Dynamic height: A key variable for identifying the spawning habitat of small pelagic fishes

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Abstract

Small pelagic fishes off southern California exhibit interannual variations in the regions they occupy. An enhanced understanding of these fluctuations could improve fisheries management and predictions of fish’s responses to climate change. We investigated dynamic height as a variable for identifying the spawning habitat of northern anchovy (Engraulis mordax), Pacific sardine (Sardinops sagax), and jack mackerel (Trachurus symmetricus). During cruises between 1998 and 2004, dynamic height was calculated from temperature and salinity profiles, while fish egg concentration was measured with obliquely towed bongo nets and the Continuous, Underway Fish Egg Sampler. Dynamic height ranged between 68 and 108 cm, with values increasing offshore. The greatest probability of encountering anchovy, sardine, and jack mackerel eggs occurred at dynamic heights of 79–83 cm, 84–89 cm, and 89–99 cm, respectively. Four mechanisms were proposed to explain how dynamic height affects egg distribution: (1) dynamic height is a proxy for upper water column temperature and salinity, which are known to influence spawning habitat. (2) Low dynamic heights are indicative of coastal upwelling, which increases primary and secondary productivity. (3) Egg concentration is greater at dynamic heights coincident with geostrophic currents that transport larvae to favorable habitats. (4) Eddies delineated by dynamic height contours retain eggs in productive habitats. To evaluate these mechanisms, a generalized linear model was constructed using dynamic height, temperature, salinity, chlorophyll, zooplankton volume, geostrophic currents, and eddies as independent variables. Dynamic height explained more variance than any other variable in models of sardine and anchovy spawning habitat. Together temperature, salinity, and chlorophyll accounted for 80–95% of the dynamic height effect, emphasizing the importance of the first two mechanisms. However, dynamic height remained statistically significant in the models of anchovy and jack mackerel spawning habitat after considering the effects of all other variables. Dynamic height shows promise as an ecological indicator of spawning habitat, because it integrates the effects of multiple oceanic variables, can be remotely sensed, and is predicted by ocean circulation models.

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1. Introduction

Populations of Pacific sardine (Sardinops sagax) and northern anchovy (Engraulis mordax) exhibit decadal-scale fluctuations in abundance related to low-frequency climate oscillations (Schwartzlose et al., 1999; Chavez et al., 2003; Alheit et al., 2009). In the California Current Ecosystem (CCE), these changes in stock size have been accompanied by shifts in the geographic extent of the habitat occupied by these species (MacCall, 1990; Rodríguez-Sánchez et al., 2002). Examining spawning habitat may be propitious for gaining an understanding of how oceanic conditions influence these changes in fish distribution, since the early life history stages of fishes have a narrower tolerance to many environmental conditions than adults (Pörtner and Farrell, 2008).

Temperature has long been identified as a factor affecting sardine spawning habitat. Tibby (1937) first noted that Pacific sardine spawning was limited to temperatures > 13 °C. While temperature can have a profound impact on fish physiology, several researchers have suggested that temperature may be a proxy for other environmental cues that more directly affect sardine (Fiedler, 1983; Jacobson and MacCall, 1995; Rodríguez-Sánchez et al., 2002). Consequently, recent research on spawning habitat of small pelagic fishes has focused on combinations of oceanic variables. Lluch-Belda et al. (1991) found sardines spawn across an array of temperatures, but their eggs only occur within a narrow range of upwelling. In contrast, the spawning habitat of anchovy corresponds to a narrower temperature range, but...
spawning occurs at both high and low upwelling. Checkley et al. (2000) observed that sardine and anchovy eggs are found in water masses with distinct temperatures and salinities. Weber and McClatchie (2010) modeled the relationship between sardine and anchovy eggs and a suite of biological and physical variables, including temperature, salinity, geostrophic flow, mean chlorophyll concentration, and depth of the chlorophyll maximum. Reiss et al. (2008) and Zwolinski et al. (2011) developed models using satellite observations of sea surface temperature (SST), ocean color, and gradients of sea surface height anomalies (SSHa) that accurately predicted seasonal and inter-annual changes in sardine and anchovy spawning area. Similarly, the boundaries of spawning habitat can be delineated by a combination of SST and zooplankton concentration for sardine (Lynn, 2003) and SST and chlorophyll concentration for anchovy (Fiedler, 1983).

One environmental variable related directly or indirectly to almost all of these predictors of spawning habitat is dynamic height. Dynamic height refers to hydrographically based measurements of sea surface height (SSH). Dynamic height is calculated from vertical profiles of temperature, salinity, and pressure that are integrated over the upper water column above a reference depth. In this manuscript, we will use the term dynamic height to specifically refer to these hydrographic measurements, whereas SSH will be used in a more general sense that includes observations from tide gauges and satellite altimetry. Since dynamic height and integrated water column density are inversely proportional (Pond and Pickard, 1995), areas with fresh, warm seawater correspond to high dynamic heights, whereas locations with salty, cool seawater have low dynamic heights. Gradients in dynamic height are also proportional to geostrophic current velocity. As a result, contours of dynamic height can be used to identify eddies and meanders (Soto-Mardones et al., 2004; Stegmann and Schwing, 2007). Seasonal patterns of dynamic height in the CCE are controlled by a combination of heating, cooling, and changes in current direction, with the first two processes exerting a greater influence in offshore areas and the effect of currents dominating in the coastal zone (Lynn and Simpson, 1987).

In the CCE, chlorophyll concentration is negatively correlated with SSH across both seasonal and inter-annual scales (Henson and Thomas, 2007; Venegas et al., 2008). Meandering SSH contours indicating the position of the California Current correspond to a boundary between eutrophic inshore waters with high chlorophyll and offshore waters that are more oligotrophic (Strub and James, 2000). Through bottom-up forcing, this relationship between phytoplankton biomass and SSH can exert an influence on zooplankton abundance (Chelton et al., 1982). Several mechanistic processes can explain these relationships. First, SSH is low where the thermocline shoals, bringing denser water closer to the surface. Since the thermocline and nutricline are frequently co-located, this is a mechanism through which surface nutrient flux can increase phytoplankton concentration in areas with low SSH (Wilson and Adamec, 2002). For example, areas with low SSH often demarcate coastal upwelling in the CCE (Kruse and Huyer, 1983). A second mechanism connecting biological productivity and SSH is transport of nutrients and organisms by currents. Strengthening of the California Current leads to increased zooplankton volume (Chelton et al., 1982) and a concurrent decrease in SSH due to the influx of cooler water (Logerwell et al., 2003). Third, eddies whose boundaries can be delineated by SSH contours are often characterized by increased primary production due to upwelling near their center. Closed circulation in eddies can retain and concentrate plankton (Mackas et al., 2005) and advect gradients in chlorophyll to new areas (Chelton et al., 2011).

The relationship between dynamic height and the spawning habitat of small pelagic fishes in the CCE has not been previously studied, although a few authors have examined the influence of closely related variables, such as indices of geostrophic flow (Weber and McClatchie, 2010; Zwolinski et al., 2011). Small pelagic species may exhibit different associations with dynamic height and geostrophic currents because spatial patterns differ between absolute values of SSH and gradients of this variable. Similarly, SSH and SSHa may display different geographic patterns and distinct relationships with fish spawning habitat, because spatial information is removed when subtracting mean values to calculate anomalies.

We hypothesize that the environmental conditions represented by dynamic height can account for spatial patterns in the spawning habitat of small pelagic fishes in the southern CCE. Secondly, we hypothesize that temporal variations in dynamic height explain interannual variability in the location and extent of spawning habitat. In addition to sardine and anchovy, we also examine the spawning habitat of jack mackerel (Trachurus symmetricus), which is an abundant, but poorly studied, species in the family Carangidae. Larvae of jack mackerel were the eighth most abundant ichthyoplankton species found between 1951 and 1998 in the southern CCE (Moser et al., 2001). The geographic distribution of jack mackerel spawning habitat has been previously studied (Farris, 1961; Ahlstrom, 1969; Ahlstrom and Stevens, 1976), but no research has explored linkages between environmental variables and their spawning habitat.

Since SSH typically varies by no more than ±1 m globally (Stewart, 2008), it is unlikely that fishes can directly sense small differences in dynamic height across the ~100-km scale of their spawning habitat. Instead, any dynamic height effect on spawning habitat could be due to dynamic height’s role as an ecological indicator that incorporates the influence of multiple oceanic variables. In the second half of this manuscript, we assess the relative importance of four mechanisms that potentially explain how dynamic height affects spawning habitat:

- **Mechanism 1**: dynamic height is a proxy for integrated, upper water column temperature and salinity, factors known to influence the spawning habitat of small pelagic fishes.
- **Mechanism 2**: since low dynamic height is indicative of coastal upwelling in the CCE, increases in fish eggs at particular dynamic heights reflect an elevated concentration of planktonic prey for adult fish or early life history stages following upwelling.
- **Mechanism 3**: given that gradients of dynamic height influence the speed and direction of geostrophic flow, increases in fish eggs at particular dynamic heights reflect spawning in currents that transport larvae to favorable habitats.
- **Mechanism 4**: eddies delineated by dynamic height contours affect spawning habitat by retaining fish eggs in biologically productive areas.

### 2. Methods

#### 2.1. Datasets

Fish eggs and hydrographic data were collected during April cruises between 1998 and 2004. All cruises were conducted by the California Cooperative Oceanic Fisheries Investigations (CalCOFI). Data from April were used because eggs of all three fish species were frequently observed this month (Moser et al., 2001). A subset of the CalCOFI time series from 1998 to 2004 was used because two independent measures of fish egg abundance (i.e., bongo net samples and the Continuous, Underway Fish Egg Sampler [CUFES]) were available these years. This period was sufficient for capturing interannual variability in egg distribution,
including extreme events observed during El Niño and La Niña. The area sampled included six CalCOFI transects (i.e., lines 76.7, 80.0, 83.3, 86.7, 90.0, and 93.3) in southern California, which extended offshore of the coastline between San Diego (33.0°N) and north of Point Conception (35.1°N; Fig. 1). During a limited number of years (i.e., 1998, 2003, and 2004), data were also available from CalCOFI transects 60.0–73.3, which encompassed the area in central California north of Morro Bay (35.6°N) to San Francisco Bay (37.8°N; Supplemental information, Section S1). Transects were separated by 72 km. Along transects, stations were spaced 36 km apart inshore of the continental slope and 72 km apart offshore.

The 3-m long bongo net used to collect fish eggs has two openings with a 0.71-m diameter and a mesh size of 505 μm (McGowan and Brown, 1966). This net was towed obliquely at a 45° angle to a depth of 210 m. Tow speed was ~0.5–1.0 m s⁻¹ for a duration of ~20 min (Kramer et al., 1972). During 2004, only one station sampled with the bongo net was positive for sardine eggs. This reflects the fact that sardine spawning occurred principally in the central CCE during 2004 (Lo et al., 2010). Since measurements of habitat electivity would not be meaningful during a year when sardine eggs were nearly absent from our study region, bongo net data from 2004 were excluded from our investigation of sardine spawning habitat. This decision did not have a significant effect on the distribution of sardine eggs observed over the full period between 1998 and 2004 (Kolmogorov–Smirnov test: D = 0.008, p = 1.000). Also, patterns of dynamic height usage by sardine spawning in central California during this year closely resembled those typically observed in southern California (Supplemental information, Section S1).

CUFES collected fish eggs along CalCOFI transects while the research vessel was underway by pumping seawater through an intake at 3 m depth (Checkley et al., 1997). Seawater flowed through CUFES at ~0.5–1.0 m³ min⁻¹. Fish eggs were concentrated and filtered through a 505-μm mesh. The sampling interval of CUFES was adjusted opportunistically depending on the abundance of fish eggs, but typically varied between 5 and 30 min (Checkley et al., 2000). The jack mackerel time series from CUFES starts in 1999.

Fig. 1. Maps of the concentration of eggs of northern anchovy (left column), Pacific sardine (middle column), and jack mackerel (right column) between 1998 and 2001. Fish egg data are from spring Continuous, Underway Fish Egg Sampler (CUFES) surveys. The scale of egg concentration varies between years. Interpolated measurements of dynamic height are shown in the background of each map. Black lines show the research cruise track, while red lines indicate the range of dynamic height across which fish eggs of each species was most frequently observed. These ranges are 80–85 cm for anchovy, 80–90 cm for sardine, and 80–95 cm for jack mackerel.
because this species’ eggs were not identified when CUFES surveys first began. Comparisons between CUFES and plankton nets have consistently demonstrated significant correlations between sampling methods (Checkley et al., 1997; Lo et al., 2001; Curtis, 2004; Planque et al., 2007). On average CUFES samples were collected every 5.3 km. Due to concerns about autocorrelation at this spatial scale (Supplemental information, Section S2), all statistical tests were performed on bongo net data. CUFES data were used solely for mapping egg distribution.

While eggs < 1 day old provide the closest proxy for the distribution of spawning fishes, we used all egg data available from CUFES and bongo net tows to identify the location of spawning habitat for the following reasons: (1) while sardine eggs were aged during some CalCOFI cruises, ages were not recorded for anchovy and jack mackerel eggs (Kramer et al., 1972); (2) due to their extremely patchy distribution, early stages of sardine eggs tended to be undersampled relative to later stages (Lo et al., 1996); (3) since fish eggs passively drifted in currents, they were advected along with water masses with approximately the same physical characteristics as where they were spawned, and; (4) studies of diffusion have indicated that this process only disperses sardine and anchovy eggs hundreds to thousands of meters (Smith, 1973; Smith and Hewitt, 1985), a negligible distance relative to the scale of the CalCOFI grid.

Hydrographic data were collected concurrently at stations where the bongo net was deployed. Dynamic height of the surface, relative to 500 m, was derived from water samples obtained from a Niskin rosette, which recorded temperature and salinity to 500 m depth. Using the equation of state, seawater density and specific volume anomalies were calculated. Dynamic height was then computed by numerically integrating specific volume anomalies across pressures found between 0 and 500 m (Pond and Pickard, 1995). At stations with depths < 500 m, linear extrapolation from adjacent sites was used to calculate the dynamic height relative to the 500 m reference level. For display purposes, data presented in maps of dynamic height were linearly interpolated to a 0.1\° grid using MATLAB (The Mathworks, Inc., Natick, MA, USA).

Other environmental covariates examined to determine their relative influence on spawning habitat include temperature, salinity, chlorophyll concentration, zooplankton displacement volume, speed and direction of geostrophic currents, and the presence/absence of eddies. Data on temperature, salinity, and chlorophyll concentration were acquired from CalCOFI seawater samples from the Niskin rosette. Observations of temperature, salinity, and chlorophyll taken at 10-m intervals from the upper 50 m of the water column were averaged, because sardine and anchovy generally spawn at depths < 50 m (Weber and McClatchie, 2010). The bongo net was deployed to obtain zooplankton displacement volume. We used zooplankton displacement volumes where gelatinous organisms with biovolumes > 5 cm\(^3\) were removed (Kramer et al., 1972). Chlorophyll concentration and zooplankton volume were log\(_{10}\) transformed prior to statistical analyses.

Geostrophic flow and the location of eddies were derived directly from calculated values of dynamic height from hydrographic measurements. Geostrophic velocity was calculated with the formulas \(u = -\left(\frac{g}{f}\right)\frac{\partial H}{\partial y}\) and \(v = \left(\frac{g}{f}\right)\frac{\partial H}{\partial x}\), where \(u\) and \(v\) are geostrophic flows in the \(x\) and \(y\) directions, respectively; \(g\) is the gravitational acceleration; \(f\) is the Coriolis parameter, and; \(H\) is the dynamic height (Stewart, 2008). Gradients of dynamic height were obtained by taking the difference between dynamic heights at adjacent stations along transects. The direction of geostrophic currents was described with a polar coordinate system in which 0° indicates eastward flow, 90° northward flow, 180° westward flow, and 270° (or −90°) southward flow.

We identified eddies with a method modified from Stegmann and Schwing (2007). Locations of eddies were delineated from closed contours of dynamic height separated by 2-cm intervals of dynamic height. If a potential eddy’s boundaries extended beyond the edge of our study area, it was categorized as an eddy only if its dynamic height contour enclosed at least two-thirds of a circle. The extent of each eddy was defined based on the minimum and maximum latitude and longitude of closed dynamic height contours. Due to the spatial resolution of the CalCOFI grid, only mesoscale eddies could be reliably detected. Closed contours whose longest dimension was < 42 km were not counted as eddies. This size limit corresponded to the smallest diameter of eddies identified in the CCE by Stegmann and Schwing (2007). Eddies were classified as cyclonic (counterclockwise) or anticyclonic (clockwise) depending on whether the dynamic height in their center was depressed or elevated, respectively. We identified 17 eddies during spring months between 1998 and 2004. Of these eddies, eight flowed in a cyclonic direction, while nine were anticyclonic.

2.2. Habitat electivity

Over the space and time domain of this study, dynamic height ranged from 68 to 108 cm. Quotient curves were constructed to assess whether eggs were observed at certain dynamic heights more frequently than expected if fishes spawned randomly (Drapeau, 2005). Data were binned into 2-cm dynamic height intervals. To ensure a minimum sample size per bin, any bin containing < 8 observations was merged with a neighboring bin. A quotient was calculated by dividing the percent of total egg abundance in a bin by the percent of stations in the bin. To prevent artifacts due to sites with extremely high egg abundance, a three-point running mean was used to smooth quotient curves (Drapeau, 2005). Since offshore sites (CalCOFI station numbers ≥ 70) were principally outside the range where anchovy spawned (Fig. 1), they were excluded from analyses of habitat electivity for anchovy. Quotient curves were developed on a year-by-year basis and for the 7-year time series mean. If a quotient was > 1, this indicated positive habitat electivity within a dynamic height interval. Positive electivity can reflect either active habitat selection by spawns or increased survival of eggs in an area. Conversely, quotients < 1 suggested avoidance by spawning fish, high mortality of eggs, or recent hatching of eggs. Since there was some overlap between areas where each species exhibited positive electivity, we used Kolmogorov–Smirnov tests to detect significant differences between species in terms of the dynamic heights used. Empirical cumulative distribution functions (CDFs) for each species were graphed to visually portray these differences.

2.3. Generalized linear models

A generalized linear model (GLM) framework was employed to compare the relative influence of oceanic variables on spawning habitat and assess the merit of the four mechanisms proposed to explain why dynamic height affects fish egg distribution. This modeling approach was selected because quotient curves from this study and Lluch-Belda et al. (1991) showed that the frequency of fish egg occurrence often peaked across a distinct range of environmental variables that could be modeled as a quadratic function incorporated into a GLM. We used the presence/absence of eggs as the dependent variable in GLMs in order to model the full extent of areas where spawning occurred. Similar results were also obtained when GLMs were constructed with data on egg concentration (Supplemental information, Section S3). Independent variables in GLMs were selected to correspond to the four mechanisms hypothesized to explain
The significance of the Pearson correlation coefficients is indicated as follows: ratio tests (Bolker, 2008). Linear and quadratic terms in GLMs was examined with likelihood which variable(s) provided the best fit to egg presence/absence maximum value. Analysis of deviance tables were used to assess defined based on the area where the GLM exceeded 90% of its encountering fish eggs across the range of each variable was probability of encountering fish eggs. The peak probability of\[\text{Table 1}\]

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<th>Zooplankton volume</th>
<th>Geostrophic current speed</th>
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<td>Dynamic height</td>
<td>0.87***</td>
<td>-0.51***</td>
<td>-0.85***</td>
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<td>Temperature</td>
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<td>Salinity</td>
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The significance of the Pearson correlation coefficients is indicated as follows:

- *p < 0.05.
- **p < 0.01.
- ***p < 0.001.

how dynamic height influences spawning habitat. These independent variables included dynamic height, temperature (Mechanism 1), salinity (Mechanism 1), chlorophyll (Mechanism 2), zooplankton volume (Mechanism 2), speed and direction of geostrophic currents (Mechanism 3), and presence/absence of eddies (Mechanism 4). Prior to constructing GLMs, we examined the covariance structure between these variables using Pearson correlation coefficients. Both linear and quadratic terms were incorporated into GLMs. Eddies were the one exception to this, since they were treated as a categorical variable. Each bongo net sample was classified as originating from either an area with no eddies, a cyclonic eddy, or an anticyclonic eddy. The form of GLMs was effectively a logistic regression with a binomial distribution and logit link (McCullagh and Nelder, 1989). All GLMs were fit within the R programming environment, version 2.11.1 (R Foundation for Statistical Computing, Wien, Austria). GLMs were varied in three ways to investigate distinct scientific questions. First, oceanic variables were examined in models individually to evaluate each variable’s relative effect on the probability of encountering fish eggs. The peak probability of encountering fish eggs across the range of each variable was defined based on the area where the GLM exceeded 90% of its maximum value. Analysis of deviance tables were used to assess which variable(s) provided the best fit to egg presence/absence data (McCullagh and Nelder, 1989; Bolker, 2008). Significance of linear and quadratic terms in GLMs was examined with likelihood ratio tests (Bolker, 2008).

Second, a full model including all statistically significant oceanic variables and two-way interaction terms was developed to determine whether the effect of dynamic height on egg distribution remained significant after the influence of other variables was taken into account. Recognizing the fact that many oceanic variables covary spatially, we added the dynamic height term last to these GLMs. This was done because analysis of deviance evaluates the deviance of each term sequentially so that a deviance estimate indicates the variation accounted for by a corresponding variable after having eliminated the effects of all terms previously added to the GLM (McCullagh and Nelder, 1989). Any remaining deviance attributed to dynamic height represented the component of the dynamic height effect that could not be explained by other oceanic variables.

A forward, stepwise process was used to develop a third set of GLMs. These GLMs were employed to assess the mechanisms proposed to explain how dynamic height influences the spatial distribution of fish eggs. Again, dynamic height was added to the model last. After the addition of each term to the GLM, the percent reduction in the deviance attributed to dynamic height was calculated to determine how much each environmental variable contributed to the dynamic height effect. The stepwise addition of terms was ended when new terms no longer resulted in a decrease in the deviance of dynamic height or when there were no new statistically significant terms to add. Linear, quadratic, and two-way interaction terms were included in these GLMs. In addition, Section S4 of the Supplemental information presents results from forward, stepwise GLMs where the order in which variables were added to the model was varied to maximize the explanatory capacity of GLMs. However, due to the fact that many of the variables considered here spatially covary (Table 1), the predictive ability of the GLMs in Section S4 may be limited.

Dynamic height observations and bongo net samples of fish eggs from spring CalCOFI cruises during 2005–2008 were used to assess the predictive skill of GLMs that included only dynamic height. The observed percentage of bongo net tows from 2005 to 2008 containing eggs of sardine, anchovy, and jack mackerel was estimated in six dynamic height bins: < 78.0 cm, 78.0–82.9 cm, 83.0–87.9 cm, 88.0–92.9 cm, 93.0–97.9 cm, and ≥ 98.0 cm. These intervals were selected so that each bin contained a minimum of 20 observations, resulting in a precision of at least 5% for estimates of the observed probability of fish eggs. A mean prediction was generated using the dynamic height GLM to estimate the probability of encountering eggs at the center of each bin. 95% confidence intervals for predictions were developed from the 2.5th and 97.5th percentiles of GLM predictions at the upper and lower edges of each bin. Prediction skill was assessed by performing a linear regression that compared the observed and predicted probabilities of encountering eggs between 2005 and 2008 (Zagaglia et al., 2004). Separate linear regressions were initially performed for each species. Since the slope and intercept of regressions did not significantly differ between species, we combined the regressions for all three species to increase sample size.

3. Results

3.1. Habitat electivity

Spring observations of dynamic height in the southern CCE ranged between 68 and 108 cm. Reflecting the equatorward flow along the California coast, low dynamic heights (75–80 cm) were usually observed nearshore, while high dynamic heights (95–105 cm) occurred offshore (Fig. 1). More specifically, cruise-wide minima and maxima of dynamic height were typically found around Point Conception and the southwestern extent of our study area, respectively. This likely reflected upwelling of cool, saline water off Point Conception and an influx of warm, subtropical water at the southwestern edge of the CalCOFI region. While a general onshore-offshore gradient in dynamic height was observed, the area was also characterized by meanders and eddies that altered this gradient. The location of the transition zone...
between nearshore and offshore values of dynamic height varied substantially between years, as was exemplified by the 1998–1999 alternation between El Niño and La Niña. During the 1998 El Niño, the region with dynamic heights > 95 cm expanded shoreward, whereas there was a large region with dynamic heights < 80 cm in 1999 (Fig. 1).

We examined data from 449 bongo net samples from cruises between 1998 and 2004. Anchovy, sardine, and jack mackerel eggs were found in 22.3%, 22.9%, and 47.9% of samples, respectively. When egg distribution was overlaid on maps of dynamic height, it was evident that eggs of each species were most frequently observed in water masses characterized by particular dynamic heights (Fig. 1). 64.1% of sardine eggs were distributed throughout waters with dynamic heights between 80 and 90 cm. When dynamic heights within this range contracted shoreward in 1998 and 2003, sardine eggs were found closer to the coast. During years when dynamic heights between 80 and 90 cm covered an extensive offshore area (1999 and 2002), the distribution of sardine eggs also expanded offshore. Compared to sardine, anchovy eggs were less abundant, distributed closer to shore, and most frequently observed within the southern CalCOFI area. 47.0% of anchovy eggs originated from dynamic heights between 80 and 85 cm. During 1999, 2000, and 2001, areas with peak concentrations of anchovy eggs roughly tracked the 80-cm dynamic height contour (Fig. 1). Jack mackerel eggs were located farther offshore than other species. 63.7% of jack mackerel eggs occurred within water with dynamic heights between 80 and 95 cm (Fig. 1). During several years (1999, 2000, and 2002), the inshore or offshore distribution of jack mackerel eggs traced the path of meandering currents indicated by dynamic height contours.

Quotient curves were used to examine whether spawning fishes inhabited certain dynamic heights at a disproportionately high frequency. When data from all cruises were analyzed jointly, quotient curves indicated that anchovy, sardine, and jack mackerel displayed positive spawning habitat electivity at dynamic heights of 78–86 cm, 79–88 cm, and 84–99 cm, respectively. During most years, the quotient curve for sardine eggs peaked at intermediate dynamic heights in between the maximum of the quotient curves for anchovy and jack mackerel eggs (Fig. 2). Exceptions to this pattern occurred in 2000 and 2003 when there was a high degree of overlap between the anchovy and sardine quotient curves. Also, peaks in spawning habitat electivity for sardine and jack mackerel were observed at similar dynamic heights in 2002.

Since there was a large overlap between dynamic heights used by anchovy and sardine when spawning, a Kolmogorov–Smirnov test was performed to detect differences in the CDFs of these species with respect to dynamic height. These tests found significant differences between the CDFs of all species (anchovy-sardine comparison: $D=0.38$, $p<0.001$; sardine-jack mackerel comparison: $D=0.32$, $p<0.001$; anchovy-jack mackerel comparison: $D=0.59$, $p<0.001$). Empirical CDFs in Fig. 3 show that anchovy favored slightly lower dynamic heights than sardine during spawning, while jack mackerel eggs were found at higher dynamic heights. Similar preferred ranges of dynamic height were observed amongst sardine and jack mackerel spawning in central California (Table S1; Fig. S1a).

3.2. Generalized linear models

Prior to constructing GLMs, we examined correlations between dynamic height, temperature, salinity, chlorophyll, zooplankton volume, and geostrophic currents to better understand the relationship between these variables. All correlations were significant at $p<0.05$, with the exception of those between salinity and geostrophic current speed, and between geostrophic current direction and temperature, salinity, chlorophyll, zooplankton volume, and geostrophic current speed (Table 1). To correct for the accumulation of type I error due to performing multiple tests, we also evaluated correlations between variables using the Bonferroni method to lower the $\alpha$ at which tests would be
considered significant ($n=21$, $z_{\text{Bonferroni}}=0.002$; Sokal and Rohlf, 1995). Following this correction, the correlations between geostrophic current speed and zooplankton volume and between geostrophic current direction and dynamic height were no longer significant. In order of the decreasing strength of correlations, elevated dynamic height was associated with warmer temperatures, lower chlorophyll, reduced zooplankton volume, lower salinity, and slower geostrophic currents.

In GLMs where each variable was examined individually, model fit was significant in all cases except for the effects of zooplankton volume on sardine, geostrophic current direction on jack mackerel, geostrophic current speed on sardine and jack mackerel, and eddies on all species (Table 2). The majority of GLMs exhibited significant quadratic terms indicating that the probability of encountering eggs was maximized across a specific range of each variable. GLM results were fairly consistent with quotient curves in terms of identifying dynamic heights where the probability of encountering eggs was maximized. The greatest probabilities of fish eggs occurred at dynamic heights of 79–83 cm, 84–89 cm, and 89–99 cm for anchovy, sardine, and jack mackerel, respectively (Fig. 4; Table S3).

Since many oceanic variables displayed cross-shelf gradients and each species typically spawned at different distances from shore, several relationships between fish eggs and environmental variables could be interpreted in terms of these gradients. For example, the maximum probability of anchovy and sardine eggs occurred at 12.0–13.9°C due to the influence of cool water associated with coastal upwelling (Fig. 4; Table S3). Jack mackerel eggs located farther offshore peaked at warmer temperatures of 13.5–15.6°C. Salinities <33.2 were found offshore in the relatively fresh water of the California Current (Checkley et al., 2000), whereas nearshore areas were characterized by higher salinities from subsurface water upwelled along the coast. Jack mackerel tended to spawn within the California Current as demonstrated by their preference for waters with salinity <33.1, while anchovy eggs were most frequently observed in coastal areas with salinities of 33.5–33.75. The presence of sardine eggs was greatest at intermediate salinities of 33.0–33.4. The maximum probability of anchovy, sardine, and jack mackerel eggs occurred at chlorophyll concentrations of 1.2–3.9 mg m$^{-3}$, 0.6–2.2 mg m$^{-3}$, and <0.5 mg m$^{-3}$, respectively. Again, this reflected the lower concentration of chlorophyll in offshore waters occupied by jack mackerel when spawning. Maps of chlorophyll concentration revealed that areas where chlorophyll dropped below 0.3 mg m$^{-3}$ closely coincided with the locations of the 90- or 95-cm contours of dynamic height (Fig. S3). Jack mackerel eggs were most commonly observed in offshore areas with <46 cm$^3$ of zooplankton per 1000 m$^3$ of seawater strained. The peak probabilities of anchovy eggs (78–264 cm$^3$/1000 m$^3$) coincided with biologically richer waters containing greater concentrations of zooplankton.

The direction of geostrophic currents was largely bi-directional with the vast majority of observations indicative of the south-eastward flow of the California Current (−30°) and a second, but much smaller, mode indicative of northeastward flow (60°). The probability of sardine eggs was maximal at <−42° (Fig. 4; Table S3), suggesting this species spawns in southerly flow of the California Current. Anchovy eggs occurred most often in currents flowing east or northeast (−6° to 23°). The probability of finding anchovy eggs also peaked in the regions with the fastest geostrophic currents (>80 cm s$^{-1}$). This preference to spawn in fast-flowing, eastward currents could help maintain anchovy eggs and larvae in coastal areas during planktonic life stages.

The relative influence of each oceanic variable on the presence/absence of fish eggs was evaluated with analysis of deviance (Table 2). Dynamic height explained more deviance than any other environmental variable in models of sardine and anchovy eggs. This result implied that dynamic height was not solely a proxy for another variable, even though it was strongly correlated with several oceanic processes. Dynamic height also exhibited a strong

**Table 2**

Deviance explained by generalized linear models (GLMs) examining the presence/absence of fish eggs. The effect of independent variables was tested individually using quadratic and linear terms. The only exception to this was the “eddies” term, which was incorporated into GLMs as a categorical variable. In the full model, dynamic height was added to the model following the inclusion of all other statistically significant independent variables and interaction terms. Therefore, the deviance explained by dynamic height in the full model is the remaining effect of dynamic height on the presence/absence of fish eggs after accounting for the effects of all other oceanographic factors. Significance levels in GLMs are indicated as follows: $^a$p < 0.05; $^b$p < 0.01; $^c$p < 0.001. The number of asterisks corresponds to the most significant term in a GLM, which could be either linear or quadratic.

<table>
<thead>
<tr>
<th>Independent variables</th>
<th>Anchovy ($n=435$)</th>
<th>Sardine ($n=378$)</th>
<th>Jack mackerel ($n=435$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deviance</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dynamic height</td>
<td>119.9$^{a}$</td>
<td>48.9$^{a}$</td>
<td>82.5$^{a}$</td>
</tr>
<tr>
<td>Temperature</td>
<td>41.9$^{b}$</td>
<td>30.6$^{b}$</td>
<td>52.3$^{b}$</td>
</tr>
<tr>
<td>Salinity</td>
<td>35.4$^{c}$</td>
<td>22.9$^{c}$</td>
<td>90.5$^{c}$</td>
</tr>
<tr>
<td>Chlorophyll</td>
<td>81.6$^{b}$</td>
<td>36.6$^{b}$</td>
<td>54.7$^{b}$</td>
</tr>
<tr>
<td>Zooplankton volume</td>
<td>19.3$^{c}$</td>
<td>4.5</td>
<td>12.9$^{b}$</td>
</tr>
<tr>
<td>Geostrophic current speed</td>
<td>9.1$^{b}$</td>
<td>2.8</td>
<td>0.6</td>
</tr>
<tr>
<td>Geostrophic current direction</td>
<td>20.3$^{b}$</td>
<td>9.2$^{a}$</td>
<td>5.7</td>
</tr>
<tr>
<td>Eddies</td>
<td>4.7</td>
<td>0.6</td>
<td>3.7</td>
</tr>
<tr>
<td>Dynamic height in full model</td>
<td>33.6$^{c}$</td>
<td>1.7</td>
<td>11.8$^{b}$</td>
</tr>
</tbody>
</table>

$^a$ Linear term significant at $p < 0.05$.

$^b$ Quadratic term significant at $p < 0.05$.

$^c$ Linear and quadratic terms significant at $p < 0.05$.
influence on the distribution of jack mackerel eggs, but more deviation was explained by salinity for this species. For sardine and anchovy, chlorophyll consistently had the second greatest effect on egg distribution, followed by temperature and salinity. Generally, zooplankton volume, geostrophic current direction and speed, and eddies had weaker effects on egg presence/absence than other variables.

Next, we assessed the deviance explained by dynamic height when it was added last to a GLM including all statistically significant environmental variables and interaction terms. A significant interaction between temperature and chlorophyll was included in this full model GLM for all three species, whereas anchovy and sardine both exhibited significant temperature × salinity and salinity × chlorophyll interactions. In addition, the distribution of anchovy and jack mackerel eggs was affected by significant temperature × zooplankton volume and chlorophyll × zooplankton volume interactions. For anchovy and jack mackerel eggs, the effect of dynamic height remained significant at \( p < 0.001 \) in the full model, although the deviance it explained was reduced (Table 2). This suggested that the combined effect of environmental variables could only partially explain the impact of dynamic height on egg distribution of these species. In contrast, dynamic height no longer had a significant effect on sardine egg distribution once all other variables were taken into account (Table 2).

Similarly, the forward, stepwise GLMs for anchovy and jack mackerel revealed a decrease in the deviance explained by dynamic height following the addition of model terms, although the overall effect of dynamic height remained significant at \( p < 0.01 \) (Table 3). By the time the final variable was added to the stepwise GLMs for anchovy and jack mackerel, the deviance explained by dynamic height was reduced by 82–91% of its original value. The influence of dynamic height on sardine egg distribution could be completely accounted for by other oceanic variables in the stepwise GLM, causing dynamic height to become non-significant when added last to this model (Table 3).

### Table 3
Stepwise generalized linear models (GLMs) used to evaluate which oceanographic variables accounted for the effect of dynamic height on the spatial distribution of fish eggs. Terms were added to the regression model in a forward, step-wise fashion, such that dynamic height was always added last. Deviance refers to the amount of variability in the model explained by dynamic height. The last column refers to the percentage by which the deviance explained by dynamic height decreased as new terms were added to the regression. Significance of dynamic height in GLMs is indicated as follows: * \( p < 0.05 \); ** \( p < 0.01 \); *** \( p < 0.001 \). The number of asterisks corresponds to the most significant dynamic height term, which could be either linear or quadratic.

<table>
<thead>
<tr>
<th>Model step</th>
<th>Variable added</th>
<th>Deviance %</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Anchovy</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Dynamic height</td>
<td>119.5***</td>
</tr>
<tr>
<td>2</td>
<td>Chlorophyll</td>
<td>41.7***</td>
</tr>
<tr>
<td>3</td>
<td>Salinity</td>
<td>33.5***</td>
</tr>
<tr>
<td>4</td>
<td>Temperature</td>
<td>27.1***</td>
</tr>
<tr>
<td>5</td>
<td>Chlorophyll × salinity</td>
<td>24.2***</td>
</tr>
<tr>
<td>6</td>
<td>Geostrophic current speed</td>
<td>22.1***</td>
</tr>
<tr>
<td><strong>Sardine</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Dynamic height</td>
<td>48.9***</td>
</tr>
<tr>
<td>2</td>
<td>Temperature</td>
<td>24.7***</td>
</tr>
<tr>
<td>3</td>
<td>Salinity</td>
<td>17.4***</td>
</tr>
<tr>
<td>4</td>
<td>Chlorophyll</td>
<td>6.0**</td>
</tr>
<tr>
<td>5</td>
<td>Temperature × salinity</td>
<td>2.5</td>
</tr>
<tr>
<td>6</td>
<td>Geostrophic current direction</td>
<td>2.2</td>
</tr>
<tr>
<td><strong>Jack mackerel</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Dynamic height</td>
<td>82.5***</td>
</tr>
<tr>
<td>2</td>
<td>Salinity</td>
<td>14.9***</td>
</tr>
<tr>
<td>3</td>
<td>Temperature</td>
<td>7.3***</td>
</tr>
</tbody>
</table>

* Quadratic effect of dynamic height significant at \( p < 0.05 \).

In models of all species, temperature, salinity, chlorophyll, and their interactions collectively accounted for 80–95% of the dynamic height effect. Geostrophic current speed or direction was included in the stepwise GLMs of anchovy and sardine eggs, but explained little of the deviance (\( \leq 1.8\% \)) originally attributed to dynamic height. The eddy and zooplankton volume terms were not incorporated into any stepwise GLM.

At the 261 CalCOFI stations sampled between 2005 and 2008, dynamic height ranged between 70 and 106 cm, indicating that there had been little change in this variable since 1998–2004 when its range extended between 68 and 108 cm. However, between 1998–2004 and 2005–2008 the probability of encountering eggs increased from 22.9% to 37.9% for sardine and from 22.3% to 42.5% for anchovy. Concurrently, the probability of jack mackerel eggs dropped from 47.9% to 36.4%. These changes affected the probability of sampling fish eggs in each dynamic height bin, but did not alter the general pattern in which the peak probability of encountering eggs occurred at low dynamic heights for anchovy (78–83 cm), intermediate dynamic heights for sardine (83–88 cm), and elevated dynamic height for jack mackerel (88–93 cm) during 2005–2008 (Fig. 5). Thus, GLMs provided robust predictions of the spatial distribution of eggs in any given year and the dynamic heights favored by spawning fishes, but could not predict interannual variations in the mean probability of encountering eggs. This may reflect differences between realized and potential spawning habitat, where realized spawning habitat is more strongly affected by interannual and seasonal variations in spawning stock biomass (SSB; Planque et al., 2007). Our model predictions correspond to Planque et al.’s definition of potential spawning habitat, while the observations from 2005 to 2008 describe realized spawning habitat.
Across our study area of several 100 km, it is unlikely that oceanic variables could give rise to the apparent influence of dynamic height on fish egg distribution. These mechanisms are that fishes may preferentially spawn in water masses with a certain temperature or salinity (Mechanism 1), elevated primary and secondary productivity (Mechanism 2), geostrophic currents with a specific direction or speed (Mechanism 3), and eddies that increase retention of ichthyoplankton (Mechanism 4). Evaluation of these mechanisms using GLMs indicated that together the first two mechanisms explained ≥ 80% of the influence of dynamic height on spawning habitat, while ≤ 1.8% could be attributed to the latter two mechanisms (Table 3). This suggests that dynamic height affects egg distribution via a combination of fish spawning in areas with optimal temperatures for their growth and survival and adequate primary production to provide prey for adult fish and/or larvae. In addition to temperature and chlorophyll, spatial variations in dynamic height reflect changes in salinity, which are indicative of distinct water masses that may contain different concentrations of ichthyoplankton. Since no single variable could completely account for the dynamic height effect on spawning habitat, we conclude that dynamic height functions as an ecological indicator that is able to incorporate the influence of multiple oceanic processes. In this way, dynamic height is similar to the Simpson–Hunter stratification parameter, temperature–salinity diagrams, and spiciness, which are all oceanic indices that integrate two or more physical processes and directly or indirectly affect the distribution of fish eggs and larvae (Iles and Sinclair, 1982; Checkley et al., 2000; Sakuma et al., 2007).

Our analysis demonstrates that anchovy, sardine, and jack mackerel spawn in areas characterized by different dynamic heights (Figs. 2 and 3). Use of distinct spawning habitats may be indicative of niche partitioning between these species, where anchovy primarily spawn in coastal waters, jack mackerel reside in the offshore waters of the California Current when spawning, and sardine use the transition zone between these habitats (Fig. 1). Since water mass characteristics (i.e., temperature and salinity) and primary production explained much of the dynamic height effect on spawning habitat, these factors may also contribute to niche differentiation among these species. In waters off Japan, congeners of these three species have distinct niches based on their optimal temperatures for maximizing growth (Takasuka et al., 2007; Takasuka et al., 2008). In addition, the niches of anchovy and sardine can be distinguished based on the size spectrum of their prey. The gill rakers of anchovy are specialized for filter feeding on larger plankters that occur in areas dominated by coastal upwelling. Finer spacing between the gill rakers of sardine allow them to retain smaller plankters found in areas farther offshore where curl-driven upwelling predominates (Rykaczewski and Checkley, 2008). The diet of jack mackerel is also distinct from sardine (Carlisle, 1971). Lastly, these species may possibly use dissimilar spawning habitats to prevent competitive exclusion. However, given their distinct dietary and temperature preferences, competition between these species may be minimal.

While our results from the GLMs highlight the importance of Mechanism 2, it is noteworthy that zooplankton volume was never included in stepwise GLMs where dynamic height was added last (Table 3). This implies that, although low dynamic height is indicative of upwelling and increased primary production, this analysis did not attribute any of the dynamic height effect on egg distribution to spatial variations in secondary production. This was unforeseen since mesozooplankton abundance in the CCE sharply decreases coincident with large gradients of dynamic height (Lynn, 2003). The weak effect of zooplankton volume could reflect the ambiguous ecological role of this indicator. Zooplankton volume is a bulk measure of the abundance of myriad species belonging to diverse functional
groups. Variations in species composition make it difficult to interpret the meaning of changes in zooplankton volume. It is often assumed that high zooplankton volume denotes increased prey for planktivorous fishes (Lynn, 2003), but some authors have identified negative correlations between zooplankton and the egg distribution and recruitment of sardine (Checkley et al., 2000; Agostini et al., 2007). These negative correlations have been attributed to increases in predatory zooplankton that consume fish larvae and eggs. Furthermore, spatial and temporal variations in zooplankton volume do not correspond to fluctuations in the carbon biomass of zooplankton (Lavaniegos and Ohman, 2007). This is because displacement volume is often dominated by gelatinous organisms with low carbon content and little nutritional value.

Based on GLM results, neither geostrophic currents nor eddies explained much of the influence of dynamic height on fish egg distribution. This may reflect the spatial resolution of the CalCOFI grid, since the gradients in dynamic height used to derive geostrophic currents are more precisely measured when observations are spaced over smaller intervals. The relatively coarse scale of the CalCOFI grid is adequate for detecting mean flow in the California Current, nearshore countercurrent flow, large meanders, and mesoscale eddies. However, smaller scale jets and filaments could not be identified. Similarly, only 1–2 bongo net samples were obtained within many eddies due to the spatial resolution of the CalCOFI grid. The scarcity of bongo net samples in eddies may have prevented us from being able to use GLMs to accurately attribute how much of the dynamic height effect was related to fishes spawning in eddies. Nevertheless, an examination of eddy effects using finer resolution CUFES data suggested that sardine, anchovy, and jack mackerel eggs were more abundant in areas outside eddies than within cyclonic eddies, possibly due to the high predation within productive eddies. This analysis using CUFES was inevitably affected by autocorrelation, but the fact that neither the bongo net nor CUFES datasets indicated a tendency for fishes to spawn in eddies implies that the results of GLMs were not strongly influenced by spatial scale.

An advantage of using SSH as an indicator of spawning habitat is that it can be remotely sensed by altimetry. Unlike in situ surveys, remote sensing can provide a synoptic view of a region, sample an area more frequently than ships, and provide higher spatial resolution. Despite these advantages of satellite data, there may be greater coherence between fish egg distribution and in situ measurements of dynamic height, because they can be collected concurrently. Contemporaneous sampling is especially important given that the egg stage of small pelagic fishes lasts only 2–4 days at temperatures in the southern CCE (Zweifel and Lasker, 1976), while satellite altimeters record SSH over a 7- to 10-day repeat cycle. The reliability of altimetry data is also reduced within 50 km of land (Martin, 2004), which could constrain the use of altimetry for identifying the habitat of coastal fish. In addition, there are subtle, but important, differences between remotely sensed SSH and SSHa. Remotely sensed sea level anomalies from the Archiving, Validation, and Interpretation of Satellite Oceanographic (AVISO) data project are calculated relative to the mean SSH between 1993 and 1999 observed in a single pixel. Since mean SSH differs between pixels, a spatial component of the altimetry dataset is removed in calculating anomalies. Consequently, certain oceanic features, such as mesoscale eddies, become more apparent in SSHa data than SSH observations (Fig. 7b and c). However, other features, such as onshore-offshore gradients, become obscured in the SSHa dataset (Fig. 7c). While similar circulation patterns can be seen in CalCOFI dynamic height measurements and AVISO SSH (Fig. 7a and b), many of these shared features are not detectable in maps of SSHa. A similar pattern emerged from correlations between dynamic height during April CalCOFI cruises from 1998 to 2008 and concurrent AVISO SSH and SSHa observations. Dynamic height and SSH were closely correlated ($r=0.93$, $p<0.001$, d.f.$=658$), while a weaker correlation between dynamic height and SSHa was detected ($r=0.49$, $p<0.001$, d.f.$=658$). Use of dynamic height versus SSHa may explain the differing results of the present study and Zwolinski et al. (2011), who found SSHa gradients to have a relatively weak effect on sardine spawning habitat.
4.2. Interannual variability in spawning habitat

Interannual variability in spawning habitat evident in Figs. 1 and 2 can be attributed to two factors. First, variations in spawning habitat reflect changes in oceanic conditions. During our study, this was exemplified by the El Niño events of 1998 and 2002/2003. Sea level in California is positively correlated with the strength of El Niño with a lag of 3–4 months (Chelton et al., 1982). During El Niño, coastal upwelling is reduced and the thermocline deepens in the CCE (McPhaden et al., 2006). Consequently, coastal waters become warmer and fresher, leading to increased dynamic height. This was evident in 1998 when dynamic heights > 95 cm expanded shoreward while the region with dynamic heights < 80 cm contracted (Fig. 1). This pattern recurred in 2002/2003, albeit to a much lesser extent since this was a weaker El Niño whose beginning and end were closely coincident with timing of the 2002 and 2003 spring cruises, respectively (NOAA Climate Prediction Center, 2012). These changes reduced the extent of areas with low dynamic height, forcing fishes that favor these habitats to either spawn in other regions, which may become suboptimal, or increase their density in remaining areas. Spawning sardine and jack mackerel responded to the 1998 El Niño via the first strategy since peaks in their cohort curves occurred at slightly higher dynamic heights than normal (Fig. 2). Anchovy utilized the second strategy since they remained in areas with low dynamic heights but exhibited greater spawning habitat electivity than usual in 1998. Song et al. (2012) observed a similar pattern, noting that sardine eggs were more concentrated in recently upwelled waters during El Niño.

Second, the size of a fish stock can influence the extent of its spawning habitat in a given year. As proposed by the basin model (MacCall, 1990), increased stock size may lead to density-dependent declines in habitat quality. In response, fish either occupy new waters that previously displayed lower habitat electivity or the density of fish may increase in areas with the highest electivity. An example of this was observed in 2005–2008 when the frequency of anchovy eggs increased to 42.5% compared to earlier years when eggs occurred at 22.3% of sites. While a stock assessment for anchovy has not been conducted since 1995 (Jacobson et al., 1995), this increased frequency of anchovy eggs is likely due to growth of this species’ SSB. This growth was not accompanied by a major change in the dynamic heights used by anchovy when spawning (Fig. 5). Instead, the distribution of anchovy eggs expanded northward, occupying a larger portion of the region with dynamic heights < 83 cm. While this finding is in accordance with the basin model, a more definitive test of this model requires data from a larger proportion of anchovy’s range (i.e., British Columbia to Baja California).

4.3. Other oceanic variables that affect spawning habitat

The novelty of our study rests in that it is the first to identify in situ measurements of dynamic height as an important variable influencing the spawning habitat of sardine and anchovy. However, we also used to GLMs to model the effect of several other oceanographic variables on the spawning habitat of small pelagic fishes. The ranges of temperature, salinity, chlorophyll concentration, zooplankton volume, and geostrophic currents preferred by spawning anchovy and sardine in our GLMs were generally similar those detected in previous studies (Fiedler, 1986; Lluch-Belda et al., 1991; Checkley et al., 2000; Lynn, 2003; Reiss et al., 2008; Weber and McClatchie, 2010; Zwolinski et al., 2011), although one noteworthy exception is discussed below.

Unique biological communities develop in eddies due to retention of planktonic organisms, upwelling in cyclonic eddies, and transport of coastal species offshore. Anchovy eggs are occasionally found offshore in eddies with similar characteristics to the nearshore habitats where they usually spawn (Fiedler, 1986). Also, abundance and production of late-stage sardine larvae can be extremely high in offshore, cyclonic eddies (Logerwell and Smith, 2001; Logerwell et al., 2001). In contrast to these studies, our results did not detect a significant effect of cyclonic or anticyclonic eddies on the presence/absence of fish eggs. This does not contradict Logerwell and Smith (2001) because our work examines a different life history stage of sardine. Our results suggest that sardine do not preferentially spawn in eddies, but late-stage larvae could still be concentrated in eddies due to retention and/or reduced mortality. Also, upwelling of water in the eddy center can concentrate larvae (Nishimoto and Washburn, 2002; Mackas et al., 2005), but the time scale of this process may be too slow to affect the short-lived egg stage. While Fiedler (1986) demonstrates that anchovy eggs may sometimes become concentrated in eddies, this author documented an unusual event that does not occur regularly.

Of the three species examined, jack mackerel has been the least studied, with no prior research identifying how environmental factors affect where it spawns in the CCE. Based on GLMs, jack mackerel spawning habitat includes oceanic regions characterized by high springtime dynamic height (89–99 cm), warm temperatures (13.5–15.6 °C), low salinity (< 33.1), and reduced biomass of phytoplankton (< 0.5 mg m⁻³ of chlorophyll) and zooplankton (< 46 cm³/1000 m² strained). Salinity played the largest role in determining which regions were likely to contain jack mackerel eggs (Table 2). The prevalence of jack mackerel eggs in salinities < 33.2 suggests that this species spawns in the main California Current, which can be delineated by salinity within this range (Checkley et al., 2000). Chilean jack mackerel (T. murphyi), a congener of this species, exhibits similar habitat requirements, spawning in oceanic waters with warm temperatures (Arcos et al., 2001).

5. Conclusions

Dynamic height was the single best oceanic variable for identifying spawning habitat of anchovy and sardine. Each species of small pelagic fish in the CCE exhibited positive spawning habitat electivity across different dynamic heights, indicating that they spawn in distinct portions of the environment, albeit with some partial overlap. In accordance with our initial hypothesis, interannual variability in the extent of each species’ preferred range of dynamic height explained year-to-year fluctuations in spawning habitat location. The skill of dynamic height GLMs when making predictions for 2005–2008 demonstrated that spawning habitat preferences remained stable across distinct time periods. The influence of dynamic height on these species’ spawning habitat can be largely attributed to the combined effects of temperature, salinity, and chlorophyll on fish egg distribution. Spatial variations in zooplankton volume, geostrophic flow, and eddies accounted for relatively little of the dynamic height effect on spawning habitat.

Spawning habitat models could potentially be used to predict shifts in fish egg distribution due to climate change, assuming the current relationship between spawning habitat and environmental variables remains constant. Climate-induced changes in the latitude and depth inhabited by fishes have been observed in many ecosystems (Beare et al., 2004; Perry et al., 2005; Hsieh et al., 2008, 2009; Nye et al., 2009). These changes are expected to accelerate under future climate change scenarios. One obstacle related to predicting changes in fish distribution is that many models of ocean dynamics, including the widely used Regional Ocean Modeling System (ROMS), are skillful at forecasting physical oceanographic conditions, but are not able to model biological variables with comparable accuracy. In light of this, the relationship between dynamic height and
spawning habitat may be particularly propitious because ROMS and other ocean general circulation models routinely output estimates of SSH.

Improved understanding of the relationship between small pelagic fishes and environmental variables may be useful for transitioning from single species fisheries management to ecosystem-based fisheries management. Sardine is one of the few species whose stock assessment has explicitly considered the effect of environmental variability, since the running mean of SST from the Scripps Pier has been used to determine the fraction of SST to be harvested (Jacobson and MacCall, 1995; Hill et al., 2011). Recently the reliability of Scripps Pier SST for predicting the recruitment success of sardine has been challenged (McClatchie et al., 2010). Therefore, this may be the right time to examine how other environmental variables could be incorporated into the management of small pelagic fishes. Dynamic height could be useful to consider within this context, because it is linked to a variety of oceanic processes, including fluctuations in temperature, salinity, biological productivity, geostrophic flow, and eddies. Two ways in which dynamic height could be used in fisheries management are: (1) remotely sensed observations of SSH could help identify regions with a potentially high concentration of fish eggs prior to annual egg surveys. Data from these surveys are used as fisheries-independent input to the sardine stock assessment. Knowledge of environmental influences on spawning habitat can increase the efficiency of these surveys by allowing researchers to target areas where eggs are abundant (Fiedler, 1983; Zwolinski et al., 2011). (2) The Magnuson–Stevens Fishery Conservation and Management Act requires that essential fish habitat (EFH) be identified for commercially fished species. Currently, EFH for coastal pelagic species in the CCE is defined based on the 10 C isotherm (PFMC, 1998). Since dynamic height has a greater influence on the spawning habitat of anchovy and sardine than temperature, this variable may be useful for refining EFH. SSSH may also be helpful for delineating fish habitat in regions with a dearth of oceanographic data given that it can be remotely sensed and influences the distribution of a variety of species.

Acknowledgments

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.dsr.2012.08.006.

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