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7 2 **The role of environmental controls in determining sardine and anchovy population cycles**
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9 3 **in the California Current: Analysis of an end-to-end model**
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Abstract

Sardine and anchovy are two forage species of particular interest because of their low-frequency cycles in adult abundance in boundary current regions, combined with a commercially relevant contribution to the global marine food catch. While several hypotheses have been put forth to explain decadal shifts in sardine and anchovy populations, a mechanistic basis for how the physics, biogeochemistry, and biology combine to produce patterns of synchronous variability across widely separated systems has remained elusive. The present study uses a 50-year (1959-2008) simulation of a fully coupled end-to-end ecosystem model configured for sardine and anchovy in the California Current System to investigate how environmental processes control their population dynamics. The results illustrate that slightly different temperature and diet preferences can lead to significantly different responses to environmental variability. Simulated adult population fluctuations are associated with age-1 growth (via age-2 egg production) and prey availability for anchovy, while they depend primarily on age-0 survival and temperature for sardine. The analysis also hints at potential linkages to known modes of climate variability, whereby changes in adult abundance are related to ENSO for anchovy and to the PDO for sardine. The connection to the PDO and ENSO is consistent with modes of interannual and decadal variability that would alternatively favor anchovy during years of cooler temperatures and higher prey availability, and sardine during years of warmer temperatures and lower prey availability. While the end-to-end ecosystem model provides valuable insight on potential relationships between environmental conditions and sardine and anchovy population dynamics, understanding the complex interplay, and potential lags, between the full array of processes controlling their abundances in the California Current System remains an on-going challenge.

Keywords

End-to-end ecosystem model; sardine and anchovy; environmental conditions; upwelling; population dynamics; eastern boundary currents.

Regional Index Terms

U.S.A. West Coast, California Current System, 116-134°W, 30-48°N.

1. Introduction

In coastal upwelling regions such as the California Current system (CCS), small pelagic forage fish (e.g., sardines, anchovies, herrings) represent a major link between the lower and higher trophic levels. As such, these forage species are intimately tied to plankton concentrations (Cury et al., 2000), and constitute a significant part of the diet of apex predators (e.g., California sea lion; Weise and Harvey, 2008). Because of their position in the food chain, small pelagic fish integrate their own natural variability with spatial and temporal changes in their environment and in the foraging of their predators (Bakun, 2006; Field et al., 2006).

Sardine and anchovy are two forage species of particular interest because of their low-frequency (decadal) cycles in adult abundance in boundary current regions (Schwartzlose et al., 1999), combined with a commercially relevant contribution (up to 50%) to the global marine food catch (Fréon et al., 2005). The low-frequency fluctuations (indexed by landings) indicate synchronous variations off Japan, California, Peru, and Chile, with species thriving for several decades and then practically vanishing for similar durations. In the Atlantic Ocean, Benguela Current sardine and anchovies appear to be in synchrony with Pacific stocks, but in opposite

phase. Based on paleo-reconstruction, it is also known that the cycles have been occurring for hundreds of years (Baumgartner et al. 1992). While fisheries in each location affect sardine and anchovy population dynamics, their intensity and management has not varied in a coherent manner among the different systems. Hence, the persistence of low-frequency cycles suggests that environmental conditions play a major role (Alheit et al. 2009; Schwartzlose et al. 1999).

The synchrony among locations has led to hypotheses involving a single global driver linked to large-scale atmospheric or oceanic forcing (Bakun 1996). The Regime Indicator series (RIS; Lluch-Cota et al. 1997), synthesized from anchovy and sardine catch data, has been related to the low-frequency component of different climate indices, including the Pacific Decadal Oscillation (PDO) (Chavez et al. 2003), and to the low-frequency signature in global ocean temperature (Tourre et al. 2007). Recently, the spatial aspect of these low-frequency cycles has been investigated, with each species showing distributional expansions and contractions and latitudinal shifts (Barange et al. 2009; McFarlane and Beamish 2001). Several hypotheses have been put forth to explain decadal shifts in sardine and anchovy populations: low-frequency boundary current variability (flow, temperature, eddy activity, nutrients), age-dependent fecundity, density-dependent habitat selection, and fishing pressure (MacCall, 2009, and references therein). However, a mechanistic basis for how the physics, biogeochemistry, and biology combine to produce patterns of synchronous variability across these widely separated systems has remained elusive.

Environmental variability in the CCS is strongly impacted by the seasonal upwelling of cold, high salinity, nutrient rich water to coastal surface waters, attributed to the prevailing alongshore wind stress. Upwelled nutrient input to the euphotic zone stimulates new primary production along the majority of the west coast of the United States. The offshore region (100-300 km from

the coast) is mainly oligotrophic and includes the meandering California Current (i.e., the eastern boundary current associated with the North Pacific subtropical gyre). Between the coastal upwelling and offshore California Current regions is an alongshore front known as the California Current transition zone (CCTZ; Brink and Cowles, 1991), which has been identified as a region largely influenced by mesoscale processes and wind stress curl (Kosro et al., 1991; Strub et al., 1991). Oceanic mesoscale features in the transition zone supports significant contributions to primary production and have been linked to increased zooplankton biomass (Huntley et al., 2000) and sardine survival rates (Logerwell and Smith, 2001). In addition to intense seasonal upwelling and mesoscale processes, the CCS is also influenced by known modes of climate variability, such as the El Niño Southern Oscillation (ENSO; e.g. Lynn and Bograd, 2002), the PDO (Mantua et al., 1997), and the North Pacific Gyre Oscillation (NPGO; Di Lorenzo et al., 2009). Differences in physical and biological environments between the coastal upwelling region and the CCTZ also define habitat for planktivorous pelagic species: anchovies are generally located on the continental shelf where larger planktonic organisms dominate (e.g., diatoms, copepods), whereas sardines are typically distributed further offshore where micro-plankton is most abundant (Rykaczewski and Chekeley, 2008). During their northward summer feeding migration, adult sardine tend to move inshore and feed on larger prey types (e.g., copepods and krill) (Emmet et al., 2005; McClatchie, 2009), although they usually avoid freshly upwelled waters with temperatures below 12°C (Schweigert and McFarlane, 2001).

The main focus of the present study is to use a long-term historical simulation of a fully coupled end-to-end ecosystem model configured for sardine and anchovy in the CCS (Rose et al., this issue) to investigate how environmental (i.e., bottom-up) processes control adult population dynamics via growth, survival, and reproduction. The analysis should establish

whether similar processes determine interannual fluctuations in adult abundance for both sardine and anchovy, or whether each species exhibits a distinct response to environmental forcing owing to slightly different temperature and diet preferences (i.e., anchovy favor coastal waters and sardine favor offshore waters). Isolating bottom-up controls on population dynamics will not only shed light on the underlying mechanisms regulating low-frequency cycles of sardine and anchovy in the CCS, but it will also help understand how these cycles may change under future climate conditions.

2. Coupled End-to-End Ecosystem Model

The end-to-end ecosystem model for the CCS is fully coupled and combines a regional ocean circulation component, a Nutrient-Phytoplankton-Zooplankton component, a multi-species, individual-based fish component, and an agent-based fishing fleet component. The model is calibrated to represent two coastal pelagic fish species (anchovy and sardine) and a migratory predator species (albacore). The various components are summarized below and the reader is referred to Rose et al. (this issue) for a detailed description of the end-to-end model and its parameterization.

2.1 Regional ocean circulation model

The ocean circulation model for the CCS is an implementation of the Regional Ocean Modeling System (ROMS; Haidvogel et al., 2008; Shchepetkin and McWilliams, 2005) and ranges geographically from 30°N to 48°N and 116°W to 134°W. The horizontal grid resolution was 1/10° (ca. 10 km), and the vertical resolution was set to 42 non-uniform terrain-following levels (Fig. 1). The ROMS model was forced on all open boundaries by monthly-averaged fields from the Simple Ocean Data Assimilation (SODA; Carton et al., 2000) reanalysis to guarantee

realistic transport values and temperature and salinity profiles. Surface forcing was derived from the datasets for Common Ocean-Ice Reference Experiments (CORE2; Large and Yeager, 2008), which consists of 6-hourly winds, air temperatures, sea level pressure and specific humidity, and daily short-wave and downwelling long-wave radiation, and monthly precipitation. ROMS is known to exhibit significant skill in producing deterministic solutions (i.e., forward simulations) across a wide range of spatial and temporal scales in many regional-scale applications (Haidvogel et al., 2008), and several configurations have already been implemented in the Northeast Pacific Ocean (Curchitser et al., 2005; Veneziani et al., 2009).

2.2 Nutrient-phytoplankton-zooplankton model

The NPZ model was based on the 11-component NEMURO model (Kishi et al., 2007), which was specifically developed and parameterized for the North Pacific. In its default configuration, NEMURO includes three limiting macro-nutrients (nitrate, ammonium and silicic acid), two phytoplankton groups (nanophytoplankton and diatoms), three zooplankton groups (micro-, meso-, and predatory zooplankton), and three detritus pools (dissolved and particulate organic nitrogen and particulate silica). NEMURO uses nitrogen as the common “currency” and, for diatoms, silicon is converted to nitrogen using a fixed Si:N ratio. Nitrogen is recycled to ammonium via particulate organic nitrogen (PON) and dissolved organic nitrogen (DON), and silicon is recycled to silicic acid via particulate silica (opal). NEMURO has been used previously to investigate seasonal (Hashioka and Yamanaka, 2007) and interdecadal (Aita et al., 2007) lower trophic level ecosystem variability in the northern Pacific, and it has been coupled to fish bioenergetics models representing herring and saury population dynamics (Megrey et al., 2007; Rose et al., 2007). More recently, a coupled ROMS-NEMURO model, augmented with a carbon

component, has been used to investigate air-sea CO₂ flux variability in the CCS (Fiechter et al., 2013).

NEMURO was coupled to the ocean circulation by solving a transport equation in ROMS for each NEMURO component at every time step. A vertical sinking velocity is also applied to PON and opal. The initial and boundary conditions for nitrate and silicic acid are derived from monthly climatological concentrations (World Ocean Atlas 2001, 1°x1° horizontal resolution; Conkright and Boyer, 2002). For lack of better information, the initial and boundary conditions for ammonium, phytoplankton, zooplankton, and detritus (PON, DON, and opal) are set to a small value (0.1 mmolN m⁻³).

2.3 Multi species, individual-based fish model

The individual-based model (IBM) tracked individuals from each of the three model fish species in continuous (Lagrangian) space within the ROMS grid. The fish IBM included two coastal pelagic species, representing an inshore anchovy population and an offshore sardine population. The IBM also included a migratory predator species (albacore) that imposed dynamically-varying predation mortality rates on anchovy and sardine. The position of each individual in 3-dimensional space was updated hourly and followed both in continuous (longitude, latitude, depth) space and grid cell location.

Growth of larval, juvenile, and age-1 and older anchovy and sardine individuals was computed based on bioenergetics and a functional response relationship. The functional response determined the hourly consumption rate and used zooplankton concentrations in the same spatial cell generated by the NEMURO model. Adult fish in the model fed on all three zooplankton types produced by the NEMURO model with vulnerabilities and half-saturation constants specific to all stages of each fish species (i.e., larva, juvenile, age-1 and older) matched with each

possible prey type (i.e., micro-, meso- and predatory zooplankton). Total consumption by each individual was calculated using a multi-species version of a type 2 functional response (Rose et al., 1999). Although the vulnerabilities and half-saturation constants were fixed for each predator-prey type combination, actual diet composition of individual sardine and anchovy varied during the simulation as individuals moved among areas on the grid where zooplankton types themselves varied spatially and temporally. Anchovy typically feeding on larger prey types and sardine on smaller ones was represented in the model by setting the diet preferences (i.e., vulnerabilities and half-saturation constants so that adult anchovy favored predatory zooplankton (i.e., krill) and adult sardine favored microzooplankton (see Rose et al., this issue).

Mortality for sardine and anchovy in the fish IBM was represented by a fixed natural mortality rate based on the stage specific values reported by Butler et al. (1993), with the addition of dynamically imposed starvation (from weight-length relationship) for feeding stages (i.e., larva to adult) and predatory mortality rates (from albacore species) for age-1 and older individuals. Adult sardines were also subjected to daily fishing mortality (see Section 2.3). Mortality from starvation was treated separately because starvation was not a rate, but rather starved super-individuals were removed from the simulation.

Reproduction for mature fish in the model kept track of egg development or resorption for each batch produced by an individual, and was configured to produce batch sizes and number of batches for anchovy and sardine similar to reported values (see Rose et al, this issue). The timing of batch releases depended mostly on the energy stores of the individual at the beginning of the spawning season (i.e., income spawning). The simulated number of batches per spawner was relatively constant with age, with a yearly average of 12-15 for anchovy and 8-10 for sardine; total annual production was approximately $2 \text{ to } 4 \times 10^{15}$ eggs.

Anchovy and sardine individuals were moved behaviorally using a kinesis approach in which horizontal displacements are based on the sum of inertial and random components depending on proximity to optimal conditions (Humston et al. 2004; Rose et al., this issue). Temperature and prey availability at the location of each individual were used as cues to determine movement by weighting the inertial component more when conditions are near optimal and weighting the random component more when conditions are far from optimal. Hence, kinesis behavior allows an individual to maintain itself in a favorable temperature and food environments (inertial component) or to perform a random search of the surrounding environments for better conditions when temperature and food deviate too far from optimal (random component). The maximum distance an individual of each species could move during a time step was based on a swimming speed of three body length per second (i.e., roughly 1.6 km h^{-1} for adult anchovy and 2.2 km h^{-1} for adult sardine). Vertical movement was more simply simulated by positioning the individuals at the depth where they maximized consumption based on local prey availability and temperature. A seasonal feeding migration was also imposed on sardine individuals by biasing kinesis movement poleward during May (i.e., towards summer feeding grounds) and equatorward during September (i.e., towards winter spawning grounds). The predator species was moved in the horizontal (surface) plane only (but ate fish located over the entire water column) based on restricted-area (neighborhood) search using growth rate as a measure of fitness (Watkins and Rose, 2013).

The overall numerics of the fish IBM were based on the use of the super-individual approach (Scheffer et al. 1995), where a fixed number of model individuals are followed, with each model individual worth some number of identical population individuals. Mortality from all sources (except starvation) acted to reduce the worth of each individual over time. Upon reaching a

maximum age, all super-individuals were removed and the empty super-individuals were then used to track the next year's production of eggs. Although super-individuals were tracked until a fixed maximum age, the worth of many of the individuals reached zero much sooner due to mortality; super-individuals with effectively zero worth were excluded from the simulation via a "dead/alive" flag. On average, age-7 and older fish represented only a small fraction of the total adult population in the model (i.e., < 1% for anchovy and < 5% for sardine).

2.3 Fishing fleet model

The daily location choice, and associated daily catch, of individual boats that fished sardine individuals was simulated using a simplified multinomial logit, agent-based approach where boats maximized their expected net revenue for each trip (e.g., Eales and Wilen, 1986). Fishing boats were moved horizontally using the surface layer of the ROMS grid, and they could encounter all sardine individuals in the water column below each surface cell. Each boat is defined by a suite of traits related to motoring speed and costs, capacity, catchability, and encounter rates. A total of 100 boats were used in the simulation with every boat having identical attributes and a maximum daily capacity of 30 metric tons of sardine (see Rose et al., this issue). A trip by a boat had to be completed within 24 hours, including the time to travel to the cells to fish and the time to return to the nearest port from the last cell fished. The expected catch per unit effort (CPUE) for each horizontal cell was defined as a 10-day moving average, and updated each day after fishing by all boats occurred. If no sardine individuals were caught in a given cell, the expected CPUE was updated based on "historical" information using either the maximum CPUE over the past 9 days or the average CPUE from the same month of the previous year. This approach assumed that fishing boats would expect that CPUE in a cell was either what occurred in the recent past (previous 9 days) in that cell or what was caught last year in that cell during the

same month. Fishing occurred every day of the year, as long as boats had access to a grid cell where expected net revenue was positive.

3. Historical Simulation and Analysis Method

3.1 Historical Simulation

The analysis was focused on a 50-year integration (1959-2008) of the fully-coupled end-to-end ecosystem. The simulation is the same as that reported and documented in Rose et al. (this issue). The objectives were to further examine model results to determine how environmental variables control the annual variation in adult anchovy and sardine adult abundances in the CCS, and to determine if the simulated environmental conditions correlated with known regional climate indices. The analyses could then provide a cascading link from climate to local environmental conditions to anchovy and sardine population cycles.

Differences in prey preference and behavior led to distinct spatial distributions between adult sardine and anchovy, with anchovy residing mainly on the shelf and sardine occupying the CCTZ (Fig. 2, far right panels). Based on their respective spawning seasons (Jan-Apr for anchovy and Feb-Jun for sardine) and temperature ranges (11.5-16.5°C for anchovy and 12-15°C for sardine), reproduction and early life development occurred principally in the southern CCS (i.e., equatorward of 40°N), as evidence by the mean abundance distributions for eggs, yolk-sacs, larvae, and juveniles (Fig. 2, far left to center right panels). While simulated abundances generally reproduced the expected spatial distributions for both species (i.e., order of magnitude higher abundances on the shelf for anchovy and in the transition zone for sardine), it is difficult to ascertain whether the results over or underestimate the actual geographical extent over which the various life stages of each species are found.

Anchovy and sardine exhibited distinct interannual and low-frequency variability in abundance during early life stages and as adults (Fig. 3). Annual abundances of eggs plus yolk-sac larvae, larvae, juveniles, and adults (age-1 and older) on January 1 were calculated by summing the worths over all super-individuals by species and life stage first, and then transforming these abundances to anomalies by removing their respective long-term mean and normalizing by the corresponding standard deviation. All showed a consistent pattern of anchovy peaking during the early 1970's and the 1980's, while sardine remained relatively low until steadily increasing from the mid 1990's to the end of the model run. The low frequency variability in simulated adult biomass for each species also compared favorably with historical observations (Barange et al., 2009; Fissel et al., 2011; Hill et al., 2009), especially in overall increase (decrease) of sardine (anchovy) population abundance starting in the early 1990's (Rose et al., this issue).

All model output variables used in the analysis were summed or averaged to obtain annual values. Variables related to sardine and anchovy were computed by accounting for the different and changing worths of the super-individuals. For a given year, adult abundances were the summed worths of all age-1 and older individuals on January 1 of that year. Survival fractions were computed as the summed worth of individuals exiting the stage divided by the summed worth that entered the stage for each year. Annual egg production (total and by age class) was the sum of eggs produced by each spawner for each batch multiplied by its worth at the time of batch release, accumulated over all spawners in that year. Averaged eggs per individual by age-class for each year were computed by dividing the total number of eggs produced by a given age-class by the total worth associated with that age-class on January 1. Weight and growth at age were based on the averaged weights on January 1. The environmental conditions experienced by

anchovy and sardine were from the ROMS and NEMURO fields interpolated hourly to the exact 3-dimensional location of each individual. Mean annual values for the ROMS and NEMURO variables and climate indices were calculated by averaging monthly values over a calendar year.

3.2 Analysis Method

A three step analysis was used to dissect the causes of the anchovy and sardine adult dynamics in the historical simulation (Fig. 4). Whenever possible, the analysis was performed in parallel for anchovy and sardine to provide a direct contrast between the two species. However, if a variable was found unimportant, the analysis was stopped for one of the species as there was no reason to look for further correlations.

The first step was to establish which biological processes controlled sardine and anchovy adult population dynamics. Since an earlier examination of the 50-year simulation (see Rose et al., this issue) already determined that annual adult mortality rates from predation and fishing imposed in the model did not exhibit sufficient interannual variation that could explain the simulated fluctuations in population abundances, the analysis presented here was focused instead on early life stage survival and reproduction as explanatory mechanisms. To that end, annual abundances of adult anchovy and sardine were first related to lagged annual age-0 (egg through juvenile) survival rates and to lagged total annual egg production. For survival, the rationale was to determine whether high survival of age-0 life stages in one year eventually led to higher abundances in subsequent years. For example, a strong correlation of adult abundances to age-0 survival from the previous year (lagged -1 year) or two years ago (lagged -2 years) would suggest that high age-0 survival resulted in high adult abundances. A strong correlation of adult abundances and age-0 survival lagged forward (e.g., the next year) is unlikely as it would suggest that high adult abundance led to high age-0 survival (i.e., the opposite of density-dependence

effects). For reproduction, the rationale was to identify if high adult abundance led to high egg production, or vice versa, by calculating correlations lagged backward and forward in time between the two variables and determining whether high egg production preceded or followed high adult abundance. Because total population fecundity combines the effects of multiple years, correlations were also calculated for age specific fecundities to allow for a clearer detection of the lagged signal associated with conditions specific to single earlier or later years.

As part of the first step, the causes of the interannual variation in age-0 survival and total egg production were further dissected. Age-0 survival was related to life stage-specific survival rates for eggs plus yolk-sac, larval, eggs through larvae, and juvenile stages. The relationship between adult abundance and egg production was more difficult to establish, as cause and effect become conflated. Since more eggs led to more adults but more adults then led to more eggs being produced; the lags between adult abundance and egg production became important to identify cause and effect. Total annual egg production was mainly contributed by age-1 to age-4 individuals (approximately 90% for anchovy and 65% for sardine). Adult abundances were therefore related to lagged age-specific (ages 1 to 4) annual egg production to identify the important age-classes whose reproductive output controlled annual adult abundances. Using the important age-specific egg production, averaged eggs per individual for this age class was related to average weight of this age and to lagged annual growth rates and weights of younger age classes.

Having established the primary biological processes driving population dynamics in the model, the second step in the analysis was to link changes in these processes to variations in environmental conditions. Temperatures and prey concentrations directly experienced by model individuals were used to quantify environmental conditions, which avoided the need to define

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4 344 spatial subregions over which to average temperature and prey. More specifically, anchovy age-1
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14 348 preferences. The relative contribution of temperature versus prey effects was determined by
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16 349 examining anomalous years. Anomalous conditions were identified as years during which
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19 350 growth or survival was above or below one standard deviation from the long-term mean (i.e.,
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21 351 normalized anomalies greater than 1 or less than -1). Spatial maps of temperature and prey
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24 352 experienced were created by first averaging over all individuals (weighted by their respective
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26 353 worth) present in a given grid cell every five days (i.e., outputting frequency), and then
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29 354 computing an annual mean for each year. Using the anomalous years, three maps were calculated
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31 355 for anchovy age-1 growth, three maps for sardine egg+yolk-sac survival, and three maps for
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33 356 sardine larval survival (juvenile survival was unimportant for determining age-0 survival of
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36 357 sardine). A map of normal years was first produced, and then differences maps corresponding to
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38 358 years of low and high growth or survival were derived. The maps for anomalous years were
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41 359 computed as the average for those years minus the average from the normal years on a cell-by-
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43 360 cell basis.

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45 361 The third and final step in the analysis was to correlate the environmental conditions
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51 363 using the ROMS and NEMURO output directly. The analysis was based on the same division of
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53 364 years into anomalously high and low growth for age-1 anchovy and survival for age-0 sardine as
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55 365 used in the second step. Annual anomalies of simulated sea surface temperature, total surface
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58 366 phytoplankton and zooplankton concentrations, and eddy kinetic energy were calculated and
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presented as spatial maps for years coinciding with anomalous growth and survival conditions. Since surface temperature, phytoplankton and zooplankton anomalies for anchovy growth and sardine survival were identified based on a collection of single anomalous years, the annual mean model fields for all years were decomposed using an empirical orthogonal function (EOF) approach to determine if the patterns identified as anomalous were robust and emerged as dominant modes of variability in the 50-year ROMS and NEMURO solutions. The correspondence between EOF patterns and anomalous growth and survival conditions was further illustrated by contrasting the time-varying amplitudes of the different modes with changes in sardine and anchovy adult population biomass. EOFs describing physical variability were not directly compared to EOFs of anchovy and sardine biomass for two reasons: (1) annual mean biomass fields at 10-km horizontal resolution are too noisy to extract meaningful modes of variability without substantial spatial smoothing, and (2) biomass is not correlated at 0-lag with the physical processes controlling its interannual variability (as demonstrated in Sections 4.1 and 4.2). Hence, the analysis is clearer if the biological processes controlling abundance (and associated lags) are first identified, and then related directly (i.e. at 0-lag) to physical variability.

Finally, the variability present in the EOF modes was related to known climate indices associated with fluctuations in the broader CCS circulation and lower trophic level ecosystem response. For this purpose, the PDO, NPGO, ENSO (Niño 3.4 Index) and coastal Upwelling Index (UI; Bakun, 1973) were averaged to obtain annual values (Fig. 5), and regressed against annual anchovy age-1 growth and sardine age-0 survival using only anomalous years (i.e., normal years removed). The PDO Index represents the first dominant mode of variability in observed monthly sea surface temperature anomalies in the North Pacific Ocean (source: jisao.washington.edu), while the NPGO Index represents the second dominant mode of observed

sea surface height variability in the Northeast Pacific Ocean (source: www.o3d.org). The Niño 3.4 Index represents a 3-month running mean of sea surface temperature anomalies in region 3.4 of the equatorial Pacific Ocean (source: www.ncdc.noaa.gov); and the UI represents an estimate of offshore Ekman transport along the coast based on mean large-scale pressure gradients over the Northeast Pacific Ocean (source: www.pfel.noaa.gov).

4. Results

4.1 Biological controls on population dynamics

For anchovy, simulated adult abundance was more closely related to variations in egg production than to variations in early life survival (Fig. 6, left panels). The causality between population abundance and egg production was based on the fact that adult abundance on a given year had the highest correlation ($r = 0.82$; Table 1) with annual egg production the year before (i.e., -1 year lag). This result was further confirmed by calculating similar lagged correlation between age specific egg productions and total population abundance (Table 1). The one year lag effect suggested that variation in adult abundance in the model first resulted from changes in egg production, rather than the opposite. In contrast, adult anchovy abundance on a given year was uncorrelated to age-0 survival the previous year ($r = 0.02$; Table 1), meaning that changes in age-0 survival were not a primary driver for variation in total population abundance. It should however be noted that years of high or low age-0 survival can enhance or mitigate the effect of egg production on adult abundance. For sardine, simulated egg production tracked abundance, and changes in abundance were primarily associated with interannual variations in age-0 survival (Fig. 6, right panels). Although the correlation coefficients between sardine adult abundance and egg production were above 0.8, the highest values occurred at lags of 0 and +1 year (Table 2),

which confirmed that changes in abundance were the primary cause for variation in egg production. In contrast, the correlation coefficient between sardine adult abundance and age-0 survival, while relatively low ($r = 0.3$; Table 2), was highest at a lag of one year, indicating that variations in age-0 survival on a given year led to changes in adult abundance one year later. In the model, age-0 survival for sardine was almost entirely determined by survival during the egg and yolk-sac stages (hereafter referred to as the “egg” stage for simplicity), as suggested by the near perfect coincidence between egg survival and age-0 survival (Fig. 7, right panels). While not a predominant factor controlling population dynamics for anchovy, changes in age-0 survival were mainly determined through the end of the larval stage (Fig. 7, left panels).

For anchovy, annual adult abundance correlated highly ($r > 0.7$) with age-2, age-3, and age-4 egg production at a lag of -1 year (Fig. 8, left panels and Table 1). However, because age-2 egg production exhibited the highest correlation coefficient ($r = 0.77$) and accounted for approximately 50% of the total number of eggs produced each year, age-2 reproductive output was critical in affecting anchovy adult variations in the model. For sardine, although egg production from the various age classes tracked adult abundance, the highest correlations occurred at a lag of +1 years, thereby indicating dependence, not causality (Fig. 8, right panels and Table 2).

Fluctuations in annual age-2 egg production of anchovy was related to the average number of eggs per individual ($r = 0.42$), which itself varied as a function of growth during the previous year ($r = 0.66$) (Fig. 9). Hence, years of low versus high growth for age-1 anchovy (and to a lesser extent age-2 and age-3 anchovy) led to a decrease or increase in reproductive output during the next year, and, ultimately, affected adult abundance the year after.

4.2 Environmental controls on biological processes

For anchovy, anomalous growth conditions were typically balanced between “good” and “bad” years prior to 1980, but became dominated by several years of markedly poor growth (i.e., 1987, 1992 and 1997) during the second half of the simulation (Fig. 10, upper panel). Years of low age-2 growth coincided with the decrease in population abundance from the late 1980’s to the late 1990’s (see Fig 3, left panel). For sardine, most anomalous years of age-0 survival occurred during the second half of the simulation (1985-2008), and were dominated by a group of several years of enhanced survival in the 1990’s (i.e., 1992, 1993 and 1997) (Fig. 10, lower panel). Years of high age-0 survival coincided with the period of rapidly increasing adult abundance (see Fig. 3, right panel). Interestingly, there were years that had anomalously low age-1 growth for anchovy and anomalously high age-0 survival for sardine (e.g., 1969, 1992, 1997). The model results thus suggest the existence of coinciding environmental conditions that would lead, if they persisted, to opposite adult abundances between anchovy and sardine.

Years of anomalously low age-1 growth for anchovy were associated with reduced prey availability in the model on the shelf along most of the U.S. west coast, and in particular in the southern California Bight (i.e., 31 to 34 °N) (Fig 11, left panels). In contrast, years of anomalously high growth were associated with substantially cooler temperatures and higher prey availability on the shelf, with the largest temperature anomalies (0.5 to 1.0 °C) occurring off central California (i.e., 34 to 38 °N) and the largest prey availability anomalies occurring in the southern California Bight (Fig. 11, right panels). Simulated temperature and prey availability anomaly patterns during years of high anchovy age-1 growth were indicative of periods of enhanced upwelling in the southern CCS, which would lead to a more productive lower trophic level ecosystem on the shelf and favor anchovy growth.

Age-0 survival of sardine was anomalously low when the egg and larval stages experienced substantially cooler temperature (anomalies up to 2.0 °C) in the CCTZ, and larvae experienced slightly higher prey availability over the same region (Fig. 12, left panels). During years of anomalously high survival, temperatures averaged 0.5 to 1.0 °C above normal and prey availability during the larval stage was slightly reduced (Fig. 12, right panels). Since egg and yolk-sac larva being non-feeding stages, this finding is consistent with their development time, and hence cumulative stage survival, being entirely determined by temperature. Furthermore, the effects of small differences in temperature were important because, combined with the high mortality rate associated with sardine eggs and yolk-sac larvae in the model ($\sim 0.7 \text{ day}^{-1}$; Butler et al., 1993), they resulted in large changes in cumulative stage survival. Because age-0 survival was controlled by survival during the egg and yolk-sac stages (see Fig. 7, right panels), years of increased (decreased) age-0 survival were characterized by anomalously high (low) temperatures. The fact that larvae typically experienced higher prey availability during years of low survival further confirms that the larval stage does not significantly affect age-0 survival, as one would expect to see a reversed effect (i.e., high prey availability should lead to higher growth and, thus, higher survival).

4.3 Connections between environmental conditions and climate variability

During years of high anchovy age-1 growth, anomalous conditions were most pronounced in the near-shore region of the southern CCS, with markedly cooler sea surface temperatures and higher total zooplankton concentrations in the southern California Bight and near Point Conception (near 34 °N) (Fig. 13, upper panels). Simulated eddy kinetic energy was also higher off the central and northern California coast (35-39 °N), suggesting an increase in mesoscale variability (i.e., jets and filaments) associated with more intense wind-driven coastal upwelling.

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4 481 In contrast, during years of low anchovy growth, anomalous conditions were more wide-spread,
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6 482 with warmer sea surface temperatures and lower zooplankton concentrations prevailing over
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9 483 most of the CCS domain (Fig. 13, lower panels).

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11 484 A similar analysis using years of high and low sardine age-0 survival indicated that
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14 485 anomalous conditions for simulated temperature, phytoplankton and zooplankton were not
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16 486 associated with specific subregions, but rather prevailed over the entire CCS domain. During
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19 487 high survival years, surface temperatures were warmer (by ca. 0.5 °C), while phytoplankton and
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21 488 zooplankton concentrations were reduced (Fig. 14, upper panels). In contrast, during years of
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24 489 low survival, surface temperatures were markedly cooler (by up to 1 °C), while phytoplankton
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26 490 and zooplankton concentrations were anomalously high over most of the CCS (Fig. 14, lower
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29 491 panels). Differences in EKE related to years of anomalous age-0 survival were not as obvious as
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31 492 for anchovy, but the results suggested slightly higher EKE in the southern (northern) CCS during
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36 494 An empirical orthogonal function (EOF) decomposition of the annual mean model fields for
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41 496 anchovy population dynamics in the model corresponded to leading modes of simulated physical
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43 497 and lower trophic level ecosystem variability in the CCS (Fig. 15). For example, the patterns of
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48 499 was associated with years of high anchovy age-1 growth emerged as the second EOF mode for
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51 500 temperature (8.5% of total variance) and third EOF mode for zooplankton (7.3% of total
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53 501 variance). Similarly, domain-wide fluctuations in temperature and zooplankton associated with
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56 502 years of anomalously high and low sardine age-0 survival emerged as the first EOF mode for
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58 503 both temperature and zooplankton (67% and 26% of total variance, respectively).

For anchovy, years of higher adult biomass in the model generally coincided with the distinctively positive amplitude in the third EOF mode for zooplankton (e.g., 1967-1973 and 1984-1988) (Fig. 16, top left panel). Similarly, years of lower anchovy adult biomass were typically correlated with periods of markedly negative amplitude in the first EOF mode for zooplankton (e.g., 1976-1978 and 1992-1995) (Fig. 16, bottom left panel). For sardine, simulated adult biomass remained low during years of the prolonged negative amplitude in the first EOF mode for temperature (e.g., 1968-1976), and increased substantially during the extended periods of positive amplitude (e.g., 1992-1998) (Fig. 16, right panels). Comparison between EOF modes and adult biomasses also hinted at potential environmental conditions leading to out-of-phase low frequency variability between the two species. Two noticeable examples were the 1967-1973 and 1992-1998 periods: zooplankton concentrations favored anchovy growth in the earlier period and limited growth in the latter period, while temperatures reduced sardine survival in the early period and increased survival in the latter period.

For the environmental conditions modulating anchovy age-1 growth, the first EOF mode for zooplankton (i.e., low growth mode) was most highly correlated (negatively) with ENSO ($r = -0.54$), while the third EOF mode for zooplankton (i.e., high growth mode) was most highly correlated (negatively) with the NPGO ($r = -0.23$) (Table 4). However, the correlation between the third mode and the NPGO was low, and the first mode also correlated with the PDO, NPGO and UI, although at a slightly lower level than for ENSO. The second EOF mode for temperature, also related to years of high anchovy growth, is weakly correlated with ENSO ($r = -0.21$) and the UI ($r = 0.21$). For the environmental conditions modulating sardine age-0 survival, the first EOF mode for surface temperature (i.e., both high and low survival mode) was most highly correlated (positively) with the PDO ($r = 0.69$) (Table 4). Because the low frequency

variability in the ENSO signal is partly related to the PDO, the first EOF mode for temperature also correlated (positively) fairly highly with ENSO ($r = 0.58$).

A direct comparison between climate indices and years of anomalous anchovy age-1 growth and sardine age-0 survival indicated that anchovy growth was negatively related to ENSO ($R^2 = 0.4$) and positively related to the UI ($R^2 = 0.3$), while sardine survival was positively related to the PDO ($R^2 = 0.6$) (Fig. 17). Since anchovy growth in the model is primarily affected by prey availability, it intuitively makes sense that growth variations depend on coastal upwelling intensity and ENSO events (during which primary production in the southern CCS is on average reduced). Similarly, the relationship between simulated sardine survival and the PDO is consistent with the fact that survival variations primarily respond to region-wide temperature fluctuations.

5. Discussion

The present study illustrates how output from a fully coupled end-to-end ecosystem model can be used to investigate linkages between environmental forcing (i.e., physical and biogeochemical), early life survival, adult growth and reproduction, and, ultimately, population dynamics sardine and anchovy in the CCS. While such models can easily generate an “overload” of information, having access to the exact environmental and feeding conditions experienced by individual fish throughout their life history (i.e., from eggs to adults) enabled identification of the physical and biological processes responsible for spatial and temporal variations in growth, survival, and abundance. Despite being dependent on model hypotheses and simplifications (e.g., behavioral cues, predation mortality), the results presented here still indicate a robust signal between environmental conditions and key biological processes impacting sardine and anchovy

population dynamics. Furthermore, the EOF analysis established that the anomalous conditions experienced by the fish corresponded to actual modes of variability in the ROMS and NEMURO solutions, and that these modes were in turn related to known climate-scale variability (i.e., PDO, ENSO, NPGO and UI). While the correlation coefficients do not unequivocally link a single index to each EOF mode, they identify potential relationships between modes of variability in the CCS and the temperature and zooplankton patterns associated with years of anomalous anchovy growth and sardine survival. Although some degree of sensitivity to the parameterization of the IBM is expected, many of the rates and relationships used in the model were derived directly from reported data for sardine and anchovy in the CCS and elsewhere (Rose et al. (this issue) describe the calibration process used and the sources for the parameter values for anchovy and sardine growth, reproduction, mortality, and movement). The only significant characteristic “imposed” in the model was that, via diet composition and horizontal behavior, sardine would primarily reside offshore and migrate seasonally, while anchovy were restricted to the shelf. The ability to feed on smaller prey types (i.e., microzooplankton from the NEMURO model), as well as migrating seasonally to exploit the more productive northern part of the CCS during summer, may in part explain why sardine were less sensitive to bottom up forcing (i.e., prey availability) than anchovy on the shelf that experience interannual variations in coastal upwelling intensity more directly. Without a comprehensive sensitivity study (which is beyond the scope of this work), it is difficult to determine the exact impact of parameter uncertainty on model results. However, the findings described here are expected to hold, as they represent mostly “emergent” properties for a sardine-like species exposed to offshore variability and an anchovy-like species exposed to coastal variability in the CCS.

From a more general point of view, the model results illustrate that two forage fish species exploiting the same marine ecosystem, but with slightly different temperature and diet preferences, can exhibit significantly different environmental controls on their respective population dynamics. Furthermore, the physical processes linked to the spatial distribution of adult fish populations may not necessarily be the same as those responsible for interannual variability in their abundances (e.g., the Rykaczewski and Checkley (2008) hypothesis that anchovy feed on larger prey types linked to coastal upwelling on the shelf and sardine feed on smaller prey types linked to wind stress curl offshore). While it is true in the model that changes in anchovy abundance are tied to variability in wind-driven coastal upwelling, simulated variability in sardine abundance is not associated with food availability for adult individuals (i.e., wind stress curl dependence), but rather with survival during the egg stage (i.e., temperature dependence). This finding has important implications for how both species may response to current and future climate conditions. Physical and biological processes affecting adult anchovy growth on the shelf may not co-vary (positively or negatively) with those impacting sardine early life stage survival farther offshore. These differences also support the hypothesis that recruitment fluctuations across species occupying similar trophic levels (e.g., small coastal pelagic forage fish species) are likely not determined by a single common mechanism, but by multiple factors acting over a wide range of spatial and temporal scales (Houde, 2012).

The modeling results presented here generally agree with the analysis of Lindegren and Checkley (2012) that identified temperature as an important covariate in the sardine spawner-recruit relationship for the CCS. Lindegren and Checkley found that annual mean temperature, averaged over the CALCOFI region (ca. 30-35°N and 118-124°W; see Figure 1), rather than at a specific location, was the best covariate when fitting a spawner-recruit function to the historical

data. The simulation also confirmed the importance of temperature in affecting pre-recruit survival: temperature affected egg and larval stage survival, and as with the data analysis, warm conditions favored higher recruitment. The analysis of simulated surface temperature on the model grid indicated that the warmer, or cooler, conditions that affected egg and larval survival generally occurred over most of the spatial extent over which individuals were distributed. Lindegren and Checkley (2012) also showed that their temperature was positively related to the Multivariate El Niño Southern Oscillation Index (MEI; Wolter and Timlin, 1998), and that both the MEI and PDO were similarly related to recruits per spawner. The analysis of the end-to-end ecosystem model revealed a similar positive relationship between the PDO, simulated temperatures averaged over the model grid, and sardine age-0 survival (Table 3).

The results from the simulation did not however concur with the role of density-dependence identified by Lindegren et al. (2013) as being an important contributor to the sardine and anchovy population cycles. Lindegren et al. repeated the spawner-recruit analysis of Lindegren and Checkley (2012) for sardine, but applied it to anchovy, and imbedded both relationships into an age-structured population dynamics model for each species. While the model results presented here agree with their analysis that the sometimes subtle differences in the life history traits between sardine and anchovy can cause markedly different, and even opposite, responses to environmental variation, the simulation did not replicate the role of density-dependent mortality that they identified as important. Simulated adult biomasses were similar to those analyzed by Lindegren et al. (2013), as the model was calibrated to the same adult biomass data (Figure 7 in Rose et al., this issue) used to estimate the spawner-recruit relationships. The potential for density-dependent feedback in the end-to-end model was included by allowing sardine and anchovy to depress their local prey concentrations (thus prolonging duration in

higher mortality life stages), and also potentially by the albacore predator and fishing fleet increasing their per capita mortality rates when sardine and anchovy abundances were high. A sensitivity analysis indicated that although density dependence effects associated with prey consumption had a moderate impact on adult abundance (10 to 20% difference), it did not significantly modify the interannual and low frequency variability exhibited by sardine and anchovy in the model (Rose et al., this issue). The other sources of density-dependent mortality were generally small in the end-to-end ecosystem model. Thus, unlike the dome-shaped spawner-recruit relationships estimated by Lindegren et al. (2013) for sardine and anchovy, recruitment (i.e., surviving to age-1) in the 50-year simulation was almost linearly related to spawning biomass (i.e., total number of eggs each year). Hence, when Lindegren et al. (2013) found that density-dependent mortality in pre-recruit life stages significantly affected sardine and anchovy population responses to favorable conditions, the model solution could not reproduce those relationships owing to a lack of sufficient density-dependent mortality. This discrepancy will need to be addressed in future simulations that explore anomalous historical conditions (e.g., many consecutive years of favorable conditions) or new conditions such as various climate change scenarios. One possibility for increasing density-dependence in the simulated spawner-recruit relationships is to specify the juvenile mortality rate as positively dependent on the local density in the cell, and then calibrating the parameters of the density-dependent mortality formulation in the model to reproduce the major features observed in the historical data (e.g., leveling off of recruitment).

With respect to the well-documented, out-of-phase low-frequency cycles between sardine and anchovy abundances in the CCS (Schwartzlose et al., 1999), the model solution identified potential mechanisms that could alternatively favor one species over the other. The asynchronous

response in the simulation stemmed from the fact that adult population dynamics were linked to prey availability for anchovy and temperature for sardine, and that these two variables are generally correlated negatively in the CCS (i.e., higher primary productivity is associated with cooler temperatures). Furthermore, since anchovy resided inshore of the shelfbreak in the model simulation, their variability occurred predominantly at interannual scales in response to local changes in coastal upwelling intensity and other processes modulating near-shore primary production (i.e., ENSO events). In contrast, sardine resided mainly in the CCTZ (i.e., 100-300 km offshore) in the model simulation, and their variability was more closely associated with regional-wide changes in environmental conditions (i.e., PDO). The connection to the PDO and ENSO is consistent with modes of interannual and decadal variability that would alternatively favor anchovy during years of cooler temperatures and higher prey availability, and sardine during years of warmer temperatures and lower prey availability.

The fact that warm and relatively low prey conditions favor sardine and cool and high prey conditions favor anchovy on decadal time scales is in general agreement with the “cool anchovy regime” and “warm sardine regime” argument proposed by Chavez et al. (2003), and the state-space model results from Hosack et al. (2013). Hosack et al. identified direct (e.g., temperature) and indirect (e.g., zooplankton) environmental conditions as the most likely hypothesis explaining low frequency cycles in anchovy and sardine landings. However, the apparent relationship between the PDO and sardine abundance over the past century may not necessarily reflect co-variability in the longer paleoclimatic record (McCaltchie, 2012). Furthermore, recent changes observed in ecosystem variability off California have been linked to increasing climate variance in the North Pacific (Sydeman et al., 2013), a process which could eventually affect the response of sardine and anchovy populations to environmental conditions in the CCS (e.g.,

dampen low-frequency cycles in favor of more pronounced interannual fluctuations). Interestingly, the temperature control on sardine abundance via egg survival emerging from the 50-year simulation parallels findings from the western Pacific Ocean where onshore intrusions of warmer water associated with large meanders of the Kuroshio Current are known to favor sardine over anchovy by increasing temperature in sardine spawning ground on the shelf and leading to higher egg abundances (Nakata et al., 2000). Annual mean sea surface temperature in the southern CCS has also been identified as an important factor influencing sardine recruitment in the southern CCS, although with a stronger connection to regional variability than to climate indices (i.e., PDO and ENSO) (Lindgren et al., 2013). Establishing the full extent to which sardine and anchovy population dynamics respond to climate variability in the CCS and elsewhere is an on-going and evolving research question that clearly needs further consideration.

It should be emphasized that the linkages identified here between environmental conditions, adult growth and early life survival are all model-generated and, presumably, not the sole processes regulating sardine and anchovy population dynamics in the CCS. For example, observational evidence suggests that larval mortality for sardine correlates more closely with anchovy abundance than with environmental variables, such as upwelling transport, temperature, and zooplankton (Butler, 1991). Since predation mortality by adult anchovy on sardine eggs and larvae is not currently included in the simulation, the results did not account for population variability associated with top-down control on early life stages. This lack of a direct feedback mechanism between sardine and anchovy (other than competition for food resources) could limit the out-of-phase response between the two species in the current model implementation, and may in part explain the discrepancies between simulated and observed biomass fluctuations (see Rose et al., this issue). Furthermore, as predation mortality was limited to just one species (albacore)

feeding solely on the adult stage of sardine and anchovy, additional simulations are warranted to examine the impact of including a more diverse array of predators (e.g., marine mammals and salmon) in the model. The present study also did not examine alternative hypotheses, such as advection/retention effects on development and mortality of egg and larval stages (e.g., mesoscale eddies), and longitudinal/latitudinal shifts in adult population distributions in response to changes in environmental conditions (McCall, 2009). However, the poleward shift in the latitudinal range over which sardine eggs are found during years of high survival (34-42 °N) compared to years of low survival (32-40 °N) suggests a certain degree of variability in adult population distribution and spawning grounds in the model (see Fig. 10, top panels). Future work should focus on this issue more carefully by identifying suitable spawning and foraging habitat characteristics in the simulation, and comparing them with those derived from observational data for sardine and anchovy in the CCS (e.g., Asch and Checkley, 2013; Zwolinski et al., 2012). Similarly, the potential impact of increased mesoscale activity in the CCTZ on early life stage dispersal during years of high anchovy survival (see Fig. 11, top panels) also deserves further examination. While changes in fishing mortality did not explain the low frequency variability of simulated sardine abundance (Rose et al., this issue), a more comprehensive sensitivity analysis to the fishing rates prescribed in the model is warranted in the future to determine harvest thresholds for which the increase in sardine biomass in the early 1990's may be reduced or no longer occur.

The complex interplay, and potential lags, between the different processes controlling population abundance of small coastal pelagic forage fish species in the CCS present an obvious challenge for accurately predicting their response to past, present and future climate conditions. While the end-to-end ecosystem model described here provides a valuable framework for

identifying potential linkages between environmental conditions and fish population dynamics,
an increase in biological realism (e.g., top down controls from predation, cues determining daily
foraging and seasonal migratory behavior) is clearly needed before such model can provide
adequate information for fisheries management.

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Tables

Lag/Variables	-2 years	-1 year	0 year.	+1 year
Adult Worth vs. Age-0 Survival	<u>0.04</u>	0.02	-0.20	-0.26
Adult Worth vs. Egg Production	0.70	<u>0.82</u>	0.69	0.60
Adult Worth vs. Age-1 Egg Prod.	<u>0.38</u>	0.37	0.12	-0.03
Adult Worth vs. Age-2 Egg Prod.	0.62	<u>0.77</u>	0.74	0.69
Adult Worth vs. Age-3 Egg Prod.	0.70	<u>0.75</u>	0.70	0.71
Adult Worth vs. Age-4 Egg Prod.	0.56	<u>0.71</u>	0.57	0.53

Table 1. Pearson rank correlation coefficients for anchovy worth. Boldfaced values indicate relationships plotted in Figs. 4 and 6. Underlined values indicate highest correlation coefficient over all lags.

Lag/Variables	-2 years	-1 year	0 year.	+1 year
Adult Worth vs. Age-0 Survival	0.15	<u>0.30</u>	-0.15	-0.14
Adult Worth vs. Egg Production	0.82	0.81	0.86	<u>0.96</u>
Adult Worth vs. Age-1 Egg Prod.	0.54	0.50	<u>0.61</u>	0.52
Adult Worth vs. Age-2 Egg Prod.	0.50	0.48	0.62	<u>0.79</u>
Adult Worth vs. Age-3 Egg Prod.	0.53	0.56	0.53	<u>0.66</u>
Adult Worth vs. Age-4 Egg Prod.	0.54	0.54	<u>0.57</u>	0.52

Table 2. Pearson rank correlation coefficients for sardine worth. Boldfaced values indicate relationships plotted in Figs. 4 and 6. Underlined values indicate highest correlation coefficient over all lags.

Lag/Variables	-2 years	-1 year	0 year.	+1 year
Age-2 Eggs/Ind. vs. Age-2 Egg Prod.	-0.03	-0.12	<u>0.42</u>	0.18
Age-2 Eggs/Ind. vs. Age-1 Weight	-0.04	0.23	<u>0.71</u>	-0.28
Age-2 Eggs/Ind. vs. Age-1 Growth	0.14	<u>0.66</u>	-0.36	-0.05
Age-2 Eggs/Ind. vs. Age-2 Growth	0.21	<u>0.60</u>	-0.55	-0.12

Table 3. Pearson rank correlation coefficients for anchovy egg production. Boldfaced values indicate relationships plotted in Fig. 7. Underlined values indicate highest correlation coefficient over all lags.

EOF Modes	PDO	NPGO	ENSO	UI 36N
Temperature				
Mode 1	0.69	-0.45	0.58	-0.39
Mode 2	-0.14	0.10	-0.21	0.20
Mode 3	-0.12	0.03	0.14	-0.20
Phytoplankton				
Mode 1	-0.46	0.37	-0.57	0.45
Mode 2	0.06	-0.04	-0.01	0.01
Mode 3	-0.10	-0.14	-0.17	-0.28
Zooplankton				
Mode 1	-0.48	0.46	-0.54	0.38
Mode 2	0.14	-0.03	0.19	-0.15
Mode 3	-0.09	-0.23	0.06	-0.19

Table 4. Pearson rank correlation coefficients between climate indices and EOF modes 1-3 for temperature, phytoplankton and zooplankton. Bold values indicate highest correlation coefficient for each mode.

Figure Captions

Figure 1. CCS geographical domain and ROMS grid. Left: horizontal grid and bottom topography (m). Right: terrain-following vertical model grid at 38°N.

Figure 2. Maps of mean abundance (log10 of number of individuals) for anchovy (top) and sardine (bottom) by life stage during 1964-2008. From left to right: eggs+yolk-sacs, larvae, juveniles, and adults.

Figure 3. Time series of annual abundance anomaly for anchovy (left) and sardine (right) by life stage: eggs and yolk-sacs (EYS = black), larvae (LRV = red), juveniles (JUV = green), and adults (ADT = blue). Anomalies are with respect 1964-2008 mean and normalized by standard deviation

Figure 4. Flow chart describing the 3-step analysis method applied to the historical, end-to-end ecosystem model simulation. Substeps specific to anchovy and sardine are indicated by (A) and (S), respectively.

Figure 5. Monthly (black line) and annually averaged (red line) Pacific Decadal Oscillation (PDO; top left), North Pacific Gyre Oscillation (NPGO; top right), NINO 3.4 index (ENSO; bottom left), and Bakun Upwelling Index at 36N (UI36N; bottom right).

Figure 6. Annual adult abundance vs. age-0 survival (top) and egg production (bottom) for anchovy (left) and sardine (right). Adult worth is for the current year; age-0 survival and egg production are for the year prior.

Figure 7. Annual age-0 survival vs. survival during (from top to bottom) eggs+yolk-sac stages (EYS), larval stage (LRV), eggs+yolk-sac+larval stages (EYL), juvenile stage (JUV) for anchovy (left) and sardine (right).

Figure 8. Annual adult abundance vs. (from top to bottom) age-1, age-2, age-3, and age-4 egg production for anchovy (left) and sardine (right). Adult worth is for the current year; egg production is for the year prior.

Figure 9. Annual anchovy age-2 egg production vs. age specific growth. Top left: egg production per individual vs. egg production. Top right: egg production per individual vs. age-1 weight the years prior. Bottom left: egg production per individual vs. age-1 growth the year prior. Bottom right: egg production per individual vs. age-2 growth the same year.

Figure 10. Annual anomalies for anchovy age-1 growth (top) and sardine age-0 survival (bottom). Anomalies are with respect to the 1964-2008 mean and normalized by standard deviation. Highlighted years indicate growth and survival anomalies below (blue) and above (red) one standard deviation from the mean.

Figure 11. Maps of temperatures (°C; top) and prey availability (non-dimensional; bottom) experienced by age-1 anchovy during years of low (left), normal (center), and high (right)

growth. Temperatures and prey availability for low and high years are expressed as differences with respect to normal conditions.

Figure 12. Maps of temperatures ($^{\circ}\text{C}$; top and middle) and prey availability (non-dimensional; bottom) experienced by sardine egg+yolk-sac (upper) and larval (middle and lower) stages during years of low (left), normal (center), and high (right) age-0 survival. Temperatures and prey availability for low and high years are expressed as differences with respect to normal conditions.

Figure 13. Annual anomalies for (from left-to-right) sea surface temperature ($^{\circ}\text{C}$), total surface phytoplankton (mmolN m^{-3}), total surface zooplankton (mmolN m^{-3}), and eddy kinetic energy ($\text{cm}^2 \text{s}^{-2}$) during years of high (top) and low (bottom) anchovy age-1 growth. Anomalies are with respect to the 1964-2008 mean.

Figure 14. Annual anomalies for (from left-to-right) sea surface temperature ($^{\circ}\text{C}$), total surface phytoplankton (mmolN m^{-3}), total surface zooplankton (mmolN m^{-3}), and eddy kinetic energy ($\text{cm}^2 \text{s}^{-2}$) during years of high (top) and low (bottom) sardine age-0 survival. Anomalies are with respect to the 1964-2008 mean.

Figure 15. First three EOF modes and normalized amplitudes for sea surface temperature ($^{\circ}\text{C}$; top), total surface phytoplankton (mmolN m^{-3} ; middle), total surface zooplankton (mmolN m^{-3} ; bottom). The percent variance explained by each mode is listed in the corresponding panel.

Figure 16. Amplitude of EOF modes (black) and adult biomass (red) for anchovy (left) and sardine (right). Top left: anchovy biomass vs. zooplankton mode 3, with shaded periods indicating conditions favorable for age-1 growth (i.e., positive mode amplitude). Bottom left: anchovy biomass vs. zooplankton mode 1, with shaded periods indicating conditions unfavorable for age-1 growth (i.e., negative mode amplitude). Top right: sardine biomass vs. temperature mode 1, with shaded periods indicating conditions favorable for age-0 survival (i.e., positive mode amplitude). Bottom right: sardine biomass vs. temperature mode 1, with shaded periods indicating conditions unfavorable for age-0 survival (i.e., negative mode amplitude).

Figure 17. Linear regressions between annual anomalies of anchovy age-1 growth (top) and sardine age-0 survival (bottom) and (from left-to-right) the Pacific Decadal Oscillation (PDO), North Pacific Gyre Oscillation (NPGO), NINO 3.4 index (ENSO), and Bakun Upwelling Index at 36°N (UI36N). Anomalies are computed as for Fig. 13. For the linear regression, only the anomalous growth and survival years are included (see Fig. 8) and the climate indices are averaged annually per calendar year.

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FIGURES

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