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1 **Climate-mediated changes in marine ecosystem regulation during El Niño**

2

3 Running title: Climate change and ecosystem regulation

4

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11

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13 model, management

14

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18

19 Abstract

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

42 Introduction

43 The degree to which terrestrial and aquatic ecosystems are regulated through bottom-up
44 (resource-driven), top-down (consumer-driven) or direct physical (climate-driven) processes
45 represents a long-standing issue in ecology (Power 1992; Strong 1992; Polis *et al.*, 2000; Worm
46 & Myers 2003; Strong & Frank 2010), with important consequences for resource management
47 and conservation (Cury *et al.*, 2003; Llope *et al.*, 2011; Blenckner *et al.*, 2015; Lynam *et al.*,
48 2017). Although it is presently recognized that these processes are not mutually exclusive, the
49 conditions under which one of these processes dominate and whether climate change can trigger
50 changes in their relative importance remain largely unknown. In marine ecosystems, the role of
51 bottom-up and top-down forcing has been shown to vary with latitude, where the former
52 dominates in areas with high temperature and species richness and vice versa (Frank *et al.*, 2007;
53 Boyce *et al.*, 2015). Upwelling areas, such as the Humboldt and Benguela Currents, have been
54 hypothesized to represent “wasp-waist” ecosystems, where mid-trophic levels dominated by a
55 few species of planktivorous fish (e.g., sardine and anchovy), may exert both top-down control
56 on their prey and bottom-up control on their predators (Rice 1995; Cury *et al.*, 2000, 2003) (Fig.
57 1). However, direct physical processes, such as related to transport and advection of nutrients
58 and organisms may also predominate in upwelling systems, including the California Current
59 (Parrish *et al.*, 1981; Brinton & Townsend 2003; Koslow *et al.*, 2014).

60

61 The relative importance of bottom-up and top-down forcing has been shown to vary over spatio-
62 temporal scales, often linked to highly variable environmental conditions (Polis *et al.*, 1997;
63 Hunt & McKinnell 2006; Litzow & Ciannelli 2007; Lindegren *et al.*, 2012), as well as the degree

64 of spatial connectivity between areas (Casini *et al.*, 2012). For instance, ecosystem dynamics in
65 the Eastern Bering Sea have been shown to alternate between bottom-up and top-down control
66 during cold and warm regimes, caused by decadal variability in temperature affecting the timing
67 of the spring bloom, the composition of the zooplankton community and recruitment of key fish
68 species, e.g., walleye Pollock (*Theragra chalcogramma*) (Coyle *et al.*, 2011; Hunt *et al.*, 2011).
69 Similar alteration between bottom-up and top-down regulation has also been suggested to occur
70 in wasp-waist ecosystems, where during periods of high abundances mid-trophic level species
71 may instead exert top-down control on their predators, either through direct predation or via food
72 competition with early life-stages of their predators (Bakun 2006).

73

74 The El Niño Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) represent
75 two major modes of climate variability across the tropical and North Pacific, affecting a suite of
76 abiotic and biotic conditions related to temperature, transport, nutrient availability and
77 productivity (Bjerknes 1966; Chelton *et al.*, 1982; Mantua *et al.*, 1997; Chavez *et al.*, 2002).
78 While the effects of ENSO events, i.e., El Niño (anomalously warm) and La Niña (anomalously
79 cold), are short-lived and occur at relatively high frequencies (Philander & Federov 2003),
80 positive and negative phases of the PDO may persist for decades with long-lasting consequences
81 for the biota (Mantua *et al.*, 1997; Minobe 1997). Furthermore, phase transitions in the PDO may
82 coincide with changes in the relative frequency of ENSO events, i.e., enhanced frequency of El
83 Niño during positive phases of the PDO and vice versa (Verdon & Franks 2006). Although not
84 studied in detail, it is suggested that potential phase differences between the ENSO and PDO
85 may serve to weaken or strengthen the effect of El Niño and La Niña events on the biota
86 (Chelton *et al.*, 1982; Chavez *et al.*, 2002). Despite pronounced climate variability, ecosystem

87 dynamics in the Northeast Pacific, including a wide range of open marine ecosystems from
88 southern California to Alaska, have been suggested to be predominately bottom-up regulated
89 (Ware & Thompson 2005). However, it remains unknown to what extent top-down forcing can
90 exert a regulatory role, or whether the relative importance of bottom-up, top-down or direct
91 physical forcing may change in response to climate variability and future climate change.

92

93 The Southern California Current System (SCCS) is a highly productive ecosystem strongly
94 impacted by climate variability across a range of spatial and temporal scales (Rykaczewski &
95 Checkley 2008; Checkley & Barth 2009; DiLorenzo and Ohman 2013). This is largely due to its
96 geographical location and interactions of both a high-frequency tropical and low-frequency
97 temperate mode of climate variability, caused by ENSO and PDO, respectively (Lluch-Cota *et*
98 *al.*, 2003). Likewise, biotic variables of the SCCS display pronounced variability ranging from
99 inter-annual to multi-decadal fluctuations of e.g., meso- and macrozooplankton, marine
100 mammals and birds, as well as mesopelagic and pelagic fish (Rebstock 2002; Brinton
101 & Townsend 2003; Smith & Moser 2003; Sydeman *et al.*, 2009; Koslow *et al.*, 2011). These
102 include non-target and commercially important prey and predatory fish species, such as sardine
103 (*Sardinops sagax*), anchovy (*Engraulis mordax*) and Pacific hake (*Merluccius productus*).
104 Although climate effects on population dynamics of single, or groups of species have been
105 extensively studied (Lavaniegos & Ohman 2007; Rykaczewski & Checkley 2008; Koslow *et al.*,
106 2011, 2013, 2014; Lindegren & Checkley 2013; Lindegren *et al.*, 2013; DiLorenzo & Ohman
107 2013), little is known regarding the combined effects of bottom-up, top-down and direct physical
108 forcing on the food web dynamics across multiple trophic levels. In this study, we investigate
109 the effects and relative importance of bottom-up and top-down forcing on the food web

110 dynamics of the SCCS during changing climate conditions using a generalized food web model.
111 The generalized model represents links between several functional groups and trophic levels but
112 does not resolve interactions at the level of individual species. This statistical approach is based
113 on non-linear threshold models, fitted and parameterized using a unique long-term data set (~60
114 year), largely based on the *California Cooperative Oceanic Fisheries Investigations* (CalCOFI)
115 monitoring program, supplemented by the *California Current Ecosystem Long-Term Ecological*
116 *Research* site, covering multiple trophic levels from phytoplankton to predatory fish. We show
117 evidence of strong bottom-up regulation throughout the food web, interacting with moderate top-
118 down forcing, but only during periods of unfavorable climate conditions primarily associated
119 with certain combinations of ENSO and PDO. Furthermore, we elaborate on the effects of major
120 El Niño events, if occurring during the positive or negative phase of the PDO, as well as
121 demonstrate potential concerns for marine- and fisheries management in the face of climate
122 change.

123

124 **Material and Methods**

125 *1.1 Data collection*

126 An inventory of data characterising the ocean-atmospheric, hydrographic, physical and biotic
127 conditions across multiple trophic levels in the SCCS over the time period from 1951 to 2010
128 was performed (Table S1). In order to reflect the ocean-atmospheric conditions affecting
129 regional climate in the area, a number of large-scale climate indices, including the PDO (Mantua
130 *et al.* 1997), the tropical Multivariate ENSO Index (MEI), the Southern Oscillation Index (SOI),
131 as well as the North Pacific Gyre Oscillation (NPGO) (DiLorenzo *et al.*, 2008) were included.

132 To reflect the hydrodynamic conditions, coastal upwelling, open-ocean (wind stress curl-driven)
133 upwelling (Rykaczewski & Checkley 2008), sea level height (detrended), alongshore (North-
134 South) transport, as well as dynamic height were used. Physical conditions were represented by
135 spring averages of 0-100 m temperature, salinity, water density (σ_t) and oxygen concentration
136 across all stations of the regular CalCOFI area (i.e., from line 76.7 to 93.3; Figure S1). Nutrient
137 conditions were represented by average concentrations of nitrate in the mixed layer. Since nitrate
138 was consistently sampled only from 1984 onwards, we extended its time series backwards until
139 1951 based on modelled estimates. These were derived from a Generalized Additive Model
140 (GAM) with upwelling, temperature and sea level as predictors, demonstrating highly significant
141 and temporally consistent relationships overall (Table S2; Figure S2, S4) and a high degree of
142 explained deviance (79.4%). Finally, a set of biotic (response) variables representing separate
143 trophic levels was compiled. The mean spring chlorophyll *a* in the mixed layer was chosen to
144 characterize primary producers. Note that due to lack of chlorophyll *a* data prior to 1984 we
145 extended the time series backwards until 1951 with modelled estimates (Table S2-S3; Figure
146 S3), based on a GAM explaining a high degree of deviance from 1984-2010 (87.8%). The
147 spring carbon biomass of mesozooplankton, excluding euphausiids, here termed ‘other
148 zooplankton’ and euphausiids, the latter divided into a warm-water (subtropical) and cold-water
149 (temperate) assemblage (Brinton & Townsend 2003), were used to represent intermediate trophic
150 levels (see details in Lavaniegos & Ohman, 2007).

151

152 To represent key consumers of both meso- and macrozooplankton (euphausiids) and prey for
153 higher trophic level predators, an aggregated index of mesopelagic fish abundance, derived from
154 ichthyoplankton samples (Koslow *et al.*, 2011), as well as the total spawning stock biomass

155 (SSB) of small pelagic fish was used. The latter group consists of the dominant consumers of
156 copepods and euphausiids including Pacific sardine, northern anchovy and Pacific mackerel
157 (*Scomber japonicus*), respectively, for which comparable biomass estimates are available from
158 stock assessments (Murphy 1966; Jacobson *et al.*, 1994; Fissel *et al.*, 2009; Hill *et al.*, 2011;
159 Crone *et al.*, 2011). Note that, in the absence of sardine stock assessments during the period of
160 low stock size from 1963 to 1980, hindcasted model estimates were used (Lindegren *et al.*,
161 2013). Finally, ichthyoplankton samples of Pacific hake, as well as stock assessment estimates of
162 hake fishing mortality (Stewart & Forrest 2011) and albacore (*Thunnus alalunga*) catch-per-unit
163 effort (CPUE) data (ALBWG 2011) were used to characterize the dominant predatory fish in the
164 area (Figure S4). Because of its highly migratory behavior and transitory residence in the
165 California Current, albacore was treated as an external covariate only. In addition to these
166 predators, sharks, billfishes (e.g., striped marlin and swordfish), as well as marine birds and
167 mammals constitute other top predators in the SCCE (Bedford & Hagerman 1983; Barlow *et al.*,
168 2008; Sydeman *et al.*, 2015). Unfortunately, the considerably shorter length of monitoring time
169 series for these groups (e.g., 1987 and 1991 onwards for birds and cetaceans, respectively;
170 Hyrenbach & Veit 2003; Barlow & Forney 2007), precludes a comparable long-term analysis of
171 climate forcing and trophic interactions on these predators. Nevertheless, we will discuss our
172 findings regarding climate effects and trophic regulation in the SCCE with reference also to these
173 top predators.

174

175 *1.2 Food web model setup and validation*

176 In order to account for potential threshold-dependent relationships, we used a modified
177 formulation of Generalized Additive Models, so-called threshold Generalized Additive Models

178 (TGAM), allowing for non-additive effects of the explanatory variables below and above a
 179 certain threshold value (ϕ) estimated from the data (Ciannelli *et al.*, 2004). Since our aim was to
 180 investigate whether bottom-up and top-down processes depend on climate, in particular the
 181 indirect or direct effects of ENSO and PDO on resource availability (Chelton *et al.*, 1982), we
 182 treated the PDO, MEI, total nitrate and chlorophyll *a* as candidate threshold variables and
 183 allowed the model to test for potential threshold values. For mesopelagic fish we treated deep-
 184 water oxygen (200-400m) as a potential threshold variable due to its proposed effect on habitat
 185 size and predator-prey overlap (Koslow *et al.*, 2011). In order to assess potential state-dependent
 186 relationships between small pelagic fish and predatory fish (Bakun 2006) we also tested an
 187 alternative model formulation where the biomass of small pelagic fish was used a threshold
 188 variable in the hake model. The following non-additive model formulation with $\log(x+1)$
 189 transformed biomass (or abundance) indices for each trophic level as response variables (y) was
 190 used:

$$191 \quad y_{i,t} = a + \begin{cases} s(x_{i-1,t}) + s(x_{i+1,t}) + s(v_{1,t}) + \dots + s(v_{n,t}) + \varepsilon_t & \text{if } TV > \Phi \\ s(x_{i-1,t}) + s(x_{i+1,t}) + s(v_{1,t}) + \dots + s(v_{n,t}) + \varepsilon_t & \text{if } TV \leq \Phi \end{cases}$$

192 where a is the intercept, s the thin plate smoothing function (Wood 2003), $x_{i,t}$ the biomass (or
 193 abundance) at time t for each trophic level i (i.e., where $i-1$ and $i+1$ represent direct predator-
 194 prey interactions between adjacent trophic levels occurring without time lags), $v_1 \dots v_n$ a number
 195 of selected climate predictors known to affect the dynamics of each trophic level, TV the
 196 threshold variable, and ε the error term. We applied a stepwise backward selection routine based
 197 on the generalized cross validation criterion (GCV) and partial F -tests to find the best possible
 198 set of predictors for each trophic level model. Furthermore, the spline smoother function (s) was
 199 constrained to three degrees of freedom ($k=3$), in order to allow for potential nonlinearities but

200 restrict flexibility during model fitting. Finally, we tested whether the non-additive models
201 proved significantly better than regular GAMs (fitted without thresholds) by comparing the
202 genuine CV, i.e., the average squared leave-one-out prediction errors (Ciannelli *et al.*, 2004). To
203 validate the predictive capabilities of the model, we hindcasted historical food web dynamics by
204 dynamically coupling each separate trophic level model into a generalized food web model,
205 where the internal dynamics (i.e., trophic interactions) are forced only by the external covariates
206 (Llope *et al.*, 2011; Blenckner *et al.*, 2015; Lynam *et al.*, 2017). The food web model was
207 initialised with the observed biomass (or abundance) values in 1966, the first year with available
208 observations for all covariates (i.e., albacore data are missing prior to 1966), and run throughout
209 the period until 2010 with observed covariate values. To account for uncertainty we added
210 process noise, resampled from the residuals of each trophic level model, and performed 1000
211 replicated model runs. In order to retain any temporal dependence (correlation) between errors
212 across trophic levels, an entire vector of errors corresponding to a randomly sampled set of
213 model residuals for a given year was used. The hindcasted estimates were then compared with
214 the actual observed values for each trophic level to validate the predictive accuracy of the food
215 web model for the study period.

216

217 *1.3 El Niño simulations and management scenarios*

218 In order to investigate the effect of major El Niño events and particularly whether phase
219 differences between the ENSO and PDO may serve to weaken or strengthen the biotic response
220 across trophic levels, we exposed the validated food web model to a simulated El Niño event,
221 represented by the observed covariate values during the record strong El Niño in 1998 (Chavez

222 *et al.*, 2002). This pulse perturbation was introduced during both a negative and positive phase of
223 the PDO, defined as the mean covariate values observed prior to and after the PDO phase shift in
224 1976-1977 (Mantua *et al.*, 1997). These simulations were initialized at the mean biomass (or
225 abundance) for each trophic level and forced with the mean covariate values, both averaged
226 during the negative and positive phases of the PDO, over a period of 10 years. Thereafter, the El
227 Niño pulse perturbation was introduced and the relative difference in non-log biomass (or
228 abundance) before and during the perturbation was estimated as a measure of the strength of the
229 biotic response (e.g., a value <1 would indicate a decline) (Figure S6). Furthermore, we
230 illustrated potential management implications by assessing the effect of exploitation on the
231 commercially important small pelagic fishery during periods of low or high productivity,
232 respectively. These were defined as periods of low and high nitrate availability, as occurring
233 during positive and negative phases of MEI, and correspond to the mean covariate values above
234 and below the estimated MEI threshold of 0.371 (Fig. S7i,j). The effect of exploitation was
235 quantified as the change in total spawning stock biomass (SSB) relative to an equilibrium SSB
236 (i.e., 0.77 and 0.44 million metric tonnes below and above the MEI threshold, respectively) when
237 forced by a range of fishing mortalities (F) from 0 to 0.6 y^{-1} for a period of 10 years (i.e., $\text{SSB}_t =$
238 $\text{SSB}_{t-1} * e(-F)$). All statistical analyses were conducted using the R software (www.r-project.org).

239

240 **Results**

241 All trophic level models demonstrate strongly significant interactions and a high degree of
242 explained deviance (Table 1). The type of interactions range from linear to non-linear
243 relationships, occurring with or without threshold-dependent dynamics and illustrate a
244 combination of bottom-up and top-down effects and direct physical forcing throughout the

245 modelled food web (Fig. 2). We recognize that these statistical relationships do not necessarily
246 reflect direct causation, but for convenience we refer to these as “effects” and provide references
247 to known relationships documented in the literature. The bottom-up effects are shown as positive
248 linear or curvilinear relationships, predominately without threshold-dependent dynamics,
249 illustrated by the positive effect of nitrate availability on chlorophyll *a* (Fig. 3c; Fig. S8e-f), as
250 well as the between lower and higher trophic levels throughout the food web (Fig.
251 3g,l,m,s,t,z,aa). In case of omnivory, positive feeding relationships may extend across several
252 trophic levels (Miller *et al.* 2010), such as shown by positive effects of chlorophyll *a* and other
253 zooplankton on euphausiids (Fig. 3l), as well as euphausiids on hake (Buckley & Livingston
254 1997) (Fig. 3z,aa). The top-down effects are indicated by opposite relationships between
255 adjacent trophic levels, where consumers are positively related to their prey and vice versa (Fig.
256 3d,h,I,n,u,v,x,ac). In addition, potential competition is illustrated by negative non-trophic
257 interactions, such as shown from cold-water to warm-water euphausiids (Fig. 3q). Interestingly,
258 the negative effects are exclusively threshold-dependent, indicating top-down effects only below
259 or above certain thresholds. Therefore, a negative grazing impact of other zooplankton on
260 primary producers (Mullin 2000) and predation on other zooplankton by mesopelagic and
261 pelagic fish (Ohman & Hsieh 2008) occurred only during periods of low nitrate availability (Fig.
262 3d,h,i). These conditions primarily exist during El Niño events when diminished upwelling of
263 nutrient rich-water into the SCCS limits primary and secondary production (Chelton *et al.* 1982;
264 Chavez *et al.* 2002). The immediate consequences for pelagic fish are illustrated by significant
265 negative effects from albacore and hake (Fig. 3u,v), but only during periods of high MEI when
266 zooplankton biomass is drastically reduced and food availability limited (Rebstock 2002;
267 Lavaniegos & Ohman 2007). While the top-down effect from albacore can be explained by

268 predation (Glaser 2010), the negative effect of hake may be due to both predation and
269 competition, especially during early life stages when diet preferences overlap (Buckley &
270 Livingston 1997).

271

272 In contrast to the threshold dependent top-down effects, the influence of direct physical forcing
273 is exclusively non-threshold dependent and is optimally described as linear (Fig.
274 3a,b,e,f,j,k,o,p,r), with the exception of deep-water oxygen which shows a curvilinear
275 relationship to mesopelagic fish (Fig. 3w). Climate effects are illustrated by negative ENSO
276 effect on zooplankton (Fig. 3f) (Rebstock 2002; Lavaniegos & Ohman 2007; Ohman *et al.*
277 2012), as well as the positive effects of warming (i.e., high PDO and low SOI; Fig. 3o,p) on
278 southern (warm-water) euphausiids (Brinton & Townsend 2003; DiLorenzo & Ohman 2013).
279 Furthermore, we demonstrate positive temperature effect on pelagic fish (Fig. 3r) (Sugihara *et*
280 *al.*, 2012; Lindegren & Checkley 2013) and positive impacts of nitrate availability (Fig. 3c) and
281 negative effects of density stratification (reduced mixing) on chlorophyll *a* (Fig. 3b) (Mantyla *et*
282 *al.* 2008). Finally, we show a positive effect of deep-water oxygen on mesopelagic fish (Fig.
283 3w), likely caused by increased habitat availability and reduced predator-prey overlap (Koslow
284 *et al.*, 2011, 2013, 2014) and a positive effect of sea surface height (i.e., a proxy for the strength of
285 passive advection by the southward flowing California current) on northern (cold-water)
286 euphausiids (Fig. 3j) (Brinton & Townsend 2003).

287 The separate trophic level models show a good fit to data, being able to accurately recreate the
288 long-term dynamics, as well as inter-annual fluctuations (Fig. S9). Likewise, the hindcast
289 simulations, using the coupled food web model where the internal dynamics (i.e., trophic

290 interactions) are forced entirely by the external covariates, are able to represent the historical
291 food web dynamics (Fig. 4). However, note that some of the variability is less well represented,
292 especially for higher trophic levels, such as the overestimation of small pelagic fish in the first
293 five years of the hindcast simulations (Fig. 4e). This is due to the coupled structure of the food
294 web model where potential deviations in lower trophic levels, in this case the slight
295 overestimation in both zooplankton and cold-water euphausiids (Fig. 4b,c), propagate through
296 the food web, thereby increasing the uncertainty of predictions at higher trophic levels. In
297 addition, higher trophic levels are not constrained by as many external covariates as the lower
298 trophic levels. Nevertheless, the observed values were within the 95% confidence intervals for
299 all trophic levels. Finally, TGAMs proved significantly better than regular GAMs, as
300 demonstrated by lower genuine CVs (Table 1). However, a regular GAM showed lower gCVs
301 for mesopelagic fish but displayed an insignificant interaction (with hake) and lower explained
302 deviance (65.7%). We therefore used the TGAM formulation, including a significant threshold
303 dependent effect of hake. In addition, the alternative hake model formulation, including pelagic
304 fish biomass as a potential threshold variable, did not show threshold-dependent relationships
305 between prey and predator (Table S4; Figure S10). Since the alternative model resulted in a
306 considerably lower deviance explained (57.2%) compared to the original model using the PDO
307 as a threshold variable (78.9%) we kept the original model. Standard diagnostics of model
308 residuals were satisfactory for all trophic-levels (Figure S11).

309

310 The El Niño simulations show a generally strong negative effect on the biota (Fig. 5),
311 particularly for lower trophic levels where chlorophyll *a*, other zooplankton and cold-water
312 euphausiids demonstrate depressed biomasses at about 20-50% of their equilibrium levels,

313 regardless whether occurring during the negative or positive phase of the PDO. In contrast,
314 higher trophic levels, pelagic and predatory fish (i.e., Pacific hake), respond less negatively to
315 the El Niño event if occurring during the negative phase of the PDO, while during the positive
316 phase of the PDO the biomasses (or abundances) are depressed to about 55% and 30% of their
317 equilibrium levels, respectively. Mesopelagic fish and warm-water euphausiids show
318 moderately, or markedly, positive responses to the El Niño event, particularly during the
319 negative phase of the PDO. However, for euphausiids the magnitude of this increase should be
320 understood in the context of the relatively lower biomass of warm-water euphausiids (Brinton &
321 Townsend 2003). In the second scenario, assessing the effect of exploitation on the
322 commercially important small pelagic fishery, the total pelagic SSB responds drastically to
323 increasing exploitation during unfavorable conditions (Fig. 6), with a minimum SSB at ~25% of
324 the respective equilibrium level at $F=0.6 \text{ y}^{-1}$. During favorable conditions the total SSB declines
325 at a more moderate rate with increasing exploitation and demonstrates a higher minimum SSB
326 amounting to ~55% of the respective equilibrium level at $F=0.6 \text{ y}^{-1}$.

327

328 **Discussion**

329 The identification of dominant modes of ecosystem regulation and the degree to which these may
330 vary in space and time and across ecosystem types, including terrestrial and aquatic ecosystems,
331 represent a long-studied field in ecology (Power 1992; Strong 1992; Polis *et al.*, 2000; Schmitz
332 *et al.*, 2000; Worm & Myers 2003; Strong & Frank 2010; Boyce *et al.*, 2015). On the basis of
333 positive correlations between adjacent trophic levels, a number of large and highly productive
334 marine ecosystems across the North Atlantic and North Pacific, including the California Current,

335 are considered to be bottom-up driven (Ware & Thompson 2005; Frank *et al.*, 2007; Boyce *et al.*,
336 2015). Our generalized food web model, using non-linear threshold regressions and a long-term
337 data set spanning six decades, also supports strong bottom-up forcing in the SCCS. This
338 highlights the important regulatory role of nutrient and prey availability, where increased
339 supplies of nitrate (i.e., caused by southern transport of nutrient-rich waters upwelled further
340 north (Chelton *et al.* 1982)) lead to higher primary and secondary production, as well as high
341 abundance of pelagic fish and upper-trophic level predators in the area (Chelton *et al.* 1982;
342 Chavez *et al.* 2003; Mantyla *et al.* 2008), including marine birds and mammals (Melin *et al.*,
343 2012; Sydeman *et al.* 2015). These resource-driven processes were found to be largely non-
344 threshold dependent. This result implies that bottom-up effects are ever-present and provide a
345 strong baseline regulation of food web dynamics in the SCCS, regardless of highly variable
346 climate conditions. While bottom-up effects on various species or trophic levels in the Northeast
347 Pacific have previously been established (Chavez *et al.* 2003; Ware & Thompson 2005;
348 Sydeman *et al.* 2009), evidence of top-down control has been shown primarily at higher latitudes
349 (Litzow & Ciannelli 2007; Hunt *et al.*, 2011; Boyce *et al.*, 2015), as well as in nearshore and
350 intertidal ecosystems (Paine 1980; Estes *et al.* 1998). Our results support these findings by
351 showing also moderate top-down effects, but interacting with stronger bottom-up forcing
352 throughout the food web. Interestingly, the negative effects are exclusively threshold-dependent,
353 indicating top-down effects only below or above certain thresholds. These thresholds generally
354 correspond to situations when positive bottom-up effects are weakened due to resource
355 limitation, or unfavorable climate conditions. These conditions primarily exist during El Niño
356 events when diminished upwelling of nutrient rich-water into the SCCS limits primary and
357 secondary production (Chelton *et al.* 1982; Chavez *et al.* 2002).

358 Furthermore, climate-mediated changes in the spatio-temporal overlap between predators and
359 prey may affect the strength of top-down effects. Hence, the negative effect of hake on pelagic
360 fish, as well as albacore on hake, may partly be due to increasing spatial overlap, especially during
361 El Niño events when hake extends its distribution range northward (Agostini *et al.* 2008).
362 Likewise, increased vertical overlap between hake and mesopelagic fish may explain the
363 negative predation effect detected during low oxygen conditions when the mid-water habitat of
364 mesopelagic fish is compressed (Koslow *et al.* 2011, Netburn & Koslow 2015) due to a shoaling
365 of the hypoxic boundary (Bograd *et al.* 2008). Similarly, a fishing effect on hake was found
366 significant only during the negative phase of the PDO. This may be due to lower abundances and a
367 contracted (southerly) distribution range, resulting from stronger equatorward flow by the
368 California current (Agostini *et al.*, 2008), which may increase the vulnerability to fishing. Note
369 that since major changes in hake management (e.g., the transition to a joint Canada-US
370 assessment in 1997; Stewart & Forrest 2011) do not coincide with transitions in the PDO,
371 changes in fishing regulations are unlikely to explain this effect. Although previous studies
372 suggest a marginal effect of hake predation on euphausiids (Mullin & Conversi 1987;
373 Tanasichuk 1999), we found a negative effect on euphausiids occurring only during high
374 chlorophyll *a*. Whether this may be explained by a concentration of hake in the southern area of
375 its distribution range during periods of limited poleward flow (Agostini *et al.* 2008) and high
376 productivity is unclear. Furthermore, whether sharks, billfishes, marine birds and mammals (that
377 were not included in this analysis) can exert a significant regulatory top-down effect on lower
378 trophic levels is unclear. While previous studies demonstrate the importance of bottom-up
379 forcing regulating sea bird populations (Sydeman *et al.*, 2015; Melin *et al.*, 2012), high
380 consumption rates may buffer their relatively low biomasses (Field *et al.*, 2006; Barlow *et al.*,

381 2008). Hence, these other predators could at least locally (i.e., in the vicinity of bird colonies)
382 and/or seasonally (i.e., during feeding migrations of these highly mobile and wide ranging
383 species) affect the dynamics of their fish and zooplankton prey in the SCCS.

384

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

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

420 As a complement to bottom-up and top-down regulation, wasp-waist control, in which mid-
421 trophic levels may exert both top-down and bottom-up control on their prey and predators,
422 respectively (Rice 1995; Cury *et al.*, 2000), and oscillating trophic control, in which an
423 ecosystem may shift between bottom-up and top-down regulation (Litzow & Ciannelli 2007;
424 Hunt *et al.* 2011), represent additional explanations for understanding ecosystem regulation. In

425 this study, we found bottom-up control to be the primary mode of ecosystem regulation in the
426 SCCS (Ware & Thompson 2005; Lindegren *et al.* 2016). However, our results indicate also an
427 alternative mode of regulation represented by combined bottom-up and top-down forcing, hence
428 analogous to wasp-waist dynamics, but occurring across multiple trophic levels and only during
429 periods of limiting resources. The shifts in regulation are caused by changes in ocean-atmosphere
430 forcing and are triggered by highly variable climate conditions, such as El Niño, hence analogous
431 to oscillating trophic control (Hunt *et al.*, 2011). Similar climate-mediated shifts between
432 bottom-up and top-down control have also been shown to occur in terrestrial ecosystems,
433 primarily as a response to increased temperature (Hoekman 2010; Rodriguez-Castañeda 2013).
434 The observed shifts in the SCCS do not seem to represent persistent alterations between
435 alternative ecosystem states (i.e., “regime shifts”), but transient events momentarily increasing
436 the relative importance of top-down effects as bottom-up forcing is weakened due to decreasing
437 nutrient concentrations and prey availability. Following these short-lived perturbations the SCCS
438 has been shown to rebound to previous conditions by rapidly regaining primary and secondary
439 production (Rebstock 2001, Ohman *et al.* 2012). In addition to providing a deeper understanding
440 of the roles and relative importance of bottom-up and top-down forces under variable climate
441 conditions, our model simulations highlight important management considerations. Such
442 management concerns are illustrated by an increased sensitivity of the commercially important
443 small pelagic fishery to exploitation during El Niño events, when food availability is limited and
444 predation pressure (natural mortality) is higher. Hence, a holistic ecosystem-based management
445 approach (McLeod & Leslie 2009) accounting for climate-mediated changes in the strength and
446 relative importance of bottom-up and top-down forcing is therefore needed to ensure a
447 sustainable use of marine living resources in the SCCS and beyond.

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457

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666

667 **Supporting Information legends**

668 **Table S1.** Biotic and abiotic variables used during model fitting.

669 **Table S2.** Summary statistics of GAM explaining mixed-layer nitrate concentrations and
670 chlorophyll a.

671 **Table S3.** Summary statistics of the Chl a TGAM when fitted to only observed data from
672 1984 onwards.

673 **Table S4.** Summary statistics of the hake TGAM when introducing small pelagic fish
674 spawning stock biomass (SSB) as a threshold variable.

675 **Figure S1.** Map of the study area and the California Cooperative Oceanic Fisheries
676 Investigations (CalCOFI) long-term monitoring program.

677 **Figure S2.** Partial smooth plots for the GAM explaining variability in mixed-layer nitrate
678 concentrations.

679 **Figure S3.** Partial smooth plots for the GAM explaining variability in mixed-layer
680 Chlorophyll a concentrations.

681 **Figure S4.** Observed vs predicted mixed layer nitrate concentrations during years with
682 a negative PDO.

683 **Figure S5.** Comparison of ichthyoplankton abundance indices and available stock
684 assessment estimates of spawning stock biomass of sardine and hake.

685 **Figure S6.** A single stochastic model run showing the effect on the biota of an
686 introduced El Niño event.

687 **Figure S7.** The estimated thresholds and time-series of threshold variables for the final
688 TGAMs.

689 **Figure S8.** Partial smooth plots for the final TGAM for Chl a when fitted on the entire
690 time-series and when fitted on observed values only from 1984 onwards.

691 **Figure S89** Observed and fitted food web dynamics based on the final models.

692 **Figure S10.** Summary plot showing the alternative hake TGAM if introducing the
693 spawning stock biomass of small pelagic fish as a threshold variable.

694 **Figure S11.** Residual diagnostic plots for the final models.

695 **Figure S12.** The response of Chl a when including or significantly limiting the threshold
696 dependent top-down effect of zooplankton grazing during a simulated El Niño event.

697 **Figure S13.** Simulated food web responses to a negative and positive phase of the
698 PDO.

699 **Appendix S1.** Additional sensitivity tests for trophic-level models.

700 **Table 1.** Summary statistics showing the intercept with p-value, the estimated threshold, the
 701 deviance explained (DEV in %), the genuine cross-validation score (gCV), comparing TGAM
 702 and GAMs, the number of observations (N), as well as smooth term statistics for each TGAM.
 703 Significant terms “above”, “below or equal to”, or without the estimated threshold are denoted
 704 by $>$, \leq and $--$, respectively. (edf, estimated degrees of freedom for the model smooth terms
 705 where $edf > 1$ indicates a nonlinear relationship).

706	<u>Response</u>	<u>Intercept</u>	<u>P-value</u>	<u>Threshold (Φ)</u>	<u>DEV (%)</u>	<u>gCV_{TGAM/GAM}</u>	<u>N</u>
707	Chl α	0.24	<0.001	0.498	77.9	0.027/0.029	58
708	Other Zooplankton	3.03	<0.001	0.735	57.0	0.211/0.235	52
709	Euphausiid (cool)	1.73	<0.001	0.279	69.3	0.242/0.243	56
710	Euphausiid (warm)	0.42	<0.001	-0.225	63.0	0.233/0.249	55
711	Pelagic fish	13.6	<0.001	0.371	68.1	0.512 /0.535	37
712	Mesopelagic fish	2.36	<0.001	1.517	73.0	0.143/0.125	45
713	Pacific hake	3.51	<0.001	-0.251	78.9	0.817/1.12	42

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715	<u>Response</u>	<u>Threshold</u>	<u>Predictor</u>	<u>edf</u>	<u>F</u>	<u>P-value</u>
716	Chl α	---	SST	1.00	14.1	<0.001
717		---	Density	1.00	50.2	<0.001
718		---	[NO ₃]	1.96	36.9	<0.001
719		[NO ₃] $\leq \Phi$	Other Zooplankton	1.00	6.36	0.015
720	Other Zooplankton	---	PDO	1.85	10.4	<0.001
721		---	MEI	1.58	7.60	0.001
722		---	Chl α	1.00	6.10	0.017
723		[NO ₃] $\leq \Phi$	Pelagic fish	1.27	4.96	0.011
724		[NO ₃] $\leq \Phi$	Mesopelagic fish	1.00	7.35	0.009
725	Euphausiid (cool)	---	Dynamic height	1.00	19.6	<0.001
726		---	Sverdrup transport	1.00	8.82	0.005
727		---	Chl α	1.64	4.00	0.025
728		Chl $\alpha \leq \Phi$	Other Zooplankton	1.00	8.55	0.005

729		Chl $\alpha > \Phi$	Pacific hake	1.91	14.2	<0.001
730	Euphausiid (warm)	---	PDO	1.02	8.60	<0.001
731		---	SOI	1.00	10.60	0.002
732		PDO $> \Phi$	Euphausiid (cool)	1.72	10.41	0.002
733	Pelagic fish	---	SST	1.00	8.23	0.007
734		---	Euphausiid cool	1.00	12.62	0.001
735		MEI $\leq \Phi$	Other Zooplankton	1.00	13.0	<0.001
736		MEI $> \Phi$	Pacific hake	1.00	10.7	0.003
737		MEI $> \Phi$	Albacore	1.00	9.86	0.004
738	Mesopelagic fish	---	[O ₂] (200-400m)	1.99	42.2	<0.001
739		[O ₂] $\leq \Phi$	Pacific hake	1.79	5.42	0.008
740	Pacific hake	---	Mesopelagic	1.86	13.7	<0.001
741		PDO $> \Phi$	Euphausiid (cool)	1.78	11.5	<0.001
742		PDO $> \Phi$	Euphausiid (warm)	1.56	7.10	0.003
743		PDO $> \Phi$	Pelagic fish	1.00	43.1	<0.001
744		PDO $> \Phi$	Albacore	1.00	8.98	0.005
745		PDO $\leq \Phi$	F	1.00	11.54	0.002

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754 **Figure 1.** A conceptual representation of the dominant modes of ecosystem regulation within a
755 simplified four-level marine food web. (a) Bottom-up regulation is typically characterized by a
756 positive relationship between trophic levels where an increase in primary producers leads to
757 increases in higher trophic levels. (b) Top-down regulation is represented by negative
758 relationship between adjacent trophic levels, usually characterized by alternating abundance
759 trends in response to a decline in top-predators. (c) Wasp-waist regulation occurs when mid-
760 trophic levels (e.g., small planktivorous fish) exert both top-down control on their prey
761 (zooplankton) and bottom-up control on their predators. (d) Finally, our results indicate an
762 alternative mode of regulation represented by strong and persistent bottom-up forcing interacting
763 with weaker top-down forcing, but only above or below certain thresholds, here associated with
764 climate-related changes in ENSO. This mode of regulation is related to wasp-waist and
765 oscillating trophic control, occurring when the modes of ecosystem regulation shift between
766 bottom-up and top-down control (usually as a result of rapid changes in the environment).
767 However, in the mode of regulation presented here the shifts are between strict bottom-up
768 forcing and a combination of both bottom-up and top-down control. (This figure is inspired and
769 partly redrawn from Cury *et al.*, 2003).

770

771 **Figure 2.** A schematic representation of the effects of climate, fishing and trophic interactions in
772 the generalized SCCS food web model, consisting of Pacific hake, mesopelagic fish, small
773 pelagic fish, euphausiids, i.e., divided into a cold (C) and warm (W) water assemblage,
774 mesozooplankton and primary producers. (Note that the top-predator albacore tuna (within
775 dotted rectangle) is treated as an external covariate). Blue and red arrows indicate threshold-
776 dependent interactions above and below an estimated threshold, respectively (Fig. S6). The

777 numbers associated with each arrow correspond to a particular covariate used as threshold
778 variable, identified by the same number in superscript. The black arrows indicate non-threshold
779 dependent effects. Although interactions may range from linear to non-linear, we have indicated
780 generally positive (+) and negative (-) interactions.

781

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

792

793 **Figure 4.** Observed (circles) and hindcasted dynamics of chlorophyll a (A), other
794 mesozooplankton (B), cold- and warm-water euphausiids (C-D), small pelagic fish (E),
795 mesopelagic fish (F) and Pacific hake (G). The simulations are initiated with observed
796 population estimates in 1966 and simulated until 2010 based on observed external covariates
797 only. Grey lines show 95% confidence intervals. (See Fig. S9 for model fits).

798

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

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808 **Figure 6.** Impact of increasing exploitation, i.e., fishing mortality (F), on small pelagic fish
809 during periods of low (black) and high (gray) MEI. The effect is quantified as the change in total
810 biomass relative to a respective equilibrium level (i.e., 0.77 and 0.44 Million metric tons at F=0)
811 when forced by mean climate conditions occurring below (black) and above (gray) the MEI
812 threshold (Fig. S7i,j), respectively. Solid and dashed lines show the mean and 95% confidence
813 intervals after 1000 random simulations.

814

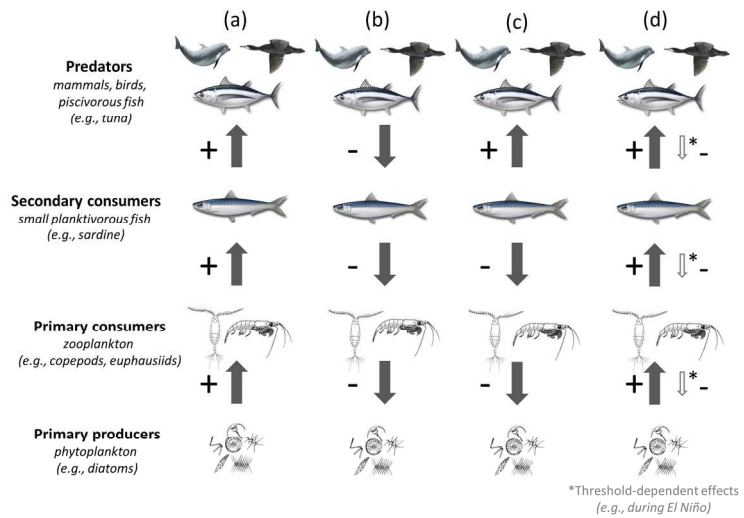


Fig 1

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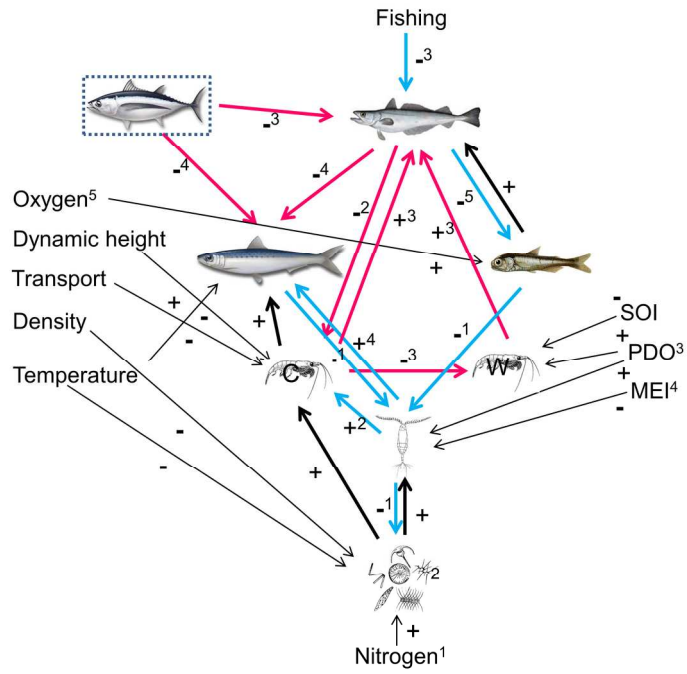


Fig 2

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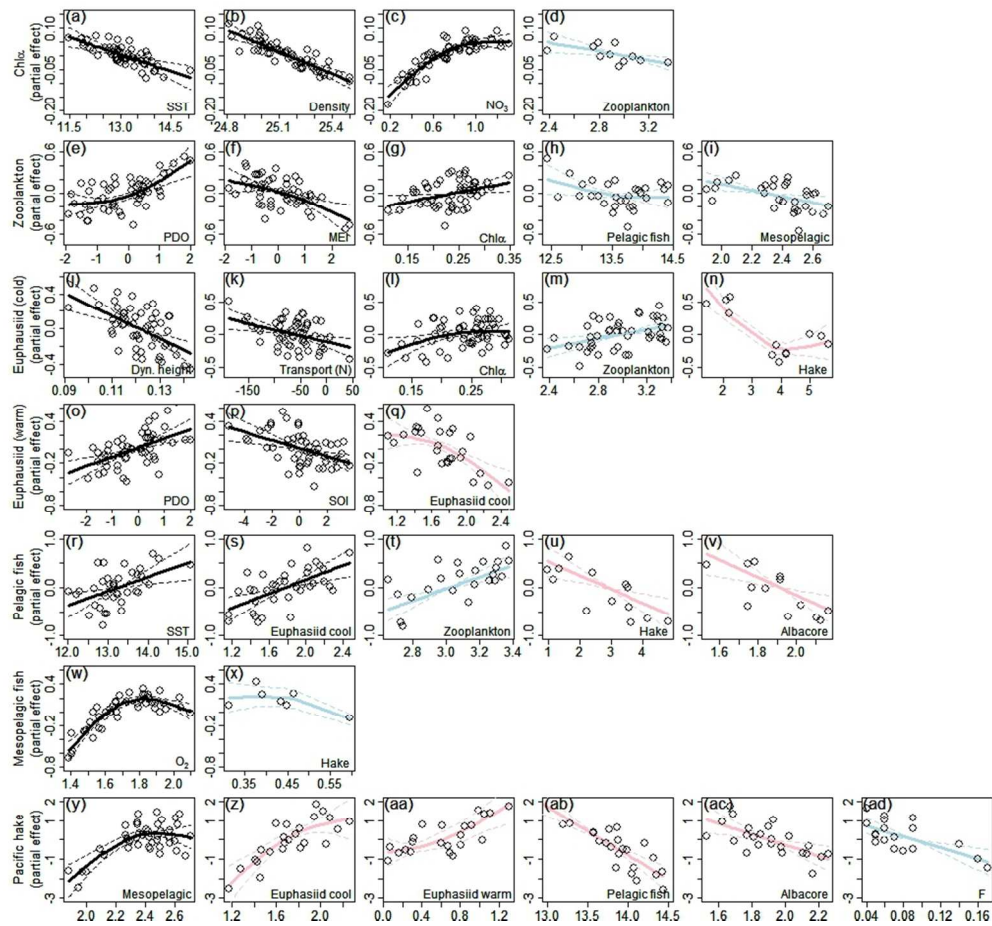
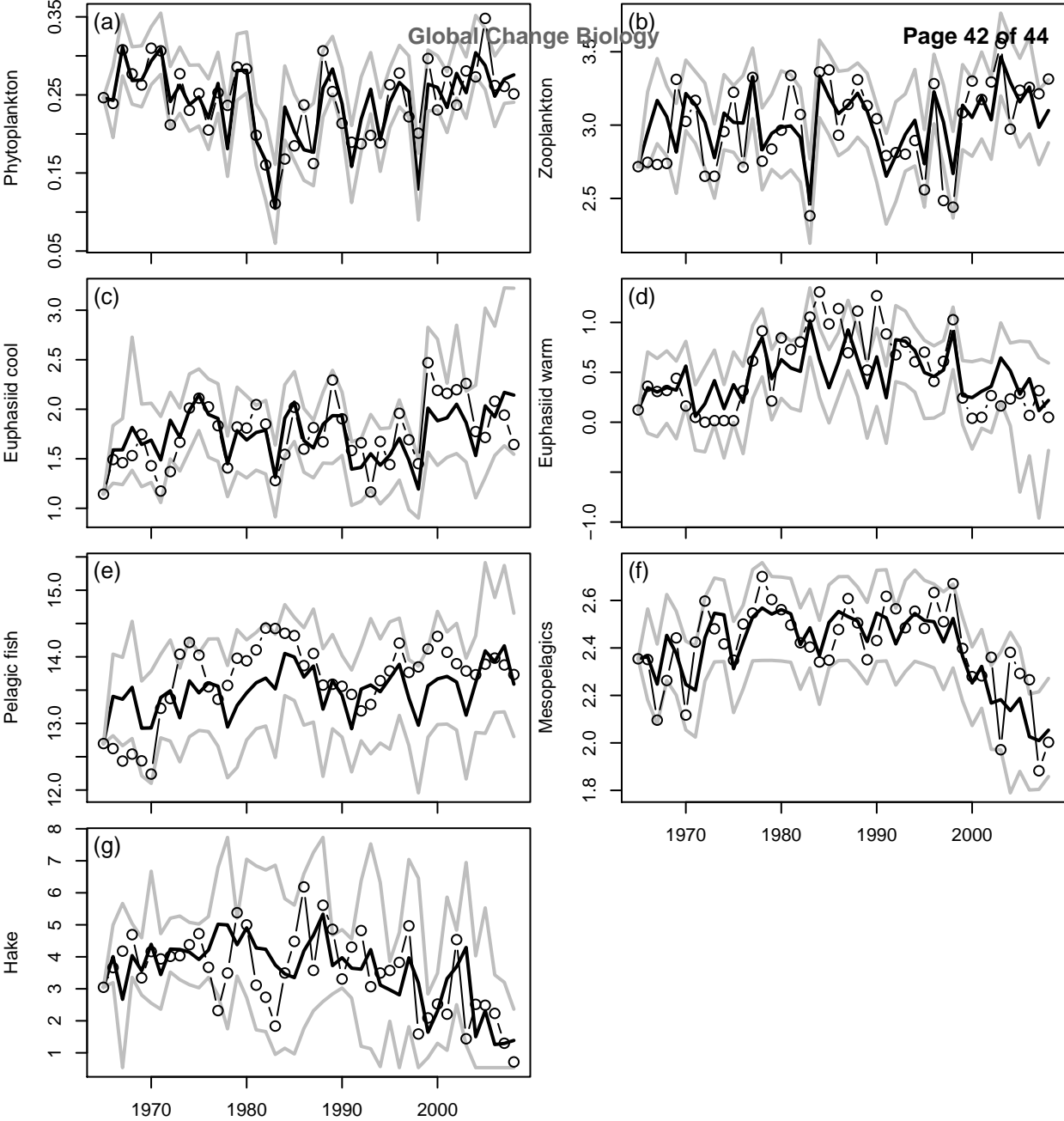


Fig 3

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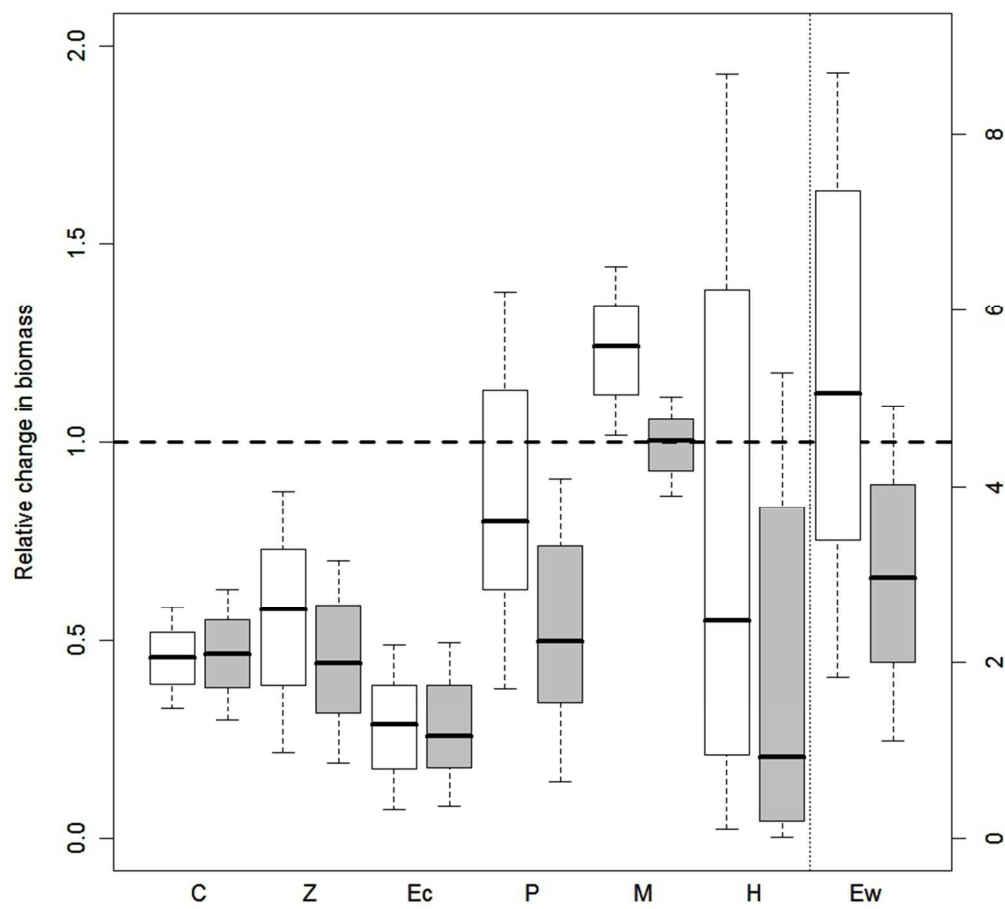


Fig 5

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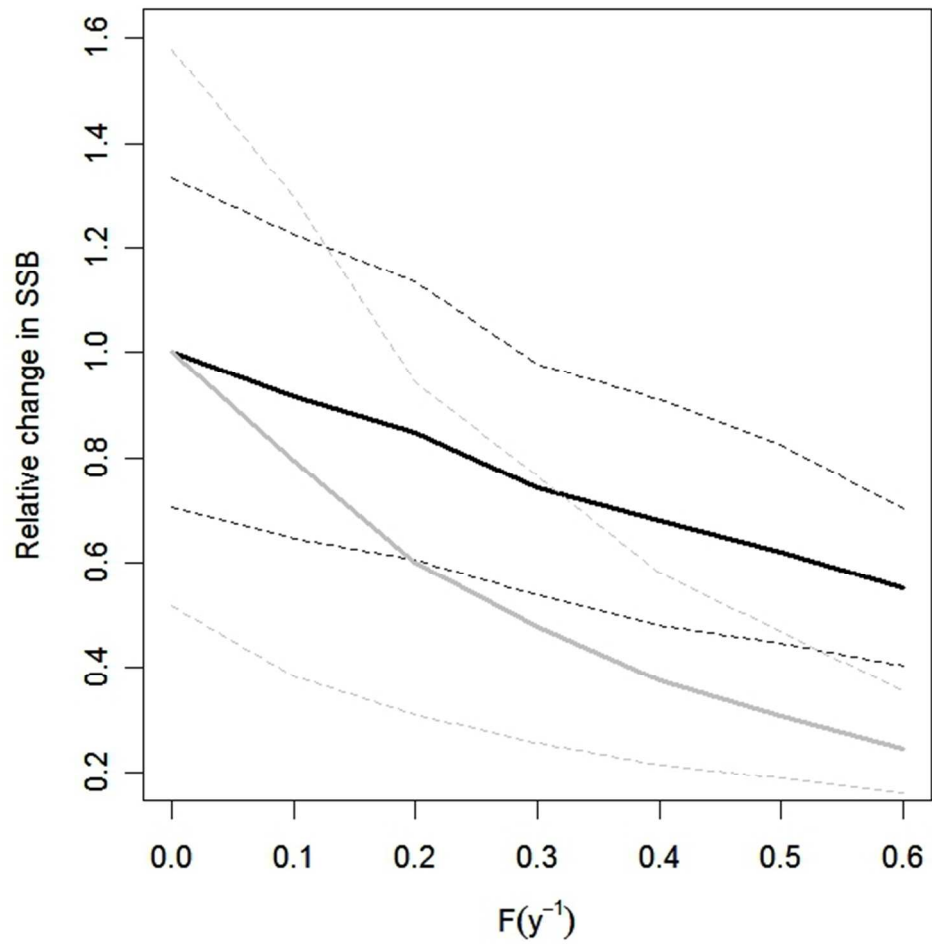


Fig 6

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