebastes spp. individual from the 2004-08 SAIP survey was collected at a station 208 km offshore along the NH line ${ }^{2}$. This was the only mid-water trawl conducted at such a far-offshore station in the five years of the SAIP survey, and represents a concentration almost three times higher than that found for Sebastes spp. juveniles at any other station to date. Not only does this suggest that early-life stages of Sebastes spp. can survive in far-offshore waters through ontogeny, but also brings into question the effectiveness of marine protected areas for this genus designated solely in coastal and shelf waters if adults are spawning in farther-offshore waters.

The results from the present study showed that not only are the dominant fish larvae in the NCC region, comprising commercially and ecologically important taxa found in normally-unsampled far-offshore waters

[^1]beyond the continental slope, but that they exist in higher concentrations in this area than in the normally-sampled coastal and shelf waters. Ongoing and future sampling designs should incorporate far-offshore stations at least 100 km beyond the continental slope if they are to truly capture the entire community structure of ichthyoplankton in the NCC. This could be accomplished with little or no additional resources of ship and personnel time by reducing the fine-scale latitudinal spacing of stations in favor of a broader and more complete cross-shelf coverage as previously suggested by Auth 2008.

## ACKNOWLEDGEMENTS

I thank the captains and crews of the RV McArthur II, RV Wecoma, and FV Piky for their cooperation and assistance in the sampling, and T. Sanford for providing the ship time on the RV Wecoma. I am indebted to A. Claiborne, W. Evans, J. Keister, B. Lindsay, H. Liu, J. Menkel, J. Peterson, W. Peterson, A. J. Phillips, L. Poppick, M. Pros, B. Reser, T. Shaw, and A. Sremba for their efforts in collecting data at sea. A special thank you goes out to R. Brodeur for his intellectual and material support, and to Sara Standerford for always being there for me when I'm California dreaming. I thank R. Brodeur, A. J. Phillips, and three anonymous reviewers for critical reviews of the manuscript. Funding was provided by NOAA's SAIP Project, Fisheries and the Environment Initiative (FATE), and Northeast Pacific GLOBEC Program. This is contribution number 638 of the U.S. GLOBEC Program.

## LITERATURE CITED

Auth, T. D. 2008. Distribution and community structure of ichthyoplankton from the northern and central California Current in May 2004-06. Fish. Oceanogr. 17(4):316-331.
Auth, T. D. and R. D. Brodeur. 2006. Distribution and community structure of ichthyoplankton off the Oregon coast, USA, in 2000 and 2002. Mar. Ecol. Prog. Ser. 319:199-213.
Auth, T. D., R. D. Brodeur, and K. M. Fisher. 2007. Diel variation in vertical distribution of an offshore ichthyoplankton community off the Oregon coast. Fish. Bull. 105:313-326.
Beamish, R. J., K. D. Leask, O. A. Ivanov, A. A. Balanov, A. M. Orlov, and B. Sinclair. 1999. The ecology, distribution, and abundance of midwater fishes of the Subarctic Pacific. Prog. Oceanogr. 43:399-442.
Boehlert, G. W., D. M. Gadomski, and B. C. Mundy. 1985. Vertical distribution of ichthyoplankton off the Oregon coast in spring and summer months. Fish. Bull. 83:611-621.
Brodeur, R. D. and O. Yamamura, eds. 2005. Micronekton of the North Pacific. PICES Sci. Rep. No. 30:1-115.
Brodeur, R. D., D. M. Gadomski, W. G. Pearcy, H. P. Batchelder, and C. B. Miller. 1985. Abundance and distribution of ichthyoplankton in the upwelling zone off Oregon during anomalous El Niño conditions. Est. Coastal Shelf Sci. 21:365-378.
Brodeur, R. D., W. G. Pearcy, and S. Ralston. 2003. Abundance and distribution patterns of nekton and micronekton in the Northern California Current Transition Zone. J. Oceanogr. 59:515-535.
Brodeur, R. D., S. Ralston, R. L. Emmett, M. Trudel, T. D. Auth, and A. J. Phillips. 2006. Anomalous pelagic nekton abundance, distribution, and apparent recruitment in the northern California Current in 2004 and 2005. Geophys. Res. Lett. 33, L22S08, doi:10.1029/2006GL026614.

Brodeur, R. D., W. T. Peterson, T. D. Auth, H. L. Soulen, M. M. Parnel, and A. A. Emerson. 2008. Abundance and diversity of coastal fish larvae as indicators of recent changes in ocean and climate conditions in the Oregon upwelling zone. Mar. Ecol. Prog. Ser. 366:187-202.
Doyle, M. J. 1992. Patterns in distribution and abundance of ichthyoplankton off Washington, Oregon, and northern California (1980-1987). AFSC Proc. Rep. 92-14:1-344.
Emmett, R. L., R. D. Brodeur, T. W. Miller, S. S. Pool, P. J. Bentley, G. K. Krutzikowsky, and J. McCrae. 2005. Pacific sardine (Sardinops sagax) abundance, distribution and ecological relationships in the Pacific Northwest. Calif. Coop. Oceanic Fish. Inves. Rep. 46:122-143.
Gray, C. A. 1996. Small-scale temporal variability in assemblages of larval fishes: implications for sampling. J. Plankton Res. 18:1643-1657.
Gray, A. K., A. W. Kendall Jr., B. L. Wing, M. G. Carls, J. Heifetz, Z. Li, and A. J. Gharrett. 2006. Identification and first documentation of larval rockfishes in southeast Alaskan waters was possible using mitochondrial markers but not pigmentation patterns. Trans. Amer. Fish. Soc. 135:1-11.
Hooff, R. C. and W. T. Peterson. 2006. Copepod biodiversity as an indicator of changes in ocean and climate conditions of the northern California current ecosystem. Limnol. Oceanogr. 51:2607-2620.
Houde, E. D. 1997. Patterns and consequences of selective processes in teleost early life histories. In Early life history and recruitment in fish populations. R. C. Chambers and E. A. Trippel, eds. London: Chapman and Hall, pp. 172-196.
Hunter, J. R. and C. Kimbrell. 1980. Egg cannibalism in the northern anchovy, Engraulis mordax. Fish. Bull. 78:811-816.
Hunter, J. R., N. C.- H. Lo, and L. A. Fuiman, eds. 1993. Advances in the Early Life History of Fishes; Part 2, Ichthyoplankton Methods for Estimating Fish Biomass. Bull. Mar. Sci. 53:723-935.
Love, M. S., M. Yoklavich, and L. Thorsteinson. 2002. The rockfishes of the Northeast Pacific. Los Angeles, California: University of California Press. 404 pp.
Lyczkowski-Shultz, J. 2006. The role of early life stages in fishery assessments. Paper presented at the 136th Annual Meeting, Am. Fish. Soc., Lake Placid, New York.
Matarese, A. C., A. W. Kendall, Jr., D. M. Blood, and B. M. Vinter. 1989. Laboratory guide to early life history stages of northeast Pacific fishes. NOAA Tech. Rep. NMFS 80:1-652.
Matarese, A. C., D. M. Blood, S. J. Piquelle, and J. L. Benson. 2003. Atlas of abundance and distribution patterns of ichthyoplankton from the northeast Pacific Ocean and Bering Sea ecosystems based on research conducted by the Alaska Fisheries Science Center (1972-1996). NOAA Prof. Paper NMFS 1:1-281.

Moser, H. G., R. L. Charter, P. E. Smith, D. A. Ambrose, W. Watson, S. R. Charter, and E. M. Sandknop. 2001. Distributional atlas of fish larvae and eggs in the Southern California Bight region: 1951-1998. CalCOFI Atlas 34:1-208.
Mundy, B. C. 1984. Yearly variation in the abundance and distribution of fish larvae in the coastal upwelling zone off Yaquina Head, OR, from June 1969-August 1972. M.S. Thesis, Oregon State University, 158 pp.
Norcross, B. L. and R. F. Shaw. 1984. Oceanic and estuarine transport of fish eggs and larvae: a review. Trans. Am. Fish. Soc. 113:153-165.
Parnel, M. M., R. L. Emmett, and R. D. Brodeur. 2008. Ichthyoplankton community in the Columbia River plume off Oregon: effects of fluctuating oceanographic conditions. Fish. Bull. 106:161-173.
Peterson, W. T. and F. B. Schwing. 2003. A new climate regime in northeast Pacific ecosystems. Geophys. Res. Lett. 30(17), 1896, doi:10.1029/ 2003 GL017528.
Phillips, A. J., R. D. Brodeur, and A. V. Suntsov. 2009. Micronekton community structure in the epipelagic zone of the northern California Current upwelling system. Prog. Oceanogr. (2009), 80:74-92.
Richardson, S. L. 1973. Abundance and distribution of larval fishes in waters off Oregon, May-October 1969, with special emphasis on the northern anchovy, Engraulis mordax. Fish. Bull. 71:697-711.
Richardson, S. L. and W. G. Pearcy. 1977. Coastal and oceanic larvae in an area of upwelling off Yaquina Bay, Oregon. Fish. Bull. 75:125-145.
Richardson, S. L., J. L. Laroche, and M. D. Richardson. 1980. Larval fish assemblages and associations in the north-east Pacific Ocean along the Oregon coast, winter-spring 1972-1975. Estuar. Coast. Mar. Sci. 11:671-699.
Schwing, F. B. and C. Moore. 2000. 1999-A year without summer for California or a harbinger of a climate shift? Eos. Trans. AGU 81:301, 304-305.
Shenker, J. M. 1988. Oceanographic associations of neustonic larval and juvenile fishes and Dungeness crab megalopae off Oregon. Fish. Bull. 86:299-317.
Suntsov, A. V. and R. D. Brodeur. 2008. Trophic ecology of three dominant myctophid species in the northern California Current region. Mar. Ecol. Prog. Ser. 373:81-96.
Waldron, K. D. 1972. Fish larvae collected from the northeastern Pacific Ocean and Puget Sound during April and May 1967. NOAA Tech. Rep. NMFS SSRF-663:1-16.


[^0]:    ${ }^{1}$ W. Peterson. Pers. commun. Hatfield Marine Science Center, Newport, OR 97365.

[^1]:    ${ }^{2}$ T. Britt and A. J. Phillips. Unpub. data. Hatfield Marine Science Center,
    Newport, OR 97365.

