Contribution to the Theme Section 'Marine ecosystems, climate and phenology: impacts on top predators'

Defining spring transition: regional indices for the California Current System

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ABSTRACT: While the physical and ecological importance of the spring transition in the California Current System (CCS) is well recognized, there is no widely agreed upon metric for tracking the phenomenon. Most metrics reflect oceanographic events of the northern CCS; few pertain to southern regions. Our goal was to compare 2 commonly used methods for identifying spring transition in the CCS that use data on wind-driven upwelling and coastal sea levels to 2 newly developed methods that use data on sea levels as well as satellite-derived sea-surface temperatures (SSTs). More specifically, we assessed whether methods typically used in northern regions of the CCS could be applied to other regions. To demonstrate the biological implications of those methods, we evaluated relationships between timing of spring transition and recruitment of 2 groundfish species, Pacific ocean perch *Sebastes alutus* and sablefish *Anoplopoma fimbria*. Our results suggest that while dramatic changes in wind-derived upwelling and coastal sea levels consistently indicate spring transition in the northern CCS, this is not the case for central and southern regions. In those regions, spring transition may be better represented by the rate of change in sea levels and/or changes in spatial patterns of SSTs. Only metrics based on wind-driven upwelling and sea levels were related to groundfish recruitment; when transitions in upwelling winds and sea levels were delayed, recruitment tended to be poor. We advise caution when identifying dates of spring transition and applying them to analyses of ecological phenomena; a combination of several methods may be required to reveal the multidimensional physical and biological changes that occur during that transition.

KEY WORDS: Spring transition · California Current · Bakun upwelling · Sea levels · Sea-surface temperatures · Groundfish recruitment

INTRODUCTION

The transition from winter to spring ocean conditions over the shelf and slope portions of the California Current System (CCS) is characterized by a shift in circulation, stratification, and biological habitat. The Aleutian low-pressure system weakens and is displaced northward by the North Pacific high-pressure cell (Strub et al. 1987, Strub & James 1988, Schwing et al. 2006), regional winds and alongshore currents shift from predominantly northward to southward (Huyer et al. 1979), coastal sea level drops, nutrients are upwelled to the euphotic zone (Huyer et al. 1979), primary productivity increases (Lynn et al. 2003, Thomas & Brickley 2006), and winter zooplankton communities over

the shelf are replaced by spring/summer communities (Peterson & Keister 2003, Hooff & Peterson 2006; Fig. 1). Delays in spring transition have also been associated with poor survival of higher trophic-level organisms, such as coho salmon (Logerwell et al. 2003), fewer colonizations of new habitat by the common murre *Uria aalga* (Zador et al. 2009), and reduced reproductive success of mussels, rockyshore barnacles (Barth et al. 2007), groundfish (e.g. Pacific ocean perch; Holt & Punt in press), and seabirds (e.g. the planktivorous auklet *Ptychoramphus aleuticus*; Sydeman et al. 2006). While the physical and ecological importance of the spring transition has been embraced by many, there is no widely agreed upon metric for tracking the phenomenon (Kosro et al. 2006).
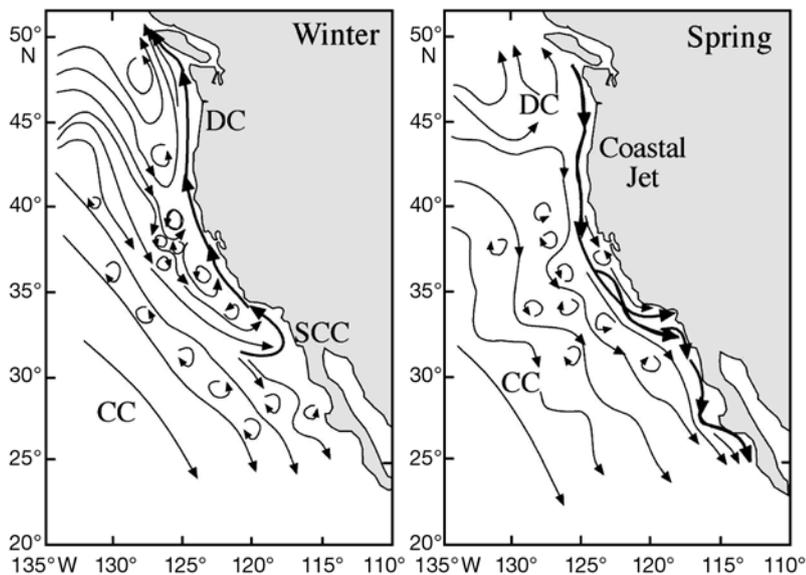
Fig. 1. Seasonal variation of large-scale and coastal currents in the California Current System (adapted with permission from Hickey & Royer 2001, originally from Strub & James 2000). CC: California Current, DC: Davidson Current, SCC: Southern California Countercurrent

Most indices of spring transition date reflect physical and biological phenomena of the northern CCS; few pertain to southern regions. The switch from downwelling-favorable winter winds to upwelling-favorable spring/summer winds is the most commonly used metric (Schwing et al. 1996, 2006, Barth et al. 2007). Closely related to wind-driven upwelling is the timing of the persistent drop in coastal sea level (also driven by local and remote wind stress) from high levels characteristic of warm, winter, downwelled waters, to lower levels characteristic of cool, spring/summer, upwelled waters (Strub et al. 1987, Bilbao 1999, Kosro et al. 2006). Other metrics include the timing of a reversal in current direction off Vancouver Island (Thomson & Ware 1996), changes in the cross-shore pressure gradients indicating the development of a spring equatorward jet (Lynn et al. 2003), variations in the spatial structure of sea-surface temperatures (SSTs) from isotherms primarily perpendicular to the coast in winter, to isotherms parallel to the coast in summer (Lynn et al. 2003), increases in chlorophyll *a* concentrations (Lynn et al. 2003), and shifts in zooplankton species composition from species found predominantly in southern regions (in winter) to those found in northern regions (in summer; Peterson & Keister 2003, Hooff & Peterson 2006). Although biological responses of physical spring transition have been documented off central California (e.g. phytoplankton; Lynn et al. 2003), the timing of the transition is not well documented for that region.

Our first goal was to compare 2 commonly used methods for identifying spring transition in the CCS that use data on wind-driven upwelling and coastal sea levels to 2 newly developed methods that use data on sea levels as well as satellite-derived SSTs, and more specifically, to assess whether methods typically used in northern regions of the CCS can be applied to central and southern regions (from Cape Mendocino, California, to the US–Mexico border). Second, to investigate the biological relevance of those time series of spring transition, we examined the relationships between spring transition and larval abundance (age-0) of 2 west coast groundfish species (sablefish *Anoplopoma fimbria* and Pacific ocean perch *Sebastes alutus*). We chose those species because previous evidence suggests that the timing of spring transition affects their recruitment (Schirripa & Colbert 2006, Holt & Punt in press). In addition, they are of management interest due to the contribution of sablefish to the commercial west coast groundfish catch (Schirripa 2007) and the designation of Pacific ocean perch as 'overfished' (Hamel 2007a). Furthermore, both stocks are currently assessed by the Pacific Fisheries Management Council and so estimates of age-specific abundances exist (Hamel 2007b, Schirripa 2007). In fact, the assessment of sablefish currently uses information on oceanographic conditions to inform estimates of recruitment and may benefit from improved characterization of the timing of favorable conditions.

We chose to investigate recruitment for those species because most hypotheses about environmental effects on groundfish pertain to early life-history stages (i.e. mortality prior to recruitment) when age-class strength is typically determined (Bakun 1996). In particular, the 2 most compelling hypotheses about mechanisms relating spring transition to recruitment of groundfish are the timing of prey availability for larvae during the critical period early in life, and the timing of favorable current conditions to transport groundfish larvae to preferred habitat (e.g. for sablefish, see Schirripa & Colbert 2006).

MATERIALS AND METHODS

Data. To identify dates of spring transition, we compiled coast-wide data on oceanographic conditions from 3 sources: Bakun upwelling wind indices, coastal sea levels, and *in situ* and satellite-measured SST

fields. Bakun upwelling indices were derived from the daily average of wind-driven cross-shore transport computed from surface atmospheric pressure gradients generated from atmospheric models (Environmental Research Division of the Pacific Fisheries Environmental Laboratory, available online at: www.pfeg.noaa.gov/, for 1967 to 2007). Although satellite-derived wind data exist for recent years (after 1999; Pickett & Schwing 2006), those time series are too short to test hypotheses about groundfish recruitment. We analyzed northern, central, and southern regions of the CCS separately because dates of spring transition (and environmental variables that determine them) tend to be coherent at spatial scales corresponding to the size of those regions (Strub et al. 1987). In particular, Strub et al. (1987) found positive covariation in the timing of the spring transition at alongshore scales of 500 to 2000 km driven predominantly by large-scale wind stress (at alongshore scales of ~1500 km). In addition, the lines between regions (at Cape Mendocino, 40.0° N, and Point Conception, California, 34.5° N) are well-recognized boundaries in physical and biological oceanographic conditions, although additional boundaries north of Cape Mendocino have also been documented (Huyer et al. 2005, Venegas et al. 2008). Furthermore, we compared dates of spring transition with recruitment time series for groundfish stocks, which are typically resolved at relatively large, regional (or sometimes, coast-wide) scales, requiring information on environmental conditions at similarly large scales. Bakun indices were averaged over coastal stations within regions (6 stations in total).

Daily sea level data were extracted from the University of Hawaii Sea Level Database (available at: http://uhslc.soest.hawaii.edu/uhslc/data.html) for Neah Bay, Washington (representing the northern region), San Francisco (representing the central region), and San Diego (representing the southern region), California. Sea levels at a single station in each region were chosen because of evidence for covariation in that metric at large spatial scales (250 to 1300 km; Roach et al. 1989). An inverse barometric correction was applied to sea level data using surface pressures from the NCEP/NCAR Reanalysis Project (available online at: www.cdc.noaa.gov/cdc/reanalysis/reanalysis.shtml, for 1967 to 2007).

Daily Reynolds-AVHRR SST data (1985 to 2006) were extracted from the NOAA National Operational Model Archive & Distribution System covering the region from the coastline to beyond the continental shelf (extending 100 km offshore in the north, increasing to 560 km in the south). The SST data were a blend between coarse-scale *in situ* (Reynolds) and fine-scale satellite (AVHRR) observations and were interpolated over points missing in the satellite record as described by Reynolds et al. (2007).

For Pacific ocean perch, maximum likelihood estimates of annual deviations in recruitment to age-3 (1970 to 2006; deviations from a stock-recruitment model, i.e. reflecting indices of recruitment success independent of spawning stock size) were taken from the most recent stock assessment (Hamel 2007b). Those data were shifted by 3 yr to generate time series of age-0 recruitment (1967 to 2003). Pacific ocean perch has a geographic distribution that spans Cape Blanco in the south to the southern US–Canada border in the north, so we compared time series of recruitment to dates of spring transition for the northern region only. For sablefish, the maximum likelihood estimates of the deviations in recruitment to age-0 (1972 to 2006) were generated from the same model used in the most recent stock assessment (Schirripa 2007) with one difference. In that assessment, an environmental covariate of recruitment, monthly average sea-surface heights from 4 locations off Washington and Oregon were included to improve model fit (i.e. generating time series of recruitment deviations independent of interannual variability in sea-surface height). For our analyses, we used estimates of recruitment deviations that did not include that environmental covariate (M. Schirripa unpublished analyses) since we were interested in testing the relationship between total interannual variation in recruitment and timing of spring transition. Because sablefish are distributed from Baja California in the south to the Gulf of Alaska in the north and the current stock assessment includes survey data from the US–Mexico border to the southern US–Canada border (Schirripa 2007), we compared recruitment time series and dates of spring transition for all 3 regions. Assessments for both species used an age-structured population dynamics model fit to catch and survey indices of abundance and length and age compositions (collected from fishery catches and surveys).

Statistical methods. Dates of spring transition were identified in 4 ways: one method that used Bakun indices (Schwing et al. 2006), another that combined Bakun indices and sea level data (as in Logerwell et al. 2003, adapted from Bilbao 1999, henceforth referred to as the 'Logerwell method'), a modified version of that method that used only sea level data, and one that used spatial patterns in SSTs.

The first method identified timing of spring transition from the start of the wind-driven coastal upwelling season, i.e. the date of minimum cumulative Bakun upwelling index (Schwing et al. 2006, Bograd et al. 2009) averaged over coastal stations within regions.

The Logerwell method uses 2 metrics of ocean conditions: the daily Bakun index averaged over coastal

stations within regions and residuals in coastal sea levels from the long-term mean at one location in each region. Both time series were low-pass filtered with a stop frequency of 1/(10 d), using complex demodulation performed in S-plus, to eliminate high frequency variation independent of a seasonal shift. Spring transition was defined as the first date when the Bakun index became positive and sea level residuals became negative, as indicated by the filtered time series. In years when the upwelling and sea-level time series crossed the zero line several times during the spring, the date that best matched the seasonal trends was chosen (as indicated by low-pass filtered time series with a stop frequency of 1/[90 d]).

The third method was a modified version of the Logerwell method with 3 differences. (1) For the modified version, we used only sea level data because they better integrate seasonal shifts in ocean conditions experienced by fish than wind data that were used to generate upwelling indices (Strub et al. 1987). Coastal sea levels on the west coast of the Americas integrate wind forcing and remotely generated, coastally trapped waves (Enfield & Allen 1980), whereas the Bakun upwelling indices are derived from smoothed atmospheric pressure fields and reflect wind-driven coastal upwelling only. (2) We computed sea-level residuals from the 3-yr running mean instead of the long-term mean to better capture seasonal changes in sea levels and remove signals related to interannual changes in mean values. (3) We defined spring transition as the date of steepest negative slope of the filtered time series using a stop frequency of 1/(90 d), since an objective selection of the date of seasonal shift was not possible with the 1/(10 d) filtered time series due to high frequency variation in those data.

We developed a fourth method for identifying dates of spring transition from changes in spatial patterns of SSTs. Although SSTs have been used to characterize the spring transition for specific locations (e.g. off central California, Lynn et al. 2003), those data have not been used to identify coast-wide time series of dates of spring transition. Spatial and temporal patterns in SSTs relate to upwelling of cold water that is characteristic of the spring transition in the north, and in the central region, to the formation of oceanographic features characteristic of spring and summer conditions (Lynn et al. 2003). Because we were interested in the seasonality of spatial patterns in SSTs independent of changes due to solar radiation (i.e. independent of common patterns across the entire region), we removed the mean spatial SST from each daily field to create time series of SST residuals. We examined those SST residuals for the first 240 d of each year because we were only interested in changes that occurred during winter, spring, and summer. Those residuals were then smoothed by computing the 3-d running mean and extracting every third day.

The dominant spatial patterns in residual SST fields were identified for each region using Empirical Orthogonal Function (EOF) analysis (also known as Principal Component Analysis), a multivariate technique that decomposes data series into a linear recombination of multiple orthogonal functions of the original data. The EOFs minimize residual variance in SST residuals and represent the dominant statistical patterns in high-dimensional data (as described by Armstrong 2000). Those functions are selected in descending order of importance (i.e. the first EOF captures the largest portion of variance; subsequent EOFs capture increasingly smaller portions). We identified dates of spring transition from time series of the amplitudes of the first EOF (the first principal component, PC1) because that function explained the largest portion of the variance (61.9, 40.2, and 49.1% for northern, central, and southern regions, respectively) and exhibited spatial patterns characteristic of spring transition. Furthermore, its amplitude (PC1) varied on a seasonal scale. We selected the date of initiation of the seasonally persistent upward slope of smoothed PC1 values (i.e. the date of maximum curvature derived from the second derivative of PC1 values, and low-pass filtered with a stop-frequency of 1/[90 d]) to represent the onset of spring SST conditions. Again, we used the 1/(90 d) filtered time series because objective dates of spring transition could not be identified from the 1/(10 d) filtered data due to high frequency variation.

We further examined latitudinal gradients in Bakun index climatologies and winter-spring differences in SST and wind stress fields to provide insights into the regional patterns of change associated with the spring transition.

To investigate the relationship between dates of spring transition and groundfish recruitment, we fit linear models for both species, Pacific ocean perch and sablefish:

$$\ln(R_{i,t}) = b_{i,0} + b_{i,1} \cdot x_t + \varepsilon_{i,t} \qquad \varepsilon_{i,t} \approx MN(0, \Phi_i) \qquad (1)$$

where $\ln(R_{i,t})$ is the natural logarithm of the recruitment deviation for species i in year t, x_t is the date of spring transition in year t calculated using 1 of the 4 methods described above, $b_{i,0}$ and $b_{i,1}$ are parameters for species i, and $\varepsilon_{i,t}$ are multivariate normally distributed random errors with a variance-covariance matrix Φ_i (dimensioned $t \times t$). Variability in recruitment time series was from natural, biological sources and errors in observations of abundances from surveys and commercial catch. A third source of uncertainty, estimation uncertainty, arose because recruitment deviations were

derived from stock assessment models and were not observed directly. Estimation uncertainty was characterized by a variance-covariance matrix of annual recruitment values from the stock assessment model. We included those 3 sources of uncertainty by using multivariate normally distributed errors in Eqn. 1 (ε_i) that included both estimation errors and natural variability combined with observation errors. Following Dichmont et al. (2003), the following objective function was minimized:

$$\ln\left[\sqrt{Det(\Omega_i + V_i)}\right]$$

$$+ \frac{1}{2}\sum_{t1}\sum_{t2}(\ln R_{i,t1} - \ln \hat{R}_{i,t1})[(V_i + \Omega_i)^{-1}]_{t1,t2}(\ln R_{i,t2} - \ln \hat{R}_{i,t2}) \quad (2)$$

where V_i is the variance-covariance matrix of estimates of $\ln(R_i)$ for species i obtained from the stock assessment model that generated those estimates, Ω_i is a matrix with diagonal elements σ^2_ε representing variance associated with natural variability and observation errors, and $\ln\hat{R}_{i,t}$ are expected recruitments (determined from $\ln\hat{R}_{i,t} = b_{i,0} + b_{i,1} \cdot x_t$). Both summations ($t1$ and $t2$) occur over all years in the time series. Therefore, unlike previous studies relating groundfish recruitment to environmental factors (e.g. Schirripa & Colbert 2006), our parameter estimates account for the relative precision of annual recruitment estimates.

We tested whether the linear model was a significantly better fit to the data than a simpler model (e.g. the null model with a *y*-intercept only) using likelihood-ratio tests, and calculated the Akaike Information Criterion (AIC) value to estimate the gain (or loss) in information content. We then compared results among the 4 methods used to identify dates of spring transition.

RESULTS

Cumulative upwelling

For the northern region of the CCS, the start of the upwelling season (i.e. date of minimum cumulative upwelling after which upwelling was generally positive) usually occurred between March and May. For the central and southern regions it occurred 1 to 3 mo

earlier (e.g. Figs. 2a, 3a, & 4a for an example time series from 1999). In fact, in most years, south of 36° N, the start of the upwelling season was identified as 1 January, because winter wind conditions were characterized by weak upwelling rather than downwelling. In those years, the cumulative upwelling index remained positive year round. Seasonally weak or intermittent winter downwelling between 33° and 39° N was reflected in the climatology of Bakun indices for 1948 to 2007, which were positive (indicating upwelling favorable winds) for most months (Fig. 5).
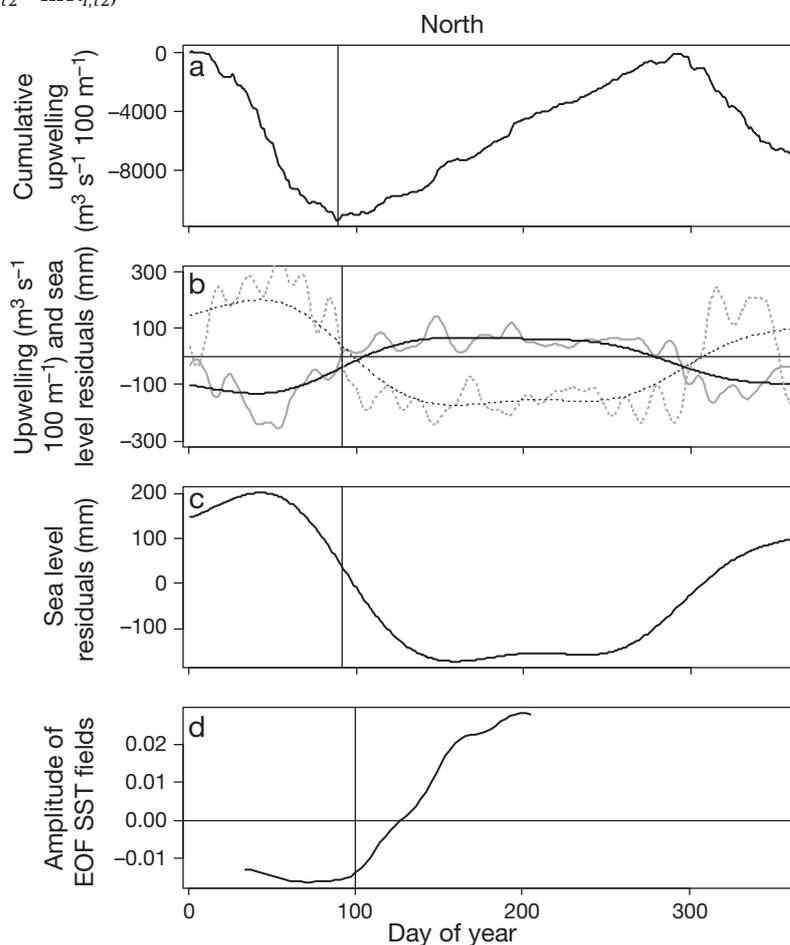

Fig. 2. (a) Cumulative Bakun upwelling indices (m³ s⁻¹ per 100 m of coastline) for one example year, 1999, in the northern California Current System. (b) Bakun upwelling indices smoothed with a low-pass filter of stop frequency 1/(10 d) (grey solid line) and low-pass filter of stop frequency 1/(90 d) (black solid line), and sea-level residuals from the long-term mean smoothed in the same ways (grey dashed lines for stop frequency of 1/[10 d] and black dashed line for the stop frequency of 1/[90 d]). (c) Sea-level residuals from a 3-yr running mean, smoothed with a low-pass filter of stop-frequency 1/(90 d). (d) Amplitudes of the first EOF of SST fields, smoothed with a low-pass frequency of 1/(90 d). Note, only days of year 1 to 240 were included in the EOF analysis, and smoothing further removed the first and last 40 d of the time series. Vertical lines denote dates of spring transition identified by (a) the method of Schwing et al. (1996) (start of upwelling season), (b) the Logerwell method, (c) the modified Logerwell method, and (d) our method using seasonal trends in SST fields
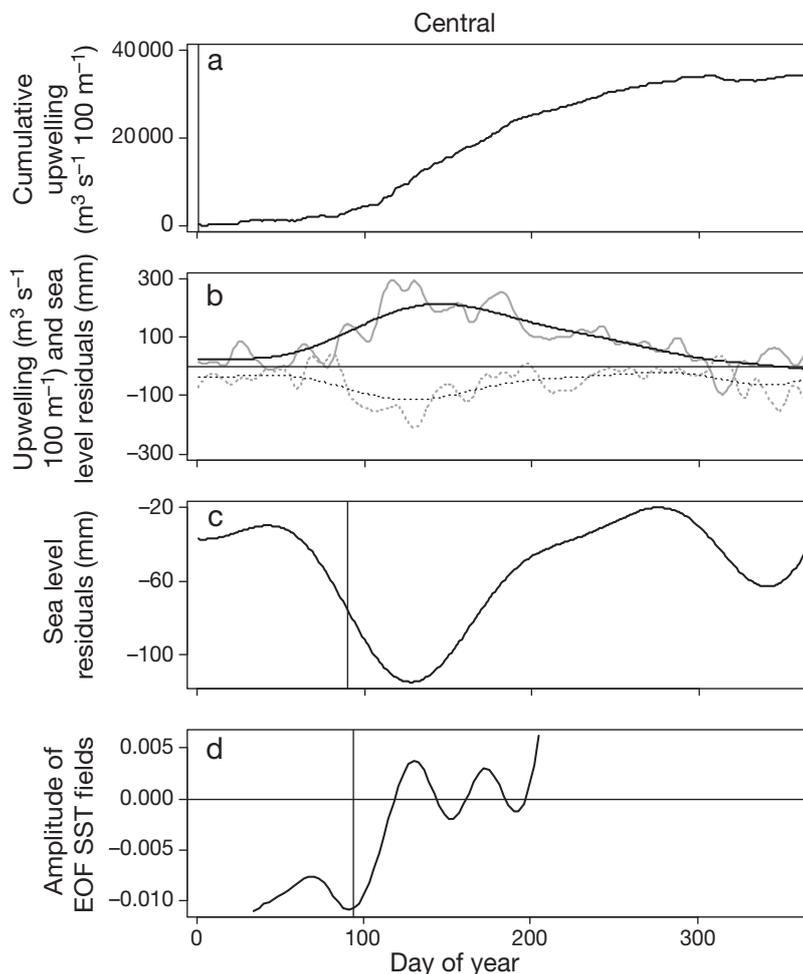
Fig. 3. As in Fig. 2, but for the central region of the California Current System

Logerwell method

When applied to the northern region, the timing of reversal in winds from downwelling favorable to upwelling favorable coincided with a rapid drop in sea levels below their long-term mean (e.g. Fig. 2b). As expected, the dates identified by the Logerwell method were highly correlated with those from the cumulative upwelling method for that region (Fig. 6, top left corner). However, in the central and southern regions, the onset of strong upwelling favorable winds occurred several weeks prior to a gradual decline in sea levels. Similar to the previous method (minimum cumulative upwelling), in some years, dates of spring transition could not be identified with the Logerwell method in the central and southern regions because winds remained upwelling favorable throughout the winter, sea levels remained below their long-term mean, or the dates identified from the 2 metrics were not coincident (e.g. Figs. 3b & 4b).

Modified Logerwell method

In contrast to the Logerwell method, dates of spring transition could be identified using the modified Logerwell method for all 3 regions because that method did not rely on wind-driven upwelling and it employed the date of most rapid decline in sea levels (an event that could be specified for each year) rather than the date of decline below the long-term mean (an event that could not be consistently specified). Rapid declines in sea levels in the southern region tended to occur 10 to 50 d earlier than in the northern and central regions (e.g. Figs. 2c, 3c, & 4c for 1999). The dates of spring transition identified from the modified Logerwell method were only weakly positively correlated with timing of upwelling derived from Bakun indices for the northern and southern regions, and were uncorrelated in the central region (Figs. 6, 7, & 8).

Spatial patterns in SST fields

In our northern CCS region (40.0° to 49° N), the first EOF represented a combination of latitudinal and cross-shore trends in SST residuals. The amplitude of the first EOF (PC1) generally increased from winter to summer each year (e.g. Fig. 9). The spatial patterns in PC1 suggest that nearshore and offshore areas exhibited opposite seasonal trends; nearshore areas were warmer than average during winter and cooler than average in summer (i.e. were negatively correlated with PC1 trends). In contrast, offshore areas (and nearshore around 46° N) exhibited opposite trends, i.e. were positively correlated with PC1 trends. See Fig. 10 for the correlation coefficients of the relationship between the PC1 and SST residuals (which reflect spatial patterns in the first EOF), and the magnitude of the slope of that relationship.

Similarly, for our central region (34.5° to 40.0° N), the first EOF exhibited strong cross-shore patterns (Figs. 9 & 10). In contrast to the northern and central regions, in the south, SST residuals were positively correlated with PC1 values near shore (i.e. SSTs were cooler than average during winter and warmer than average in summer) and negatively correlated offshore.

In the northern region, dates of spring transition identified from SST fields were positively correlated with the timing of the onset of upwelling and dates
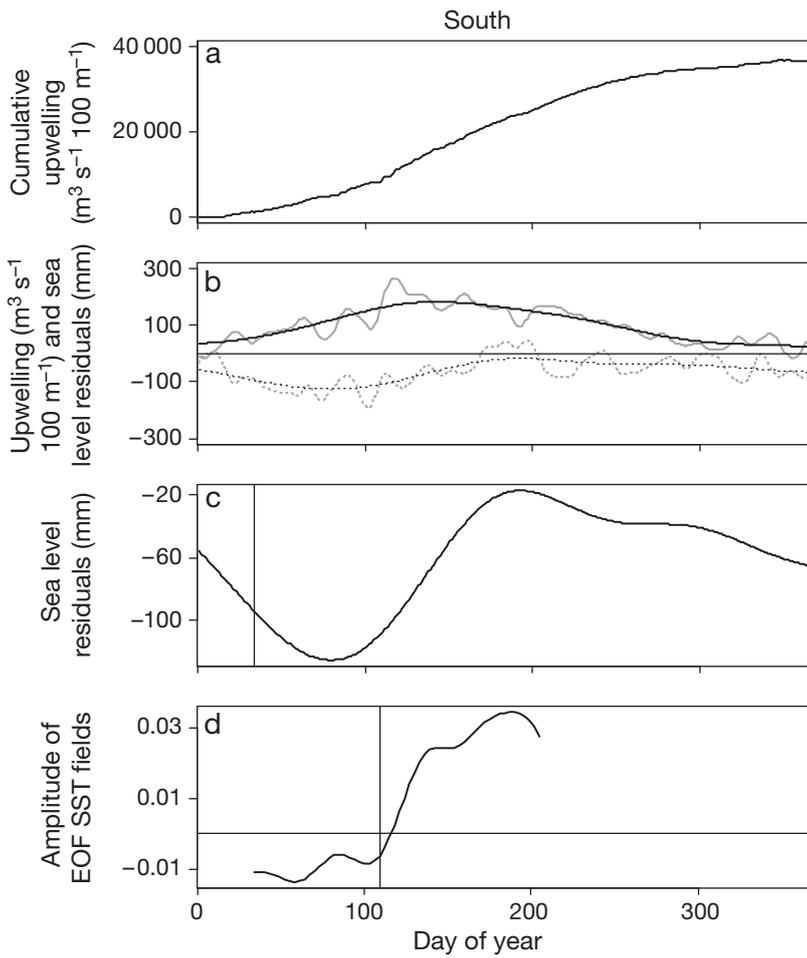
Fig. 4. As in Fig. 2, but for the southern region of the California Current System
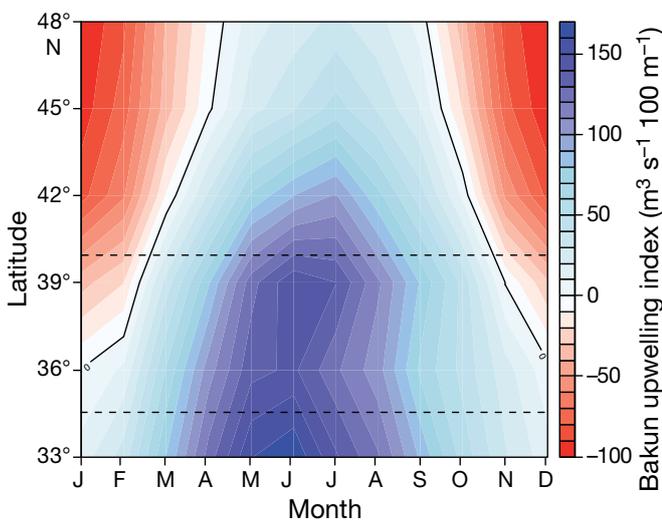

Fig. 5. Hovmöller diagram of monthly average Bakun upwelling index (m³ s⁻¹ per 100 m of shoreline) arranged by latitude on the *y*-axis. The horizontal dashed lines delineate 3 regions of the California Current System: northern, central, and southern

identified from the Logerwell method (Fig. 6). However, those relationships were either not calculated (Logerwell method) or near zero (upwelling method) in the central and southern regions (Figs. 7 & 8). Relationships between the modified Logerwell dates and those from SST fields were consistently near zero for all regions (Figs. 6, 7, & 8).

The relationships between dates of spring transition and recruitment deviations varied according to species, region, and the method used to identify dates. For sablefish, the models that included spring transition identified from cumulative upwelling and the Logerwell method were significantly better fits to the data than the null models for the northern region (p = 0.04 and p = 0.001, respectively), and the model based on the modified Logerwell method approached significance (p = 0.06; Table 1, Fig. 11). However, this was not the case for the central or southern regions, or the model based on dates identified from SSTs for any region. Indeed, those models had higher AIC values (lower information content) than their null versions. For Pacific ocean perch, only the relationship based on dates of spring transition identified from the Logerwell method approached significance (p = 0.05; Table 1, Fig. 12). The remaining 3 models had higher AIC values than their null counterparts, suggesting no gain in information by including dates of spring transition.

DISCUSSION

Our results suggest that using the Logerwell approach, or the Bakun wind-derived index alone, provides an informative spring transition index in the northern region. However, these metrics may not be appropriate in the central and southern regions because of diminished, intermittent, or absent winter downwelling in those regions. For the central region, for 10 of the 40 years, either smoothed time series of Bakun winds remained positive during the winter or smoothed time series of coastal sea levels remained below their long-term mean. Furthermore, for most years in that region, the timing of onset of upwelling favorable winds differed from the timing of declines in sea levels (e.g. Fig. 3b). For the southern region, the smoothed time series of Bakun winds remained positive for 34 of 40 years. One possible explanation for the
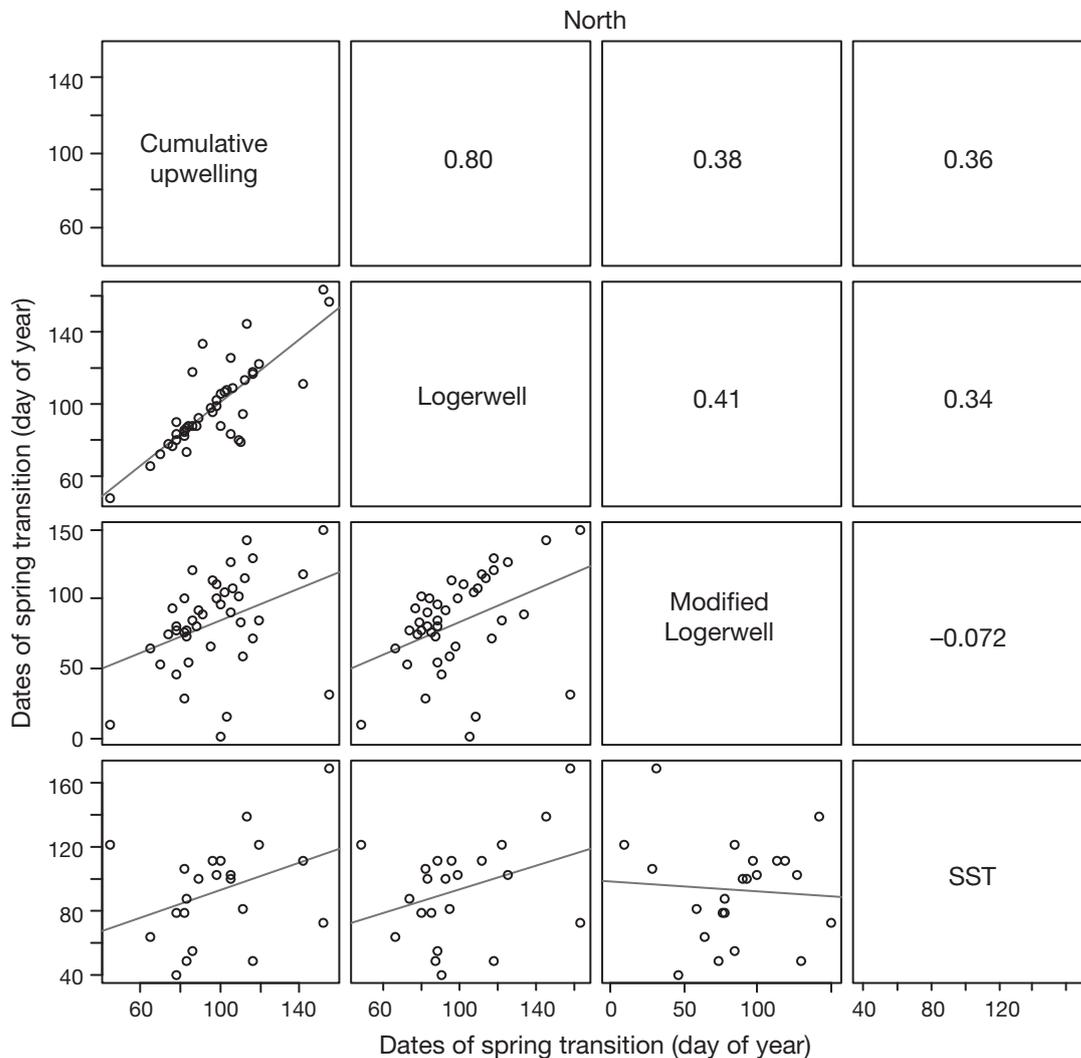
Fig. 6. Correlations between dates of spring transition (day of year) for the northern region of the California Current System identified from 4 methods: the start of the upwelling season (date of minimum cumulative upwelling), the Logerwell method, the modified Logerwell method, and an index of the dominant patterns in SST from EOF analysis that uses the date of maximum curvature in smoothed PC1 values

divergence in the timing of transition among metrics in central and southern regions is strong vertical stratification in the upper ocean during spring. That stratification can negate the impact of wind stress on the upwelling of cold, nutrient-rich water and can confound the relationship between upwelling winds and ecologically-important ocean conditions, as documented in 2005 (Kosro et al. 2006). Another possibility is that remotely forced, coastally trapped waves (Hickey et al. 2006) must be considered in conjunction with local wind forcing to account for seasonal changes in coastal sea levels and SSTs in the southern region (Enfield & Allen 1980). Although sea levels tend to covary at large spatial scales (i.e. exhibiting coherence within regions), Denbo & Allen (1987) found that the magnitude of those fluctuations varied by latitude and

were largest several hundreds of kilometers north of maxima in wind stress. Our observations of sea levels at San Francisco and San Diego for the central and southern regions, respectively, may be more closely related to variability in wind stress south of the southern boundary of the respective region than within it. In contrast, sea-level data for the northern region were collected near the northern boundary (Neah Bay) and likely integrate conditions over that region.

In contrast, we were able to identify dates of spring transition in all 3 regions using our modified version of the Logerwell method. That method had 2 additional advantages. The choice of the date (the date of steepest decline in low-pass filtered time series in sea levels) was more objective than the date chosen using the Logerwell method in years when multiple dates of
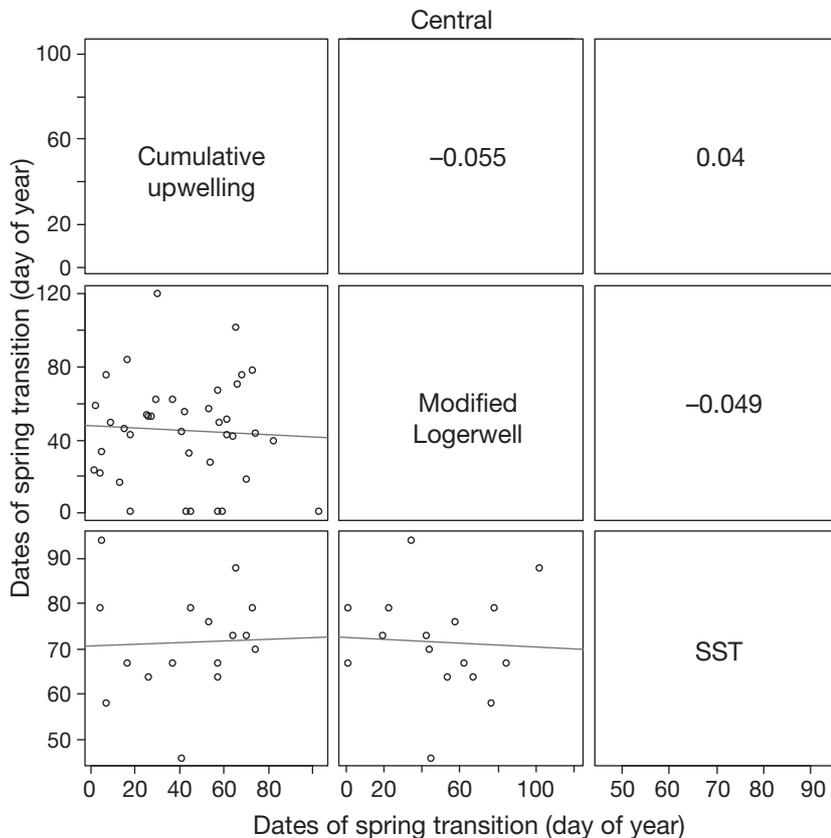
Fig. 7. Correlations between dates of spring transition (day of year) for the central region of the California Current System identified from 3 methods: the start of the upwelling season (date of minimum cumulative upwelling), the modified Logerwell method, and an index of the dominant patterns in SST from EOF analysis that uses the date of maximum curvature of smoothed PC1 values

zero-crossing existed in Bakun winds and sea-level residuals. Furthermore, our method more accurately reflected the timing of seasonal changes in ocean conditions that define the spring transition (date of steepest change) than previous methods that use arbitrary point thresholds (e.g. declines below the long-term mean sea level). However, the ability of our method to detect sudden declines in sea levels was limited by the smoothing of time-series data, which may have excluded high-frequency variation associated with spring transition.

Strong seasonal signals were also evident in our EOF-based indices of SSTs (Fig. 9). In the northern and central regions, differences between spring (April to June) and winter (January to March) SST fields indicate an incursion of cold upwelled water at the coast and/or the presence of remotely forced, coastally trapped waves (see the left panel of Fig. 10). However, the timing of SST changes was weakly (positively) correlated with the start of upwelling in the north only. South of Point Conception, the seasonal trends in SSTs are characterized by a local maximum in warming waters inside the Southern

California Bight, a local minimum in warming in a narrow band offshore, and a region of intermediate warming farther offshore (right panel of Fig. 10). The band of minimal seasonal warming is a southeastward extension of the seasonally cooling coastal upwelling waters in the central CCS region. The leading EOF from our analysis of SSTs in the southern region captures these features with an east-west dipole hinging on a line that extends southeastward from Point Conception. Once the regionally averaged seasonal warming is accounted for, the characteristics of the total winter-to-spring SST changes in the 3 regions of the CCS examined here are all consistent with the EOF loadings shown in the right panel of Fig. 10.

Comparison to previous literature

The sequence of seasonal changes in oceanographic variables that we examined generally agree with previous studies. Similar to our results, most studies have found the onset of upwelling favorable winds to either coincide or precede declines in sea level, depending on the region (Strub et al. 1987, Strub & James 1988, Logerwell et al. 2003). In contrast to our findings, Strub et al. (1987) found that seasonal cycles in sea levels lead those of mid-shelf SSTs by 1 to 2 mo across the US west coast (35° to 48° N). The differences in relative timing of SST changes between our results and those of Strub et al. (1987) can be explained in at least 3 ways. First, our measure was of spatial patterns in SSTs (i.e. we used ordination techniques to extract dominant spatial patterns in SST residuals), whereas Strub et al. (1987) used raw SST values. Second, our measure was independent of trends common within regions. In other words, our measure of SST changes was designed to filter out the seasonal trends due to increasing solar radiation that may have been captured by Strub et al. (1987). Third, we chose the date of maximum curvature in smoothed PC1 values as the date of spring transition, which preceded large absolute changes in SSTs described by Strub et al. (1987).

Few studies have examined differences in seasonal patterns in oceanographic conditions across regions in the CCS; most have focused on a single region (usually in the north). In one exception, Strub et al. (1987) found that the seasonal cycle of currents was more dramatic
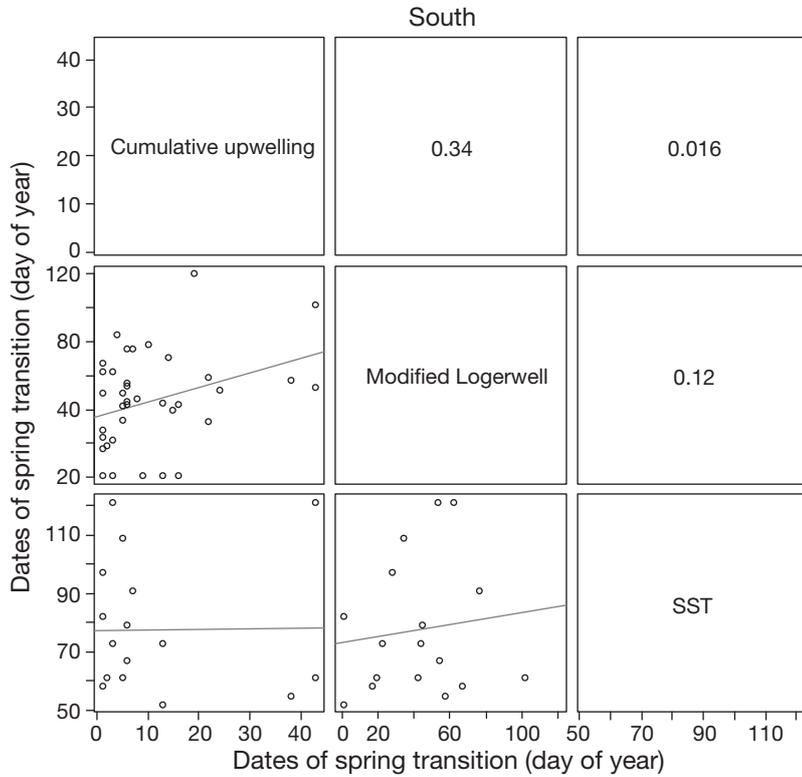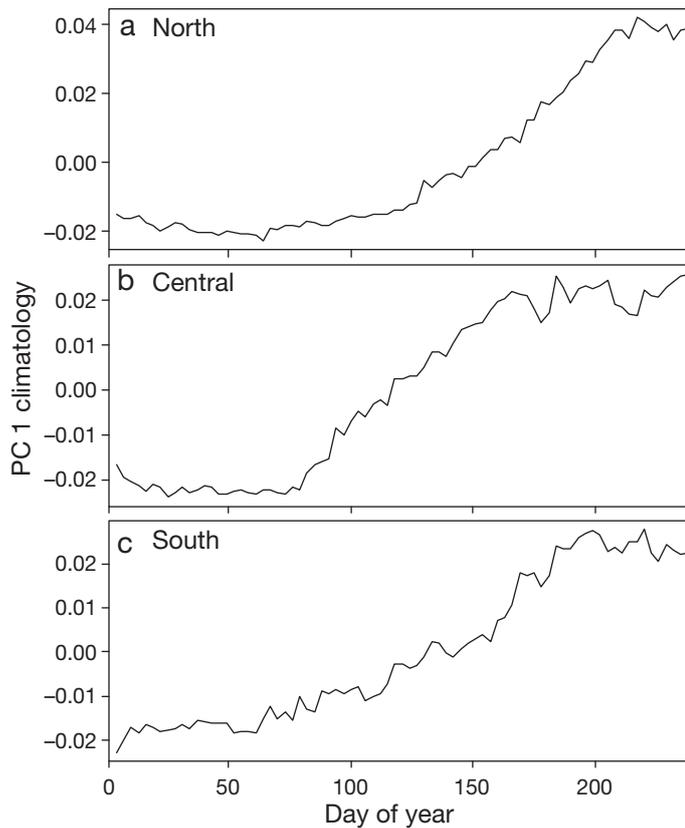
Fig. 8. Correlations between dates of spring transition (day of year) for the southern region of the California Current System (as described in the caption of Fig. 7)

Fig. 9. Climatologies of PC1 values for (a) northern, (b) central, and (c) southern regions of the California Current System for January through August (day of year 1 to 240, 1985 to 2007)

north of 45° N (accounting for 30 to 50% of variance in those currents) compared to the rest of the US west coast. Similar to our results, they found that the magnitude of seasonal cycles in winds and sea levels in the northern CCS exceeded the magnitude in southern regions.

Also similar to our results, south of 35° N, Strub et al. (1987) found that the onset of strong southward winds was followed by a more gradual decline in sea levels than observed in the north. They suggested that those sea-level declines tended to progress northward along the US west coast via coastally trapped waves over a period of 3 to 10 d. We found that declines in sea levels in the north occurred 1 to 4 wk later than in the south, suggesting that, in at least some years, sea levels may be forced by different mechanisms between regions, or the same mechanism (e.g. wind-derived upwelling and poleward propagating coastally-trapped waves) combined withregionally independent atmospheric forcing.

Again similar to our results, Enfield & Allen (1980) found strong correlations between coastal sea levels and wind stress north of San Francisco that were not apparent in the south. They attributed declines in coastal sea levels in the south to forcing by wind stress over the equatorial wave guide (e.g. associated with the Southern Oscillation) modified by annual insolation cycles, rather than local wind stress (which was responsible for declines in sea levels in the north). In another study comparing time series of sea levels across the margins of the Pacific Ocean, Roach et al. (1989) also suggested that sea levels were forced remotely by large-scale disturbances in the southern part of the CCS and locally in the north, as evidenced by higher correlations in sea levels among stations south of 38° N than north of that latitude.

Comparison to other metrics of spring transition

The timing of spring transition derived from other physical and biological indicators of ocean conditions from previous studies were either uncorrelated or pos-
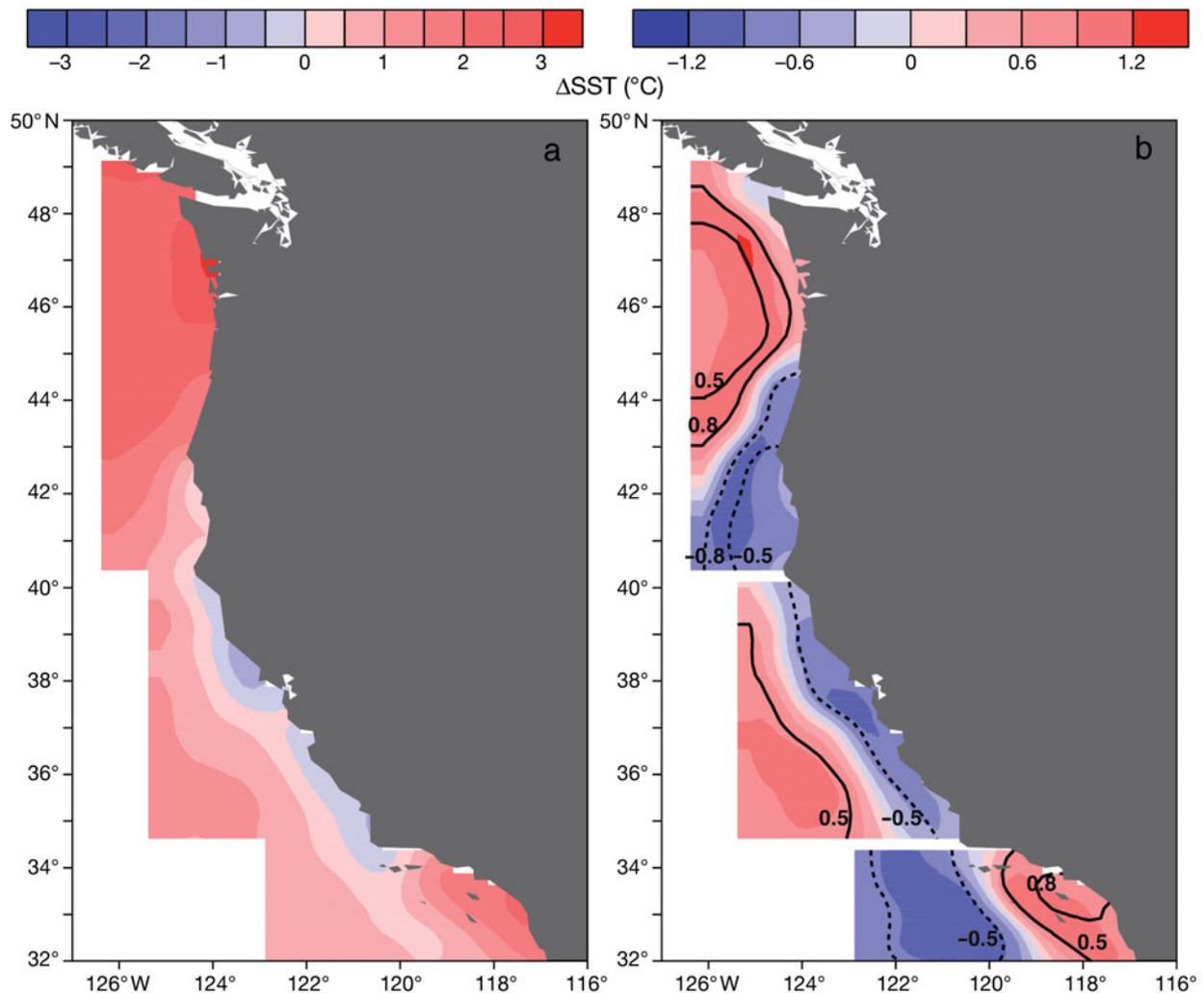
Fig. 10. (a) Change in raw sea-surface temperatures (SSTs) in °C between winter (averaged over January, February, and March) and spring (averaged over April, May, and June) for northern, central, and southern regions of the California Current System. (b) Correlation coefficients between SSTs (residuals from the spatial mean) and the first principal component (PC1) from EOF analysis for each grid point in the northern, central, and southern regions (contours), and slope of the relationship between PC1 (divided by its SD) and SST values for each SST location (colors)

itively correlated with our time series of spring transition. Consistent with the results of Thomson & Ware (1996), we found that dates of spring transition in the vertical shear of currents off Vancouver Island were uncorrelated with dates of spring transition identified from Bakun winds using the Logerwell method in the northern region (r = −0.33, p = 0.53), and the same was true for dates derived from the cumulative upwelling index (r = −0.42, p = 0.40) and the modified Logerwell method (r = −0.45, p = 0.37). These discrepancies can be explained in at least 3 ways. (1) the Bakun up-welling index (used in the cumulative upwelling and both Logerwell methods) is solely based on estimates of local alongshore windstress forcing that causes coastal upwelling, whereas current velocities used by Thomson & Ware (1996) represent integrated oceanic

processes more directly. (2) Thomson & Ware's (1996) index of current velocity smoothes out high-frequency wind-induced variation of the upper ocean not related to seasonal shifts, which may be captured by the Bakun upwelling index. (3) Thomson & Ware (1996) examined conditions off Vancouver Island, north of our study region. In addition, the dates derived from SST fields were uncorrelated with those of Thomson & Ware (1996) (r = −0.22, p = 0.67), suggesting that variation in SST is driven by processes other than (or in addition to) coastal currents.

Biological dates of spring transition derived from zooplankton community structure (Peterson 2008) tend to be approximately 1 mo later than dates derived from upwelling indices (Bakun winds and sea level data) perhaps due to a delay in zooplankton response to

Table 1. Summary statistics for linear relationships between dates of spring transition and ln(recruitment deviations) for Pacific ocean perch *Sebastes alutus* and sablefish *Anoplopoma fimbria*. Four methods for identifying dates of spring transition are listed in the third column: the date when the cumulative upwelling is minimized ('Start of upwelling'), the method used by Logerwell et al. (2003) ('Logerwell'), date of steepest change in smoothed sea levels ('Sea level', or modified Logerwell method), and date of seasonal shift in spatial patterns in sea-surface temperatures 'SST'. AIC_c: Akaike Information Criterion for small sample sizes; L ratio: likelihood-ratio test statistic that compares log-likelihoods of the linear and null models, where the null model has an intercept but no slope. p-values are based on a chi-squared distribution of L ratios

Species Region	Method for identifying date of spring transition	No. of years	Null model AIC_c	b_0	b_1	σ_ε	ΔAIC_c from null model	L ratio	p
Sablefish									
North	Start of upwelling	35	3.8	0.90	−0.00926	0.54	−2.02	4.42	0.036
	Logerwell	35	3.8	1.20	−0.0122	0.50	−7.82	10.22	0.001
	Sea level	35	3.8	0.46	−0.00552	0.55	−1.18	3.58	0.059
	SST	22	12.0	−0.23	0.00134	0.70	2.63	0.07	0.787
Central	Start of upwelling	35	3.8	0.08	−0.00191	0.57	2.15	0.25	0.616
	Sea level	33	−1.1	−0.24	0.0039	0.54	1.86	0.56	0.453
	SST	18	8.0	0.87	−0.0123	0.61	0.47	2.23	0.135
South	Start of upwelling	35	3.8	0.12	−0.0116	0.56	0.69	1.71	0.190
	Sea level	34	3.8	0.20	−0.00409	0.57	1.40	1.02	0.314
	SST	19	8.0	0.57	−0.0078	0.62	1.03	1.67	0.197
Perch									
North	Start of upwelling	37	20.2	0.58	−0.00848	0.62	0.24	2.13	0.144
	Logerwell	37	20.2	0.76	−0.0101	0.60	−1.31	3.69	0.055
	Sea level	37	20.2	0.13	−0.00444	0.63	1.14	1.23	0.267
	SST	22	16.3	−1.10	0.00949	0.65	0.10	2.75	0.098

favorable feeding conditions. Despite differences in average timing, positive correlations between those biological dates and our dates for the northern region (e.g. Logerwell method r = 0.80, p = 0.0004; modified Logerwell method r = 0.74, p = 0.01) suggest that the oceanographic mechanisms associated with spring upwelling and the drop in sea levels may also advect zooplankton species typical of summer conditions (originating from northern regions) into the CCS, replacing species typical of winter conditions (originating from southern regions).

Biological responses to the timing of spring transition

Although persistent changes during spring were evident in all 4 oceanographic time series that we examined, only those related to wind-driven upwelling and sea levels showed significant (negative) relationships with recruitment of Pacific ocean perch or sablefish. Those oceanographic variables reflect upwelling in coastal waters during spring (decreased sea levels and shift from poleward to equatorward winds) and may reflect increases in upwelling-derived productivity important during larval stages of groundfish. However, time series of spring transition derived from spatial-temporal patterns in SST residuals were uncorrelated with recruitment of Pacific ocean perch and sablefish.

In contrast to our results for SSTs, Lynn et al. (2003) observed changes in spatial patterns in SSTs concurrent with biological metrics of spring transition. However, they examined fine-scale spatial features in SSTs during spring rather than large-scale spatial trends, and in only a small region off of central California. Furthermore, they used primary productivity, as measured by nearshore vertically integrated fluorescence and beam attenuation coefficients, to demonstrate changes in biological conditions over spring and not higher trophic levels. Our measure of spatial gradients in SST may also be related to biological processes at lower trophic levels, not captured by our metric of groundfish recruitment.

We investigated the relationships between timing of spring transition and groundfish recruitment to demonstrate the biological implications of various methods for identifying timing of spring transition, and not to rigorously test those methods. Our interpretation of those examples is limited for at least 3 reasons. (1) Instead of a single physical driver (e.g. influx of food resources), recruitment may depend on the complex interaction of productivity, currents transporting larvae offshore away from zones of productivity, and distribution of predators. Those factors may be reflected in the different oceanographic variables used to identify spring transition, limiting the application of a single method for detecting that phenomenon. (2) Although both species are assessed as single popula-
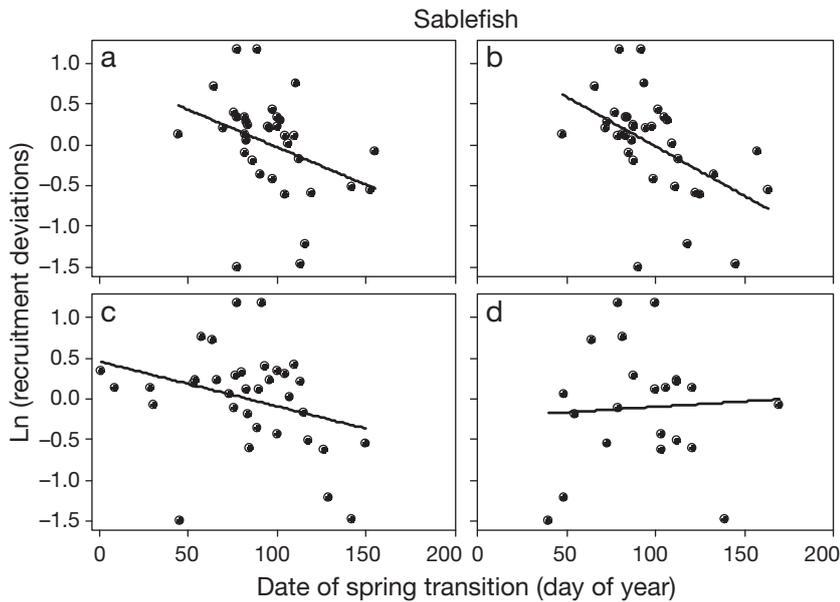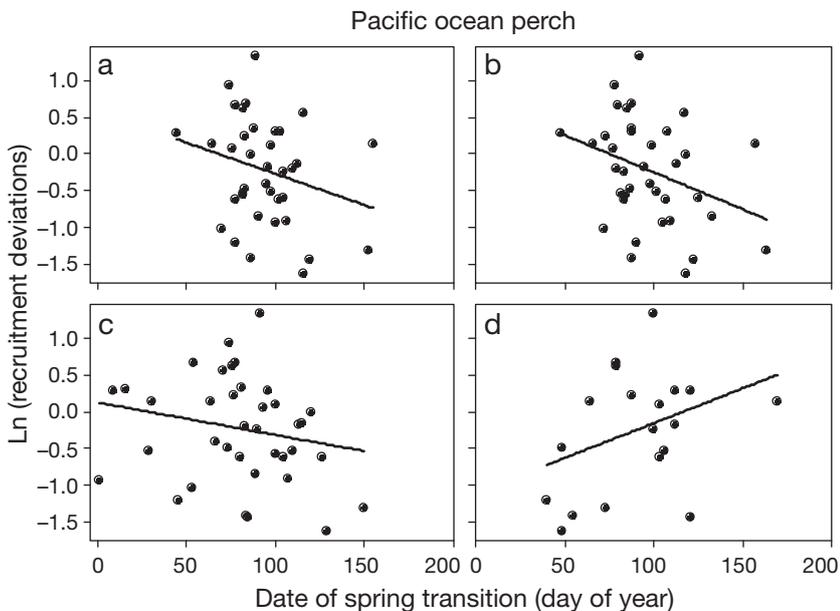
Fig. 11. Relationships between dates of spring transition and ln(recruitment deviations) for sablefish *Anoplopoma fimbria* using 4 methods for identifying spring transition: (a) the date when the cumulative upwelling first becomes positive, (b) the method used by Logerwell et al. (2003), (c) date of the steepest decline in smoothed sea levels, (d) and date of the seasonal shift in spatial patterns in sea-surface temperatures. Note the only difference in ln(recruitment deviations) for each plot is the number of years included. The relationships in plots (a), (b), and (c) were significant (i.e. $p < 0.05$) or approached significance (likelihood-ratio tests, $p = 0.04$, $p = 0.001$, and $p = 0.06$, respectively)

Fig. 12. Relationships between dates of spring transition and ln(recruitment deviations) for Pacific ocean perch *Sebastes alutus*, as described in the caption of Fig. 11. The relationship in plot (b) was marginally significant (likelihood-ratio test $p = 0.05$)

tions, there is some evidence for stock structure within populations (e.g. for sablefish see Schirripa (2007)), and those sub-populations may respond in different

ways to delays in spring transition. (3) For Pacific ocean perch, estimates of recruitment include variability in survival experienced over the first 3 yr of life, potentially swamping signals from larval life stages (the first year). Although the timing of spring transition may also influence maternal condition, which may in turn influence recruitment (Sogard et al. 2008), we found no significant relationships between timing of spring transition in the year prior to recruitment and abundance of recruits for either species.

CONCLUSIONS

Spring transition in the CCS is not a single, easily defined phenomenon. We advise caution when identifying dates of spring transition; individual methods for selecting those dates do not capture the complex multidimensional changes that occur. For example, in the southern CCS, dates derived by locally wind-driven upwelling, coastal sea levels, and SSTs differed by 1 to 2 mo of each other, and their time series were not significantly correlated.

The choice of an appropriate method depends on the specific oceanographic conditions relevant for hypotheses being tested (e.g. related to upwelling, temperatures, and/or biological habitat) and the spatial extent of investigation (e.g. regionally-specific or spanning the entire CCS). Metrics related to upwelling may be appropriate when transport constrains the ability of fish larvae to access high quality habitat and/or prey, and metrics derived from spatial patterns in SSTs may be related to other trophic levels (e.g. primary productivity). Instead of developing multiple time series of spring transition that reflect individual physical drivers, multivariate ordination techniques could be used to combine information across metrics (within or among regions). Environmental signals that are common among metrics could be extracted in a series of orthogonal ordination axes. Further studies at large spatial scales, multi-decadal temporal scales, and multiple trophic levels are required to identify

metrics that will be relevant to different components of the ecosystem.

Spatially comprehensive metrics of the timing of spring transition (i.e. that include the entire CCS) are warranted given the growing recognition for the ecological importance of this phenomenon and the large spatial scale of physical drivers (and hence biological responses). However, coast-wide metrics of upwelling may not be feasible given region-specific responses to physical drivers (e.g. interactions between coastally trapped waves and local winds). We developed 2 new methods to identify dates of spring transition that use the timing of rapid declines in sea levels and spatial patterns in SSTs, which may be more appropriate than previous methods when comparing northern, central, and southern regions of the CCS. Although not related to recruitment of sablefish or Pacific ocean perch, those methods may be related to other biological phenomena not investigated here. Metrics that span the CCS will be especially relevant with projected changes in the timing of spring transition under global warming scenarios (Snyder et al. 2003).

LITERATURE CITED

Armstrong EM (2000) Satellite derived sea surface temperature variability off California during the upwelling season. Remote Sens Environ 73:1–17

Bakun A (1996) Patterns in the ocean: ocean processes and marine population dynamics. University of California Sea Grant in cooperation with Centro de Investigaciones Biologicas de Noroeste, San Diego, CA

Barth JA, Menge BA, Lubchenco J, Chan F and others (2007) Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California current. Proc Natl Acad Sci USA 104:3719–3724

Bilbao P (1999) Interannual and interdecadal variability in the timing and strength of the spring transitions along the United States West Coast. MSc thesis, Oregon State University, Corvallis, OR

Bograd SJ, Schroeder I, Sarkar N, Qiu X, Sydeman WJ, Schwing FB (2009) Phenology of coastal upwelling in the California Current. Geophys Res Lett 36:L01602, doi:10.1029/2008GL035933

Denbo DW, Allen JS (1987) Large-scale response to atmospheric forcing of shelf currents and coastal sea level off the west coast of North America. J Geophys Res 92: 1757–1782

Dichmont CM, Punt AE, Deng A, Dell Q, Venables W (2003) Application of a weekly delay-difference model to commercial catch and effort data for tiger prawns in Australia's Northern Prawn Fishery. Fish Res 65:335–350

Enfield DB, Allen JS (1980) On the structure and dynamics of monthly mean sea level anomalies along the Pacific coast of North and South America. J Phys Oceanogr 10:557–578

Hamel O (2007a) Rebuilding update for Pacific ocean perch. Pacific Fishery Management Council, Portland, OR

Hamel O (2007b) Status and future prospects for the Pacific ocean perch resource in waters off Washington and Oregon as assessed in 2007. Pacific Fishery Management Council, Portland, OR

Hickey BM, Royer TC (2001) California and Alaska Currents. In: Steele JH, Thorpe SA, Turekian KK (eds) Encyclopedia of ocean sciences. Academic Press, Oxford, p 368–379

Hickey B, MacFadyen A, Cochlan W, Kudela R, Bruland K, Trick C (2006) Evolution of chemical, biological, and physical water properties in the northern California Current in 2005: remote or local wind forcing? Geophys Res Lett 33:L22S02 doi:10.1029/2006GL026782

Holt CA, Punt AE (in press) Incorporating climate information into rebuilding plans for overfished groundfish species of the U.S. west coast. Fish Res

Hooff RC, Peterson WT (2006) Recent increases in copepod biodiversity as an indicator of changes in ocean and climate conditions in the northern California current ecosystem. Limnol Ocean 51:2042–2051

Huyer A, Sobey EJC, Smith RL (1979) The spring transition in currents over the Oregon continental shelf. J Geophys Res 84:6995–7011

Huyer A, Fleischbein JF, Keister J, Kosro PM, Perlin N, Smith RB, Wheeler PA (2005) Two coastal upwelling domains in the northern California Current system. J Mar Res 63:901–929

Kosro PM, Peterson WT, Hickey BM, Shearman RK, Pierce SD (2006) Physical versus biological spring transition: 2005. Geophys Res Lett 33:L22S03 doi:10.1029/2006GL027072

Logerwell EA, Mantua N, Lawson PW, Francis RC, Agostini VN (2003) Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (*Oncorhynchus kisutch*) marine survival. Fish Oceanogr 12:554–568

Lynn R, Bograd S, Chereskin T, Huyer A (2003) Seasonal renewal of the California Current: the spring transition off California. J Geophys Res 108:3279

Peterson WT (2008) The biological spring transition. Northwest Fisheries Science Center, NOAA. Available at www.nwfsc.noaa.gov/research/divisions/fed/oeip/ec-biological-spring-trans.cfm

Peterson WT, Keister JE (2003) Interannual variability in copepod community composition at a coastal station in the northern California Current: a multivariate approach. Deep-Sea Res 50:2499–2517

Pickett MH, Schwing FB (2006) Evaluating upwelling estimates off the west coasts of North and South America. Fish Oceanogr 15:256–269

Reynolds RW, Smith TM, Liu C, Chelton DB, Casey KS, Schlax MG (2007) Daily high-resolution blended analyses for sea surface temperature. J Clim 20:5473–5496

Roach D, Mitchum G, Wyrtki K (1989) Length scales of interannual sea level variations along the Pacific margin. J Phys Oceanogr 19:122–128

Schirripa MJ (2007) Status of the sablefish resource off the continental U.S. Pacific coast in 2007. Pacific Fisheries Management Council, Portland, OR

Schirripa MJ, Colbert JJ (2006) Interannual changes in sablefish (*Anoplopoma fimbria*) recruitment in relation to oceanographic conditions within the California Current System. Fish Oceanogr 15:25–36

Schwing FB, O'Farrell M, Steger JM, Baltz K (1996) Coastal upwelling indices, west coast of North America, 1946–95. Report No. NOAA-TM-NMFS-SWFSC-231, US Department of Commerce, NOAA Technical Memorandum

Schwing FB, Bond NA, Bograd SJ, Mitchell T, Alexander MA, Mantua N (2006) Delayed coastal upwelling along the U.S. West Coast in 2005: a historical perspective. Geophys Res Lett 33:L22S01, doi:10.1029/2006GL026911

Snyder MA, Sloan LC, Diffenbaugh NS, Bell JL (2003) Future climate change and upwelling in the California Current. Geophys Res Lett 30:1823 doi:10.1029/2003GL017647

Sogard SM, Berkeley SA, Fisher R (2008) Maternal effects in rockfishes *Sebastes* spp.: a comparison among species. Mar Ecol Prog Ser 360:227–236

Strub TP, James C (1988) Atmospheric conditions during the spring and fall transitions in the coastal ocean off western United States. J Geophys Res 93:15561–15584

Strub PT, James C (2000) Altimeter-derived variability of surface velocities in the California Current System: 2. Seasonal circulation and eddy statistics. Deep-Sea Res II Top Stud Oceanogr 47:831–870

Strub PT, Allen JS, Huyer A, Smith RL (1987) Large-scale structure of the spring transition in the coastal ocean off western North America. J Geophys Res 92:1527–1544

Sydeman WJ, Bradley RW, Warzybok P, Abraham CL and others (2006) Planktivorous auklet *Ptychoramphus aleuticus* responses to ocean climate, 2005: unusual atmospheric blocking? Geophys Res Lett 33:L22S09, doi:10.1029/2006 GL026736

Thomas AC, Brickley P (2006) Satellite measurements of chlorophyll distribution during spring 2005 in the California Current. Geophys Res Lett 33:L22S05, doi:10.1029/ 2006GL026588

Thomson RE, Ware DM (1996) A current velocity index of ocean variability. J Geophys Res 101:14297–14310

Venegas RM, Strub PT, Beier E, Letelier R and others (2008) Satellite-derived variability in chlorophyll, wind stress, sea surface height, and temperature. J Geophys Res 113: C03015, doi:10.1029/2007JC004481

Zador SG, Parrish JK, Punt AE (2009) Factors influencing subcolony colonization and persistence in a colonial seabird, the common murre *Uria aalge*. Mar Ecol Prog Ser 376: 283–293