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Climate-mediated changes in marine ecosystem regulation during El Niño

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Abstract

The degree to which ecosystems are regulated through bottom-up, top-down, or direct physical processes represents a long-standing issue in ecology, with important consequences for resource management and conservation. In marine ecosystems, the role of bottom-up and top-down forcing has been shown to vary over spatio-temporal scales, often linked to highly variable and heterogeneously distributed environmental conditions. Ecosystem dynamics in the Northeast Pacific have been suggested to be predominately bottom-up regulated. However, it remains unknown to what extent top-down regulation occurs, or whether the relative importance of bottom-up and top-down forcing may shift in response to climate change. In this study, we investigate the effects and relative importance of bottom-up, top-down, and physical forcing during changing climate conditions on ecosystem regulation in the Southern California Current System (SCCS) using a generalized food web model. This statistical approach is based on nonlinear threshold models and a long-term data set (~60 years) covering multiple trophic levels from phytoplankton to predatory fish. We found bottom-up control to be the primary mode of ecosystem regulation. However, our results also demonstrate an alternative mode of regulation represented by interacting bottom-up and top-down forcing, analogous to wasp-waist dynamics, but occurring across multiple trophic levels and only during periods of reduced bottom-up forcing (i.e., weak upwelling, low nutrient concentrations, and primary production). The shifts in ecosystem regulation are caused by changes in ocean-atmosphere forcing and triggered by highly variable climate conditions associated with El Niño. Furthermore, we show that biota respond differently to major El Niño events during positive or negative phases of the Pacific Decadal Oscillation (PDO), as well as highlight potential concerns for marine and fisheries management by demonstrating increased sensitivity of pelagic fish to exploitation during El Niño.

KEYWORDS
bottom-up, climate, ecosystem regulation, El Niño, food web model, management, Pacific Decadal Oscillation, top-down

1 | INTRODUCTION

The degree to which terrestrial and aquatic ecosystems are regulated through bottom-up (resource-driven), top-down (consumer-driven), or direct physical (climate-driven) processes represents a long-standing issue in ecology (Polis, Sears, Huxel, Strong, & Maron, 2000; Power, 1992; Strong, 1992; Strong & Frank, 2010; Worm & Myers, 2003), with important consequences for resource management and conservation (Blenckner et al., 2015; Cury, Shannon, & Shin, 2003; Llope et al., 2011; Lynam et al., 2017). Although it is presently recognized that these processes are not mutually exclusive, the conditions under which one of these processes dominate and whether climate change can trigger changes in their relative importance remain largely unknown. In marine ecosystems, the role of bottom-up and top-down forcing has been shown to vary with latitude, where the former dominates in areas with high temperature and species richness and vice versa (Boyce, Frank, Worm, & Leggett, 2015; Frank, Petrie, & Shackell, 2007). Upwelling areas, such as the Humboldt and Benguela Currents, have been hypothesized to represent “wasp-waist” ecosystems, where mid-trophic levels dominated by a few species of planktivorous fish (e.g., sardine and anchovy), may exert both top-down control on their prey and bottom-up control on their predators (Cury et al., 2000, 2003; Rice, 1995) (Figure 1). However, direct physical processes, such as related to transport and advection of nutrients and organisms may also predominate in upwelling systems, including the California Current (Brinton & Townsend, 2003; Koslow, Davison, Lara-Lopez, & Ohman, 2014; Parrish, Nelson, & Bakun, 1981).

The relative importance of bottom-up and top-down forcing has been shown to vary over spatio-temporal scales, often linked to highly variable environmental conditions (Hunt & McKinnell, 2006; Lindegren, Blenckner, & Stenseth, 2012; Litzow & Ciannelli, 2007; Polis, Anderson, & Holt, 1997), as well as the degree of spatial connectivity between areas (Casini et al., 2012). For instance, ecosystem dynamics in the Eastern Bering Sea have been shown to alternate between bottom-up and top-down control during cold and warm regimes, caused by decadal variability in temperature affecting the timing of the spring bloom, the composition of the zooplankton community and recruitment of key fish species, e.g., walleye Pollock (*Theragra chalcogramma*) (Coyle et al., 2011; Hunt et al., 2011). Similar alteration between bottom-up and top-down regulation has also been suggested to occur in wasp-waist ecosystems, where during periods of high abundances mid-trophic level species may instead exert top-down control on their predators, either through direct predation or via food competition with early life stages of their predators (Bakun, 2006).

The El Niño Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) represent two major modes of climate variability across the tropical and North Pacific, affecting a suite of abiotic and biotic conditions related to temperature, transport, nutrient availability, and productivity (Bjerknes, 1966; Chavez et al., 2002; Chelton, Bernal, & McGowan, 1982; Mantua, Hare, Zhang, Wallace, & Francis, 1997). While the effects of ENSO events, i.e., El Niño (anomalously warm) and La Niña (anomalously cold), are short-lived and occur at relatively high frequencies (Philander & Fedorov, 2003), positive and negative phases of the PDO may persist for decades with long-lasting consequences for the biota (Mantua et al., 1997; Minobe, 1997). Furthermore, phase transitions in the PDO may coincide with changes in the relative frequency of ENSO events, i.e., enhanced frequency of El Niño during positive phases of the PDO and vice versa (Verdon & Franks, 2006). Although not studied in detail, it is suggested that potential phase differences between the ENSO and PDO may serve to weaken or strengthen the effect of El Niño and La Niña events on the biota (Chavez et al., 2002; Chelton et al., 1982). Despite pronounced climate variability, ecosystem dynamics in the Northeast Pacific, including a wide range of open marine ecosystems from southern California to Alaska, have been suggested to be predominately bottom-up regulated (Ware & Thomson, 2005). However, it remains unknown to what extent top-down forcing can exert a regulatory role, or whether the relative importance of bottom-up, top-down or direct physical forcing may change in response to climate variability and future climate change.

The Southern California Current System (SCCS) is a highly productive ecosystem strongly impacted by climate variability across a range of spatial and temporal scales (Checkley & Barth, 2009; Di Lorenzo & Ohman, 2013; Rykaczewski & Checkley, 2008). This is largely due to its geographical location and interactions of both a high-frequency tropical and low-frequency temperate mode of climate variability, caused by ENSO and PDO, respectively (Lluch-Cota, Wooster, Hare, Lluch-Belda, & Pares-Sierra, 2003). Likewise, biotic variables of the SCCS display pronounced variability ranging from inter-annual to multi-decadal fluctuations of, e.g., meso- and macrozooplankton, marine mammals, and birds, as well as mesopelagic and pelagic fish (Rebstock, 2002; Brinton & Townsend, 2003; Smith & Moser, 2003; Sydeman et al., 2009; Koslow, Goericke, Lara-Lopez, & Watson, 2011). These include nontarget and commercially important prey and predatory fish species, such as sardine (*Sardinops sagax*), anchovy (*Engraulis mordax*), and Pacific hake (*Merluccius productus*). Although climate effects on population dynamics of single, or groups of species have been extensively studied (Di Lorenzo & Ohman, 2013; Koslow, Goericke, & Watson, 2013; Koslow et al., 2011, 2014; Lavaniegos & Ohman, 2007; Lindegren & Checkley, 2013; Lindegren, Checkley, Rouyer, MacCall, & Stenseth, 2013; Rykaczewski & Checkley, 2008), little is known regarding the combined effects of bottom-up, top-down, and direct physical forcing on the food web dynamics across multiple trophic levels. In this study, we investigate the effects and relative importance of bottom-up and top-down forcing on the food web dynamics of the SCCS during changing climate conditions using a generalized food web model. The generalized model represents links between several functional groups and trophic levels but does not resolve interactions at the level of individual species. This statistical approach is based on nonlinear threshold models, fitted and parameterized using a unique long-term dataset (~60 years), largely based on the *California Cooperative Oceanic Fisheries Investigations* (CalCOFI) monitoring program,

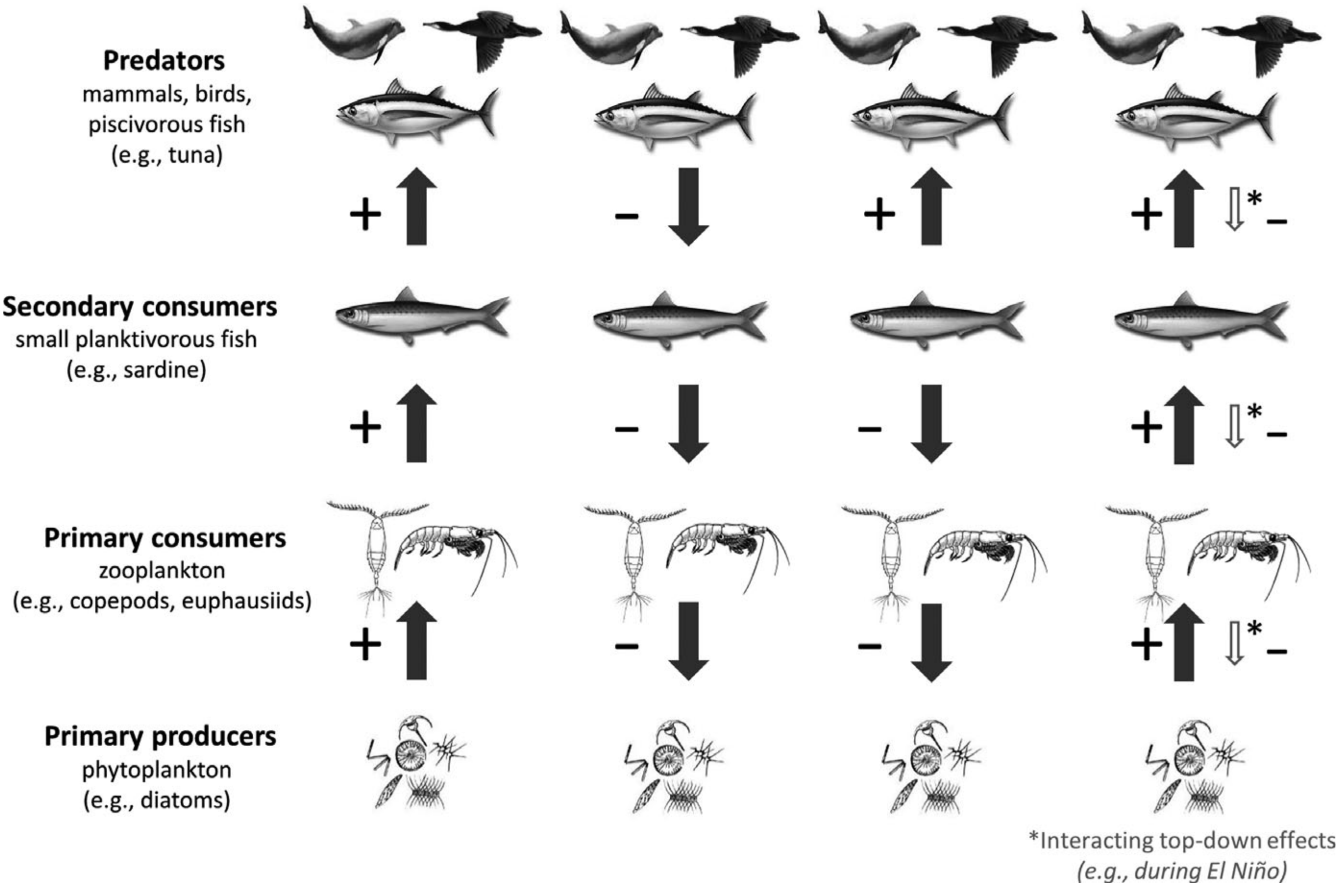

FIGURE 1 A conceptual representation of the dominant modes of ecosystem regulation within a simplified four-level marine food web. (a) Bottom-up regulation is typically characterized by a positive relationship between trophic levels where an increase in primary producers leads to increases in higher trophic levels. (b) Top-down regulation is represented by negative relationship between adjacent trophic levels, where an increase in a predator leads to a decline in its prey. (c) Wasp-waist regulation occurs when mid-trophic levels (e.g., small planktivorous fish) exert both top-down control on their prey (zooplankton) and bottom-up control on their predators. (d) Finally, our results indicate an alternative mode of regulation represented by strong and persistent bottom-up forcing interacting with weaker top-down forcing, but only above or below certain thresholds, here associated with El Niño. (This figure is inspired and partly redrawn from Cury et al., 2003)

supplemented by the *California Current Ecosystem Long-Term Ecological Research* site, covering multiple trophic levels from phytoplankton to predatory fish. We show evidence of strong bottom-up regulation throughout the food web, interacting with moderate top-down forcing, but only during periods of unfavorable climate conditions primarily associated with certain combinations of ENSO and PDO. Furthermore, we elaborate on the effects of major El Niño events, if occurring during the positive or negative phase of the PDO, as well as demonstrate potential concerns for marine- and fisheries management in the face of climate change.

2 | MATERIALS AND METHODS

2.1 | Data collection

An inventory of data characterizing the ocean-atmospheric, hydrographic, physical and biotic conditions across multiple trophic levels in the SCCS over the time period from 1951 to 2010 was performed (Table S1). To reflect the ocean-atmospheric conditions affecting regional climate in the area, a number of large-scale climate indices, including the PDO (Mantua et al., 1997), the tropical Multivariate ENSO Index (MEI), the Southern Oscillation Index (SOI), as well as the North Pacific Gyre Oscillation (NPGO) (Di Lorenzo et al., 2008) were included. To reflect the hydrodynamic conditions, coastal upwelling, open-ocean (wind stress curl-driven) upwelling (Rykaczewski & Checkley, 2008), sea level height (detrended), alongshore (North-South) transport, as well as dynamic height were used. Physical conditions were represented by spring averages of 0–100 m temperature, salinity, water density (σ_t), and oxygen concentration across all stations of the regular CalCOFI area (i.e., from line 76.7 to 93.3; Figure S1). Nutrient conditions were represented by average concentrations of nitrate in the mixed layer. Since nitrate was consistently sampled only from 1984 onwards, we extended its time series backwards until 1951 based on modeled estimates. These were derived from a Generalized Additive Model (GAM) with upwelling, temperature, and sea level as predictors, demonstrating highly significant and temporally consistent relationships overall (Table S2; Figures S2 and S4) and a high degree of explained deviance (79.4%).

Finally, a set of biotic (response) variables representing separate trophic levels was compiled. The mean spring chlorophyll *a* in the mixed layer was chosen to characterize primary producers. Note that due to lack of chlorophyll *a* data prior to 1984 we extended the time series backwards until 1951 with modeled estimates (Tables S2 and S3; Figure S3), based on a GAM explaining a high degree of deviance from 1984 to 2010 (87.8%). The spring carbon biomass of mesozooplankton, excluding euphausiids, here termed “other zooplankton” and euphausiids, the latter divided into a warm-water (subtropical) and cold-water (temperate) assemblage (Brinton & Townsend, 2003), were used to represent intermediate trophic levels (see details in Lavaniegos & Ohman, 2007).

To represent key consumers of both meso- and macrozooplankton (euphausiids) and prey for higher trophic level predators, an aggregated index of mesopelagic fish abundance, derived from ichthyoplankton samples (Koslow et al., 2011), as well as the total spawning stock biomass (SSB) of small pelagic fish was used. The latter group consists of the dominant consumers of copepods and euphausiids including Pacific sardine, northern anchovy, and Pacific mackerel (*Scomber japonicus*), respectively, for which comparable biomass estimates are available from stock assessments (Crone, Hill, McDaniel, & Lynn, 2011; Fissel, Lo, & Herrick, 2011; Hill et al., 2011; Jacobson, Lo, & Barnes, 1994; Murphy, 1966). Note that, in the absence of sardine stock assessments during the period of low stock size from 1963 to 1980, hindcasted model estimates were used (Lindegren et al., 2013). Finally, ichthyoplankton samples of Pacific hake, as well as stock assessment estimates of hake fishing mortality (Stewart & Forrest, 2011) and albacore (*Thunnus alalunga*) catch-per-unit effort (CPUE) data (ALBWG 2011) were used to characterize the dominant predatory fish in the area (Figure S4). Because of its highly migratory behavior and transitory residence in the California Current, albacore was treated as an external covariate only. In addition to these predators, sharks, billfishes (e.g., striped marlin and swordfish), as well as marine birds and mammals constitute other top predators in the SCCE (Barlow, Kahru, & Mitchell, 2008; Bedford & Hagerman, 1983; Sydeman et al., 2015). Unfortunately, the considerably shorter length of monitoring time series for these groups (e.g., 1987 and 1991 onwards for birds and cetaceans, respectively; Hyrenbach & Veit, 2003; Barlow & Forney, 2007), precludes a comparable long-term analysis of climate forcing and trophic interactions on these predators. Nevertheless, we will discuss our findings regarding climate effects and trophic regulation in the SCCE with reference also to these top predators.

2.2 | Food web model setup and validation

To account for potential threshold-dependent relationships, we used a modified formulation of Generalized Additive Models, so-called threshold Generalized Additive Models (TGAM), allowing for nonadditive effects of the explanatory variables below and above a certain threshold value (ϕ) estimated from the data (Ciannelli, Chan, Bailey, & Stenseth, 2004). Since our aim was to investigate whether bottom-up and top-down processes depend on climate, in particular the indirect or direct effects of ENSO and PDO on resource availability (Chelton et al., 1982), we treated the PDO, MEI, total nitrate, and chlorophyll *a* as candidate threshold variables and allowed the model to test for potential threshold values. For mesopelagic fish we treated deep-water oxygen (200–400 m) as a potential threshold variable due to its proposed effect on habitat size and predator-prey overlap (Koslow et al., 2011). To assess potential state-dependent relationships between small pelagic fish and predatory fish (Bakun, 2006) we also tested an alternative model formulation where the biomass of small pelagic fish was used a threshold variable in the hake model. The following nonadditive model formulation with log(x + 1) transformed biomass (or abundance) indices for each trophic level as response variables (y) was used:

$$y_{i,t} = a + \begin{cases} s(X_{i-1,t}) + s(X_{i+1,t}) + s(V_{1,t}) + \cdots + s(V_{n,t}) + \varepsilon_t & \text{if TV} > \Phi \\ s(X_{i-1,t}) + s(X_{i+1,t}) + s(V_{1,t}) + \cdots + s(V_{n,t}) + \varepsilon_t & \text{if TV} \leq \Phi \end{cases}$$

where *a* is the intercept, *s* the thin plate smoothing function (Wood, 2003), $x_{i,t}$ the biomass (or abundance) at time *t* for each trophic level *i* (i.e., where $i - 1$ and $i + 1$ represent direct predator-prey interactions between adjacent trophic levels occurring without time lags), $v_{i}. . ..v_{n}$ a number of selected climate predictors known to affect the dynamics of each trophic level, TV the threshold variable, and ε the error term. We applied a stepwise backward selection routine based on the generalized cross-validation criterion (GCV) and partial *F*-tests to find the best possible set of predictors for each trophic level model. Furthermore, the spline smoother function (*s*) was constrained to three degrees of freedom ($k = 3$), to allow for potential nonlinearities but restrict flexibility during model fitting. Finally, we tested whether the nonadditive models proved significantly better than regular GAMs (fitted without thresholds) by comparing the genuine CV, i.e., the average squared leave-one-out prediction errors (Ciannelli et al., 2004). To validate the predictive capabilities of the model, we hindcasted historical food web dynamics by dynamically coupling each separate trophic level model into a generalized food web model, where the internal dynamics (i.e., trophic interactions) are forced only by the external covariates (Blenckner et al., 2015; Llope et al., 2011; Lynam et al., 2017). The food web model was initialised with the observed biomass (or abundance) values in 1966, the first year with available observations for all covariates (i.e., albacore data are missing prior to 1966), and run throughout the period until 2010 with observed covariate values. To account for uncertainty we added process noise, resampled from the residuals of each trophic level model, and performed 1,000 replicated model runs. To retain any temporal dependence (correlation) between errors across trophic levels, an entire vector of errors corresponding to a randomly sampled set of model residuals for a given year was used. The hindcasted estimates were then compared with the actual observed values for each trophic level to validate the predictive accuracy of the food web model for the study period.

2.3 | El Niño simulations and management scenarios

To investigate the effect of major El Niño events and particularly whether phase differences between the ENSO and PDO may serve to weaken or strengthen the biotic response across trophic levels, we exposed the validated food web model to a simulated El Niño event, represented by the observed covariate values during the record strong El Niño in 1998 (Chavez et al., 2002). This pulse perturbation was introduced during both a negative and positive phase of the PDO, defined as the mean covariate values observed prior to and after the PDO phase shift in 1976–1977 (Mantua et al., 1997). These simulations were initialized at the mean biomass (or abundance) for each trophic level and forced with the mean covariate values, both averaged during the negative and positive phases of the PDO, over a period of 10 years. Thereafter, the El Niño pulse perturbation was introduced and the relative difference in non-log biomass (or abundance) before and during the perturbation was estimated as a measure of the strength of the biotic response (e.g., a value <1 would indicate a decline) (Figure S6). Furthermore, we illustrated potential management implications by assessing the effect of exploitation on the commercially important small pelagic fishery during periods of low or high productivity, respectively. These were defined as periods of low and high nitrate availability, as occurring during positive and negative phases of MEI, and correspond to the mean covariate values above and below the estimated MEI threshold of 0.371 (Figure S7i,j). The effect of exploitation was quantified as the change in total spawning stock biomass (SSB) relative to an equilibrium SSB (i.e., 0.77 and 0.44 million metric tonnes below and above the MEI threshold, respectively) when forced by a range of fishing mortalities (*F*) from 0 to 0.6 year^{-1} for a period of 10 years (i.e., $\mathrm{SSB}_t = \mathrm{SSB}_{t-1}{*}e(-F)$). All statistical analyses were conducted using the R software (www.r-project.org).

3 | RESULTS

All trophic level models demonstrate strongly significant interactions and a high degree of explained deviance (Table 1). The type of interactions range from linear to nonlinear relationships, occurring with or without threshold-dependent dynamics and illustrate a combination of bottom-up and top-down effects and direct physical forcing throughout the modelled food web (Figure 2). We recognize that these statistical relationships do not necessarily reflect direct causation, but for convenience we refer to these as “effects” and provide references to known relationships documented in the literature. The bottom-up effects are shown as positive linear or curvilinear relationships, predominately without threshold-dependent dynamics, illustrated by the positive effect of nitrate availability on chlorophyll *a* (Figures 3c and S8e–f), as well as the between lower and higher trophic levels throughout the food web (Figure 3g,l,m,s,t,z,aa). In case of omnivory, positive feeding relationships may extend across several trophic levels (Miller, Brodeur, Rau, & Omori, 2010), such as shown by positive effects of chlorophyll *a* and other zooplankton on euphausiids (Figure 3l), as well as euphausiids on hake (Buckley & Livingston, 1997) (Figure 3z,aa). The top-down effects are indicated by opposite relationships between adjacent trophic levels, where consumers are positively related to their prey and vice versa (Figure 3d,h,I,n,u,v,x,ac). In addition, potential competition is illustrated by negative nontrophic interactions, such as shown from cold-water to warm-water euphausiids (Figure 3q). Interestingly, the negative effects are exclusively threshold-dependent, indicating top-down effects only below or above certain thresholds. Therefore, a negative grazing impact of other zooplankton on primary producers (Mullin, 2000) and predation on other zooplankton by mesopelagic and pelagic fish (Ohman & Hsieh, 2008) occurred only during periods of low nitrate availability (Figure 3d,h,i). These conditions primarily exist during El Niño events when diminished upwelling of nutrient-rich water into the SCCS limits primary and secondary production (Chavez et al., 2002; Chelton et al., 1982). The immediate consequences for pelagic fish are illustrated by significant negative effects from albacore and hake (Figure 3u,v), but only during periods of high MEI when zooplankton biomass is drastically reduced and food availability limited (Lavaniegos & Ohman, 2007; Rebstock, 2002). While the top-down effect from albacore can be explained by predation (Glaser, 2010), the negative effect of hake may be due to both predation and competition, especially during early life stages when diet preferences overlap (Buckley & Livingston, 1997).

In contrast to the threshold-dependent top-down effects, the influence of direct physical forcing is exclusively nonthreshold dependent and is optimally described as linear (Figure 3a,b,e,f,j,k,o,p, r), with the exception of deep-water oxygen which shows a curvilinear relationship with mesopelagic fish (Figure 3w). Climate effects are illustrated by negative ENSO effect on zooplankton (Figure 3f) (Lavaniegos & Ohman, 2007; Ohman, Rau, & Hull, 2012; Rebstock, 2002), as well as a positive effect of warming (i.e., high PDO and low SOI; Figure 3o,p) on southern (warm-water) euphausiids (Brinton & Townsend, 2003; Di Lorenzo & Ohman, 2013). Furthermore, we demonstrate positive temperature effect on pelagic fish (Figure 3r) (Lindegren & Checkley, 2013; Sugihara et al., 2012) and positive impacts of nitrate availability (Figure 3c) and negative effects of density stratification (reduced mixing) on chlorophyll *a* (Figure 3b) (Mantyla, Bograd, & Venrick, 2008). Finally, we show a positive effect of deep-water oxygen on mesopelagic fish (Figure 3w), likely caused by increased habitat availability and reduced predator-prey overlap (Koslow et al., 2011, 2013, 2014) and a positive effect of sea surface height (i.e., a proxy for the strength of passive advection by the southward flowing California current) on northern (cold-water) euphausiids (Figure 3j) (Brinton & Townsend, 2003).

The separate trophic level models show a good fit to data, being able to accurately recreate the long-term dynamics, as well as interannual fluctuations (Figure S9). Likewise, the hindcast model predictions based on the coupled food web model where the internal dynamics (i.e., trophic interactions) are forced entirely by the external covariates, are able to represent the historical food web dynamics (Figure 4). However, note that some of the variability is less well represented, especially for higher trophic levels, such as the overestimation of small pelagic fish in the first 5 years of the hindcast simulations (Figure 4e). This is due to the coupled structure of the food web model where potential deviations in lower trophic levels, in this case the slight overestimation in both zooplankton and cold-water

TABLE 1 Summary statistics showing the intercept with *p*-value, the estimated threshold, the deviance explained (DEV in %), the genuine cross-validation score (gCV), comparing threshold Generalized Additive Model (TGAM) and Generalized Additive Models, the number of observations (*N*), as well as smooth term statistics for each TGAM

Response	Intercept	*p*-Value	Threshold (Φ)	DEV (%)	$gCV_{TGAM/GAM}$	*N*
Chl α	0.24	<.001	0.498	77.9	0.027/0.029	58
Other zooplankton	3.03	<.001	0.735	57.0	0.211/0.235	52
Euphausiid (cold)	1.73	<.001	0.279	69.3	0.242/0.243	56
Euphausiid (warm)	0.42	<.001	−0.225	63.0	0.233/0.249	55
Pelagic fish	13.6	<.001	0.371	68.1	0.512/0.535	37
Mesopelagic fish	2.36	<.001	1.517	73.0	0.143/0.125	45
Pacific hake	3.51	<.001	−0.251	78.9	0.817/1.12	42

Response	Threshold	Predictor	*edf*	*F*	*p*-Value
Chl α	–	SST	1.00	14.1	<.001
	–	Density	1.00	50.2	<.001
	–	$[NO_3]$	1.96	36.9	<.001
	$[NO_3] \le \Phi$	Other zooplankton	1.00	6.36	.015
Other zooplankton	–	PDO	1.85	10.4	<.001
	–	MEI	1.58	7.60	.001
	–	Chl α	1.00	6.10	.017
	$[NO_3] \le \Phi$	Pelagic fish	1.27	4.96	.011
	$[NO_3] \le \Phi$	Mesopelagic fish	1.00	7.35	.009
Euphausiid (cold)	–	Dynamic height	1.00	19.6	<.001
	–	Sverdrup transport	1.00	8.82	.005
	–	Chl α	1.64	4.00	.025
	Chl $\alpha \le \Phi$	Other zooplankton	1.00	8.55	.005
	Chl $\alpha > \Phi$	Pacific hake	1.91	14.2	<.001
Euphausiid (warm)	–	PDO	1.02	8.60	<.001
	–	SOI	1.00	10.60	.002
	PDO $> \Phi$	Euphasiid (cold)	1.72	10.41	.002
Pelagic fish	–	SST	1.00	8.23	.007
	–	Euphausiid cool	1.00	12.62	.001
	MEI $\le \Phi$	Other Zooplankton	1.00	13.0	<.001
	MEI $> \Phi$	Pacific hake	1.00	10.7	.003
	MEI $> \Phi$	Albacore	1.00	9.86	.004
Mesopelagic fish	–	$[O_2]$ (200–400 m)	1.99	42.2	<.001
	$[O_2] \le \Phi$	Pacific hake	1.79	5.42	.008
Pacific hake	–	Mesopelagic fish	1.86	13.7	<.001
	PDO $> \Phi$	Euphausiid (cold)	1.78	11.5	<.001
	PDO $> \Phi$	Euphausiid (warm)	1.56	7.10	.003
	PDO $> \Phi$	Pelagic fish	1.00	43.1	<.001
	PDO $> \Phi$	Albacore	1.00	8.98	.005
	PDO $\le \Phi$	*F*	1.00	11.54	.002

Significant terms "above," "below or equal to," or without the estimated threshold are denoted by >, ≤ and –, respectively. (*edf*, estimated degrees of freedom for the model smooth terms where $edf > 1$ indicates a nonlinear relationship).

euphausiids (Figure 4b,c), propagate through the food web, thereby increasing the uncertainty of model predictions at higher trophic levels. In addition, the higher trophic level models are not constrained by as many external covariates as the lower trophic levels which serves to increase the influence of stochastic noise and propagating deviations from lower trophic levels. Nevertheless, the observed values were within the 95% confidence intervals for all trophic levels. Finally, TGAMs proved significantly better than regular

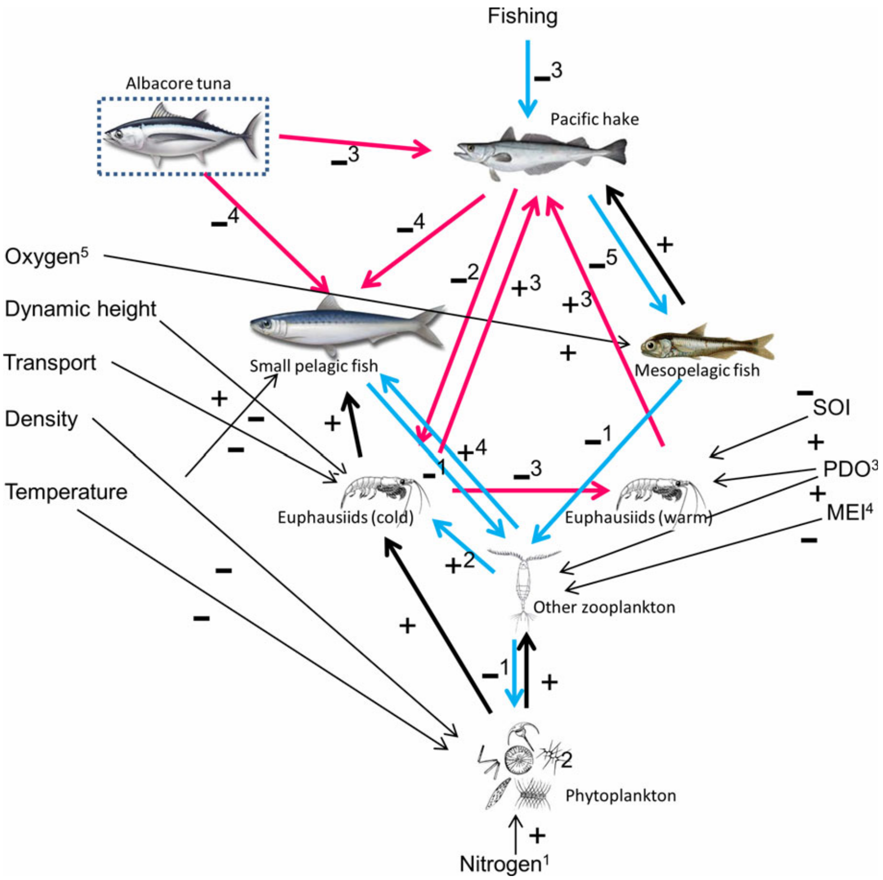

FIGURE 2 A schematic representation of the generalized Southern California Current System food web model, consisting of Pacific hake, mesopelagic fish, small pelagic fish, euphausiids, i.e., divided into a cold and warm-water assemblage, mesozooplankton and primary producers. (Note that the top-predator albacore tuna (within dotted rectangle) is treated as an external covariate). Blue and red arrows indicate threshold-dependent interactions above and below an estimated threshold, respectively (Figure S6). The black arrows indicate nonthreshold-dependent effects. Although interactions may range from linear to nonlinear, we have indicated generally positive (+) and negative (−) interactions. The numbers associated with certain arrows correspond to a particular covariate used as threshold variable, identified by the corresponding number in superscript

GAMs, as demonstrated by lower genuine CVs (Table 1). However, a regular GAM showed lower gCVs for mesopelagic fish but displayed an insignificant interaction (with Pacific hake) and lower explained deviance (65.7%). We therefore used the TGAM formulation instead, including a significant threshold-dependent effect of hake. In addition, the alternative hake model formulation, including pelagic fish biomass as a potential threshold variable, did not show threshold-dependent relationships between prey and predator (Table S4; Figure S10). Since the alternative model resulted in a considerably lower deviance explained (57.2%) compared to the original model using the PDO as a threshold variable (78.9%) we kept the original model. Standard diagnostics of residuals were satisfactory for all trophic-level models (Figure S11).

The El Niño simulations show a generally strong negative effect on the biota (Figure 5), particularly for lower trophic levels where chlorophyll *a*, other zooplankton and cold-water euphausiids demonstrate depressed biomasses at about 20%–50% of their equilibrium levels, regardless whether occurring during the negative or positive phase of the PDO. In contrast, higher trophic levels, pelagic, and predatory fish (i.e., Pacific hake), respond less negatively to the El Niño event if occurring during the negative phase of the PDO, whereas during the positive phase of the PDO the biomasses (or abundances) are depressed to about 55% and 30% of their equilibrium levels, respectively. Mesopelagic fish and warm-water euphausiids show moderately, or markedly, positive responses to the El Niño event, particularly during the negative phase of the PDO. However, for warm-water euphausiids the magnitude of this increase should be understood in the context of their relatively lower biomasses (Brinton & Townsend, 2003). In the second scenario, assessing the effect of exploitation on the commercially important small pelagic fishery, the total pelagic SSB responds drastically to increasing exploitation during unfavorable conditions (Figure 6), with a minimum SSB at ~25% of the respective equilibrium level at $F = 0.6$ year^{-1}. During favorable conditions the total SSB declines at a more moderate rate with increasing exploitation and demonstrates a higher minimum SSB amounting to ~55% of the respective equilibrium level at $F = 0.6$ year^{-1}.

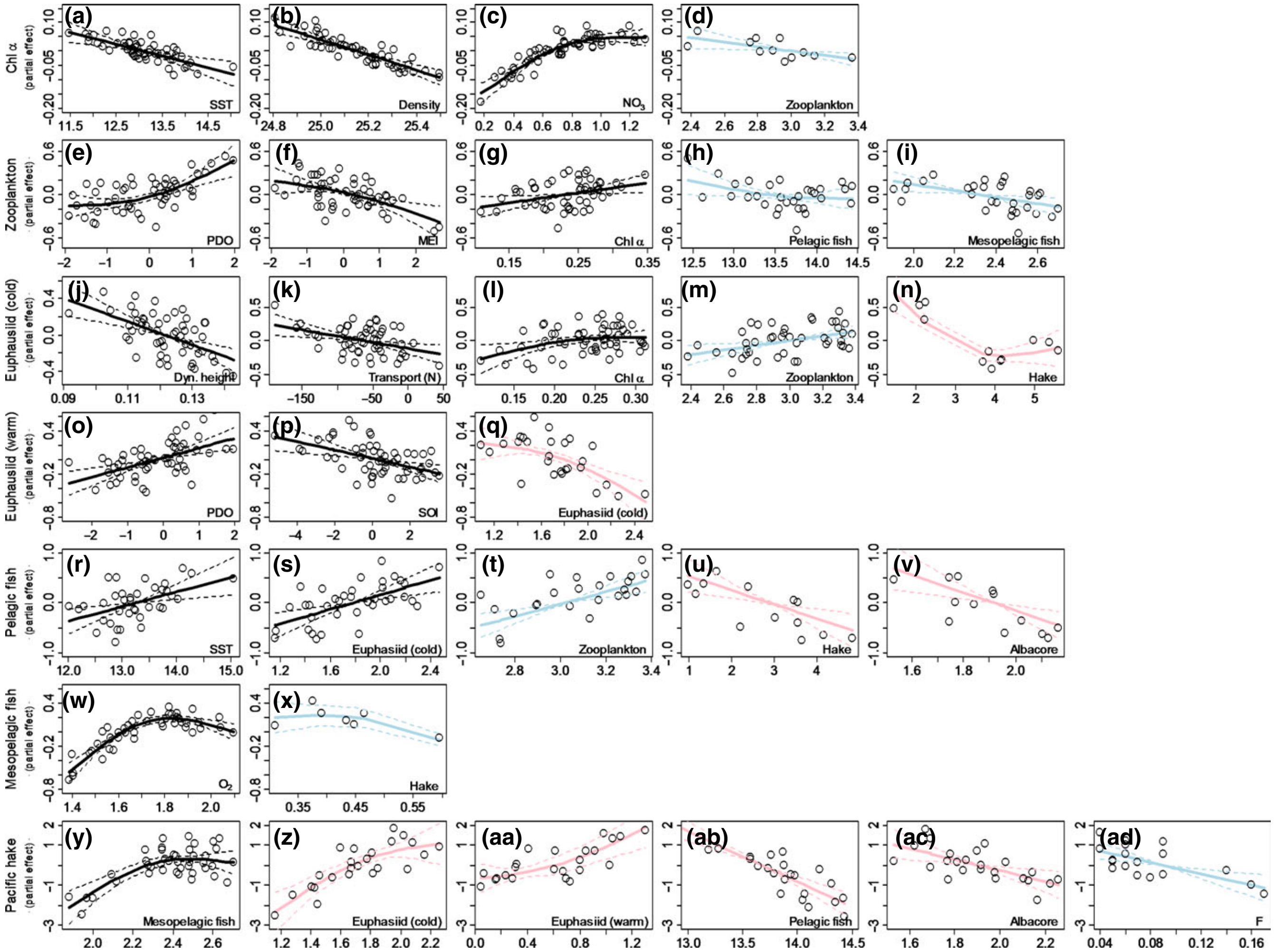

FIGURE 3 Partial effect plots from the final set of trophic level models showing the relationship between abiotic and biotic variables and chlorophyll a (a–d), other mesozooplankton (e–i), euphausiids divided into a cold- (j–n) and warm-water (o–q) assemblage, small pelagic fish (r–v), mesopelagic fish (w–x) and Pacific hake (y–ad). The names of each significant predictor are shown in the bottom-right corner of each panel. The associated *x*-axis show the range of values within which the relationships are fitted. Light blue and red lines indicate threshold-dependent interactions above and below the estimated thresholds, respectively (Figure S7; Table 1), whereas black lines indicate nonthreshold-dependent effects. Dashed lines show the 95% confidence intervals for each partial effect. (See Appendix S1 for additional sensitivity tests of partial effects and threshold estimates)

4 | DISCUSSION

The identification of dominant modes of ecosystem regulation and the degree to which these may vary in space and time and across ecosystem types, including terrestrial and aquatic ecosystems, represent a long-studied field in ecology (Boyce et al., 2015; Polis et al., 2000; Power, 1992; Schmitz, Hambäck, & Beckerman, 2000; Strong, 1992; Strong & Frank, 2010; Worm & Myers, 2003). On the basis of positive correlations between adjacent trophic levels, a number of large and highly productive marine ecosystems across the North Atlantic and North Pacific, including the California Current, are considered to be bottom-up driven (Boyce et al., 2015; Frank et al., 2007; Ware & Thomson, 2005). Our generalized food web model, using nonlinear threshold regressions and a long-term data set spanning six decades, also supports strong bottom-up forcing in the SCCS. This highlights the important regulatory role of nutrient and prey availability, where increased supplies of nitrate (i.e., caused by southern transport of nutrient-rich waters upwelled further north; Chelton et al., 1982) lead to higher primary and secondary production, as well as high abundance of pelagic fish and upper-trophic level predators in the area (Chavez, Ryan, Lluch-Cota, & Niquen, 2003; Chelton et al., 1982; Mantyla et al., 2008), including marine birds and mammals (Melin, Orr, Harris, Laake, & DeLong, 2012; Sydeman et al., 2015). These resource-driven processes were found to be largely nonthreshold dependent. This result implies that bottom-up effects are ever-present and provide a strong baseline regulation of food web dynamics in the SCCS, regardless of highly variable climate conditions. While bottom-up effects on various species or trophic levels in the Northeast Pacific have previously been established (Chavez et al., 2003; Sydeman et al., 2009; Ware & Thomson, 2005), evidence of top-down control has been shown primarily at higher latitudes (Boyce et al., 2015; Hunt et al., 2011;

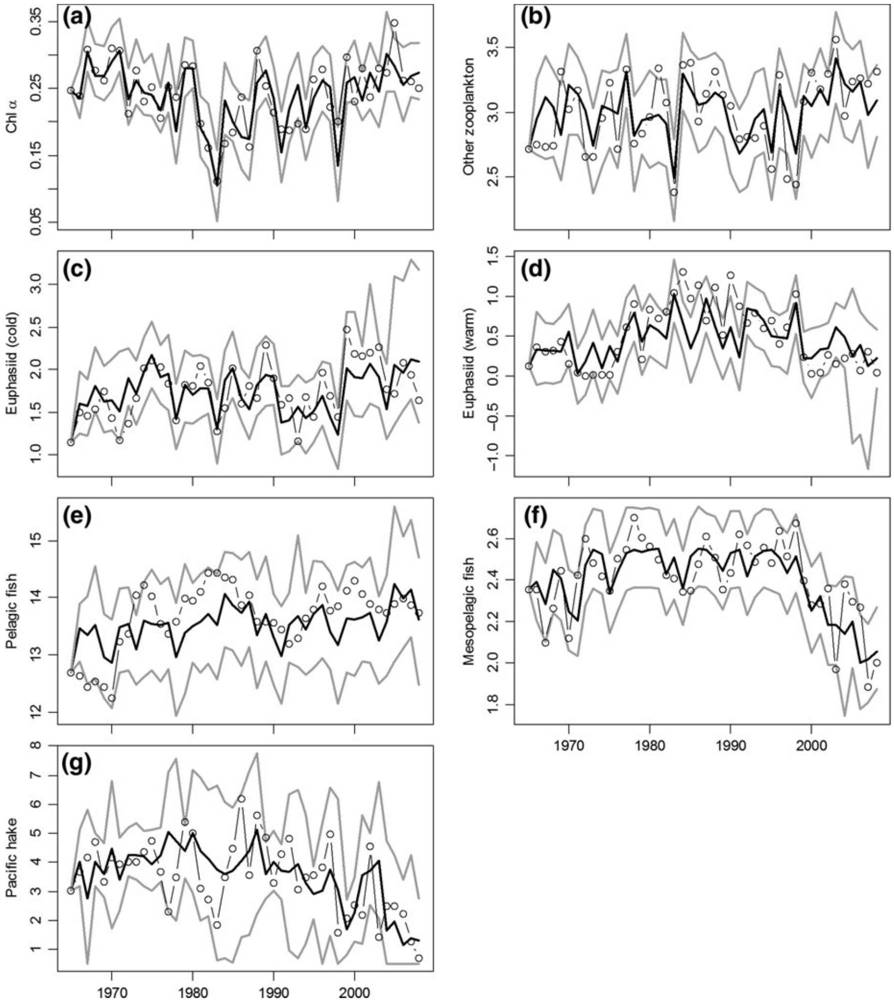

FIGURE 4 Observed (circles) and hindcasted model predictions of chlorophyll a (a), other mesozooplankton (b), cold- and warm-water euphausiids (c and d), small pelagic fish (e), mesopelagic fish (f) and Pacific hake (g). The simulations are initiated with observed population estimates in 1966 and simulated until 2010 based on observed external covariates only. Gray lines show 95% confidence intervals based on 1,000 stochatsic model runs. (See Figure S9 for model fits)

Litzow & Ciannelli, 2007), as well as in nearshore and intertidal ecosystems (Estes, Tinker, Williams, & Doak, 1998; Paine, 1980). Our results support these findings by showing also moderate top-down effects, but interacting with stronger bottom-up forcing throughout the food web. Interestingly, the negative effects are exclusively threshold-dependent, indicating top-down effects only below or above certain thresholds. These thresholds generally correspond to situations when positive bottom-up effects are weakened due to resource limitation, or unfavorable climate conditions. These conditions primarily exist during El Niño events when diminished upwelling of nutrient rich-water into the SCCS limits primary and secondary production (Chavez et al., 2002; Chelton et al., 1982).

Furthermore, climate-mediated changes in the spatio-temporal overlap between predators and prey may affect the strength of top-down effects. Hence, the negative effect of hake on pelagic fish, as well albacore on hake, may partly be due to increasing spatial overlap, especially during El Niño events when hake extends its distribution range northward (Agostini et al., 2008). Likewise, increased vertical overlap between hake and mesopelagic fish may explain the negative predation effect detected during low oxygen conditions when the mid-water habitat of mesopelagic fish is compressed (Koslow et al., 2011; Netburn & Koslow, 2015) due to a shoaling of the hypoxic boundary (Bograd et al., 2008). Similarly, a fishing effect on hake was found significant only during the negative phase of the PDO. This may be due lower abundances and a contracted (southerly) distribution range, resulting from stronger equatorward flow by the California current (Agostini et al., 2008), which may increase the vulnerability to fishing. Note that since major changes in hake management (e.g., the transition to a joint Canada-US assessment in 1997; Stewart & Forrest, 2011) do not coincide with transitions in the PDO, changes in fishing regulations are unlikely to explain this effect. Although previous studies suggest a marginal effect of hake predation on euphausiids (Mullin & Conversi, 1989; Tanasichuk, 1999), we found a negative effect on euphausiids occurring only during high chlorophyll *a*. Whether this may be explained by a concentration of hake in the southern area of its distribution range during periods of limited poleward flow (Agostini et al., 2008) and high productivity remains unclear. Furthermore, whether sharks, billfishes, marine birds, and mammals (that were not included in this analysis) can exert a significant regulatory top-down effect on lower trophic levels remains unclear. While previous studies demonstrate the importance of bottom-up forcing regulating sea bird populations (Melin et al., 2012; Sydeman et al., 2015), high consumption rates may buffer their relatively low biomasses (Barlow et al., 2008; Field,

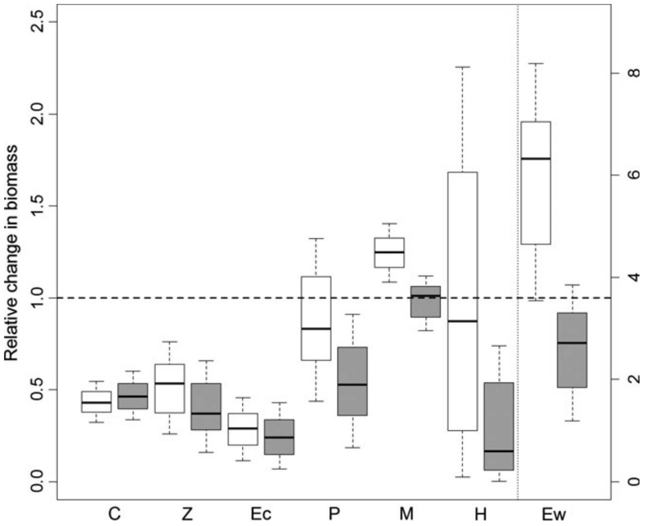

FIGURE 5 Simulated effects of a major El Niño event on chlorophyll a (C), other mesozooplankton (Z), cold- and warm-water euphausiids (Ec, Ew), small pelagic fish (P), mesopelagic fish (M), and Pacific hake (H). The effects are quantified as the change in (non-log) biomass (or abundance) relative to a baseline level during a negative (white) or a positive phase of the PDO (gray). (A value of 1 indicates no change shown by the dashed horizontal line). The additional *y*-axis (right) applies to warm-water euphausiids demonstrating a considerably larger relative change in biomass in response to El Niño

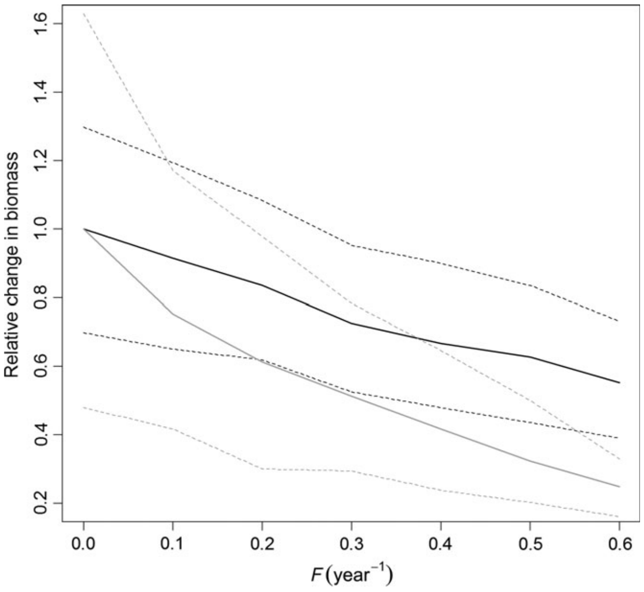

FIGURE 6 Impact of exploitation on small pelagic fish during El Niño and La Nina. The effect is quantified as the change in total biomass under increasing levels of fishing mortality (*F*), relative to a respective equilibrium level (i.e., 0.77 and 0.44 million metric tons at $F = 0$) when forced by mean climate conditions occurring below (black) and above (gray) the Multivariate ENSO Index threshold (Figure S7i,j), respectively. Solid and dashed lines show the mean and 95% confidence intervals after 1,000 stochastic simulations

Francis, & Aydin, 2006). Hence, these other predators could at least locally (i.e., in the vicinity of bird colonies) and/or seasonally (i.e., during feeding migrations of these highly mobile and wide ranging species) affect the dynamics of their fish and zooplankton prey in the SCCS.

In addition to bottom-up and top-down effects, our food web model demonstrates pronounced direct physical forcing (Checkley & Barth, 2009). These effects are exclusively nonthreshold dependent and are illustrated by a suite of interlinked hydrographic processes ranging from regional climate forcing to local impacts acting through temperature, oxygen, upwelling and patterns of transport and advection. This demonstrates the importance of climate and especially alongshore transport on community composition in the SCCS. Depending on the strength and direction of the California Current (as well as the poleward flowing counter current) species with either southern or northern affinities are being advected from, or into the area (Brinton & Townsend, 2003; Di Lorenzo & Ohman, 2013; Koslow et al., 2014). This applies also to marine birds where community composition has been shown to shift between cold-water species that dive in pursuit of prey and warm-water species that plunge dive and feed at the surface (Hyrenbach & Veit, 2003). In general, we found a stronger influence of direct climate forcing at the base of the food web compared to upper trophic levels where the relative importance of trophic interactions is greater. However, the trophic interactions provide important indirect pathways channeling climate effects from lower trophic levels (Stenseth et al., 2002), as well as propagating stochastic and climate-induced variability up the food web, thereby increasing the uncertainty of model predictions at higher trophic levels.

By integrating bottom-up, top-down and direct physical effects our food web model framework allows for scenario explorations regarding the effect of El Niño events and its potential phase dependence with the PDO (Verdon & Franks, 2006). Our simulations show a drastic reduction in biomass (or abundance) across multiple trophic levels during El Niño. The marked decline in lower trophic levels is similar during the negative and positive phase of the PDO and results from weaker bottom-up forcing and increased top-down effects during periods of reduced nutrient supply (Figure S12). In contrast, the response to El Niño events at higher trophic levels is less pronounced during a negative PDO. In case of pelagic fish this is due to slightly higher biomass of prey (other zooplankton and euphausiids) and considerably lower abundance of predators (hake) when simulated under a negative compared to a positive phase of the PDO (Figure S13). The lower hake abundance is caused by the negative fishing effect and a lack of positive foraging effects under a negative PDO. In contrast to the other trophic levels, showing a negative response to El Niño, the positive effect on mesopelagic fish reflects a combination of increasing deep-water oxygen and hypothesized reduced predator-prey overlap together with increased northward transport of warm-water species by the northward flowing counter current (Koslow et al., 2014). Likewise, the positive effect on warm-water euphausiids may be explained by a northward shift in distribution due to increased poleward flow and advection (Brinton & Townsend, 2003; Di Lorenzo & Ohman, 2013).

As a complement to bottom-up and top-down regulation, wasp-waist control, in which mid-trophic levels may exert both top-down and bottom-up control on their prey and predators, respectively (Cury et al., 2000; Rice, 1995), and oscillating trophic control, in which an ecosystem may shift between bottom-up and top-down regulation (Hunt et al., 2011; Litzow & Ciannelli, 2007), represent additional explanations for understanding ecosystem regulation. In this study, we found bottom-up control to be the primary mode of ecosystem regulation in the SCCS (Lindegren, Checkley, Ohman, Koslow, & Goericke, 2016; Ware & Thomson, 2005). However, our results indicate also an alternative mode of regulation represented by combined bottom-up and top-down forcing, hence analogous to wasp-waist dynamics, but occurring across multiple trophic levels and only during periods of limiting resources. The shifts in regulation are caused by changes in ocean-atmosphere forcing and are triggered by highly variable climate conditions, such as El Niño, hence analogous to oscillating trophic control (Hunt et al., 2011). Similar climate-mediated shifts between bottom-up and top-down control have also been shown to occur in terrestrial ecosystems, primarily as a response to increased temperature (Hoekman, 2010; Rodrıguez-Castañeda, 2013). The observed shifts in the SCCS do not seem to represent persistent alterations between alternative ecosystem states (i.e., "regime shifts"), but transient events momentarily increasing the relative importance of top-down effects as bottom-up forcing is weakened due to decreasing nutrient concentrations and prey availability. Following these short-lived perturbations the SCCS has been shown to rebound to previous conditions by rapidly regaining primary and secondary production (Ohman et al., 2012; Rebstock, 2002). In addition to providing a deeper understanding of the roles and relative importance of bottom-up and top-down forces under variable climate conditions, our model simulations highlight important management considerations. Such management concerns are illustrated by an increased sensitivity of the commercially important small pelagic fishery to exploitation during El Niño events, when food availability is limited and predation pressure (natural mortality) is higher. Hence, a holistic ecosystem-based management approach (McLeod & Leslie, 2009) accounting for climate-mediated changes in the strength and relative importance of bottom-up and top-down forcing is therefore needed to ensure a sustainable use of marine living resources in the SCCS and beyond.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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