

# Dynamics of larval fish assemblages in the California Current System: a comparative study between Oregon and southern California

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**ABSTRACT:** Boundary currents influence near-shore ecosystems worldwide, and understanding how fish assemblages change spatially and temporally throughout these systems is important for establishing the scale at which ecosystem-based management (EBM) should be conducted. Because most research on boundary currents in general, and the California Current System (CCS) in particular, have been restricted to only small portions of the systems, it is largely unknown whether fish assemblages in boundary currents form one coherent ecosystem or if changes in assemblage structure are locally independent. We expand the geographic scope of previous analyses on ichthyoplankton assemblages within boundary currents by comparing dynamics in 2 widely separated regions of the CCS: Oregon (~45° N) and southern California (~34° N) in spring and summer from 2004 to 2011. Both region and season affected assemblage structure. Some taxa that were moderately common in California were consistently rare or absent in Oregon (and vice versa), and the presence of most decreased in summer in both regions. However, the assemblages were very similar in some years. Off Oregon, the assemblage most resembled California's when the ocean temperature was relatively high and northern anchovy *Engraulis mordax* was abundant. Assemblage dynamics were well explained by environmental change in Oregon. By contrast, California's assemblage and environmental variability correlated poorly. Population sizes of taxa common to both regions did not fluctuate coherently in Oregon and California. These findings are important for EBM because they indicate that it is not possible to extrapolate results from spatially restricted localities to understand assemblage dynamics throughout the entire CCS.

**KEY WORDS:** Ichthyoplankton · Fisheries · Ecosystem dynamics · Oceanography · California Current

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## INTRODUCTION

Boundary currents greatly impact the oceanographic and biological conditions of many near-shore pelagic ecosystems worldwide (Carr & Kearns 2003). Eastern boundary systems, in particular, account for extremely high proportions of the global fish catch even though they take up only a small fraction of the total ocean volume (Pauly & Christensen 1995).

Within each boundary current system, the ecosystem is potentially linked by water flowing alongshore in the same direction, and can be viewed as a cohesive unit. However, many of these systems span thousands of kilometers, and thus there are potential regional differences in factors such as temperature and productivity that can influence the composition of a local community (Hickey & Banas 2008). Furthermore, oceanographic conditions that vary temporally

at seasonal and interannual scales also impact assemblage structure, and the degree of change can vary among regions within the geographic range of a boundary current. Therefore, it is difficult to determine, *a priori*, how biological assemblages vary through space and time in response to changing environmental conditions within different locations of a particular boundary current ecosystem.

Elucidating the scales at which fish assemblage dynamics vary is important for modern fisheries management (Levin et al. 2009). In particular, there is now global interest in ecosystem-based management (EBM) borne from the recognition that fishing can have indirect effects on multiple trophic levels within an ecosystem (Hall & Mainprize 2004, Garcia & Cochrane 2005, Scandol et al. 2005). For example, an EBM approach would attempt to understand how changes to the pelagic fish assemblage affect lower (e.g. zooplankton) and higher (e.g. birds) trophic levels as well as the economics of the fishing community (Levin et al. 2009, Pikitch et al. 2014). Because of the vagile nature of pelagic species, however, and the fact that EBM is ultimately 'place-based' (Lackey 1998), defining the extent of a marine ecosystem within a boundary current system, and determining how and why assemblages change within particular study regions is not straightforward (Levin et al. 2009). For example, if we observe in the Humboldt Current boundary ecosystem that sardine *Sardinops sagax* populations have increased in 2010 off Ilo, Peru (17° S), what implication does this have for sardine abundance in Chicama (8° S)? If anchovy *Engraulis mordax* abundance increases off San Diego, California (32° N) within the California Current ecosystem, is a similar dynamic found 1300 km north off Coos Bay, Oregon (43° N)? A critical first step for developing an EBM strategy is to discern how fish assemblages fluctuate through space and time, and whether these changes can be explained by natural environmental variation (Tolimieri & Levin 2006).

Given the inherent dynamic nature of pelagic ecosystems and the broad geographic ranges of many pelagic species, it is necessary to sample broadly to determine if taxa respond similarly to environmental variation in different spatial locations. Unfortunately, most marine monitoring programs encompass only a small portion of the biogeographic range of sampled taxa. This limited spatial perspective could obscure understanding of, for example, how individual taxa or whole assemblages respond to environmental variation throughout the biogeographic range of that species (Myers 1998). For instance, large-scale sampling revealed that Irish Sea cod *Gadus morhua*

recruitment correlates positively with sea surface temperature in northern, but negatively in southern parts of its range (Planque & Fox 1998). In this study, we expand the geographic range of sampling off the west coast of North America to better elucidate spatial and temporal variability in ichthyoplankton assemblages, and the processes that influence these dynamics, in the California Current System (CCS).

The CCS includes the marine ecosystem along the west coast of North America between approximately 20 and 50° N (Hickey 1979, Checkley & Barth 2009, McClatchie 2013). The CCS includes 3 prominent water masses: relatively cool, fresh, nutrient-rich subarctic water transported equatorward by the California Current (CC) from Alaska towards Mexico; warm, saline, nutrient-poor Central Pacific water that lies offshore from the CC; and cool, saline nutrient-rich water introduced to the system through coastal upwelling (Lynn & Simpson 1987, McClatchie 2013). The distribution and prominence of these water masses varies both seasonally and interannually. The presence of upwelled water is characterized by a spring transition when the intensity of equatorward coastal winds intensifies and cool, saline, nutrient rich water is upwelled from depth towards the surface. The influx of nutrients following the spring transition typically leads to enhanced primary production in the CCS (McClatchie 2013). The timing of the spring transition varies among years, but, on average, begins in March and peaks in June in southern California, and initiates in May and climaxes in July in Oregon (Schwing et al. 2006). In general, the rate of equatorward flow of the CC is greatest in spring and summer (Lynn & Simpson 1987). Interannual variability in the characteristics of each of these water types is affected prominently by El Niño–La Niña events. During El Niño conditions, the intensity of coastal upwelling and primary production is typically reduced, surface waters warm, and the rate of the equatorward flow of the CC decreases; the opposite occurs during La Niña conditions (McClatchie 2013). In addition, relatively warm and saline Central Pacific water can be advected poleward and shoreward under El Niño conditions (Moser et al. 1987). In the northern regions of the CCS, freshwater input from river outflow can also impact oceanographic conditions by reducing surface salinity, elevating temperature, and augmenting nutrient availability (Hickey & Banas 2008). The plume of outflow from the Columbia River, in particular, can be advected south towards the California border when CC flow is high, and thus can affect the oceanography of much of the northern CCS. Even though ocean tempera-

tures tend to be cooler in the northern part of the CCS, the magnitude of the latitudinal difference varies among years due to factors such as the timing of the spring transition in each region and outflow from the Columbia River (Mendelssohn & Schwing 2002, Checkley & Barth 2009).

Although several studies have examined spatial and/or temporal variability in ichthyoplankton assemblages within the CCS, most utilized data has been collected within geographically restricted regions relative to the CCS as a whole (e.g. within the Pacific Northwest: Richardson et al. 1980, Doyle et al. 2002, Auth 2011, Auth et al. 2011, Auth & Brodeur 2013; southern California: Hsieh et al. 2005, Thompson et al. 2012, Koslow et al. 2013; or Baja California: Funes-Rodriguez et al. 2002, 2011; but see Moser et al. 1987, Sunstov et al. 2011). The degree to which assemblages differ in widely separated regions of the CCS and whether they respond similarly to oceanographic variability in each region, however, is largely unknown. To provide a more complete understanding of patterns and processes of ecosystem dynamics throughout the CCS, we compared ichthyoplankton assemblage structure from samples collected between 2004 and 2011 over the continental margin off Oregon and southern California. Specifically, we first determined how the ichthyoplankton assemblage varied between regions and seasons (spring and summer) during this time period. Second, we compared how much of the variation in assemblage structure was explained by oceanographic variability and depth in each region and season. Third, we evaluated whether taxa found both in Oregon and California fluctuated synchronously among years.

## MATERIALS AND METHODS

### Sampling

We analyzed data collected by the Northwest Fisheries Science Center (NWFS) in Oregon and the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program in

California. In Oregon, ichthyoplankton and oceanographic samples were collected consistently along 2 cross-shelf transects from 2004 to 2011 in spring (May or June) and summer (August) (see Table S1 in Supplement 1 at [www.int-res.com/articles/suppl/m506p193\\_supp.pdf](http://www.int-res.com/articles/suppl/m506p193_supp.pdf)). Here, the distance from the shoreline to the endpoint of the transect was 95 km for the northern ('Columbia River line') and 84 km for the southern ('Newport line') transect (Fig. 1). The stations were all located at the outer shelf and slope region. These 2 transect lines were identified as important foci for long-term monitoring of the Northern California Current ([http://pacoos.org/SCI\\_PLAN/LJ-04-06b.pdf](http://pacoos.org/SCI_PLAN/LJ-04-06b.pdf)). Further details on ichthyoplankton sampling by the NWFS are provided in Auth

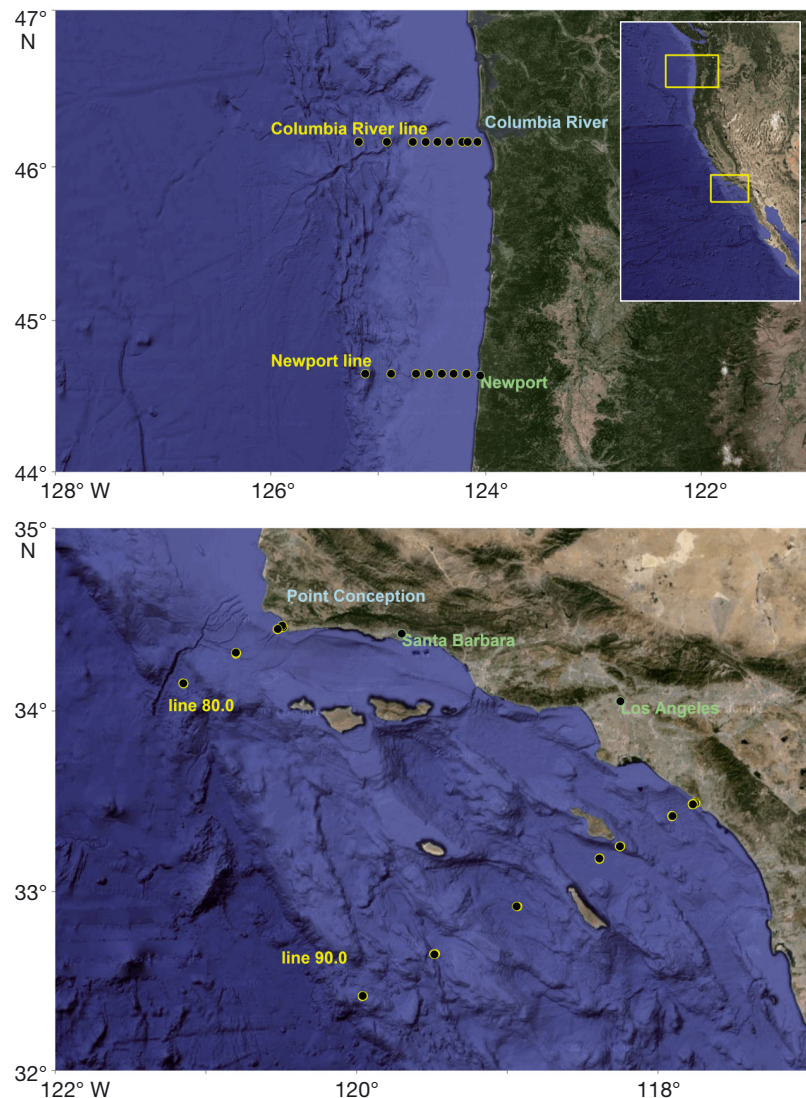


Fig. 1. Location of sampling stations in Oregon (top) and California (bottom), as well as major landmarks (blue font), and cities (green). Yellow rectangles on the inset map show the spatial extent of the fine-scale maps

(2011). CalCOFI has collected ichthyoplankton from 6 transects (i.e. 'the core CalCOFI lines') nearly continuously since 1951, and the sampling techniques are reviewed thoroughly by McClatchie (2013). We did not analyze all 6 transects for this study, however, because sampling intensity per se can impact measures of biological diversity (Gotelli & Colwell 2001). Instead, because 2 transects were used in Oregon, we selected *a priori* stations over the continental margin from 2 CalCOFI lines that were sampled in both spring (March or April) and summer (July or August) between 2004 and 2011. The 2 CalCOFI transects that we analyzed ('line 80.0' in the north and 'line 90.0' in the south; Fig. 1) were shown previously to represent well the suite of taxa found in southern California (Roemmich & McGowan 1995). Stations in California were between 3 and 240 km from the shoreline (the continental shelf is much wider on line 90.0 than 80.0; Fig. 1).

The nearest transects in Oregon and California were separated by an at-sea distance of approximately 1220 km (Fig. 1). Due to weather and logistic constraints, not each targeted station was sampled in each yr. On average, 9 stations season<sup>-1</sup> yr<sup>-1</sup> were sampled in Oregon and 11 stations were sampled in California (Table S1 in Supplement 1).

Obliquely-towed bongo nets were used to collect ichthyoplankton following standard CalCOFI protocols in both Oregon and California (Kramer et al. 1972, Smith & Richardson 1977). The nets had 71 cm diameter openings in California and 60 cm diameter openings (but 70 cm diameter in spring 2006) in Oregon, with 0.505 mm mesh in both regions. Nets were fished to 100 m (or 5 m from the bottom at shallow stations) and 212 m (or 15 m from the bottom) in Oregon and California, respectively. Although the discrepancy in tow depth among regions potentially biases inter-region comparisons of assemblage structure, depth-stratified ichthyoplankton distributions in both Oregon and California consistently show that almost all individuals of most taxa are found in the upper 100 m, thus likely minimizing the impact of the different methodologies (Ahlstrom 1959, Moser & Smith 1993, Auth et al. 2007). Nets were equipped with flowmeters to determine the amount of water filtered during each tow.

Ichthyoplankton samples were preserved at sea in buffered formalin. Fish larvae were identified to the lowest possible taxonomic level in the laboratory. Most taxa were identified to the species level with some important exceptions. First, all rockfishes *Sebastes* spp. in Oregon were identified only to genus. In California, although some rockfish species are dis-

cernible based on morphology (*S. aurora*, *S. diploproa*, *S. goodei*, *S. jordani*, *S. levis*, and *S. paucispinis*), most also fell into the *Sebastes* spp. category. Second, sanddabs *Citharichthys* spp. were identified to species in California but not in Oregon. However, previous analyses showed that the majority of *Citharichthys* spp. in Oregon are either *C. sordidus* or *C. stigmaeus* (Auth & Brodeur 2006, Auth 2011). Because these 2 species were also both common in California, we grouped *C. sordidus* and *C. stigmaeus* in California into one *Citharichthys* spp. category.

One of our goals was to determine how well environmental conditions could explain the variation of ichthyoplankton assemblages through time and space. Thus, vertical profiles of temperature and salinity were taken at each station using either a Seabird SBE 19, 25 or 911 CTD instrument. In addition, bathymetric depth (henceforth 'depth') was recorded at each station.

### Regional, seasonal and interannual variation

Our first goal was to characterize the degree to which ichthyoplankton assemblages varied temporally (seasonally and interannually) and spatially (between Oregon and California). We used a multivariate model selection approach based on Akaike's Information Criterion (AIC) scores (calculated from deviance) to test the relative plausibility of 5 *a priori* candidate redundancy analysis (RDA) models (Burnham & Anderson 2002) with different combinations of region and season as explanatory variables, and a null, unconstrained model without explanatory variables (i.e. a principal component analysis; PCA) (see Table 1). Larval concentrations (no. 1000 m<sup>-3</sup>) were averaged from each station within a cruise resulting in 31 samples for the multivariate analyses. We removed *Sebastes* spp. from the inter-region-season analysis because species identifications based on mitochondrial DNA sequences showed that many of the species within this genus differ between regions (A. R. Thompson & T. D. Auth unpubl. data). We did, however, include *Citharichthys* spp. as a species complex because this genus includes primarily *C. sordidus* and *C. stigmaeus* in both regions (Auth 2011, Thompson et al. 2012). We applied a Hellinger transformation (square-root standardized within each sample; see Supplement 2 at [www.int-res.com/articles/suppl/m506p193\\_supp.pdf](http://www.int-res.com/articles/suppl/m506p193_supp.pdf)) to larval concentrations to meet assumptions of linear multivariate analyses (Legendre & Gallagher 2001, Thompson et al. 2013), and AIC values were calculated for each

model. Notably, this transformation standardizes abundances within sampling units, and thus should alleviate bias that could occur due to differences in relative concentrations resulting from the variable tow depth between Oregon and California. We calculated  $\Delta$ AIC values for each candidate model to interpret the relative plausibility of each model. Next, we determined the amount of variation explained (adjusted  $R^2$ ) and significance of the overall best model and of the individual explanatory variables based on 1000 permutations. To better explain how season versus region affected assemblage structure, we conducted a variance partitioning analysis. To help visualize patterns, we plotted sample and species scores on the first 2 axes of a PCA. In addition, we conducted a 2-way cluster analysis of the Hellinger-transformed data for the 18 most common taxa, where separate dendrograms based on Euclidian distances and complete linkages were calculated first across samples and then taxa. These 2 dendrograms were coupled with a heat map of Hellinger-transformed values. To illustrate how concentrations of taxa varied across region, season, and year, we produced stacked bar charts of mean values of the most common taxa. Because adult habitat affinity is known to affect the degree to which particular taxa fluctuate through time in the CCS, we classified each taxon as residing in coastal, coastal-oceanic or oceanic habitats (Hsieh et al. 2005).

### Impact of environment

The second main goal was to determine whether environmental variability affected assemblage structure, and to compare the amount of explained variation between regions and seasons. Because the previous analyses showed that both season and region impacted assemblage structure (see 'Results'), and because temperature and salinity covary with region and season, we performed separate analyses for each of the 4 region by season combinations. We utilized temperature and salinity at 20 m for subsequent analyses because previous research on the vertical distribution of fish larvae in pre-transformation stages in California and Oregon showed that peak concentrations are at approximately this depth for most of the most abundant taxa (Ahlstrom 1959, Auth et al. 2007). The correlation between temperature and salinity at 20 m was low to moderate in each region by season combination ( $R^2 = 0.03$  to  $0.52$ ), so we retained both variables for subsequent analyses. In

addition, many studies have demonstrated that ichthyoplankton assemblage composition can change from near the shore to the edge of a continental shelf, due, in part, to depth preferences of adult fishes (Young et al. 1986, Hernandez-Miranda et al. 2003). Thus, we included depth as a covariate to help characterize cross-shelf larval fish spatial distribution patterns.

We also examined how 3 large-scale environmental indices that are known to affect biological conditions in the CCS (Moser et al. 1987, Parnel et al. 2008, Auth 2011, Auth et al. 2011) impacted local environmental conditions and assemblage dynamics. Specifically, we calculated from each region by season combination (March, April, May for spring and June, July, August for summer) values of the Multivariate El Niño Southern Oscillation Index (MEI), which is used to assess the magnitude of El Niño-La Niña conditions; the Upwelling Index (UPW) from Oregon ( $45^\circ$  N,  $125^\circ$  W) and southern California ( $33^\circ$  N,  $119^\circ$  W); and outflow from the Columbia River (COL) as measured at the Bonneville Dam 235 km upstream of the mouth of the river in Oregon. These indices were downloaded from publically available websites (MEI: [www.cdc.noaa.gov/ENSO/enso.mei\\_index.html](http://www.cdc.noaa.gov/ENSO/enso.mei_index.html), UPW: [www.pfeg.noaa.gov/products/las.html](http://www.pfeg.noaa.gov/products/las.html), COL: [www.cbr.washington.edu/dar/query/river\\_daily](http://www.cbr.washington.edu/dar/query/river_daily)).

We first examined the degree to which mean values of temperature and salinity for each region by year combination and the large-scale environmental indices fluctuated during the study, and the degree to which these variables were correlated with each other. For all subsequent analyses of the effect of environment on assemblages or individual taxa, we utilized individual stations as the sample unit as opposed to means from a particular cruise. To quantify how well the local environmental covariates explained assemblage variability among stations, we assessed the amount of variation (adjusted  $R^2$ ) and significance (based upon 1000 permutations) of an assemblage ~depth+salinity+temperature RDA model. Because our dataset spanned only 8 yr, we took a conservative approach (to avoid overfitting) when including the large-scale covariates in the models. Specifically, we evaluated how much additional variation could be explained by including into the RDA models indices of MEI, UPW and, in Oregon, the COL, and conducting variance partitioning to determine the unique and shared effects of the local versus large-scale environmental measures. Thus, we were able to assess the degree to which the large scale indices explained variability that was not captured by the *in situ* measurements.

We followed this with an analysis to determine whether the environmental parameters affected the presence or absence of individual taxa that were found in at least 20% of the stations in each region or season. For each of these taxa, we tested the relative plausibility (based on  $AIC_c$  scores) of 7 logistic models (i.e. depth, salinity, temperature, depth+salinity, depth+temperature, temperature+salinity, depth+temperature+salinity) in predicting their presence or absence in each of the 4 region by season combinations. Logistic models were utilized because the data were zero-inflated for most taxa. We initially explored the utility of generalized additive models (GAMs), but ultimately chose to use linear models because these typically performed as well as the GAMs and are more readily interpretable. We used model averaging, where parameter estimates are weighed by the relative strength of each candidate model, to determine mean slopes and 95% confidence intervals for each parameter for each taxon (Burnham & Anderson 2002). To discern how well the models fit the data, we calculated the area under the receiver operating characteristic (ROC) curve (AUC) for the full model (depth+temperature+salinity). The AUC statistic measures the degree to which a model fits the sample data (Fawcett 2006, Zwolinski et al. 2011). If an AUC value is 1, this indicates that the model predicted perfectly the presence or absence of a given taxon. Conversely, a score of 0.5 indicates that the model did no better than random in predicting the presence or absence of each of the modelled taxa. Notably, we tested whether results differed if the *in situ* environmental variables were taken from the surface or integrated from the surface to 100 m. Because results were qualitatively similar when using the covariates from various depths (see Supplement 3 at [www.int-res.com/articles/suppl/m506p193\\_supp.xls](http://www.int-res.com/articles/suppl/m506p193_supp.xls) and Table S2 in Supplement 1), we present only results from measurements at 20 m.

As with the multivariate analyses, we used a conservative approach to evaluate which large-scale parameters may have affected each taxon. Specifically, we determined if the large-scale indices improved model performance by comparing AUC scores from the full model utilizing only the *in situ* measurements with a model containing both the local and large-scale (depth+temperature+salinity+MEI+UPW+COL; COL was excluded in California) covariates. For taxa where AUC scores increased by at least 10% when large-scale indices were included, we performed a stepwise logistic regression (in both directions) where model efficacy was assessed based on AIC scores. We then recorded the large-scale

indices that were significant and whether the variable was positively or negatively correlated with the presence of particular taxa.

### Coherence in fluctuation

The final goal was to evaluate whether interannual trends for taxa that are common in both Oregon and California were similar among regions. Five taxa were found in at least 20% of the stations in both Oregon and California in at least one of the seasons: northern anchovy *Engraulis mordax*, northern lampfish *Stenobranchius leucopsarus*, eared blacksmelt *Lipolagus ochotensis*, slender sole *Lyopsetta exilis* and *Citharichthys* spp. In addition, *Sebastes* spp. were common in both regions and thus we compared their dynamics even though it is likely that different species are found between regions. To determine if taxa fluctuate synchronously between Oregon and California, we first calculated (1) the proportion of stations at which each of the 6 taxa occurred, and (2) compared the mean larval densities of a given taxon among years within each region by season combination. Next, we conducted a linear correlation of these variables among years for each taxon between regions in spring and summer. In addition, we assessed whether environmental parameters fluctuated in concert between regions by correlating mean temperature  $\text{yr}^{-1}$  and  $\text{season}^{-1}$ , and mean salinity  $\text{yr}^{-1}$  and  $\text{season}^{-1}$  between Oregon and California. To account for multiple tests, we used a sequential Bonferroni correction to adjust the significance thresholds (Rice 1989).

All statistics were performed and graphs created with R v.3.0.0 ([www.r-project.org](http://www.r-project.org)). The ROCR package (Sing et al. 2005) was used to obtain AUC scores; the vegan package (Oksanen et al. 2012) for PCA, RDA, and variance partitioning analyses; and the  $AIC_c$  package (Mazerolle 2013) for model-averaging. All of the plots were made using ggplot2 (Wickham 2009) except for the 2-way cluster plots, which were created with latticeExtra (Sarkar & Andrews 2012).

## RESULTS

### Regional, seasonal and interannual variation

Assemblage structure was affected by both region and season (Table 1) as evidenced from both PCA (Fig. 2) and hierarchical cluster (Fig. 3) analyses. Further, permutation-based multivariate ANOVA indi-

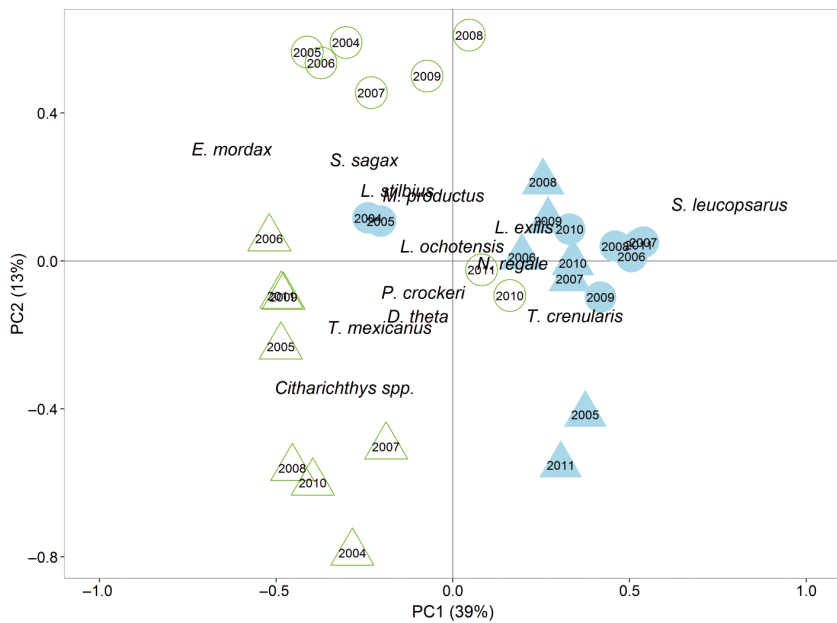


Fig. 2. Principal component analysis of sample (region by season by year combinations) and species scores on the first 2 principal components. Circles are from spring and triangles from summer. Filled icons are from Oregon and unfilled from California. Loadings are given in parentheses for each axis. To enhance readability, only the scores of the most important taxa are presented

cated that the region+season model was highly significant (adj.  $R^2 = 0.34$ ,  $p < 0.005$ ). Variance partitioning indicated that assemblage structure was influenced more by region alone (i.e. region with season partitioned out; partial RDA adj.  $R^2 = 0.27$ ,  $p < 0.005$ ) than season alone (adj.  $R^2 = 0.08$ ,  $p < 0.005$ ).

Despite the geographic separation and statistical differences between regions and seasons, some taxa were common in samples from both California and Oregon (Table 2). In spring, *Stenobranchius leucopsarus* (which utilizes oceanic habitat) was the most frequently occurring species off both Oregon (found in 78% of samples) and California (75%), *Engraulis*

Table 1. Redundancy analysis (RDA) model selection based on Akaike's Information Criterion (AIC) values where  $k$  is the number of parameters in a model and  $\Delta AIC$  the difference between a given model and the one with the lowest AIC score. The adjusted  $R^2$  and  $p$ -values for the top model are based on a permutation-based ANOVA

Model	$k$	AIC	$\Delta AIC$	Adj $R^2$	$p$
Region + season	3	-29.55379	0	0.34	<0.005
Region	2	-26.87035	-2.68344		
Season	2	-19.87001	-9.68378		
No covariates	1	-18.51482	-11.03897		

*mordax* (coastal–oceanic) ranked fourth off California (60%) and sixth off Oregon (32%), *Citharichthys* spp. (coastal) were eighth off California (33%) and fifth off Oregon (38%) (Table 2). Inter-regional differences were driven largely by variability in the presence of California smoothtongue *Leuroglossus stilbius* (coastal–oceanic; 67% in spring California, absent in Oregon), Pacific sardine *Sardinops sagax* (coastal–oceanic; 38% in spring California, absent in Oregon), Pacific hake *Merluccius productus* (coastal–oceanic; 59% in spring California, 3% in spring Oregon) blue lanternfish *Tarletonbeania crenularis* (oceanic; 9% in California, 42% in Oregon), and pinpoint lampfish *Nannobranchium regale* (oceanic; 32% in spring Oregon, <5% off California) (Table 2). Seasonal variation was generally characterized by a decrease in the proportion of stations occupied by most taxa from spring to summer (Table 2). However, the presence of some oceanic (e.g. Mexican lampfish *Triphoturus mexicanus*, California headlightfish *Diaphus theta*) and coastal (mussel blenny *Hypsoblennius jenkinsi*, bass *Paralabrax* spp., blacksmith *Chromis punctipinnis*) taxa off California, and one oceanic species off Oregon (northern flashlightfish *Protomyctophum thompsoni*) increased between spring and summer (Table 2).

Ichthyoplankton assemblages displayed seasonal variation that was regionally distinct (Figs. 2 to 4). For example, *E. mordax*, *S. leucopsarus* and *S. sagax* were abundant in California spring samples in most years (Fig. 4). In 2010 and 2011, however, the California spring assemblage diverged from other years due largely to a lack of *E. mordax* and *S. sagax* (Figs. 2 to 4). Conversely, *E. mordax* were usually absent or relatively uncommon off Oregon but were more abundant than all other taxa combined in spring 2004 and 2005 (Figs. 3 & 4). Indeed, the cluster analysis (Fig. 3) indicated that the 2004 and 2005 Oregon assemblage grouped more closely with California than other Oregon assemblages. Other notable assemblage splits included California summers 2004, 2007, 2008 and 2010 that had reduced influence of *S. sagax* and *E. mordax* relative to other California summers, and Oregon summers 2005 and 2011 where *E. mordax* were absent but *T. crenularis* were relatively important (Fig. 3).

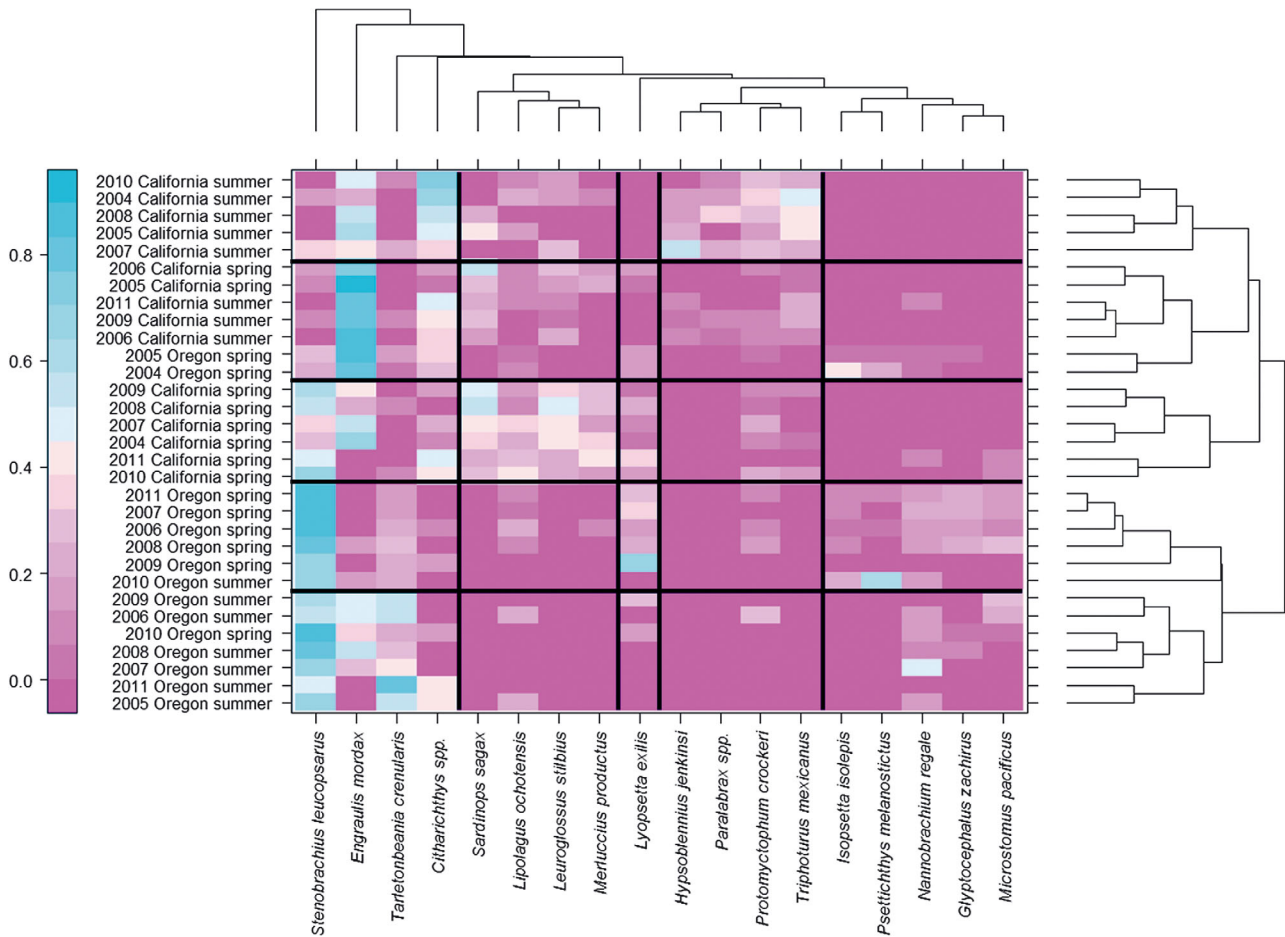


Fig. 3. Two-way cluster analysis grouping taxa (top; label on bottom) and cruises (right; labels on left) with a heat map depicting Hellinger-transformed values for each taxon. These values range from 0 to 1 and are depicted on the figure by the color of each unique year by region by season by taxon combination, where low values are in pink and high values in blue. Black lines are used to help visualize strong clustering of particular taxa (vertical lines) and cruises (horizontal lines)

### Impact of environment

The study period included both El Niño (spring and summer of 2004, 2005 and 2009; spring 2010; summer 2006) and La Niña (spring 2008 and 2011; summer 2010) conditions as depicted by the MEI (Fig. 5). Mean temperature at 20 m depth was much more variable in Oregon (mean spring range = 8.4 to 12.5°C; summer range = 8.7 to 13.0°C) than California (spring = 13.2 to 13.95°C; summer = 14.8 to 17.3°C) between 2004 and 2011 (Fig. 5). UPW was relatively high in California in spring 2008 and 2009 and in summer 2010, and was more variable in California than Oregon during spring. In Oregon, UPW during the summer was relatively high in 2006 and low in 2007. COL was also variable with high outflow in spring 2006 and 2011 and summer 2011. There was a clear response of local conditions to larger-

scale variability in spring as temperature correlated positively with the MEI in both Oregon and California (Table 3), and mean salinity correlated positively with UPW in California. The influence of large-scale processes on local conditions was less pronounced in summer but there was a positive correlation between UPW and salinity in Oregon (Table 3).

Redundancy analysis showed that more of the variation in assemblage structure among individual sampling stations was explained by the local environmental variables off Oregon (adj.  $R^2$  spring = 0.27,  $p < 0.001$ ; summer = 0.13,  $p < 0.001$ ) than off California (adj.  $R^2$  spring = 0.08,  $p < 0.001$ ; summer = 0.09,  $p < 0.001$ ). Variance partitioning examining the contribution of the *in situ* environmental measurements and larger-scale indices indicated that the local variables always explained more of the overall variation than the indices, and that influence of the large-scale



Table 2. Species rankings by proportion of stations occupied in each region during spring and summer. Only species found in at least 5% of samples in at least 1 region by year are shown. Taxa are sorted based first on their rank in spring, California then by spring, Oregon (for taxa that did not occur during spring off California) and color-coded by the magnitude of their occurrence

Scientific name	Common name	Adult habitat affinity	California		Oregon	
			Spring	Summer	Spring	Summer
<i>Stenobranchius leucopsarus</i>	Northern lampfish	Oceanic	0.75	0.08	0.78	0.5
<i>Sebastes</i> spp.	Rockfish	Coastal	0.71	0.23	0.76	0.52
<i>Leuroglossus stilbius</i>	California smoothtongue	Coastal–oceanic	0.67	0.08	0	0
<i>Engraulis mordax</i>	Northern anchovy	Coastal–oceanic	0.6	0.38	0.32	0.21
<i>Merluccius productus</i>	Pacific hake	Coastal–oceanic	0.59	0.01	0.03	0
<i>Lipolagus ochotensis</i>	Eared blacksmelt	Oceanic	0.45	0.09	0.22	0.03
<i>Sardinops sagax</i>	Pacific sardine	Coastal–oceanic	0.38	0.11	0	0
<i>Citharichthys</i> spp.	Sanddab	Coastal	0.33	0.33	0.38	0.08
<i>Lyopsetta exilis</i>	Slender sole	Coastal–oceanic	0.22	0	0.68	0.02
<i>Protomyctophum crockeri</i>	California flashlightfish	Oceanic	0.22	0.16	0.07	0.05
<i>Sebastes jordani</i>	Shortbelly rockfish	Coastal	0.19	0	0	0
<i>Nannobranchium ritteri</i>	Broadfin lampfish	Oceanic	0.12	0.08	0	0
<i>Tarletonbeania crenularis</i>	Blue lanternfish	Oceanic	0.09	0.03	0.42	0.42
<i>Triphoturus mexicanus</i>	Mexican lampfish	Oceanic	0.09	0.24	0	0
<i>Trachurus symmetricus</i>	Jack mackerel	Coastal–oceanic	0.09	0.03	0	0
<i>Rhinogobiops nicholsii</i>	Blackeye goby	Coastal	0.08	0.04	0	0.02
<i>Cataetyx rubrirostris</i>	Rubynose brotula	Coastal	0.08	0	0	0
<i>Parophrys vetulus</i>	English sole	Coastal	0.07	0	0.04	0
<i>Bathylagoides wesethi</i>	Snubnose blacksmelt	Oceanic	0.06	0.06	0	0
<i>Danaphos oculatus</i>	Bottlelight	Oceanic	0.05	0.06	0	0
<i>Scomber japonicus</i>	Pacific mackerel	Coastal–oceanic	0.05	0.03	0	0
<i>Argentina sialis</i>	Pacific argentine	Coastal	0.05	0.01	0	0
<i>Paralichthys californicus</i>	California halibut	Coastal	0.05	0.06	0	0
<i>Argyropelecus sladeni</i>	Lowcrest hatchetfish	Oceanic	0.05	0.02	0	0
<i>Cyclothone signata</i>	Showy bristlemouth	Oceanic	0.05	0.02	0	0
<i>Microstomus pacificus</i>	Dover sole	Coastal	0.03	0.01	0.19	0.03
<i>Symbolophorus californiensis</i>	California lanternfish	Oceanic	0.03	0.06	0	0
<i>Icichthys lockingtoni</i>	Medusafish	Coastal–oceanic	0.03	0.01	0.07	0
<i>Chauliodus macouni</i>	Pacific viperfish	Oceanic	0.03	0.06	0.04	0.02
<i>Pleuronichthys verticalis</i>	Hornyhead turbot	Coastal	0.03	0.06	0	0
<i>Diaphus theta</i>	California headlightfish	Oceanic	0.01	0.12	0.03	0.02
<i>Nannobranchium regale</i>	Pinpoint lampfish	Oceanic	0.01	0.03	0.32	0.16
<i>Icosteus aenigmaticus</i>	Ragfish	Coastal–oceanic	0.01	0	0.13	0
<i>Glyptocephalus zachirus</i>	Rex sole	Coastal–oceanic	0	0.01	0.28	0.02
<i>Liparis fucensis</i>	Slipskin snailfish	Coastal	0	0	0.22	0.05
<i>Isopsetta isolepis</i>	Butter sole	Coastal	0	0	0.14	0.02
<i>Psettichthys melanostictus</i>	Sand sole	Coastal	0	0	0.14	0.02
<i>Sebastolobus</i> spp.	Thornyhead	Coastal–oceanic	0	0	0.14	0
<i>Artedius harringtoni</i>	Scalyhead sculpin	Coastal	0	0	0.07	0.05
<i>Ronquilus jordani</i>	Northern ronquil	Coastal	0	0	0.06	0
<i>Ruscarius meanyi</i>	Puget Sound sculpin	Coastal	0	0	0.04	0.02
<i>Protomyctophum thompsoni</i>	Northern flashlightfish	Oceanic	0	0	0.03	0.08
<i>Hypsoblenius jenkinsi</i>	Mussel blenny	Coastal	0	0.09	0	0
<i>Paralabrax</i> spp.	Bass	Coastal	0	0.08	0	0
<i>Chromis punctipinnis</i>	Blacksmith	Coastal	0	0.05	0	0

parameters added between 0 and 7% explanatory power to models that considered only local variables (Table 4).

Logistic models of the correlation between local environmental variables (depth, temperature and salinity) and individual taxa revealed several main points (Table 5). First, 95% confidence intervals did not overlap with zero for model-averaged slopes for

the dynamical environmental variables (temperature and salinity) for a higher proportion of the Oregon (spring: 64%, summer: 80%) than California (spring: 30%, summer: 25%) taxa that were present in at least 20% of the samples. Second, with one exception (rex sole *Glyptocephalus zachirus*), the relationship with temperature was positive for Oregon taxa. By contrast, off California in the spring, for the 2 taxa

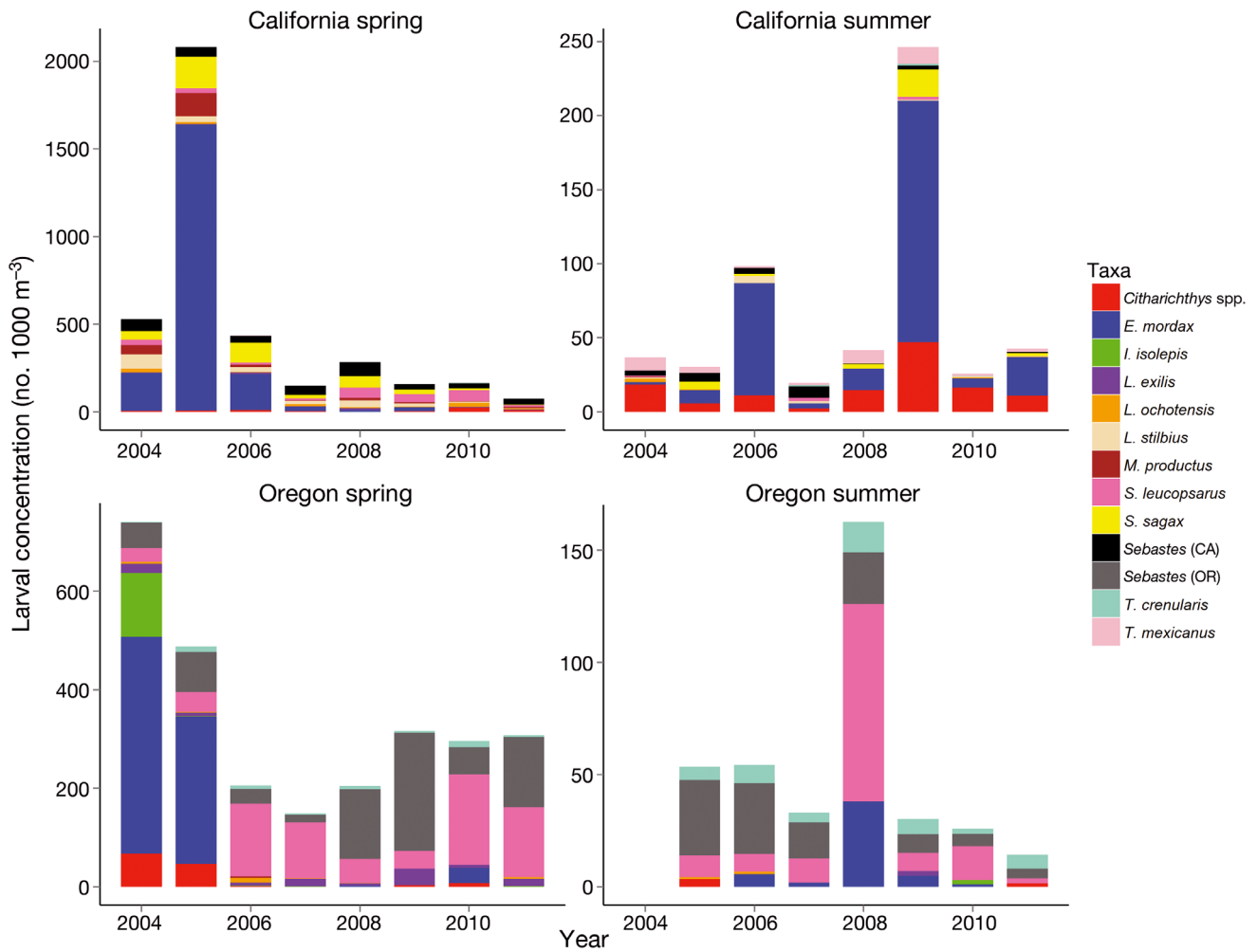


Fig. 4. Mean concentration of the 13 most common taxa in California and Oregon in spring and summer. Samples were not collected in 2004 during the summer in Oregon. See Table 1 for full species names

Table 3. Correlation matrix (Pearson's *r*) of mean temperature and salinity at 20 m and large-scale environmental indices in Oregon and California in spring (below diagonal) and summer (above diagonal). MEI: Multivariate El Niño–Southern Oscillation Index; UPW: Upwelling Index measured off Oregon and California; COL: outflow of the Columbia River

	Temperature	Salinity	MEI	UPW	COL
<b>Oregon</b>					
Temperature	–	–0.80	–0.07	–0.09	–0.03
Salinity	–0.40	–	0.06	0.58	0.16
MEI	0.78	–0.42	–	0.26	–0.23
UPW	–0.11	–0.17	0.48	–	–0.01
COL	–0.55	0.26	–0.78	–0.56	–
<b>California</b>					
Temperature	–	–0.06	0.27	–0.36	
Salinity	–0.60	–	–0.21	0.09	
MEI	0.72	–0.61	–	–0.84	
UPW	–0.50	0.94	–0.40	–	

Table 4. Variance partitioning of redundancy analysis (RDA) models explaining the amount of variation (adj.  $R^2$ ) explained by *in situ* environmental variables (temperature, depth and salinity) alone, by large-scale indices (MEI, UPW in California and MEI, UPW and COL in Oregon; see Table 3 for definitions) alone, and the shared variation between the local and large scale measures

Region	Season	Local   Large	Shared	Large   Local	Total
Oregon	Spring	0.16	0.04	0.07	0.27
Oregon	Summer	0.13	0	0	0.13
California	Spring	0.04	0.01	0.03	0.08
California	Summer	0.07	0	0.02	0.09

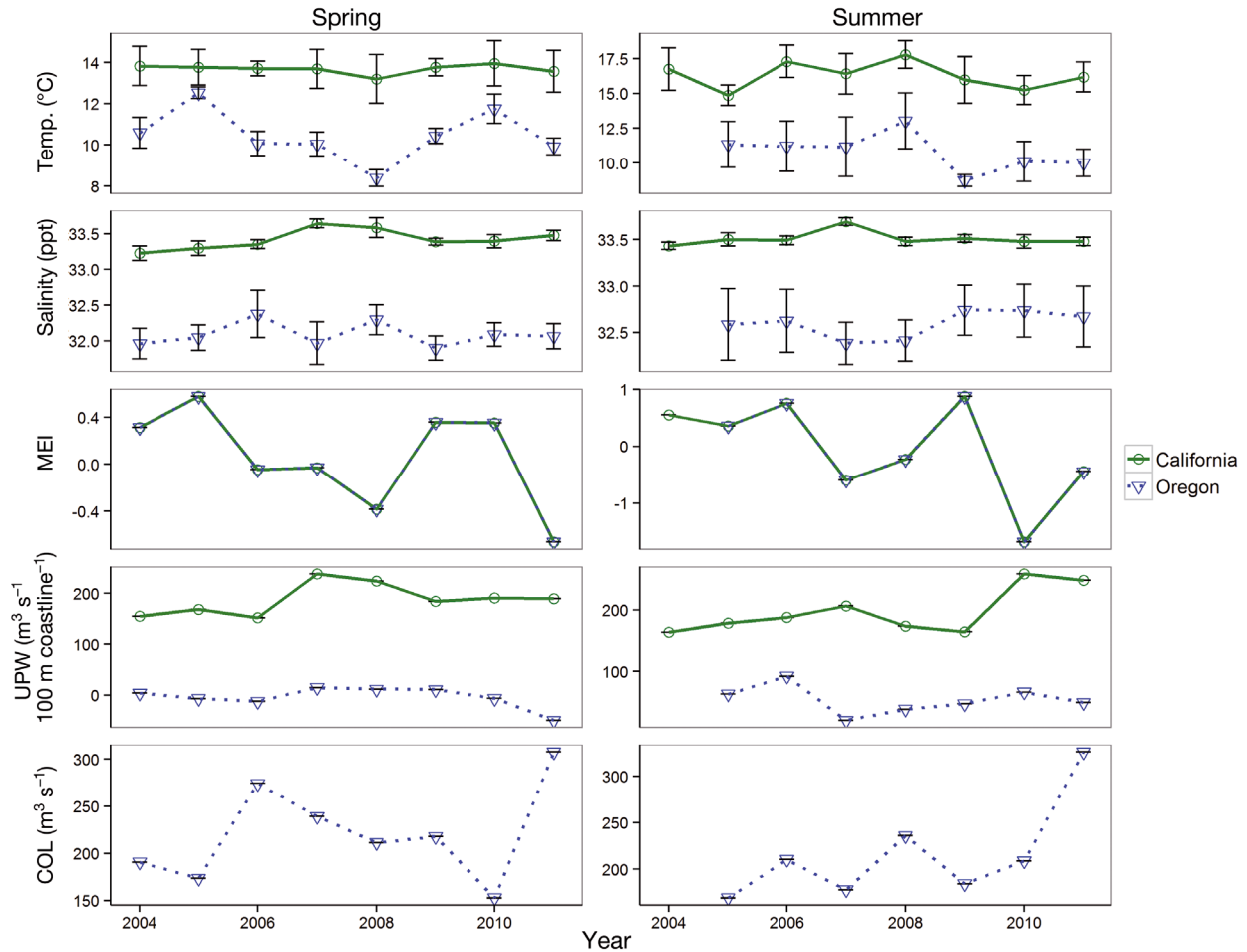


Fig. 5. Mean ( $\pm 2$  SE) values of temperature and salinity among years at 20 m depth, Multivariate El Niño–Southern Oscillation Index (MEI), Upwelling Index (UPW), and Columbia River outflow (COL) in California and Oregon in spring and summer. Spring MEI, UPW and COL values are averaged for March, April and May, and summer values for June, July and August

that exhibited a significant correlation with temperature (*M. productus* and *Sebastes* spp.), the relationship was negative. Third, model performance was much better in Oregon (mean AUC in spring: 0.80, summer: 0.88) than California (spring: 0.68, summer: 0.71). In particular, for taxa found in both regions (*Citharichthys* spp., *E. mordax*, and *S. leucopsarus*), the relationship with temperature and salinity was stronger off Oregon than California.

Inclusion of the large-scale indices improved model performance by more than 10% for 7 of the 30 models. The impact of the large-scale covariates was most evident for *E. mordax*, as the presence of this species correlated positively with MEI in spring in both California and Oregon and in summer in California. In addition, in Oregon in spring, COL correlated positively with the presence of *L. ochotensis*, UPW correlated positively with *Microstomus pacificus*, and MEI negatively with *N. regale*. In California during the

spring, UPW correlated positively with the presence of *Citharichthys* spp.

### Coherence in fluctuation

There was not much evidence that taxa fluctuated synchronously in Oregon and California between 2004 and 2011. Of the 6 taxa that were compared, only the proportion of sites per year in which *L. exilis* was found in spring correlated positively between regions. The proportion of stations occupied per year by *S. leucopsarus* did exhibit a negative correlation in spring, but this relationship was not significant following the sequential Bonferroni adjustment (Table S3 in Supplement 1). None of the correlations of mean taxon concentration per year were significant. In addition, none of the correlations between the environmental variables were significant, although

Table 5. Individual taxon slopes (95% confidence intervals) and area under curve (AUC) scores for the environmental variables by region by season for the dominant species. The 95% confidence intervals for values in **bold** do not overlap with zero. See Table 3 for abbreviations

Species	Model-averaged slope			AUC		Significant large-scale parameters
	Depth	Temperature	Salinity	Depth + temperature + salinity	Depth + temp. + salinity + MEI + UPW + COL	
<b>Oregon spring</b>						
<i>Citharichthys</i> spp.	<b>-0.0044 (-0.0076 to -0.0013)</b>	<b>1.1 (0.56 to 1.7)</b>	0.9 (-0.85 to 2.7)	0.88	0.90	
<i>Engraulis mordax</i>	<b>-0.0023 (-0.0045 to -6.9e-05)</b>	<b>0.92 (0.43 to 1.4)</b>	0.43 (-1.4 to 2.2)	0.80	0.90	MEI (+)
<i>Glyptocephalus zachirus</i>	<b>0.0024 (8e-04 to 0.004)</b>	<b>-0.58 (-1.1 to -0.098)</b>	-0.97 (-2.8 to 0.88)	0.79	0.84	
<i>Liparis fucensis</i>	0.0011 (-0.0013 to 0.0015)	-0.043 (-0.44 to 0.35)	-0.59 (-2.2 to 1)	0.61	0.66	
<i>Lipolagus ochotensis</i>	0.001 (-0.00029 to 0.0023)	0.39 (-0.029 to 0.82)	0.78 (-1 to 2.6)	0.72	0.85	
<i>Lypopsetta exilis</i>	0.00035 (-0.001 to 0.0017)	0.27 (-0.14 to 0.68)	<b>-2.7 (-4.8 to -0.66)</b>	0.76	0.82	COL (+)
<i>Microstomus pacificus</i>	<b>0.003 (0.0012 to 0.0049)</b>	-0.51 (-1.1 to 0.075)	-2.2 (-4.8 to 0.37)	0.85	0.94	MEI (-), UPW (+)
<i>Nannobranchium regale</i>	<b>0.0015 (0.00016 to 0.0028)</b>	<b>0.49 (0.09 to 0.89)</b>	0.58 (-1.1 to 2.3)	0.75	0.86	MEI (-), UPW (+)
<i>Sebastes</i> spp.	<b>0.0055 (0.00068 to 0.01)</b>	<b>0.62 (0.016 to 1.2)</b>	-4 (-7.3 to -0.75)	0.91	0.91	
<i>Stenobranchius leucopsarus</i>	<b>0.038 (0.0018 to 0.073)</b>	<b>1.8 (0.34 to 3.2)</b>	1.6 (-1.8 to 5)	0.97	0.97	
<i>Tarletonbeania crenulans</i>	<b>0.0018 (0.00034 to 0.0032)</b>	<b>0.65 (0.23 to 1.1)</b>	0.58 (-1.1 to 2.3)	0.79	0.82	
<b>Oregon summer</b>						
<i>Engraulis mordax</i>	-0.00093 (-0.0034 to 0.0015)	<b>0.4 (0.032 to 0.76)</b>	-1.9 (-5.1 to 1.4)	0.80	0.84	
<i>Nannobranchium regale</i>	-0.0011 (-0.0037 to 0.0015)	<b>0.65 (0.2 to 1.1)</b>	0.17 (-4 to 4.3)	0.90	0.92	
<i>Sebastes</i> spp.	<b>0.0038 (0.00064 to 0.0069)</b>	0.32 (-0.16 to 0.79)	-1.2 (-3.5 to 1.1)	0.86	0.86	
<i>Stenobranchius leucopsarus</i>	-0.00053 (-0.0032 to 0.0022)	<b>0.63 (0.11 to 1.2)</b>	-2.5 (-5.8 to 0.69)	0.88	0.91	
<i>Tarletonbeania crenulans</i>	<b>0.0047 (0.00083 to 0.0086)</b>	<b>0.96 (0.19 to 1.7)</b>	2.5 (-1.3 to 6.3)	0.95	0.96	
<b>California spring</b>						
<i>Citharichthys</i> spp.	0.00042 (-0.00029 to 0.0011)	0.097 (-0.29 to 0.48)	0.39 (-2.4 to 3.2)	0.59	0.72	UPW (+)
<i>Engraulis mordax</i>	-0.00048 (-0.0012 to 0.00024)	-0.046 (-0.49 to 0.39)	-2.5 (-5.3 to 0.35)	0.64	0.74	MEI (+)
<i>Leuroglossus stilbicus</i>	<b>0.0014 (0.00053 to 0.0023)</b>	0.0037 (-0.4 to 0.41)	-1.2 (-4.2 to 1.7)	0.76	0.76	
<i>Lipolagus ochotensis</i>	<b>0.0011 (0.00034 to 0.0019)</b>	0.23 (-0.2 to 0.66)	-2.2 (-5.3 to 0.85)	0.73	0.75	
<i>Lypopsetta exilis</i>	-9.9e-05 (-0.00084 to 0.00064)	-0.18 (-0.56 to 0.21)	0.84 (-2 to 3.7)	0.56	0.64	none
<i>Merluccius productus</i>	0.00027 (-0.00049 to 0.001)	<b>-0.69 (-1.2 to -0.17)</b>	<b>-3.5 (-6.9 to -0.027)</b>	0.69	0.74	
<i>Protomyctophum crockeri</i>	0.00078 (-0.00012 to 0.0017)	0.24 (-0.3 to 0.77)	-2.2 (-5.9 to 1.4)	0.69	0.71	
<i>Sardinops sagax</i>	0.00051 (-0.00026 to 0.0013)	0.0071 (-0.48 to 0.5)	-2.8 (-5.9 to 0.34)	0.66	0.70	
<i>Sebastes</i> spp.	<b>0.0021 (0.00085 to 0.0033)</b>	-0.36 (-0.83 to 0.11)	-0.5 (-4.6 to 3.6)	0.79	0.79	
<i>Stenobranchius leucopsarus</i>	<b>0.0011 (0.00026 to 0.0019)</b>	-0.098 (-0.48 to 0.29)	-0.29 (-3.2 to 2.7)	0.71	0.71	
<b>California summer</b>						
<i>Citharichthys</i> spp.	0.00028 (-0.00037 to 0.00094)	0.11 (-0.11 to 0.33)	-1.6 (-5.1 to 1.9)	0.59	0.59	
<i>Engraulis mordax</i>	<b>-0.0011 (-0.0019 to -0.00028)</b>	-0.2 (-0.46 to 0.065)	-0.74 (-4.6 to 3.1)	0.73	0.80	MEI (+)
<i>Sebastes</i> spp.	<b>0.00098 (2e-04 to 0.0018)</b>	-0.21 (-0.51 to 0.095)	4 (-0.44 to 8.5)	0.74	0.79	
<i>Triphoturus mexicanus</i>	-0.00072 (-0.0017 to 0.00023)	<b>0.51 (0.2 to 0.82)</b>	-3.4 (-7.9 to 1.1)	0.77	0.77	

mean temperature was positively correlated between regions in spring, but was not significant following the Bonferroni adjustment.

## DISCUSSION

Our study produced several insights into the dynamics of ichthyoplankton assemblages throughout the CCS. First, although there was an overall difference in assemblage structure between regions, the degree of differentiation (when controlling for seasonality) was quite variable among years. Indeed, in some years the Oregon and California assemblages were very similar and dominated by the same species: *Engraulis mordax* and *Stenobranchius leucopsarus*. Second, the interannual variation in assemblages off Oregon correlated well with temperature and/or salinity; in years when the water off Oregon was relatively warm, taxa that were more commonly associated with California tended to become important in the Oregon assemblage. By contrast, although assemblage structure also changed greatly among years off California, this variability was relatively poorly correlated with environmental covariates. Third, there was no indication that taxa common to both regions fluctuated in concert.

Our finding that the ichthyoplankton assemblages differed overall between Oregon and California was not wholly surprising as the sampling regions were separated by more than 1000 km, and there are 2 potential biogeographic barriers (Point Conception and Cape Mendocino) separating the sites. Although this is the first comparative analysis of ichthyoplankton assemblage dynamics between these 2 regions, several studies have examined the spatial structure of marine fishes off the coast of California. For example, both Loeb et al. (1983) and Sunstov et al. (2011) detected shifts in ichthyoplankton assemblage structure at Point Conception, supporting previous research on marine biogeography of fishes on the west coast of North America that suggests Point Conception separates Oregonian from San Diegan zoogeographic provinces (reviewed by Horn et al. 2006). In addition, Cape Mendocino was recently identified as an impediment to gene flow for multiple intertidal organisms with pelagic early life history stages (Kelly & Palumbi 2010). In the northern CC region, ichthyoplankton assemblages differed among Washington–Oregon, the Gulf of Alaska, and the Southeast Bering Sea (Doyle et al. 2002). In addition, Auth (2008) documented latitudinal variability in ichthyoplankton assemblage structure between northern California

and northern Oregon. Thus, our results build on previous research documenting latitudinal variability in ichthyoplankton assemblage structure within the CCS. A goal for future research will be to regularly sample the area between Oregon and Washington to better define the precise locations where breaks in assemblage structure occur in different years.

Spatial variation in ichthyoplankton assemblages has also been found in other boundary current systems. For example, larval fish assemblages within the Benguela Current System off the coast of Namibia changed dramatically over a relatively short distance across the Angola-Benguela frontal zone (John et al. 2001, 2004). Similarly, larval fish composition changed significantly within the East Australian Current (EAC) in the region where the southward-flowing EAC abutted the cooler Tasman Sea (Keane & Neira 2008). Further, a latitudinal change in assemblage structure from samples collected over the continental shelf was detected within the Leeuwin Current off Western Australia (Holliday et al. 2012). These results from boundary current systems around the world provide insight into how fish assemblages can change in a marine environment even in the absence of obvious barriers to dispersal during either adult or early life history stages.

In addition to the effect of latitude on assemblage structure, we found that seasonality impacted the ichthyoplankton assemblages off both California and Oregon. Specifically, the presence of all taxa off Oregon and most off California declined between spring and summer, suggesting that spawning by many marine teleosts occurs in spring in these areas. A decline in larval abundance and diversity was also documented between spring and summer at 2 near-shore stations in Oregon (Brodeur et al. 2008) and throughout California (Loeb et al. 1983, Moser et al. 2001). This likely reflects an evolutionary strategy of fishes to time reproduction with the availability of resources for feeding larvae following the spring transition, when upwelled nutrients stimulate phytoplankton blooms and thus provide a food source for the larvae (Cushing 1975). In both regions, however, the presence of a number of oceanic taxa (California: *Triphoturus mexicanus* and *Diaphus theta*; Oregon: *Nannobranchium regale*) increased during summer. These fishes are associated with offshore water that can intrude shoreward when coastal upwelling and/or offshore transport is low (Auth 2008, Thompson et al. 2012). In addition, the presence of some coastal taxa (e.g. *Hypsoblennius jenkinsi*, *Paralabrax* spp. and *Chromis punctipinnis*) in California increased during the summer, suggesting that these taxa have

a different life history strategy than the majority of coastal taxa (Sunstov et al. 2011).

Seasonality was also identified as an important factor affecting ichthyoplankton assemblage composition in other boundary current ecosystems. For example, larval assemblages differed significantly in the Leeuwin Current off southwestern Australia between winter and summer (Muhling & Beckley 2007, Beckley et al. 2009) and changed seasonally within the EAC in southeastern Australia (Gray & Miskiewicz 2000, Keane & Neira 2008). In addition, seasonal variation in larval fish assemblage structure was detected in the Gulf Stream off the east coast of the United States (Marancik et al. 2005), the Agulhas Current off southeast Africa (Harris et al. 1999), the Benguela Current off southwest Africa (Olivar & Shelton 1993), the Canary Current off northwest Africa (Rodriguez et al. 2009, Moyano & Hernandez-Leon 2011) and the Humboldt Current off of the west coast of South America (Hernandez-Miranda et al. 2003, Landaeta et al. 2008). These results highlight the need to be cognizant of seasonal effects when evaluating interannual change in ichthyoplankton assemblage structure.

Although we detected overall differentiation in taxonomic composition between California and Oregon, the assemblages varied considerably interannually within each season and region, and were actually quite similar between the regions in some years. To our knowledge, this is the first study to evaluate how ichthyoplankton assemblage structure changed over multiple years (when controlling for season) in such widely separated portions of a boundary current ecosystem. However, several researchers have documented the dynamic nature of ichthyoplankton assemblages in relatively spatially-restricted portions of various boundary current systems around the world. For example, off the west coast of North America, interannual changes in assemblage composition was documented near the southern extent of the of the CCS in the 1950s by Moser et al. (1987) and in the early 1980s by Funes-Rodriguez et al. (2006); off southern California in the mid-2000s by Thompson et al. (2012); off Oregon and Washington between 1999 and 2004 by Parnel et al. (2008); and off Alaska from 1996 to 2000 by Duffy-Anderson et al. (2006). In a relatively long-term study (1964 to 1983), Loeb & Rojas (1988) also found dramatic interannual changes in larval assemblage structure in the Humboldt Current off the coast of northern Chile; these dynamics were highlighted by changes of multiple orders of magnitude in the abundance of commercially important pelagic fishes such as *Sardinops sagax* and anchovetta

*Engraulis ringens*. In addition, larval assemblages changed significantly within the Labrador Current in the North Atlantic offshore of Canada between the summers of 2000 and 2003 (Evseenko et al. 2006). These findings stress the importance of developing a long time-series to adequately describe the composition of fish assemblages in marine ecosystems.

Given the propensity of ichthyoplankton assemblages to exhibit large interannual changes, an important question is whether we can determine the factors that drive this variation. In the present study, we found that taxa–environment relationships are affected strongly by the geographic location of the sampling sites. Specifically, variability in temperature and salinity at 20 m explained much more of the variation in the overall ichthyoplankton assemblage structure in Oregon than California. Further, the presence of taxa found in both locations (e.g. *E. mordax*, *Citharichthys* spp., *S. leucopsarus* and *Lipolagus ochotensis*) exhibited higher correlation with temperature-salinity variation in northern than southern locations. In one of the few studies to examine marine population dynamics across a similar geographic region, Broitman et al. (2008) found that the relationship between sea surface temperature and recruitment patterns of 3 species of intertidal invertebrates differed regionally between Washington and California, and that in general the correlation was positive in northern localities. This highlights the need for geographically broad-scale sampling to understand trends in fish population dynamics in the CCS.

Previous research in southern portions of the CCS also showed that environmental variability explained only a small amount of the variation in the abundance of fishes that live in coastal or coastal–oceanic habitats. For example, Hsieh et al. (2005) found that the abundance of coastal (e.g. *E. mordax*, *Merluccius productus*) or coastal–oceanic (e.g. *Leuoglossus stilbius*) larvae in southern California did not correlate significantly with environmental fluctuations (e.g. sea surface temperature, the Pacific Decadal Oscillation Index) between 1951 and 2002. Similarly, dynamics of coastal or coastal–oceanic taxa were also not strongly affected by a transition from cooler La Niña to warmer El Niño conditions across California and Baja California between 1954 and 1960 (Moser et al. 1987). By contrast, both Hsieh et al. (2005) and Moser et al. (1987) found that the abundances of oceanic taxa did correlate strongly with environmental change. Because our sampling was restricted to the continental margin, we covered only a very small edge of the habitat of oceanic taxa. However, the only oceanic taxon that was present in at least 10% of

the stations in California during the summer, *T. mexicanus*, correlated positively with temperature. In the spring, the presence of the 3 oceanic taxa in California correlated significantly only with depth, but not temperature or salinity. Thus, in general, the correlations between temperature/salinity and taxon fluctuations were low over the continental shelf off California.

Changing the focus to the northern CC painted a much different picture. Off Oregon, the majority of taxa responded significantly to local environmental variability regardless of whether they had coastal, coastal–oceanic or oceanic habitat affinities. These findings reflect previous analysis of the ichthyoplankton assemblages in the Pacific Northwest (Auth & Brodeur 2006, Brodeur et al. 2006, Auth 2008, 2011, Auth et al. 2011). For example, Auth (2008) found a positive correlation between temperature and the concentration of *Citharichthys* spp. and *E. mordax* larvae from samples collected between 2004 and 2006 from northern California to southern Washington. At a longer time-scale, Brodeur et al. (2008) showed that ichthyoplankton assemblage structure changed significantly between warm and cold periods from 1997 to 2005. These analyses, along with ours, demonstrate that ichthyoplankton sampled over the continental margin are sensitive indicators of variability in ocean conditions in the northern CC.

In addition to the influence of the dynamic environmental factors (temperature and salinity) on the distribution of larval species, we found that a static variable (depth) consistently affected the distribution of many species. Because depth tends to increase away from shore, this reflects cross-shelf changes in assemblage structure. Indeed, several of the oceanic taxa (e.g. *N. regale*, *S. leucopsarus*, *Tarletonbeania crenularis*; Table 1) in our study correlated positively with depth. Notably, our sample area was restricted to the continental margin; had we included samples over the abyssal plain, depth likely would have affected the presence of more taxa. Depth has also been shown to affect ichthyoplankton assemblage composition in many other boundary current regions such as the Leeuwin Current (Muhling & Beckley 2007), the Humboldt Current (Hernandez-Miranda et al. 2003) and the Gulf Stream (Marancik et al. 2005). Thus, variability in bottom depth is clearly a factor that ubiquitously impacts larval fish associated with boundary currents worldwide.

We identified local environmental conditions that predicted the presence of several ichthyoplankton taxa in Oregon and, to a lesser extent, California. Changes in local physical and biological conditions

in the CCS are often induced by El Niño–La Niña events (Brodeur et al. 2005, 2008, Hooff & Peterson 2006, Auth 2008, Auth et al. 2011, McClatchie 2013), and the period during which our study took place included both El Niño (2004, 2005, spring 2010) and La Niña (2008–2009, summer 2010) conditions (Auth 2011, Bjorkstedt et al. 2012). During El Niños, near-shore water temperatures tend to increase and upwelling-favorable, equatorward winds tend to be reduced in the CCS (McClatchie 2013). Indeed, we documented a positive correlation between the MEI and water temperature at 20 m in Oregon and California during the spring. However, with the exception of California in the summer, there was not a strong correlation between the MEI and UPW indices. Upwelling intensity, however, was strongly correlated with salinity in California during the spring. In addition to the intensity of upwelling, the timing of the spring transition can impact local conditions. For example, upwelling-favorable winds were suppressed through early summer 2005, resulting in extremely low upwelling and elevated water temperature through the early part of that year (Brodeur et al. 2006). This elevated water temperature likely increased the abundance and presence of *E. mordax* larvae in 2005. Thus, it appears large-scale El Niño–La Niña and upwelling dynamics affected the fluctuation of local environmental variables that ultimately affected the ichthyoplankton assemblages.

Analysis of the amount of additional variation explained by the large-scale variables over local measurements of temperature, salinity and depth indicated that in most cases the large-scale variables did not have an added large-impact on model performance. In Oregon during spring, however, the unique contribution of the large-scale parameters was relatively important, and AUC scores improved by at least 10% for 4 taxa. It is plausible that the large-scale indices captured effects of environmental conditions that occurred prior to the date of collection (Auth 2011) or that large-scale processes influenced larvae in a manner not reflected by local conditions (Thompson et al. 2012). In particular, 2 taxa in Oregon (*Microstomus pacificus* and *N. regale*) correlated positively with UPW and negatively with MEI, and *Citharichthys* spp. correlated positively with UPW in California during the summer. Because primary production is typically high when upwelling is high and under La Niña conditions, this may be a result of higher food availability. Although we did not have access to consistent measures of primary production for this study, quantifying a proxy for this variable (e.g. chlorophyll *a*) would be valuable for future in-

vestigations. In addition, MEI added additional explanatory power to the presence of *E. mordax* in Oregon during the spring as well as in California in both spring and summer. Because MEI typically correlates positively with temperature, this could reflect the presence of appropriate spawning habitat prior to the implementation of surveys. Finally, the presence of *L. ochotensis* correlated positively with COL. This species typically resides in deep shelf and oceanic habitat; it is thus possible that it moved into the study area to feed within the river plume where primary production tends to be relatively high in years with high outflow. Overall, these findings suggest that oceanographic factors occurring on a different spatial or temporal scale from the *in situ* measurements might have influenced the ichthyoplankton assemblages.

Although temperature at 20 m correlated positively with MEI in California, the El Niño–La Niña contrasts between 2004 and 2011 did not induce large fluctuations in temperature and salinity at 20 m in California (particularly in spring). By contrast, the range of temperature variation in Oregon was much greater over this period. This may partly explain the lack of response of most taxa to the local environmental dynamics in California. It is possible that a more clear response to El Niño-induced environmental fluctuation (and ichthyoplankton reaction) would have been evident in southern California if these oscillations were more extreme. For example, changes in the ichthyoplankton assemblage were documented in the southern portions of the CCS during the stronger El Niños of 1957–1958 (Moser et al. 1987, Watson et al. 2002, Moser & Watson 2006) and 1997–1998 (Funes-Rodriguez et al. 2011). Future comparative analyses that include more extreme El Niño events would shed further light on how assemblages in Oregon and California are affected by this large-scale event.

We found that shifting water temperatures greatly affected the structure of the ichthyoplankton assemblage in Oregon. Discerning how environmental parameters affect ichthyoplankton assemblage dynamics is an active area of research throughout the world. A common finding from many of these studies is that pelagic fishes often associate with water masses that are characterized by specific environmental conditions, and that movement of these water masses can change the spatial distribution of these fishes. For example, shifting boundaries of the warm EAC and cool Tasman Sea waters off New South Wales, Australia predictably influenced the distribution of ichthyoplankton assemblages between October 2002 and 2004 (Keane & Neira 2008). In addition,

the distribution of ichthyoplankton changed dramatically in the Benguela Current region off southwestern Africa, as this region is influenced by 3 primary water masses: the cool, northward flowing Benguela Current, and the warm Angolan and Angulhas Currents in the north and south, respectively. As the boundaries of these water masses changed, so did the location of particular pelagic fish assemblages off southeastern Africa (Olivar & Shelton 1993). An analogous result was documented in the Mediterranean Sea, where distinct larval assemblages were associated with cool Atlantic Waters entering the Mediterranean through the Strait of Gibraltar and the warm Mediterranean water off Mallorca Island (Alemany et al. 2006). These results illustrate a mechanism by which the spatial distribution of ichthyoplankton assemblages can shift through time.

Oregon and California assemblages most resembled one another in years when *E. mordax* was common in Oregon, and this species was affected by environmental fluctuation in Oregon but not California. A factor that may have imparted the stronger response of *E. mordax* to temperature variability in the north is that Oregon is closer to the edge of its biogeographical range than California (Lecomte et al. 2004). *E. mordax* spawns in water between 11.5 and 16.5°C (Lluch-Belda et al. 1991), and thus a small reduction in temperature (e.g. 1°C) in Oregon would result in intolerable conditions whereas a comparable reduction in California would still be within the optimal thermal range for this taxon (Fig. 5). Many studies have also demonstrated that species are more sensitive to climate fluctuations when found at the edge rather than center of their biogeographical distribution (Myers 1998). For example, a recent analysis of cod recruitment found that stocks are most sensitive to climatic fluctuation at the southern (warmer) part of their range (Beaugrand & Kirby 2010). Further, Pacific sardine recruitment correlated positively with temperature in the northern, but negatively in the southern extent of their range (Galindo-Cortes et al. 2010). This suggests that biogeographic range of individual taxa is an important factor to consider when studying the response of assemblages to environmental change.

Although assemblages in Oregon and California resembled one another in some years, we did not find evidence of synchronous fluctuation of taxa that were common in both regions. This result differs from past studies that demonstrated that the CCS is highly advective, and that physical or biological conditions varied in tandem across large (1000 km) spatial scales. For example, trends in sea surface tempera-



ture were highly coupled over a 50 yr period across 20° of latitude between southern Baja California and northern California (Mendelssohn & Schwing 2002). Similarly, zooplankton displacement volumes were highly spatially correlated between 1949 and 1969 off of the entirety of the California coast (Bernal & McGowan 1981). A potential explanation for the lack of interregional coupling in ichthyoplankton dynamics in our study is that these 2 regions are not consistently linked by southerly CC flow. The CC originates from the southeastern-flowing North Pacific Current and bifurcates into northward and southward branches when it abuts the west coast of North America. Although the point of contact varies among years (Sydeman et al. 2011), it tends to be just south of the California–Oregon border (Cummins & Freeland 2007), thus potentially disconnecting the sampling regions. Indeed, Mendelssohn & Schwing (2002) found that trends in sea surface temperature north of 40° latitude tended to decouple from the southern parts of the CC. Because the influence of the CC is evident at depth up to 300 m (and we found that temperatures at the surface and at 20 m are significantly correlated; data not shown), it is probable that this divide influences most of the taxa analyzed in our study. Another potential explanation for the lack of interregional cohesion is that trends in wind stress, which affects upwelling intensity, are not spatially coherent through time (Mendelssohn & Schwing 2002). Indeed, there was no correlation between the upwelling index off Oregon and California in spring or summer (Table S4). Finally, the influence of freshwater input could further decouple assemblage dynamics between the 2 regions as the Columbia and other rivers affect the temperature, salinity and turbidity of surface waters in the northern region, whereas a comparable riverine influence is lacking in southern California. The Columbia plume, in particular, is an important spawning ground for *E. mordax* in the northern CCS (Richardson 1980) and supports a fishery for *S. sagax* (Emmett et al. 2005). Although we did not detect a high correlation between COL and temperature at 20 m, the degree of outflow was correlated with water at 3 m in the spring ( $r = -0.83$ ), and it is possible that some taxa were affected by oceanographic conditions near the surface. Further, Auth (2011) detected a positive relationship between the presence of several larval taxa and COL that was lagged by 1 to 2 mo. Thus, it is possible that the Columbia River impacted the assemblage in a way that was not directly evident based on our analyses, and further desynchronized the dynamics of larval fishes in Oregon and California.

From an EBM perspective, most of the taxa we sampled form an important forage base (either in their juvenile or adult stages) for higher trophic level species such as birds and marine mammals (Smith et al. 2011, Pikitch et al. 2014). As such, the large fluctuation in larval concentration that we documented (Fig. 4) has the potential to cascade through the marine food web and impact the growth and survival of top predators. For example, reproduction (Wells et al. 2008) and survival (Ainley et al. 1995) of several piscivorous seabirds has been linked to availability of juvenile rockfishes in the central California region of the CCE. An important question, then, is how does the composition of the larval assemblage in a given year impact higher trophic levels? Thayer & Sydeman (2007) found that the primary prey in the diets of piscivorous rhinoceros auklets *Cerorhinca monocerata* reflected the availability of prey, and that mass of prey as opposed to the actual identity of prey species correlated with fledgling survival. It is largely unknown, however, how shifts in forage composition affects different predator species. For example, *S. leucopsarus*, *Citharichthys* spp., and/or *L. stilbius* were important members of the larval assemblage in some years (Figs. 2 to 4). Because these fish migrate to the surface at night as juveniles and adults and/or are pelagic during their early life history phases (N. Bowlin unpubl. data), they are potentially available for consumption by surface-feeding predators and thus could play an important, yet currently underappreciated role in ecosystem dynamics. Here, we show that the abundance and composition of the forage base for many top marine predators is highly dynamic throughout the CCS; discerning the implications of these shifts in the identity of forage assemblage taxa is an important next step for developing appropriate indicators of ecosystem change.

Another important implication of our results to EBM is that scale has a large impact on our perception of assemblage structure and dynamics. Indeed, a key challenge of integrated ecosystem assessment is to define appropriate scales for management (Levin et al. 2009). Our results show that the dynamics of key taxa and the assemblages in general are largely independent between southern California and Oregon, and therefore this is too large of a scale to consider as a single management unit. Thus, for example, it is unlikely that a change in anchovy population size off California will have any impact on seabird fledgling success in Oregon, as these are essentially separate subpopulations. Indeed, Sydeman et al. (2006) documented almost complete auklet reproductive failure in 2005 in British Columbia and cen-

tral California due to extremely low zooplankton biomass, but high reproductive success in southern California where zooplankton biomass was relatively high. Taken collectively, these results illustrate the need for broad-scale spatial and temporal sampling to fully understand the dynamics of individual taxa, assemblages and ecosystems. A fruitful direction for future work, therefore, would be to delineate in more detail the spatial boundaries within which assemblages fluctuate similarly by sampling at regular, systematic intervals between Oregon and California. This would build on our current research and help better resolve appropriate spatial units for EBM.

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