Climate-mediated changes in marine ecosystem regulation during El Niño

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3 Running title: Climate change and ecosystem regulation

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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

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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

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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

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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

8

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

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), $v_i\ldots v_n$ 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 to1966), 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., $SSB_t =$

238    $SSB_{t-1}*e(-F)$). 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

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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

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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, 213, 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

13

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,

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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 $F=0.6\ y^{-1}$. 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 $F=0.6\ y^{-1}$.

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).

16

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 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 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.*,

17

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.

18

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

19

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.

457

458   **References**

459   Agostini, V. N., Hendrix, A.N., Hollowed, A.B., Wilson, C.D., Pierce, S.D., Francis, R.C.

460   (2008). Climate-ocean variability and Pacific hake: A geostatistical modeling approach. Journal

461   of Marine Systems, 71, 237-248.

462   ALBWG (2011). Stock assessment of albacore in the North Pacific Ocean in 2011. ISC,

463   Shizuoka, Japan.

464   Bakun, A. (2006). Wasp-waist populations and marine ecosystem dynamics: Navigating the

465   "predator pit" topographies. Progress in Oceanography, 68, 271-288.

466   Barlow, J., & Forney, K.A. (2007). Abundance and population density of cetaceans in the

467   California Current ecosystem. Fisheries Bulletin, 105, 509–526.

468   Barlow, J., Kahru, M., Mitchell, B.G. (2008). Cetacean biomass, prey consumption, and primary

469   production requirements in the California Current ecosystem. Marine Ecology Progress Series,

470   371, 285-295.

471   Bedford, D.W., & Hagerman, F.B. (1983). The Billfish fishery resource of the California

472   Current. CalCOFI Reports, 24, 70-78.

473   Bjerknes, J. (1966). A possible response of the atmospheric Hadley circulation to equatorial

474   anomalies of ocean temperature. Tellus, 18, 820–829.

475   Blenckner T, Llope M, Möllmann C, Voss R, Quaas MF, Casini M, Lindegren M, Folke C,

476   Stenseth NC (2015) Climate and fishing steer ecosystem regeneration to uncertain economic

477   futures. Proc R Soc B, 282: 20142809.

478   Bograd, S.J., Castro, C.G., Di Lorenzo, E., Palacios, D.M., Bailey, H., Gilly, W., Chavez, F.P.

479   (2008). Oxygen declines and the shoaling of the hypoxic boundary in the California Current.

480   Geophysical Research Letters, 35, L12607.

481   Boyce, D.G., Frank, K.T., Worm, B., Leggett, W. (2015). Spatial patterns and predictors of

482   trophic control in marine ecosystems. Ecology Letters, 18, 1001-1011.

483   Brinton, E., & Townsend, A. (2003). Decadal variability in abundances of the dominant

484   euphausiid species in southern sectors of the California Current. Deep-Sea Research Part II, 50,

485   2449-2472.

486   Buckley, T., & Livingston, P. (1997). Geographic variation in the diet of Pacific hake, with a

487   note on cannibalism. CalCOFI Reports, 38, 53-62.

22

488   Casini, M., Blenckner, T., Moellmann, C. et al. (2012). Predator transitory spillover induces

489   trophic cascades in ecological sinks. Proceedings of the National Academy of Sciences of the

490   United States of America, 109, 8185-8189.

491   Chavez, F.P., Ryan, J., Lluch-Cota, S.E., Niquen, M. (2003). From anchovies to sardines and

492   back: Multidecadal change in the Pacific Ocean. Science, 299, 217-221.

493   Chavez, F., Pennington, J., Castro, C. et al. (2002). Biological and chemical consequences of the

494   1997-1998 El Niño in central California waters. Progress in Oceanography, 54, 205-232.

495   Checkley, D.M., & Barth, J.A. (2009). Patterns and processes in the California Current System.

496   Progress in Oceanography, 83, 49-64.

497   Chelton, D., Bernal, P., McGowan, J. (1982). Large-scale interannual physical and biological

498   interaction in the California Current. Journal of Marine Research, 40, 1095-1125.

499   Ciannelli, L., Chan, K., Bailey, K., Stenseth, N. (2004). Nonadditive effects of the environment

500   on the survival of a large marine fish population. Ecology, 85, 3418-3427.

501   Coyle, K.O., Eisner, L.B., Mueter, F.J., Pinchuk, A.I., Janout, M.A., Cieciel, K.D., Farley, E.V.,

502   Andrews, A.G. (2011). Climate change in the southeastern Bering Sea: impacts on pollock

503   stocks and implications for the oscillating control hypothesis. Fisheries Oceanography, 20, 139-

504   156.

505   Crone, P.R., Hill, K.T., McDaniel, J.D., Lynn, K. (2011). Pacific mackerel (Scomber japonicus)

506   stock assessment for USA management in the 2011-2012 fishing year. PFMC, Portland, USA.

507 Cury, P., Bakun, A., Crawford, R.J.M., Jarre, A., Quiñones, R.A., Shannon, L.J., Verheye, H.M.

508 (2000). Small pelagics in upwelling systems: patterns of interaction and structural changes in

509 "wasp-waist" ecosystems. ICES Journal of Marine Science, 57, 603-618.

510 Cury, P., Shannon, L., & Shin, Y.-J. (2003). The functioning of marine ecosystems: a fisheries

511 perspective. In M. Sinclair & G. Valdimarsson (Eds.), Responsible fisheries in the marine

512 ecosystem (pp. 103–123). Wallingford: CAB International.

513 Di Lorenzo, E., Schneider, N., Cobb, K.M. et al. (2008). North Pacific Gyre Oscillation links

514 ocean climate and ecosystem change. Geophysical Research Letters, 35, L08607.

515 Di Lorenzo, E., & Ohman, M.D. (2013). A double-integration hypothesis to explain ocean

516 ecosystem response to climate forcing. Proceedings of the National Academy of Sciences of the

517 United States of America, 110, 2496-2499.

518 Estes, J., Tinker, M., Williams, T., Doak, D. (1998). Killer whale predation on sea otters linking

519 oceanic and nearshore ecosystems. Science, 282, 473-476.

520 Field, J.C., Francis, R.C., Aydin, K. (2006). Top-down modeling and bottom-up dynamics:

521 Linking a fisheries-based ecosystem model with climate hypotheses in the Northern California

522 Current. Progress in Oceanography, 68, 238–270.

523 Fissel, B.E., Lo, N.C.H., Herrick, S.F., Jr. (2011). Daily Egg Production, Spawning Biomass and

524 Recruitment for the Central Subpopulation of Northern Anchovy 1981-2009. CalCOFI Reports,

525 52, 116-135.

526   Frank, K.T., Petrie, B., Shackell, N.L. (2007). The ups and downs of trophic control in

527   continental shelf ecosystems. Trends in Ecology & Evolution, 22, 236-242.

528   Glaser, S.M. (2010). Interdecadal variability in predator-prey interactions of juvenile North

529   Pacific albacore in the California Current System. Marine Ecology Progress Series, 414, 209-

530   221.

531   Hill, K., Crone, P.R., Lo, N., Macewicz, B., Dorval, E., McDaniel, J., Gu,, Y. (2011).

532   Assessment of the Pacific sardine resource in 2011 for U.S. management in 2012. U.S

533   Department of Commerce, La Jolla, USA.

534   Hoekman, D. (2010). Turning up the heat: temperature influences the relative importance of top-

535   down and bottom-up effects. Ecology, 91, 2819–2825.

536   Hunt, G.L., & McKinnell, S. (2006). Interplay between top-down, bottom-up, and wasp-waist

537   control in marine ecosystems. Progress in Oceanography, 68, 115-124.

538   Hunt, G.L., Jr., Coyle, K.O., Eisner, L.B. et al. (2011). Climate impacts on eastern Bering Sea

539   foodwebs: a synthesis of new data and an assessment of the Oscillating Control Hypothesis.

540   ICES Journal of Marine Science, 68, 1230-1243.

541   Hyrenbach, K.D., & Veit, R.R. (2003). Ocean warming and seabird assemblages of the

542   California Current System (1987–1998): response at multiple temporal scales. Deep Sea Res.

543   Part II, 50, 2537–2565.

544   Jacobson, L., Lo, N., Barnes, J. (1994). A Biomass-Based Assessment Model for Northern

545   Anchovy, Engraulis-Mordax. Fishery Bulletin, 92, 711-724.

546 Koslow, J.A., Goericke, R., Lara-Lopez, A., Watson, W. (2011). Impact of declining

547 intermediate-water oxygen on deepwater fishes in the California Current. Marine Ecology

548 Progress Series, 436, 207-218.

549 Koslow, J.A., Goericke, R., Watson, W. (2013). Fish assemblages in the Southern California

550 Current: relationships with climate, 1951-2008. Fisheries Oceanography, 22, 207-219.

551 Koslow, J.A., Davison, P., Lara-Lpoez, A., Ohman, M.D. (2014). Epipelagic and mesopelagic

552 fishes in the southern California Current System: Ecological interactions and oceanographic

553 influences on their abundance. J. Mar. Sys. 138, 20-28.

554 Lavaniegos, B.E., Ohman, M.D. (2007). Coherence of long-term variations of zooplankton in

555 two sectors of the California Current System. Progress in Oceanography, 75, 42-69.

556 Lindegren, M., Blenckner, T., Stenseth, N.C. (2012). Nutrient reduction and climate change

557 cause a potential shift from pelagic to benthic pathways in a eutrophic marine ecosystem. Global

558 Change Biology, 18, 3491-3503.

559 Lindegren, M., Checkley, D.M., Jr. (2013). Temperature dependence of Pacific sardine

560 (Sardinops sagax) recruitment in the California Current Ecosystem revisited and revised.

561 Canadian Journal of Fisheries and Aquatic Sciences, 70, 245-252.

562 Lindegren, M., Checkley, D.M., Jr., Rouyer, T., MacCall, A.D., Stenseth, N.C. (2013). Climate,

563 fishing, and fluctuations of sardine and anchovy in the California Current. Proceedings of the

564 National Academy of Sciences of the United States of America, 110, 13672-13677.

565   Lindegren, M., Checkley, D.M., Ohman, M.D., Koslow, J.A., Goericke, R. (2016). Resilience

566   and Stability of a Pelagic Marine Ecosystem. Proceedings of the Royal Society B-Biological

567   Science, 283, 20151931.

568   Litzow M.A., & Ciannelli L (2007) Oscillating trophic control induces community

569   reorganization in a marine ecosystem. Ecology Letters, 10, 1124–1134.

570   Llope, M., Daskalov, G.M., Rouyer, T.A., Mihneva, V., Chan, K., Grishin, A.N., Stenseth, N.C.

571   (2011). Overfishing of top predators eroded the resilience of the Black Sea system regardless of

572   the climate and anthropogenic conditions. Global Change Biology, 17, 1251-1265.

573   Lluch-Cota, D., Wooster, W., Hare, S., Lluch-Belda, D., Pares-Sierra, A. (2003). Principal

574   modes and related frequencies of sea surface temperature variability in the Pacific Coast of North

575   America. Journal of Oceanography, 59, 477-488.

576   Lynam CP, Llope M, Möllmann C, Helaouët P, Bayliss-Brown GA, Stenseth NC (2017)

577   Interaction between top-down and bottom-up control in marine food webs. . Proceedings of the

578   National Academy of Sciences of the United States of America, 114: 1952-1957.

579   Mantua, N., Hare, S., Zhang, Y., Wallace, J., Francis, R. (1997). A Pacific interdecadal climate

580   oscillation with impacts on salmon production. Bulletin of the American Meteorological Society,

581   78, 1069-1079.

582   Mantyla, A.W., Bograd, S.J., Venrick, E.L. (2008). Patterns and controls of chlorophyll-a and

583   primary productivity cycles in the Southern California Bight. Journal of Marine Systems, 73, 48-

584   60.

27

585   Melin, S.R., Orr, A.J., Harris, J.D., Laake, J.L., DeLong, R.L. (2012). California Sea Lions: an

586   indicator for integrated ecosystem assessments of the California Current System. CalCOFI

587   Reports, 53, 140-152.

588   McLeod, K., & Leslie, H. (2009). Ecosystem-based management for the oceans. Island Press,

589   Washington, D.C., USA.

590   Miller, T.W., Brodeur, R.D., Rau, G., Omori, K. (2010). Prey dominance shapes trophic

591   structure of the northern California Current pelagic food web: evidence from stable isotopes and

592   diet analysis. Marine Ecology Progress Series, 420, 15-26.

593   Minobe, S. (1997). A 50-70 year climatic oscillation over the North Pacific and North America.

594   Geophysical Research Letters, 24, 683-686.

595   Mullin, M. (2000). Large-celled phytoplankton, the nitricline, and grazing during the California

596   1997-98 El Nino. CalCOFI Reports, 41, 161-166.

597   Mullin, M., Conversi, A. (1989). Biomasses of euphausiids and smaller zooplankton in the

598   California Current - geographic and interannual comparisons relative to the Pacific whiting,

599   Merluccius productus, fishery. Fishery Bulletin, 87, 633-644.

600   Murphy, G.I. (1966). Population biology of the Pacific sardine (Sardinops caerulea). Proc. Cal.

601   Acad. Sci. 34, 1-84.

602   Netburn, A.N., Koslow, J.A., (2015). Dissolved oxygen as a constraint on daytime deep

603   scattering layer depth in the southern California current ecosystem. Deep-Sea Research Part I,

604   104, 149-158, doi 10.1016/j.dsr.2015.06.006.

28

605   Ohman, M.D., Hsieh, C. (2008). Spatial differences in mortality of Calanus pacificus within the

606   California Current System. Journal of Plankton Research, 30, 359-366.

607   Ohman, M.D., Rau, G.H., Hull, P.M.(2012). Multi-decadal variations in stable N isotopes of

608   California Current zooplankton. Deep Sea Research I 60, 46-55.

609   Paine, R.T. (1980). Food webs - linkage, interaction strength and community infrastructure – The

610   3rd Tansley Lecture. Journal of Animal Ecology, 49, 667-685.

611   Parrish, R.H., Nelson, C.S., Bakun, A. (1981). Transport mechanisms and reproductive success

612   of fishes in the California Current. Biological Oceanography 1, 175-203

613   Philander, S., Fedorov, A. (2003). Is El Niño sporadic or cyclic? Annual Review of Earth and

614   Planetary Sciences, 31, 579-594.

615   Polis, G.A., Anderson, W.B., Holt, R.D. (1997). Toward an integration of landscape and food

616   web ecology: The dynamics of spatially subsidized food webs. Annual Review of Ecology and

617   Systematics, 28, 289-316.

618   Polis, G.A., Sears, A.L.W., Huxel, GR., Strong, D.R., Maron, J. (2000). When is a trophic

619   cascade a trophic cascade? Trends in Ecology & Evolution, 15, 473-475.

620   Power, M.E. (1992). Top-down and bottom-up forces in food webs - do plants have primacy?

621   Ecology, 73, 733-746.

622   Rebstock, G.A. (2002). Climatic regime shifts and decadal-scale variability in calanoid copepod

623   populations off southern California. Global Change Biology, 8, 71-89.

624   Rice, J. (1995). Food web theory, marine food webs, and what climate change may do to

625   northern fish populations. In: Beamish, R.J.(Ed.), Climate Change and Northern Fish

626   populations. Canadian Special Publication in Fisheries and Aquatic Science, vol. 121, pp. 561–

627   568.

628   Rodrıguez-Castañeda, G. (2013). The world and its shades of green: a meta-analysis on trophic

629   cascades across temperature and precipitation gradients. Global Ecology and Biogeography, 22,

630   118–130.

631   Rykaczewski, R.R., Checkley, D.M., Jr. (2008). Influence of ocean winds on the pelagic

632   ecosystem in upwelling regions. Proceedings of the National Academy of Sciences of the United

633   States of America, 105, 1965-1970.

634   Schmitz, O.J., Hambäck, P.A., Beckerman, A.P. (2000) Trophic cascades in terrestrial systems: a

635   review of the effects of carnivore removal on plants. American Naturalist,155, 141–153.

636   Smith. P., Moser, H. (2003). Long-term trends and variability in the larvae of Pacific sardine and

637   associated fish species of the California Current region. Deep-Sea Research Part II, 50, 2519-

638   2536.

639   Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.S., Lima, M. (2002).

640   Ecological effects of climate fluctuations. Science, 297, 1292-1296.

641   Stewart, I.J., Forrest, R.E. (2011). Status of the Pacific Hake (Whiting) stock in U.S. and

642   Canadian Waters in 2011. PFMC, Portland, USA.

643   Strong, D.R. (1992). Are trophic cascades all wet - differentiation and donor-control in speciose

644   ecosystems. Ecology, 73, 747-754.

645   Strong, D.R., Frank, K.T .(2010). Human involvement in food webs. Annual Review of

646   Environment and Resources, 35, 1-23.

647   Sugihara, G., May, R., Ye, H., Hsieh, C., Deyle, E., Fogarty, M., Munch, S. (2012). Detecting

648   causality in complex ecosystems. Science, 338, 496-500.

649   Sydeman, W.J., Mills, K.L., Santora, J.A. et al. (2009). Seabirds and climate in the California

650   Current - a synthesis of change. CalCOFI Reports, 50, 82-104.

651   Sydeman, W.J., Thompson, S.A., Santora, J.A., Koslow, J.A., Goericke, R., Ohman, M.D.

652   (2015). Climate–ecosystem change off southern California: time-dependent seabird predator–

653   prey numerical responses. Deep-Sea Res. II, 112, 158–170.

654   Tanasichuk, R. (1999). Interannual variation in the availability and utilization of euphausiids as

655   prey for Pacific hake (Merluccius productus) along the south-west coast of Vancouver Island.

656   Fisheries Oceanography, 8, 150-156.

657   Verdon, D., Franks, S. (2006). Long-term behaviour of ENSO: Interactions with the PDO over

658   the past 400 years inferred from paleoclimate records. Geophysical Research Letters, 33,

659   L06712.

660   Ware, D.M., Thomson, R.E. (2005). Bottom-up ecosystem trophic dynamics determine fish

661   production in the northeast Pacific. Science, 308, 1280-1284.

662   Wood, S.N. (2003). Thin plate regression splines. Journal of the Royal Statistical Society Series

663   B-Statistical Methodology, 65, 95-114.

664   Worm, B., Myers, R.A. (2003). Meta-analysis of cod-shrimp interactions reveals top-down

665   control in oceanic food webs. Ecology, 84, 162-173.

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 ichytoplankton 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 >, ≤ and --, respectively. (edf, estimated degrees of freedom for the model smooth terms

705 where edf > 1 indicates a nonlinear relationship).

	Response	Intercept	P-value	Threshold (Φ)	DEV (%)	gCV$_{TGAM/GAM}$	N
706							
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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	Response	Threshold	Predictor	edf	F	P-value
715						
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$_3$] ≤ Φ	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$_3$] ≤ Φ	Pelagic fish	1.27	4.96	0.011
724		[NO$_3$] ≤ Φ	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 α ≤ Φ	Other Zooplankton	1.00	8.55	0.005

729		Chl α > Φ	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 > Φ	Euphasiid (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 ≤ Φ	Other Zooplankton	1.00	13.0	<0.001
736		MEI > Φ	Pacific hake	1.00	10.7	0.003
737		MEI > Φ	Albacore	1.00	9.86	0.004
738	Mesopelagic fish	---	$[O_2]$ (200-400m)	1.99	42.2	<0.001
739		$[O_2]$ ≤ Φ	Pacific hake	1.79	5.42	0.008
740	Pacific hake	---	Mesopelagic	1.86	13.7	<0.001
741		PDO > Φ	Euphausiid (cool)	1.78	11.5	<0.001
742		PDO > Φ	Euphausiid (warm)	1.56	7.10	0.003
743		PDO > Φ	Pelagic fish	1.00	43.1	<0.001
744		PDO > Φ	Albacore	1.00	8.98	0.005
745		PDO ≤ Φ	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

36

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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807

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.

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Fig 1
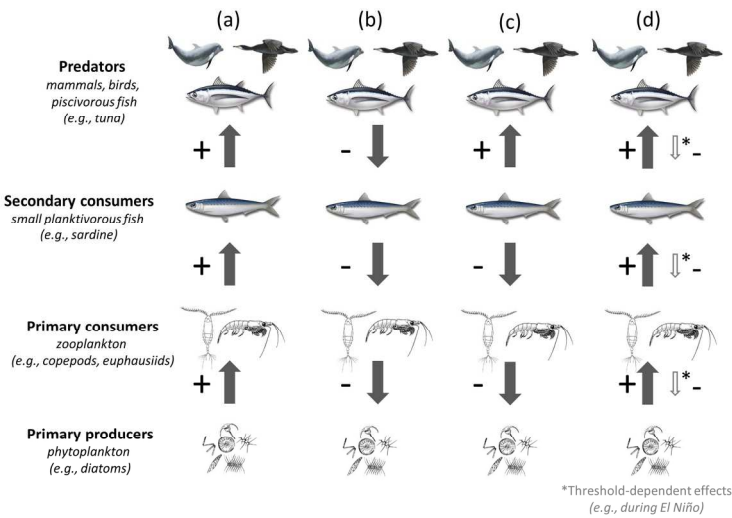
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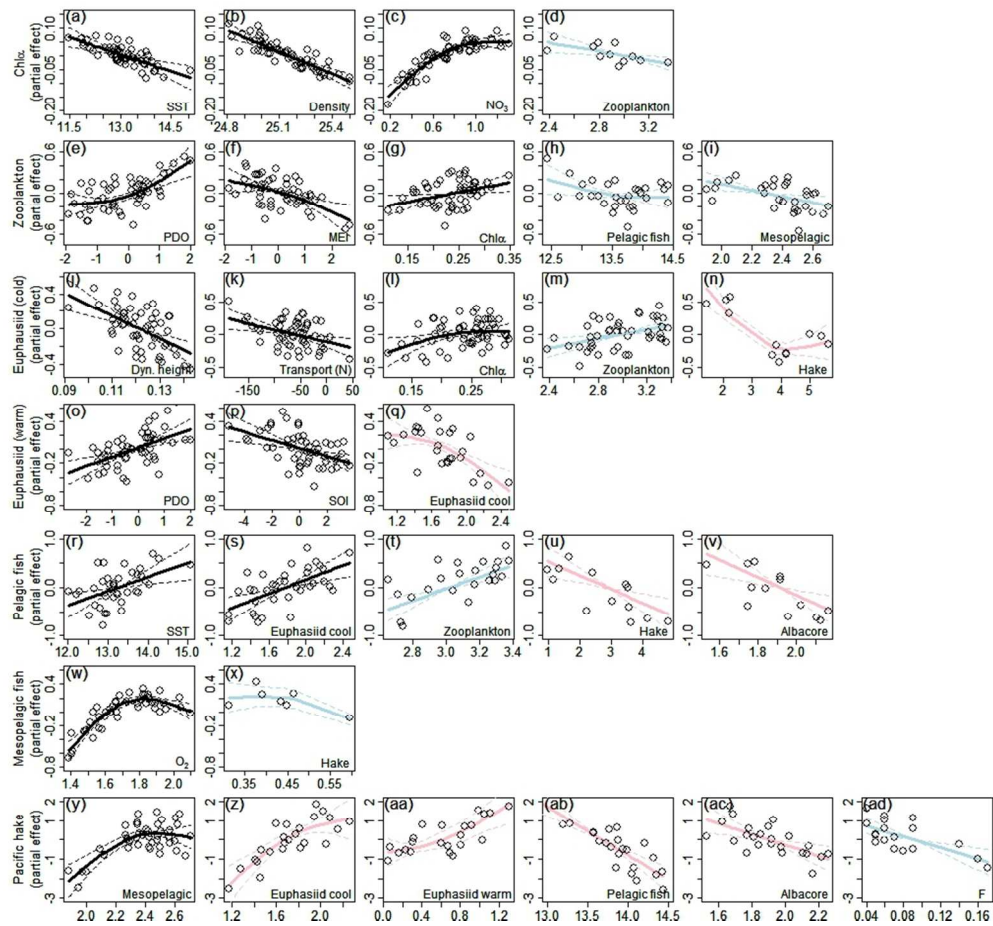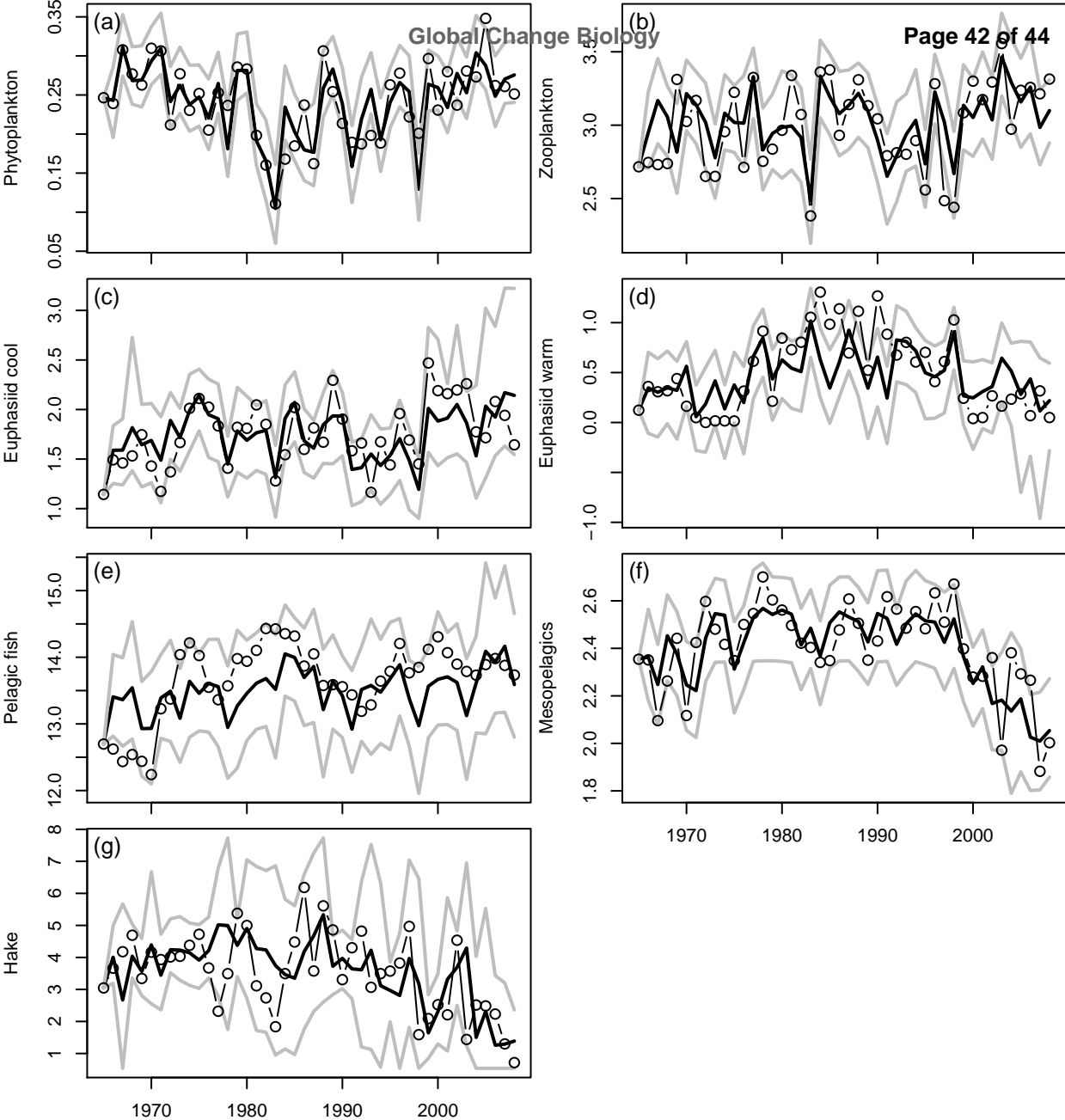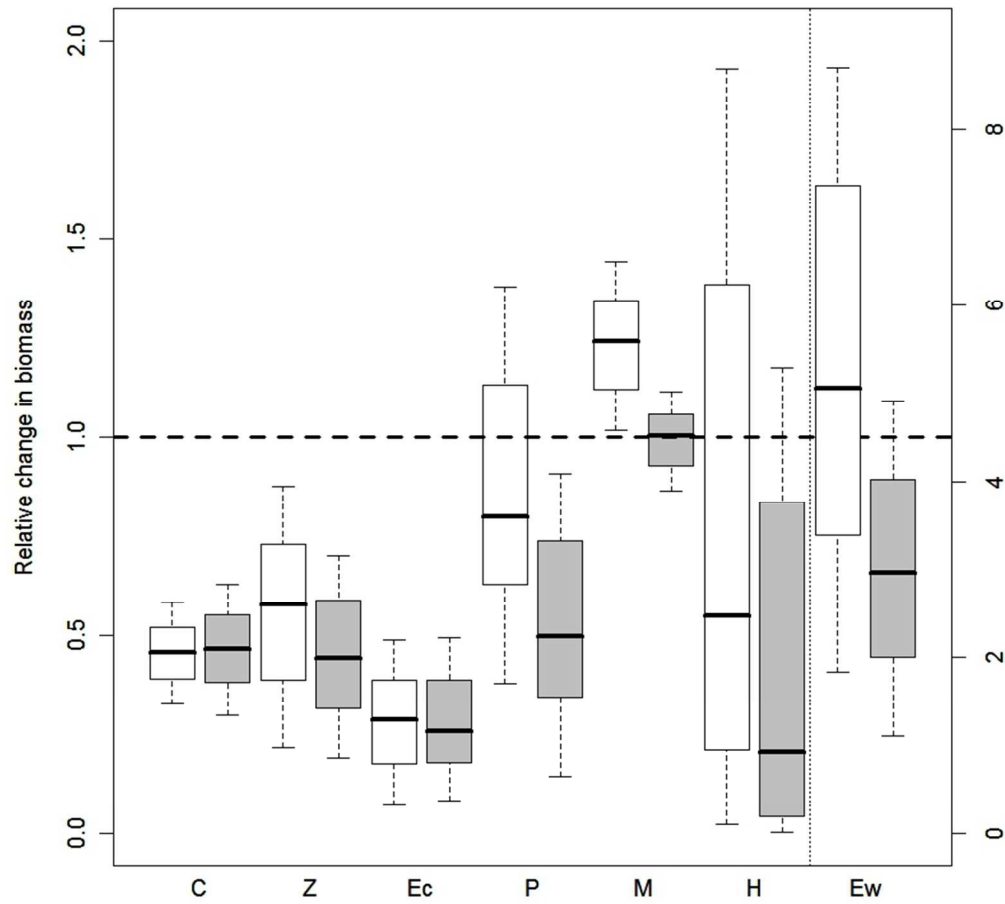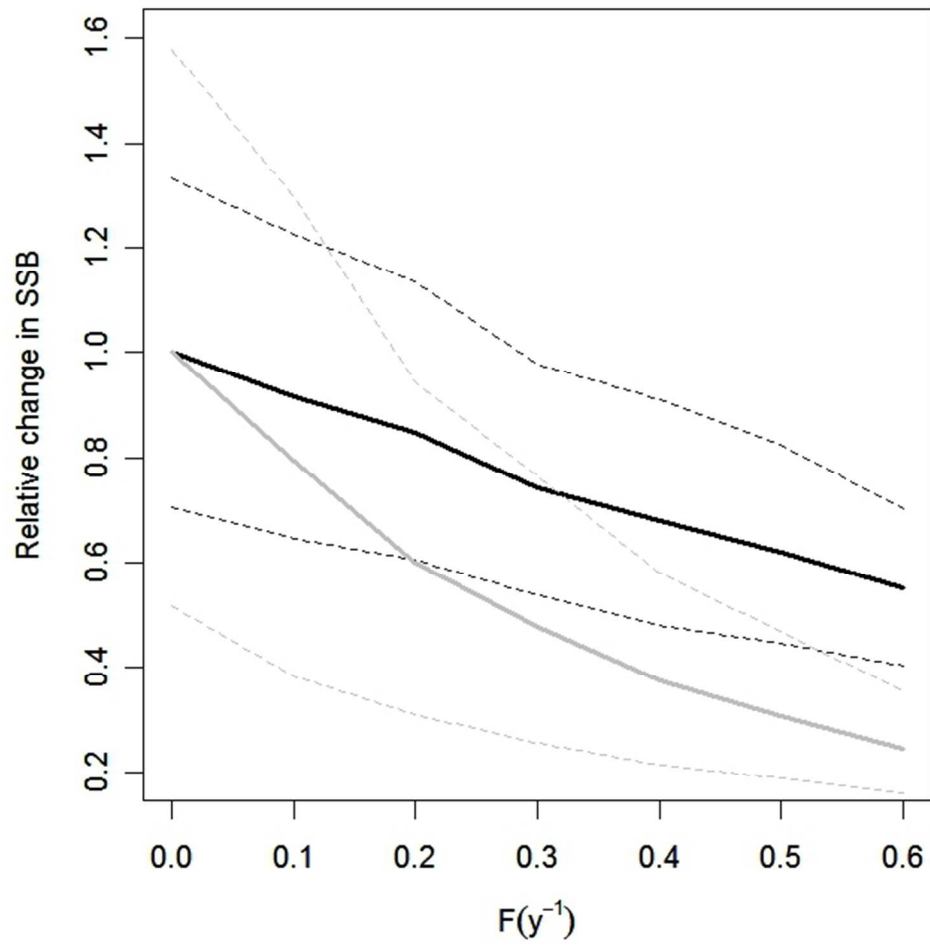Fig 2

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Fig 3

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Fig 6

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