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**Oceanographic drivers of sablefish recruitment in the California Current**

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31 **ABSTRACT**

32 Oceanographic processes and ecological interactions can strongly influence recruitment success  
33 in marine fishes. Here, we develop an environmental index of sablefish recruitment with the  
34 goal of elucidating recruitment-environment relationships and informing stock assessment. We  
35 start with a conceptual life-history model for sablefish *Anoplopoma fimbria* on the US west coast  
36 to generate stage- and spatio-temporally-specific hypotheses regarding the oceanographic and  
37 biological variables likely influencing sablefish recruitment. Our model includes seven stages  
38 from pre-spawn female condition through benthic recruitment (age-0 fish) for the northern  
39 portion of the west coast U.S. sablefish stock (40-50 °N). We then fit linear models and use  
40 model comparison to select predictors. We use residuals from the stock-recruitment relationship  
41 in the 2015 sablefish assessment as the dependent variable (thus removing the effect of spawning  
42 stock biomass). Predictor variables were drawn primarily from ROMS model outputs for the  
43 California Current Ecosystem. We also include indices of prey and predator abundance and  
44 freshwater input. Five variables explained 57% of the variation in recruitment not accounted for  
45 by the stock-recruitment relationship in the sablefish assessment. Recruitment deviations were  
46 positively correlated with (1) colder conditions during the spawner preconditioning period, (2)  
47 warmer water temperatures during the egg stage, (3) stronger cross shelf transport to near-shore  
48 nursery habitats during the egg stage, (4) stronger long-shore transport to the north during the  
49 yolk-sack stage, and (5) cold surface water temperatures during the larval stage. This result  
50 suggests that multiple mechanisms likely affect sablefish recruitment at different points in their  
51 life history.

52

53 **Key Words:** Sablefish, *Anoplopoma fimbria*, recruitment, oceanic drivers, California Current

54 **INTRODUCTION**

55 Climate plays an important role in coastal marine ecosystems, driving changes in horizontal and  
56 vertical transport that affect nutrient availability and primary production that, in turn, propagate  
57 through both lower and upper trophic levels (Di Lorenzo *et al.*, 2013; Chavez *et al.*, 2003; Hunt  
58 Jr and McKinnell, 2006). In coastal upwelling systems the bottom-up forcing hypothesis has  
59 been the prevailing paradigm (Di Lorenzo *et al.*, 2013). However, recent synthesis by the Global  
60 Ecosystems Dynamics Program (GLOBEC) of four regions (Gulf of Alaska, Northern California

61 Current, Northwest Atlantic and Southern Ocean) suggests that horizontal transport (cross-shelf,  
62 long-shore) is also highly important, providing the foundation for a new horizontal-advection  
63 bottom-up-forcing paradigm (Di Lorenzo *et al.*, 2013). This new paradigm suggests that—in  
64 addition to the indirect effects of climate manifested through variability in primary production  
65 and the timing of the availability of food resources—horizontal transport directly affects the  
66 reproductive success of taxa like fish by influencing their transport to suitable settlement habitat  
67 (reviewed by Di Lorenzo *et al.*, 2013). At the same time, other oceanographic parameters like  
68 temperature can affect growth, which can mediate an individual’s vulnerability to predation and  
69 the susceptibility of larvae to starvation (Litvak and Leggett, 1992; Houde, 1987; Leggett and  
70 DeBlois, 1994; Chezik *et al.*, 2014). Likewise, ecological interactions such as prey availability,  
71 predator abundance and density dependence may also be important in determining reproductive  
72 success for marine fishes and other species (Tolimieri, 2015; Hunt Jr and McKinnell, 2006;  
73 Frank *et al.*, 2007; Field *et al.*, 2006). Recruitment, in turn, directly affects age structure and  
74 population size in marine fishes (Bailey, 1981; Hjort, 1914; Myers, 1998; Maunder and Watters,  
75 2003). Therefore, it is important to understand the role of oceanographic processes and  
76 ecological interactions in determining recruitment success in marine fishes—both to gain a better  
77 understanding of their population dynamics and to better manage these species.

78 Sablefish (*Anoplopoma fimbria*) inhabit waters along the west coast of North America  
79 from the Baja California through Alaska and extend west (and south) to Japan (Allen and Smith,  
80 1988; Hart, 1973; Johnson *et al.*, 2016). Traditionally, two stocks have been recognized in the  
81 northeastern Pacific: (1) an Alaskan/British Columbian stock extending from the Bering Sea to  
82 Vancouver Island, and (2) a U.S. west coast population extending from southwest Vancouver  
83 Island to Baja California (Johnson *et al.*, 2016; Schirripa and Colbert, 2006), with each stock  
84 being subject to independent management. The spawning stock biomass (SSB) of the U.S. west  
85 coast sablefish stock (the focus of this work) has declined steadily since the 1980’s (Fig. 1a),  
86 concurrent with high landings during 1976-1990 (Johnson *et al.*, 2016) and highly variable, but  
87 declining recruitment (Fig. 1b). The stock-recruitment relationship appears weak (Fig. 1c)  
88 suggesting that environmental factors are likely important.

89 Sablefish recruitment-environment investigations have generally focused on large-scale  
90 climate or oceanographic variables (Schirripa and Colbert, 2006; Schirripa *et al.*, 2009; Schirripa  
91 and Methot, 2001; Coffin and Mueter, 2015; Shotwell *et al.*, 2014; Sogard, 2011). For example,

92 in the California Current Ecosystem along the U.S. west coast, sablefish recruitment has been  
93 correlated with changes in sea surface height (SSH) and both northward and eastward Ekman  
94 transport (Schirripa and Colbert, 2006). SSH has been used as an index of recruitment success in  
95 recent sablefish stock assessments (Schirripa *et al.*, 2009; Stewart and Forrest, 2011; Johnson *et*  
96 *al.*, 2016), in part as a proxy for abundance of copepods (Schirripa and Colbert, 2006; Schirripa  
97 *et al.*, 2009; Schirripa and Methot, 2001), which are an important food source for larvae and  
98 juveniles (McFarlane and Beamish, 1992; Grover and Olla, 1987). Changes in SSH serve as a  
99 proxy for large-scale climate forcing that drives regional changes in alongshore and cross-shelf  
100 ocean transport. These changes directly impact the transport of water masses, nutrients, and  
101 organisms. SSH tracks these changes on a gross scale, explaining the weak but significant  
102 relationship with sablefish recruitment (Di Lorenzo *et al.*, 2013; Schirripa and Colbert, 2006).

103 The relationship between sablefish recruitment and SSH is compelling from an ecological  
104 standpoint. However, the use of the index has not had a large effect on stock-assessment results  
105 because good data on year-class strength from fishery and fishery-independent survey data  
106 already inform the stock assessment regarding variability in recruitment (Stewart *et al.*, 2011).  
107 While a significant predictor ( $r^2 = \sim 0.3$ ), SSH provides too little additional information to lower  
108 uncertainty enough in the stock assessment to improve the precision of future recruitment  
109 predictions. To do so, an environmental index would need to explain more than 50% of the  
110 variability in recruitment unrelated to the stock-recruitment relationship and age structure  
111 (Basson, 1999; Johnson *et al.*, 2016). Ideally, such an index should derive from environmental  
112 variables at scales relevant to the sablefish life history and be able to forecast into the future,  
113 potentially allowing managers and fishers to better respond to potential shifts in sablefish  
114 recruitment. Given a robust environmental index with greater explanatory power, hind-casting  
115 recruitment strength on the basis of past environmental data can better inform recruitment  
116 estimates during time periods in which there is no information on fishery or survey length and  
117 age compositions.

118 Here, we (1) develop a literature-based, conceptual life-history model for sablefish that  
119 includes seven stages from female conditioning through benthic recruitment (age-0 fish) for the  
120 northern portion of the west coast U.S. sablefish stock (40-50° N). We then (2) use this  
121 conceptual model to generate stage-specific and spatio-temporally-specific hypotheses regarding  
122 the physical and biological variables likely to influence sablefish recruitment. Next we (3) use

123 linear models and model comparison to develop predictive models of sablefish recruitment using  
124 oceanographic drivers taken from a Regional Ocean Modeling System (ROMS) model of the  
125 California Current System (Neveu *et al.*, 2016). We also evaluate support for biological indices  
126 like predator and prey abundance, temperature impacts on growth rates (e.g., Sogard and Olla,  
127 2001), and freshwater input from the Columbia River as a proxy for nutrient input or effects on  
128 ocean currents. Our goal is to develop an ecologically meaningful, robust environment-  
129 recruitment relationship that has higher explanatory power than those developed in the past, with  
130 the end goal of enhancing the sablefish stock assessment and improving short term forecasts of  
131 sablefish recruitment required by fishery managers.

132

## 133 **METHODS**

134 We investigate predictors of recruitment for the northern portion of the U.S. west coast stock  
135 from 40-50° N. We focus on the northern portion of the stock because recruitment estimates  
136 from the coast-wide stock assessment model are most strongly informed by age and length  
137 composition data from the north (Johnson *et al.*, 2016). Although the two-stock definition for  
138 eastern Pacific sablefish (Alaskan/British Columbian and U.S. west coast) is commonly  
139 accepted, there is evidence that the dynamics of the U.S. west coast stock differs north and south  
140 of Cape Mendocino (~40.4° N). Head *et al.* (2014) concluded that the sablefish population south  
141 of Cape Mendocino may be a separate subpopulation based on differentiation in ages and lengths  
142 at 50% maturity, as well as potential differences in reproductive success. Maximum body size is  
143 larger and growth rates are slower north of Cape Mendocino. North of Cape Mendocino, the  
144 highest concentration of age-0 fishes observed in the West Coast Groundfish Bottom Trawl  
145 Survey (WCGBTS) is between 44-45° N, just south of the Columbia River (Fig. S1).

146

### 147 *Sablefish life history: female preconditioning to age-0 recruits*

148 We began our conceptual life-history model by first identifying each life-history stage that could  
149 potentially contribute to determining the size of each sablefish year class, beginning with female  
150 condition prior to the start of the spawning season (Table 1). The energetic status of females  
151 may influence their propensity to spawn, and the quality and number of eggs produced (Sogard  
152 *et al.*, 2008; Rodgveller *et al.*, 2016). Thus, the summer and fall prior to spawning (June-Dec)  
153 may be important for female preconditioning. Spawning occurs from December to March with a

154 peak in February. Most spawning takes place at the edge of the continental shelf at depths  
155 greater than 300 m with eggs initially found from 200 m to greater than 825 m (Hunter *et al.*,  
156 1989; Kendall and Matarese, 1987; Moser *et al.*, 1994; Mason *et al.*, 1983). Eggs are buoyant,  
157 rising to 200-300 m in the water column but are most common between 240 and 480 m, where  
158 they remain for approximately 12-17 days until hatching (Moser *et al.*, 1994; Mason *et al.*, 1983;  
159 Kendall and Matarese, 1987; Boehlert and Yoklavich, 1985; McFarlane and Beamish, 1992).  
160 Post hatch, larvae sink to 1000-1200 m where they can be found between February and May as  
161 yolk-sack larvae. By 14-17 days post-hatch larvae have consumed about 50% of their yolk sack  
162 and may show initial attempts at feeding approximately a week later. By 40-days post hatch  
163 larvae are in surface waters from the 500-m isobath out to 150 nautical miles (277 km) from  
164 shore where they are found between February and May (Moser *et al.*, 1994; Brock, 1940;  
165 McFarlane and Beamish, 1992). Pelagic juveniles are also found in these surface waters and are  
166 present from April through November (Mitchell and Hunter, 1970; Kendall and Matarese, 1987).  
167 Sablefish settle to the benthos as age-0 recruits between August and November with most fish  
168 likely settling to habitats 250 m or shallower.

169

#### 170 *Regional Ocean Modeling System (ROMS)*

171 The majority of our predictors were physical oceanographic parameters including temperature,  
172 long-shore and cross-shelf currents, and mixed layer depth. We derived these variables from a  
173 California Current System (CCS) configuration of the Regional Ocean Modeling System  
174 (ROMS) with 4-Dimensional Variational (4D-Var) data assimilation (Neveu *et al.*, 2016). The  
175 ROMS model domain covers the region 30-48°N and from the coast to 134W at 0.1° (~10 km)  
176 horizontal resolution, with 42 terrain-following vertical levels. In the 1980-2010 CCS reanalysis  
177 used for this study, satellite observations (SST, SSH) and in situ data (temperature and salinity  
178 from ships, floats, moorings) are assimilated into the model to improve its representation of the  
179 true ocean state. This reanalysis has been used extensively to study spatial upwelling variability  
180 (Jacox *et al.*, 2014), basin-scale climate influences (Jacox *et al.*, 2015a; Jacox *et al.*, 2015b), and  
181 bottom-up controls on primary production (Jacox *et al.*, 2016) in the CCS. All ROMS output  
182 was averaged in 4-day increments and then either averaged or summed over the appropriate  
183 period (as defined in Table 1) for each of the 30 years ( $n = 30$  for each time series in the  
184 analysis). Additional predictors are described in relation to their specific hypotheses below.

185 Oceanographic data are scarcer at depth than at the surface. As a result, the ROMS  
186 output, which assimilates available data, is not as strongly constrained by observations at the  
187 subsurface as it is at the surface. It is therefore likely that the ROMS output deviates from nature  
188 more at the subsurface than it does at the surface, though the scarcity of subsurface  
189 measurements (or transport metrics at any depth) precludes a definitive model evaluation in this  
190 regard. The paucity of subsurface data, however, is the motivation for using model output in this  
191 study, and despite our inability to validate the subsurface transport in the model, there is reason  
192 to believe it provides useful information. First, the purpose of data assimilation is to further  
193 improve a model that already captures the dynamics of the California Current faithfully without  
194 data assimilation. The fidelity of this model to nature has been documented extensively for  
195 applications with and without data assimilation (e.g., Jacox *et al.*, 2015a; Veneziani *et al.*, 2009).  
196 The model is forced by realistic winds, surface heat fluxes, and lateral boundary conditions,  
197 which drive realistic physical variability even in the absence of data assimilation. Second, the  
198 data that are assimilated, even if only available at the ocean surface, can impact the subsurface  
199 dynamics. For example, assimilating sea surface height measurements constrains the geostrophic  
200 flow and therefore transport at the surface and in the subsurface. The impact of assimilated data  
201 on different metrics of the CCS circulation is discussed in detail in Moore *et al.* (2017). For a  
202 transport example, see Fig. 4e in that paper.

203

#### 204 *Hypotheses and additional data sources*

205 We developed 21 a priori, life-stage-specific and space-specific (considering time, depth, and  
206 longitude) hypotheses for ecological and environmental covariates that may drive variation in  
207 sablefish recruitment (Table 1). Two hypotheses were represented by two predictors, and we  
208 included SSH for historical reasons (see below). Thus, we tested 24 total predictors. While the  
209 current sablefish stock assessment estimates coast-wide spawning biomass and recruitment time  
210 series, we limited the predictor time series to 40-50 °N because a majority of the length and age  
211 composition data come from the northern California Current (Johnson *et al.*, 2016). For each  
212 hypothesis, we specified the time period, depth and longitudinal extent of the potential  
213 predictor—for example, net cross-shelf transport between January and April at 300-825 m depth,  
214 between 40-50 °N and from the 500-m isobath to 170 nautical miles off shore may affect  
215 transport and distribution of sablefish eggs (Table 1).

216 We focused on hypotheses for which we had data (or model output) available for testing.  
217 We excluded some potential hypotheses for which data were not available rendering these  
218 hypotheses untestable. These hypotheses are not included in Table 1. The most obvious  
219 omission is food availability for larvae and pelagic juveniles (McFarlane and Beamish, 1992).  
220 Unfortunately, continuous data for northern copepod biomass anomaly begin in 1996<sup>1</sup>, long after  
221 recruitment estimates are available for sablefish. We also did not include potential mechanisms  
222 with indirect effects such as upwelling, which might affect larval survival by influencing food  
223 availability. Note, however, that upwelling effects will likely be caught in many of the transport  
224 and temperature indices we did include. Finally, in some cases, the literature suggested multiple  
225 potential depth ranges over which environmental or biological variables might influence  
226 recruitment: one broad and one more restricted. For example, sablefish eggs are found between  
227 240-825 m (Hunter *et al.*, 1989; Kendall and Matarese, 1987; Mason *et al.*, 1983; Moser *et al.*,  
228 1994) with the highest occurrence between 240-480 m (Moser *et al.*, 1994). When selecting  
229 environmental predictors for inclusion in model selection, we initially evaluated variables (e.g.,  
230 total cross shelf transport) for each depth range. However, preliminary analyses showed these  
231 paired predictors (i.e., net cross shelf transport between 300-825 m and 240-480 m) to be highly  
232 correlated ( $r > 0.88$ ), and we chose to include only the broader depth range version of each in our  
233 analyses to reduce the number of predictors. The resulting testable hypotheses fall into six  
234 general categories, which may overlap life-history stages (Table 1): temperature, transport,  
235 mixing, prey, predators, and nutrient fertilization or effects on oceanic currents from freshwater  
236 input from rivers.

237

### 238 Temperature

239 Ambient temperature may affect the production of recruits through multiple mechanisms.  
240 During the preconditioning period for spawning females (Table 1, hypothesis 2, hereafter, H2)  
241 warmer temperatures may increase energy demands (H2), forcing female sablefish to allocate  
242 less energy to reproduction, reducing the production of eggs. Temperature may also act as a  
243 spawning cue (H4). For eggs and larvae, temperature may also affect growth, development,

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<sup>1</sup> <http://www.noaa.gov/iea/regions/california-current-region/indicators/climate-and-ocean-drivers.html>



244 survival, and susceptibility to predation through multiple mechanisms, among which we cannot  
245 distinguish (H7, H10, H13, H17 and H19). For example, warmer temperatures allow for faster  
246 growth allowing larvae to outgrow potential predators (e.g., stage duration or 'bigger-is-better'  
247 hypotheses; Houde, 1987; 1997), but warm waters may also increase energy demands making  
248 larvae more susceptible to starvation, especially if warmer waters bring poor feeding conditions.  
249 Temperature data were obtained from ROMS outputs. In most cases, we include temperature as  
250 degree days (cumulative temperature above a threshold value, Chezik *et al.*, 2014), setting a  
251 slightly conservative threshold temperature of 3.5 °C (Alderdice *et al.*, 1988; Sogard and  
252 Spencer, 2004).

253

#### 254 Transport

255 Transport to or advection away from appropriate settlement habitat can strongly affect larval  
256 supply and settlement of marine species with pelagic eggs and larvae (Schirripa and Colbert,  
257 2006; Montgomery *et al.*, 2001). Transport to settlement habitat was characterized by ROMS  
258 estimates of net long-shore transport (LST: H8, H11, H14 & H17) and net cross-shelf transport  
259 (CST: H6, H9, H12, H15 & H18) at specific depths and time periods for each sablefish life-  
260 history stage.

261 Sablefish spawn at depth but eggs are initially buoyant, rising in the water column. The  
262 mixed-layer depth (MLD) may influence how high eggs rise in the water column, thereby  
263 affecting transport (H5). We include the ROMS estimates of MLD (mean depth and standard  
264 deviation) from Jan-Apr when eggs are in the water column.

265

#### 266 Prey availability and female condition

267 Prey availability (H1) during the months prior to spawning (June-Dec) may affect female  
268 condition and in turn, egg quality, egg production or even the probability of spawning in a given  
269 year. For example, given poor prey availability, individual sablefish in Alaskan waters may skip  
270 spawning in some years (Rodgveller *et al.*, 2016). We included the abundance of age-0 hake  
271 *Merluccius productus* (Prey<sub>Hake</sub>) and age-0 longspine thornyhead *Sebastolobus altivelis* (Prey<sub>Lsp</sub>)  
272 from their most recent stock assessments (Taylor *et al.*, 2015; Stephens and Taylor, 2014) as  
273 indices of prey abundance for female sablefish. Both species make up substantial proportions of  
274 the sablefish diet (Laidig *et al.*, 1997). We included them as separate indices because hake were

275 much more abundant than thornyheads and a combined index was highly correlated with  
276  $\text{Prey}_{\text{Hake}}$  ( $r = 0.99$ ).

277

#### 278 Predation on recruits

279 Predation (H20) in the period immediately following settlement can strongly affect population  
280 size and structure for benthic fishes (Hixon and Jones, 2005; Tolimieri, 2015). Therefore, an  
281 index of predator abundance was developed based on known sablefish predators including:  
282 lingcod *Ophiodon elongatus*, arrowtooth flounder *Atheresthes stomias*, Pacific halibut  
283 *Hippoglossus stenolepis*, widow rockfish *Sebastes entomelas*, yelloweye rockfish *S. ruberrimus*  
284 and black rockfish *S. melanops*. Data were drawn from two sources: (1) stock assessments for  
285 each species (Hamel *et al.*, 2009; Taylor and Wetzel, 2011; He *et al.*, 2011; Stewart *et al.*, 2015;  
286 Wallace *et al.*, 2008; Kaplan and Helser, 2007), and (2) West Coast Groundfish Bottom Trawl  
287 Survey (Keller *et al.*, 2008). Stock assessments for some of these species did not cover the  
288 period under investigation (1980-2010). Therefore, we used multivariate autoregressive state-  
289 space (MARSS) models to combine the stock assessment and trawl time series for each species  
290 into one population trend. We then summed the trends for each species and year to create a  
291 single index of sablefish predator abundance (Holmes *et al.*, 2014; Holmes *et al.*, 2012; Tolimieri  
292 *et al.*, 2017; see Supplementary Material for more detail).

293

#### 294 Freshwater input effects on nutrient fertilization and circulation

295 Freshwater outflow (H21) from major rivers influence the nearby marine environment. For  
296 example, freshwater discharge from the Fraser River appears to play a role in sablefish  
297 recruitment in the Gulf of Alaska, possibly through its influence on nearshore currents (Coffin  
298 and Mueter, 2015). While total catch was low for age-0 fishes, preliminary analysis of the West  
299 Coast Groundfish Bottom Trawl Survey data showed a preponderance individuals in the vicinity  
300 of the mouth of the Columbia River suggesting a similar effect and the possibility of nutrient  
301 fertilization (Fig. S1). Annual discharge from the Columbia River measured at The Dalles<sup>2</sup>,  
302 Oregon is included as an index of potential fertilization or influence on currents.

303

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<sup>2</sup> [www.cbr.washington.edu/dart/query/streamflow\\_daily](http://www.cbr.washington.edu/dart/query/streamflow_daily)

304 Sea-surface height

305 Finally, for historical purposes we include an index of north coast spring sea surface height  
306 (SSH, H22), which has been evaluated in recent stock assessments (Johnson *et al.*, 2016; Taylor  
307 *et al.*, 2015). While not spatio-temporally specific like the other predictor variables, including  
308 the SSH index aids in testing the consistency of mechanisms hypothesized to impact sablefish  
309 recruitment and whether or not the more specific mechanistic variables identified in this study  
310 allow for better recruitment prediction. For 1980-1992 the index is derived from tide-gauge data  
311 and is the average of monthly SSH at Neah Bay and Toke Point, Washington and Astoria and  
312 Newport, Oregon from April-June. From 1993 onwards, the data come from JASON and  
313 TOPEX satellites and represents a north coast spring index of SSH for 44-50° N (Schirripa,  
314 2007).

315 Since, in this analysis, the 1980 recruitment deviation depends upon data on the  
316 preconditioning period in 1979, our analysis covers recruitment residuals from 1981-2010.

317

318 *Preliminary Analyses*

319 We conducted two sets of preliminary analyses prior to model fitting. First, we evaluated  
320 correlations among predictor variables (Tables S1 and S2). As noted above, paired predictors  
321 that were the same variable but with different spatial extents were highly correlated (Table S1),  
322 and we eliminated the smaller-scale version from the model fitting to reduce the number of  
323 potential predictors. Some of the remaining predictors showed strong correlation (Table S2,  $r >$   
324  $0.75$ ), and we required both correlated variables not appear together in any model under  
325 consideration.

326 Next, we ran individual linear and quadratic regressions for each predictor against  
327 recruitment deviations to determine if the data supported non-linear relationships. Quadratic  
328 terms were included in the main modeling exercise for those terms where, in these preliminary  
329 analyses, the individual quadratic model fit better than the individual linear model (Akiake's  
330 Information Criterion, AIC, was  $<2.0$  that of the linear model, see Table S1, Burnham and  
331 Anderson, 1998). Based on preliminary analyses, a quadratic term for long-shore transport  
332 during the benthic juvenile stage ( $LST_{bjuv}$ ) was included as a potential predictor in the final  
333 model selection. Additionally, SSH was included as a potential quadratic term based on the  
334 observed relationship in Schirripa and Colbert (2006).

335

336 *Recruitment residuals*

337 Estimates of sablefish recruitment and spawning stock biomass (SSB) were taken from the most  
338 recent stock-assessment (Fig. 1c, Johnson *et al.*, 2016). The recruitment time-series from the  
339 stock assessment is generated, in part, by an asserted stock-recruitment relationship (asserted  
340 because the form is assumed to be Beverton-Holt; steepness, unfished spawning biomass, and  
341 recruitment at unfished biomass are fixed; and the data are derived data from the stock  
342 assessment process, see Eqs. 1-3 below). If the environmental indices are to be useful for  
343 prediction within the stock assessment, it is necessary to remove this relationship to avoid double  
344 counting the effect of SSB on recruitment. Moreover, the stock-recruitment relationship is  
345 known, and we want to predict the variability in recruitment unaccounted for by the SSB. In  
346 order to remove the effect of the asserted stock-recruitment relationship, recruitment residuals  
347 for this study were calculated as the difference between the estimated recruitments from the  
348 stock assessment and the assumed stock-recruitment relationship, and are given by:

349

$$350 \quad \text{Recruitment residuals} = R_{\text{assessment}} - R_{\text{sr.curve}} \quad (1)$$

351

352 where  $R_{\text{assessment}}$  are the estimated recruitments from the stock assessment and  $R_{\text{sr.curve}}$  are  
353 the predicted recruitments from the stock-recruitment relationship. Note that the recruitment  
354 residuals calculated for this study are not the same as the estimated recruitment deviations from  
355 the stock assessment, which are constrained to sum to zero over the time period during which  
356 recruitments are estimated in the stock assessment model.  $R_{\text{sr.curve}}$  is calculated as:

357

$$358 \quad R_{\text{sr.curve}} = R_0 * S / (b + S) \quad (2)$$

359

360 where  $R_0$  is recruitment at unfished biomass (equilibrium recruitment),  $S$  is the spawning  
361 biomass, and  $b$  is:

362

$$363 \quad b = (R_0 * 0.2 * S_0) / (h - R_0) - (0.2 * S_0) \quad (3)$$

364

365 where,  $S_0$  is unfished biomass and  $h$  is steepness (the ratio of recruitment at 20% vs. 100% of  
366 unfished biomass). From the 2015 assessment,  $R_0 = 115,622$  thousand age-0 fish,  $S_0 = 17,198$   
367 metric tons, and  $h = 0.6$ .

368

### 369 *Model selection*

370 We fit a series of generalized linear models (GLMs) including all possible permutations of the 24  
371 covariates ( $n = 27,191$  models) with the above restrictions for total number of parameters and  
372 exclusion of highly correlated terms ( $|r| > 0.75$ ) from the same model. Each covariate matched a  
373 specific hypothesis in Table 1 with the exceptions of  $Prey_{Hake}$  and  $Prey_{LSP}$ , which both mapped  
374 to H1, prey availability. The number of predictors in a candidate model was limited to five (one  
375 covariate per six data points in the time series) to prevent over-fitting. The two potentially  
376 quadratic predictors ( $LST_{bjuv}$ , and SSH) were allowed to enter the models as linear, quadratic  
377 only, or linear + quadratic forms. The best-fit model(s) was selected using  $\Delta AICc$  values,  
378 retaining models with  $\Delta AICc < 2.0$  (Burnham and Anderson, 1998).

379

### 380 *Model validation and testing*

381 We conducted additional analyses to evaluate the performance of the best-fit models. First,  
382 recruitment deviations were resampled with replacement to estimate  $r^2$  values for randomized  
383 data (1000 permutations) for the final, best-fit model. Second, standard bootstrapping  
384 (resampled whole years with replacement) was used to estimate bias and calculate standard error  
385 of the parameter estimates. Third, jackknife resampling was used to determine the effect of any  
386 single year on the  $r^2$  of the best-fit model. Fourth, since the dependent variable was based on  
387 estimated recruitments from a stock-assessment, there is error for each recruitment residual that  
388 is not accounted for in the best-fit model. Therefore, we resampled the recruitment values for  
389 each year from a log-normal distribution where the mean was the value for that year and  
390 recruitment standard deviation for each year was taken from the sablefish stock assessment  
391 (Johnson *et al.*, 2016, Table 15). We then recalculated the recruitment residuals and refit the  
392 best-fit model repeating the process 1000 times. Fifth, we refit the best-supported model using  
393 data for 1981-2005 and used this model to predict recruitments for 2006-2010. Sixth, jackknife  
394 resampling was used to re-run the entire model fitting and comparison exercise, rather than re-  
395 fitting only the best fit model, to determine if removal of any individual year would change the

396 oceanographic/biological variables in the final model. Finally, we re-ran the entire model fitting  
397 exercise 100 times using the re-sampled sablefish recruitments with error (from Step 4 above)  
398 and compared top models from each run.

399

#### 400 *Northern copepod biomass anomaly*

401 Previous work has suggested that recruitment success in sablefish is influenced by the abundance  
402 of northern copepods (McFarlane and Beamish, 1992), which are larger and fatter than southern  
403 species. Sablefish stock assessments have included zooplankton indices as environmental  
404 predictors (Schirripa, 2002; Schirripa, 2007). We could not test the northern copepod biomass  
405 anomaly directly in our main analyses because the continuous time series begins in 1996  
406 (although there are some earlier data). However, after selecting a best-fit model from the main  
407 analysis, we refit this model for years 1996-2010 both with and without this index. Data were  
408 the northern copepod biomass anomaly,  $\log_{10}(\text{mg C/m}^3)$ , taken from the California Integrated  
409 Ecosystem Assessment<sup>3</sup>. We averaged monthly values over the summer months (July-Sept) in  
410 each year.

411

## 412 **RESULTS**

413 Model fitting produced a clear best-fit model, with no other candidate models with a  $\Delta\text{AICc} <$   
414 2.0 (Table 2, Table 3). In fact, the next best model had  $\Delta\text{AICc} > 3.9$ . The best-fit model  
415 included five covariates (Fig. 2) related to temperature and transport, which explained 57% of  
416 the variation in recruitment residuals (from the stock-recruitment relationship) during 1981-  
417 2010. Model predictions closely followed the estimated recruitments from the stock assessment  
418 with the exception of 2006-2009 when the model over or under-predicted recruitment (Fig. 3).  
419 Recruitment residuals were negatively correlated with degree days during the period of female  
420 preconditioning ( $\text{DD}_{\text{pre}}$ ) and larval stage ( $\text{DD}_{\text{larv}}$ ). Conversely, cross-shelf transport during the  
421 egg stage ( $\text{CST}_{\text{egg}}$ ), degree days during the egg stage ( $\text{DD}_{\text{egg}}$ ), and long-shore transport during  
422 the yolk-sack stage ( $\text{LST}_{\text{yolk}}$ ) were positively correlated with recruitment residual (Fig. 4, Table

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<sup>3</sup> <https://www.integratedecosystemassessment.noaa.gov/regions/california-current-region/indicators/ecological-integrity.html>

423 3). Standardized coefficients suggest that  $DD_{\text{egg}}$  had the strongest effect on recruitment  
424 deviations, while the other predictors had similar impact (Table 3).

425 Only three additional models had  $\Delta AICc < 4.0$  and all had  $\Delta AICc > 3.9$ . These models  
426 were generally consistent in structure with the best-fit model (Table 2). The terms  $DD_{\text{egg}}$  and  
427  $LST_{\text{yolk}}$  occurred in all three models, and  $DD_{\text{pre}}$  and  $DD_{\text{egg}}$  in two. Model 4 was a subset of  
428 Model 1 minus the  $DD_{\text{larv}}$  term ( $r^2 = 0.43$ ). The other two models included alternate terms that  
429 had less support from the data including prey abundance, long-shore transport during the pelagic  
430 juvenile stage and SSH.

431 There was some moderate correlation between the covariates with the highest being for  
432  $DD_{\text{pre}}$  and  $DD_{\text{egg}}$  ( $r = 0.62$ , Table 4). Generalized variance inflation factor values (VIF; which  
433 measure how much the variance of the estimated regression coefficients are inflated as compared  
434 to when the predictor variables are not linearly related) were low to moderate with the exception  
435 of  $DD_{\text{egg}}$ , which was moderate (Table 4). Because there was moderate correlation between  
436  $DD_{\text{egg}}$  and the other two DD terms, we refit the best-fit model adding interactions between  
437  $DD_{\text{egg}}$  and the other two DD terms. These additional models included all nested possibilities  
438 from an individual interaction term to all interaction terms including a three-way interaction.  
439 Adding interactions increased AICc values by 2.99 – 14.78 points for all models suggesting that  
440 non-interaction model best fit the data. Residuals from the best-fit model did not show signs of  
441 autocorrelation (Fig. S2).

442

#### 443 *Model testing and validation: best-fit model*

444 Randomly resampling the recruitment deviations (with replacement) gave a median  
445 expected  $r^2 = 0.17$  (95% confidence limits of 0.03-0.40) for a five-parameter model suggesting  
446 that the observed value of  $r^2 = 0.57$  was unlikely to be observed at random.

447 Removing individual years and refitting the best-fit model (jackknifing) had little impact  
448 on the model fit (Figs. 3 and 5, median  $r^2 = 0.57$ ). Predicting the missing year from any  
449 iteration produced estimates very similar to those for the full model (Fig. 3). The three years that  
450 showed the highest impact on the model's ability to explain the data were 1999, 2000 and 2006.  
451 Removing 1999 reduced the explained variance the most ( $r^2 = 0.51$ ), while removing 2000 or  
452 2006 increased the  $r^2$  to 0.63. Recruitment was higher than predicted in 1999 and 2000 but lower

453 than predicted in 2006. Predicting recruitments for 2006-2010 based on a 1981-2005 model  
454 produced estimates very close to those for the 1981-2010 model (Fig. 3).

455 Resampling individual recruitments with error had little effect on the model's predictive  
456 power with median  $r^2 = 0.55$  (95% C.I. = 0.59-0.70) across all trials. This result suggests that  
457 uncertainty in the recruitment time series (given the current assessment parameters) did not  
458 greatly affect the results.

459 Using the jackknife resampling and re-running the entire model fitting process produced  
460 results that were largely consistent with the primary analysis. However, removing 1984, 1987,  
461 1989 and 1991 did result in different best-fit models. Three of these models included  $\text{Prey}_{\text{Hake}}$  as  
462 a predictor. Hake recruitment was above the 95% confidence intervals for estimated recruitment  
463 at unfished biomass in 1984 and 1987 but below it in 1989 and 1991 (see Figure e and Table c in  
464 Taylor *et al.*, 2015). However, there were other extreme years as well, which did not alter the  
465 terms included in the model here. SSH was also selected in three models. Removal of any other  
466 year produced the same set of predictors as in the primary analysis (Table 5). Model predictions  
467 for the best-fit model closely followed observed model data for 1984, 1987 and 1989 but  
468 recruitment in 1991 was lower than predicted. Interestingly, there was no overlap between the  
469 three years that had the largest impact on the explanatory value of the best-fit model and those  
470 years that affected the re-fitting process.

471 Finally, the results from resampling the recruitment values (with error) and re-running the  
472 entire model fitting exercise one hundred times were also generally consistent with the best-fit  
473 model from the primary analysis. The predictors from the best-fit model also occurred in the  
474 majority of best-fit models from each iteration:  $\text{DD}_{\text{pre}}$  (72% of models),  $\text{CST}_{\text{egg}}$  (73%),  $\text{DD}_{\text{egg}}$   
475 (89%),  $\text{LST}_{\text{yolk}}$  (83%), and  $\text{DD}_{\text{larv}}$  (70%). Additional predictors included  $\text{Prey}_{\text{Hake}}$  (18%),  
476  $\text{LST}_{\text{pjuv}}$  (18%) and  $\text{SSH}^2$  (21%).

477

#### 478 *Northern copepod biomass anomaly*

479 When refit to 1996-2010 data, the best-fit model explained 67% of the variation around the stock  
480 recruitment-relationship from the stock assessment. Alone the copepod index explained 24% of  
481 the variation in recruitment over the 1996-2010 period. However, adding the northern copepod  
482 biomass anomaly did not increase the variation explained (also 67%). The anomaly was  
483 moderately correlated with most other predictors in the best-fit model with the exception of



484  $CST_{egg}$ :  $DD_{pre}$  ( $r = -0.46$ ),  $CST_{egg}$  ( $r = -0.01$ ),  $DD_{egg}$  ( $r = 0.56$ ),  $LST_{yolk}$  ( $r = 0.48$ ), and  $DD_{larv}$  ( $r$   
485  $= -0.57$ ). Thus, while food supply is likely important, the other physical parameters may act as  
486 sufficient proxies in the absence of a full time series of copepod data.

487

## 488 DISCUSSION

489 Our results suggest that multiple mechanisms acting at different stages the life history of  
490 sablefish drive recruitment (Fig. 6). The best-fit model explained approximately 57% of the  
491 variation around the stock-recruitment curve and fit the recruitment data well (specifically  
492 residuals from the stock-recruitment relationship in the assessment in Fig. 3). Nevertheless, it is  
493 not unreasonable to consider this work as an effort to formalize potential hypotheses that should  
494 be investigated further.

495 Colder conditions during the spawner pre-conditioning period led to higher recruitment.  
496 Given sufficient food, warmer temperatures allow for faster growth and larger female size, which  
497 results in higher fecundity (Harvey, 2009). However, colder water temperatures may lower  
498 metabolic costs allowing female sablefish to divert more energy to egg production. However,  
499 the variability in the ROMS output for this parameter is likely driven primarily by temperature  
500 variation at shallower depths, and may not represent female exposure in deeper regions. More  
501 likely, colder conditions may be linked to stronger upwelling, which leads to productivity and  
502 food availability (Harvey, 2005; Chavez *et al.*, 2003; Peterson, 2009; Sydeman *et al.*, 2011).  
503 While we are unaware of data connecting female condition to egg production in sablefish,  
504 individuals may skip spawn (Rodgveller *et al.*, 2016) given limited energy reserves and degraded  
505 body condition as seen in other species like Atlantic cod *Gadus morhua* (Skjæraasen *et al.*, 2009;  
506 Skjæraasen *et al.*, 2012) and Pacific ocean perch (Hannah and Parker, 2007). The results from  
507 the jackknife refitting of the entire selection process support the hypothesis that food resources  
508 are likely important for females during the period leading up to spawning. For three of the four  
509 years that were omitted produced different best-fit models,  $Prey_{Hake}$  (positive correlation with  
510 recruitment) replaced  $DD_{pre}$  as a predictor suggesting that a large hake prey base may also lead  
511 to better female condition and recruitment.

512 Recruitment was positively correlated with water temperature during the egg stage  
513 ( $DD_{egg}$ ). In marine fishes, increased temperature results in faster development, shorter stage  
514 duration, earlier hatch date and increased hatching rates, up to a species-specific temperature

515 maxima after which developmental abnormalities occur (Llopiz *et al.*, 2014; Pepin, 1991; Peck *et*  
516 *al.*, 2012; Tsoukali *et al.*, 2016). Growth in sablefish is strongly related to temperature (Sogard  
517 and Olla, 2001; Sogard, 2011) suggesting that a similar physiological response would be likely  
518 for development. Moving more quickly through the egg state may reduce susceptibility to egg  
519 predators and reduce dispersal, the latter potentially important for match-mismatch dynamics  
520 with prey resources (Peck *et al.*, 2012). Offshore transport due to upwelling occurs primarily in  
521 surface waters. Since eggs are buoyant but yolk-sack larvae found at depth (1000-1200 m),  
522 entering deep water sooner may help to avoid advection offshore.

523 Cross-shelf transport was important from January to April corresponding to life-history  
524 stages for which sablefish are non- or only minimally motile: eggs and yolk-sack larvae. The  
525 positive correlation with  $CST_{\text{egg}}$  is fairly straightforward: being transported to near-shore nursery  
526 environments leads to higher recruitment. At first glance this result may seem at odds with  
527 Schirripa and Colbert (2006) who found a negative correlation between recruitment strength and  
528 on-shore cross-shelf transport during June. However, the time periods (Jan to Apr versus June)  
529 and the depths (300-825 m vs. approximately 0-150 m) differ suggesting that the two predictors  
530 relate to different processes: (1) transport of eggs onshore following spawning (our analysis) and  
531 (2) and upwelling leading to higher productivity and food resources later in the season.

532 Recruitment was also positively correlated with transport to the north during the yolk-  
533 sack stage ( $LST_{\text{yolk}}$ : Feb to May at 1000-1200 m). Again this result may initially appear to  
534 contradict Schirripa and Colbert (2006) who found that stronger southerly transport of surface  
535 waters (50-100 m) in February correlated with higher recruitment. However, the depths differ,  
536 and these two results may tell different parts of the same story. Southerly transport of surface  
537 waters brings boreal copepods into the Northern California Current Ecosystem. These copepods  
538 are larger, higher in fatty acids, and a better food source than southern copepods (McFarlane and  
539 Beamish, 1992; Peterson, 2009; Peterson and Keister, 2002). Yolk-sack larvae, however, are  
540 found at much deeper depths (1000-1200 m). Northern transport at these depths likely brings  
541 these larvae to the north where they are more likely encounter these energy-rich copepods once  
542 the larvae rise to the surface, start feeding, and eventually grow large enough to feed on the  
543 copepods. Access to this food resource might then result in high recruitment through any  
544 number of mechanisms including faster growth rates (size-related predation avoidance) and  
545 reduced starvation risk.

546 Temperature during the larval stage ( $DD_{\text{larv}}$ , Feb-May, surface waters) was negatively  
547 correlated with recruitment. Sogard (2011) found increased growth at warmer temperatures and  
548 higher recruitment in years with good growth, the latter after adjusting for fish size and  
549 temperature. However, Schirripa and Colbert (2006) found higher recruitment with offshore  
550 transport of surface waters, which coincides with colder upwelled water. Combined, these  
551 results suggest a trade-off between better food resources under colder conditions but faster  
552 growth for metabolic reasons in warm water. Colder temperatures may index two different  
553 mechanisms that result in higher prey availability or quality: enhanced upwelling and higher  
554 primary production, and the southerly transport of northern copepods. At the same time, larvae  
555 may be more susceptible to starvation under warm conditions due to increased metabolism and  
556 lack of prey. Both daily growth and daily mortality are positively correlated with temperature in  
557 marine fish larvae in general, although stage-duration decreases (Houde, 2008). Growth of early  
558 juvenile sablefish increases with increasing water temperature, but this effect requires sufficient  
559 food resources (Sogard, 2011; Sogard and Olla, 2001). Since sablefish have limited capacity or  
560 compensatory growth (Sogard and Olla, 2002), they appear to have a risk-prone strategy growing  
561 as quickly as possible (Sogard and Olla, 2002; Sogard, 2011) and may be susceptible to  
562 starvation under warm conditions. In the lab larvae will move to colder water as rations are  
563 decreased, indicating an energy-conservation strategy when food is limited (Sogard and Olla,  
564 2001; 1998). Adjusting for water temperature and fish size, Sogard (2011) found higher than  
565 expected growth under cold conditions in some years suggesting better food resources under cold  
566 conditions.

567 Rapid growth may help individuals avoid predation through a number of mechanisms  
568 (e.g., 'bigger-is-better', stage-duration) that cannot be untangled in this study. However, Sogard  
569 (2011) did not find evidence for size-selective mortality, possibly because the higher  
570 temperatures also lead to increased predator activity and consumption (e.g., Akimova *et al.*,  
571 2016). One might also expect the offshore transport associated with cold, upwelled waters to  
572 advect sablefish larvae away from suitable settlement habitat. Sablefish larvae are found in these  
573 surface waters where most of this offshore transport occurs. However, sablefish larvae develop  
574 large pectoral fins suggesting that they may have evolved to control their position in the water  
575 column (Shotwell *et al.*, 2014; Kendall and Matarese, 1987), and many fish larvae are strong  
576 swimmers, especially prior to settlement (Montgomery *et al.*, 2001). Thus, rapid development

577 earlier in the season (warm waters during  $DD_{egg}$ ) may allow sablefish larvae to develop the  
578 swimming capacity to utilize high quality food resources later in the year ( $DD_{larv}$ , indexed by  
579 cold water) while maintaining position in the water column and staying closer to appropriate  
580 settlement habitat.

581 Many of the years that either affected the model fit in the jackknife exercises or in which  
582 observed recruitment fell outside the 95% confidence intervals for the best-fit model appear to be  
583 associated with El Niño or La Niña events in some way. For example, recruitment was higher  
584 than predicted in 2000 and 2008 coincident with La Niña conditions as measured by the ONI<sup>4</sup>  
585 from the summer of 1998 through spring of 2001 and late summer 2007 through late spring of  
586 2008. Observed recruitment was lower than predicted 2005-2007, with variable El Niño  
587 conditions between late summer of 2005 and early 2007. However, in other El Niño or La Niña  
588 years the observed recruitment was within the 95% confidence limits for the model predictions.  
589 We did try adding both the tri-monthly ONI and bi-monthly MEI<sup>5</sup> indices to the best-fit model to  
590 determine if El Niño/La Niña information would improve the model fit, but all such models had  
591 higher AICc values than the best-fit model. This result does not necessarily mean that El  
592 Niño/La Niña events do not affect sablefish recruitment as the effects on food availability,  
593 temperature, and transport are likely already caught in the ROMS parameters.

594 In summary, multiple mechanisms likely drive recruitment of sablefish (Fig. 6). Cold  
595 conditions during the pre-conditioning period for spawners may allow females to divert more  
596 energy to egg production due to lower metabolic costs, or these colder temperatures may be  
597 indicative of upwelling or southerly transport of boreal copepods and better food resources also  
598 allowing for more egg production. Warmer temperatures during the egg stage likely allow for  
599 higher growth rates and predation avoidance through bigger-is-better mechanisms. On shore  
600 transport during the egg and yolk-sack stages retains individuals on shore near settlement habitat  
601 and reduces losses due to advection. Northern long-shore transport appears to bring larvae to  
602 regions where they are more likely to encounter food resources as they rise to surface waters to  
603 start feeding. The mechanism behind the negative correlation between recruitment and water  
604 temperature (degree days) during the larval stage is less clear. However, colder water may index

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<sup>4</sup>Oceanic Niño Index (ONI) [http://www.cpc.ncep.noaa.gov/products/analysis\\_monitoring/ensostuff/ensoyears.shtml](http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml)

<sup>5</sup>Multivariate ENSO Index (MEI) <https://www.esrl.noaa.gov/psd/enso/mei/>

605 better or alternate food resources due to upwelling or the southerly transport of boreal copepods,  
606 and may also reduce basal metabolism and reduce the risk of starvation.

607

#### 608 *Implications for stock assessment*

609 This study provides the underlying process-orientated hypotheses to address three issues in the  
610 stock assessment and management of U.S. west coast sablefish: 1) the reconstruction of what  
611 historical recruitment could have been in the absence of length- and age-composition data to  
612 inform recruitment during the period when the fishery was operating, 2) sub-annual to one year  
613 ahead forecasting of recruitment based on both observed oceanographic conditions and  
614 potentially sub-annual forecasts of environmental conditions, and 3) long-term projections of  
615 potential future stock productivity and the evaluation of the robustness of harvest control rules  
616 (HCRs) to changes in stock productivity evaluation via Management Strategy Evaluation (MSE).

617 The five oceanographic indicators identified as important drivers of sablefish recruitment  
618 in this study can inform recruitments for historical periods that lack fishery age- and length-  
619 composition data and for near-term forecasts. These historical and near-term forecasts generally  
620 rely upon average recruitment from the stock recruitment curve. However, recruitment is often  
621 far above or below the average, with large annual deviations around the stock-recruitment curve.  
622 Furthermore, the most uncertain periods in the stock assessment model are those that either lack  
623 age and length composition data, or have sparse data. Hind-casting recruitments during periods  
624 of high fishery removals without good age and length composition data should result in a  
625 reduction in uncertainty during early model years. The oceanographic indices identified during  
626 this study could be used as a survey index of recruitment in the stock assessment during the  
627 historical time period. Using the five oceanographic indicators from this study to estimate what  
628 recruitment deviations could have been, or may be into the near-term future, can provide both  
629 better estimates of historical recruitment, and therefore the un-fished spawning biomass  
630 reference point used for managing the fishery, as well as the incoming recruitment one year  
631 ahead, providing better catch advice based on what recruitment is likely to be entering the fishery  
632 in the near term (Kaplan *et al.*, 2016; Siedlecki *et al.*, 2016). Finally, if long-term forecasts of  
633 these five oceanographic drivers of sablefish recruitment are available from either Global or  
634 downscaled regional Climate Models (GCMs), they could be used to provide long-term strategic  
635 projections for fishery management planning that could include not only the fishing industry and

636 managers (PFMC) but those groups interested in the identification of potential climate-  
637 adaptation strategies given the long-term outlook for the sablefish fishery. This could include  
638 societal adaptations that build community resilience to climate driven changes in the sablefish  
639 resource such as: 1) market development for a higher quality and priced product, 2) evaluation of  
640 the resilience of the sablefish supply chain to projected changes in catch, and 3) aquaculture  
641 research and development (Norman-López *et al.*, 2013; Norman-LATA *et al.*, 2014)

642 A number of issues with respect to the oceanographic modeling and data availability will  
643 need continuing work. First, the easily available ROMS outputs that were used for this study  
644 span the period from 1980-2010. However, the current recruitment estimates from the sablefish  
645 stock assessment model continue through 2014, and will continue into the future. There is  
646 currently a discontinuity in the ROMS model outputs between 2010 and 2011 because drivers for  
647 the surface forcing (heat flux, wind) come from different products for 2011-2015, as does the  
648 input for the ocean boundary conditions. This discontinuity prevents the use of the most recent  
649 recruitment estimates in evaluating the hypotheses posed in this study. Continuous ROMS model  
650 outputs for both the pre-1980 and the post-2010 periods are necessary for fully using the results  
651 of this study in sablefish stock assessment and management. Future oceanographic modeling  
652 work should investigate the ability of ROMS models to provide informative, short-term seasonal  
653 to annual forecasts of relevant oceanographic covariates. Skillful ROMS forecasts could better  
654 inform recruitments entering the fishery prior to the availability of survey data.

655 It is important that the oceanographic drivers of sablefish recruitment identified in this  
656 study continue to be periodically re-evaluated as the fundamental relationships could change  
657 through time, particularly if the impacts of global climate change cause variability in the  
658 California Current to exceed recent historical levels (Cheung *et al.*, 2016). This continued re-  
659 evaluation depends upon both maintaining current oceanographic and biological monitoring  
660 programs that will allow for tracking of potential non-stationarity. Finally, best methods for  
661 integrating these relationships into the stock assessment model should be investigated. The  
662 current stock assessment (Johnson *et al.*, 2016) uses the environmental data as a survey index of  
663 recruitment, but new tools to incorporate environmental drivers in the population dynamics with  
664 uncertainty are becoming available (Methot Jr and Wetzel, 2013).

665

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935

### 936 **Figure Legends**

937 Figure 1. Sablefish biological parameters from the 2015 stock assessment for 1981-2010. (a)  
938 spawning stock biomass (SSB) in metric tons, (b) thousands of age-0 recruits, and (c) stock-  
939 recruitment relationship asserted in the assessment (line) versus observed data (points).

940

941 Figure 2. Time-series of independent variables in the best-fit model. (a) degree days during  
942 female preconditioning, (b) net cross-shelf transport during the egg stage, (c) degree days during  
943 the yolk-sack stage, (d) long-shore transport during the yolk-sack stage, and (e) degree days  
944 during the larval stage.

945  
946 Figure 3. Fit of the best-supported model ( $r^2 = 0.57$ ) to the estimated recruitment residuals from  
947 the stock assessment. Solid line is the predicted recruitment residuals from the full time series.  
948 Dotted lines= 95% confidence limits. Black points are recruitment residuals from the Beverton-  
949 Holt stock recruitment relationship from the 2015 sablefish assessment. Stars are predicted  
950 values from jackknife analysis removing individual years one at a time. Grey points are  
951 predicted values for the retrospective analysis of the last five years. Note, all three points  
952 overlap in 2010.

953  
954 Figure 4. Partial residual plots for (a) degree days during female pre-conditioning , (b) net cross-  
955 shelf transport during the egg stage, (c) degree days during the yolk-sack stage, (d) long-shore  
956 transport during the yolk-sack stage, and (e) degree days during the larval stage.

957  
958 Figure 5. Results of jackknife resampling showing distribution of  $r^2$  values. (a) Frequency  
959 distribution of  $r^2$  values, (b)  $r^2$  for when the indicated year was removed from the model.

960  
961 Figure 6. Conceptual model for sablefish showing the environmental drivers at specific life-  
962 history stages that lead to higher recruitment. Signs in parentheses indicate the partial  
963 correlation of each term with residuals from the sablefish stock-recruitment relationship. See  
964 Figure 4 for plots of these relationships.

965



Table 1 Life history model. See the text for data sources.

Life-history stage	Time period	Depth	Sablefish location	Hypothesis	Stage	Covariates	Depth extent	Longitudinal extent	Data source
<i>Preconditioning</i>	Jun - Dec (Yr 0)	50-1200m	Bottom	(H1) Food availability affects energy allocation to reproduction with higher recruitment when more prey are available during the preconditioning period	Prey <sub>Hake</sub> Prey <sub>Lsp</sub>	Index of age-0 hake and age-0 longspine thornyhead abundance	50-1200 m	50-1200 m isobath	Stock Assessments
				(H2) Higher temperature increases food demand resulting in lower egg production, egg quality, or probability of spawning resulting in lower recruitment	DD <sub>pre</sub>	Degree days	50-1200 m (150-400 m)	50-1200 m isobath (150-400 m isobath)	ROMS
<i>Spawning</i>	Dec - Mar	300-500 m	Bottom	(H3) Temperature acts as a spawning cue with fish less likely to spawn at high temperature resulting in lower recruitment	Temp <sub>spawn</sub>	Mean temperature	300-500 m	300-500 m isobath	ROMS
				(H4) As H3 but degree days not mean temperature	DD <sub>spawn</sub>	Degree days	300-500 m	300-500 m isobath	ROMS
<i>Eggs</i>	Jan-Apr	300-825 m	Open water	(H5) Eggs are buoyant so Layer Depth may limit how far they rise in the water column affecting later transport	Mixed MLD <sub>egg;mn</sub> MLD <sub>egg;sd</sub>	Location of mixed layer depth (m); mean and standard deviation	300-825 m (240-480 m)	Inshore limit: 500 m bottom depth, Seaward to 170 nmi	ROMS
				(H6) Transport to settlement habitat affects recruitment	CST <sub>egg</sub>	Net cross-shelf transport	300-825 m (240-480 m)	Inshore limit: 500 m bottom depth, Seaward to 170 nmi	ROMS
				(H7) Growth/Predation hypothesis: growth rate is faster in warm water leading to reduced time vulnerable to predators	DD <sub>egg</sub>	Degree days	300-825 m (240-480 m)	Inshore limit: 500 m bottom depth, Seaward to 170 nmi	ROMS
<i>Yolk-sack larvae</i>	Feb-May	1000-1200 m	Open water	(H8) Longshore transport to settlement habitat affects recruitment	LST <sub>yolk</sub>	Net long-shore transport	1000-1200 m	1000 m to 170 nmi	ROMS

					(H9) Cross-shore transport to settlement habitat affects recruitment	CST <sub>yolk</sub>	Net cross-shelf transport	1000-1200 m	1000 m to 170 nmi	ROMS
					(H10) Growth/Predation hypothesis: growth rate is faster in warm water leading to reduced time vulnerable to predators	DD <sub>yolk</sub>	Degree days	1000-1200 m	1000 m to 170 nmi	ROMS
<i>Larvae feeding</i>	(start Feb-May <sup>2</sup> )	Surface waters	Open water		(H11) Longshore transport to settlement habitat affects recruitment	LST <sub>larv</sub>	Net long-shore transport	Surface waters	0-150 nautical nmi	ROMS
					(H12) Cross-shore transport to settlement habitat affects recruitment	CST <sub>larv</sub>	Net cross-shelf transport	Surface waters	0-150 nautical nmi	ROMS
					(H13) Growth/Predation hypothesis: growth rate is faster in warm water leading to reduced time vulnerable to predators	DD <sub>larv</sub>	Degree days	Surface waters	0-150 nautical nmi	ROMS
<i>Pelagic (feeding pelagics)</i>	<i>juveniles</i> Apr-Nov	Surface waters	Open water		(H14) Longshore transport to settlement habitat affects recruitment	LST <sub>pjuv</sub>	Net long-shore transport	Surface waters	0-150 nautical nmi	ROMS
					(H15) Cross-shore transport to settlement habitat affects recruitment	CST <sub>pjuv</sub>	Net cross-shelf transport	Surface waters	0-150 nautical nmi	ROMS
					(H17) Growth/Predation hypothesis: growth rate is faster in warm water leading to reduced time vulnerable to predators	DD <sub>pjuv</sub>	Degree days	Surface waters	0-150 nautical nmi	ROMS
<i>Benthic (Age-0)</i>	<i>Juvenile</i> Aug-Nov	0 - 250 m	Bottom		(H17) Longshore transport to settlement habitat affects recruitment	LST <sub>bjuv</sub>	Net long-shore transport	to 250 m	0-250 m isobath	ROMS
					(H18) Cross-shore transport to settlement habitat affects recruitment	CST <sub>bjuv</sub>	Net cross-shelf transport	to 250 m	0-250 m isobath	ROMS
					(H19) Growth/Predation hypothesis: growth rate is faster in warm water leading to reduced time vulnerable to predators	DD <sub>bjuv</sub>	Degree days	to 250 m	0-250 m isobath	ROMS
					(H20) Predation	Pred <sub>bjuv</sub>	Some index of predator abundance	to 250 m	0-250 m isobath	Trawl Survey & Stock Assessments

(H21) Nutrient input (fertilization) affects productivity, food availability and therefore survival or river discharge may affect currents.	$FW_{bjuv}$	Annual discharge from Columbia River measured at The Dalles.	NA	NA	Columbia River DART
(H22) Sea surface height as an indicator of basin- scale processes. Used in previous assessments.	SSH				Spring north coast SSH 44-50° N

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Table 2. Results of model selection showing models with a  $\Delta\text{AICc} < 6.0$ . CST = cross-shelf transport, LST = long-shore transport, DD = degree days, Prey = prey index, pre = preconditioning, egg = egg stage, yolk = yolk-sack larvae, larv = larval stage, pjuv = pelagic juvenile, and bjuv = benthic juveniles. AICc = Akaike's Information Criterion adjusted for small sample size.

Model							R <sup>2</sup>	$\Delta\text{AIC}$
Model 1	DD <sub>pre</sub>	CST <sub>egg</sub>	DD <sub>egg</sub>	LST <sub>yolk</sub>	DD <sub>larv</sub>		0.57	0
Model 2			DD <sub>egg</sub>	LST <sub>yolk</sub>	LST <sub>pjuv</sub>	SSH <sup>2</sup>	0.46	3.92
Model 3	Prey <sub>Hake</sub>		DD <sub>egg</sub>	LST <sub>yolk</sub>	LST <sub>pjuv</sub>	SSH <sup>2</sup>	0.51	3.94
Model 4	DD <sub>Pre</sub>	CST <sub>egg</sub>	DD <sub>egg</sub>	LST <sub>yolk</sub>		SSH	0.51	3.95

Table 3 Coefficients for the best-fit model (Model 1 from Table 2) showing both raw and standardized (beta) coefficients. Bias and standard error (s.e.) are from bootstrap resampling. DD = degree days, CST = cross-shelf transport, LST = long-shore transport, pre= preconditioning, egg = egg stage, yolk = yolk-sack larvae, larvae = larval stage.

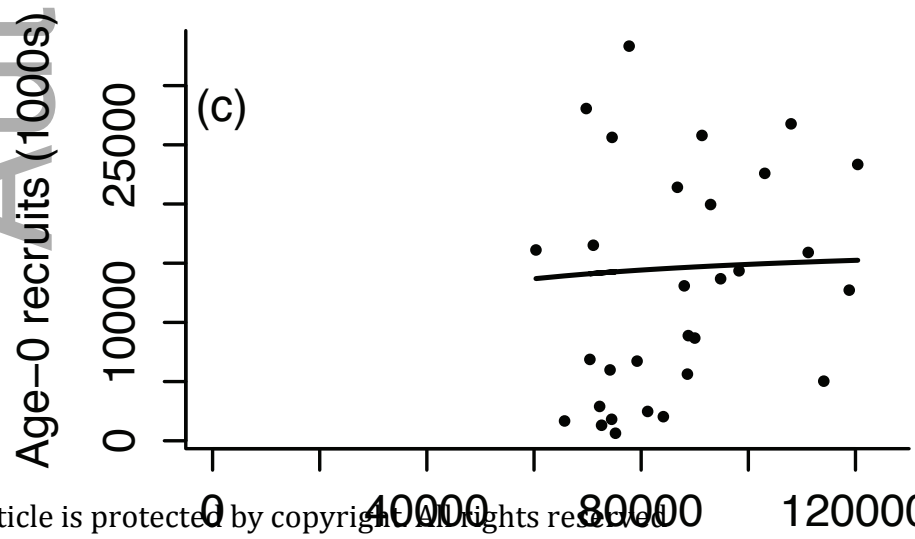
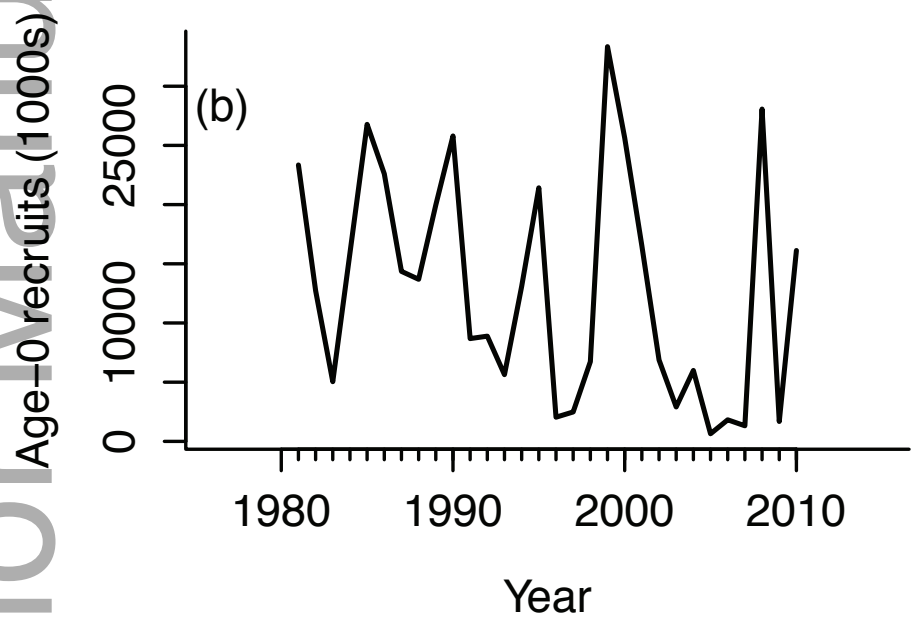
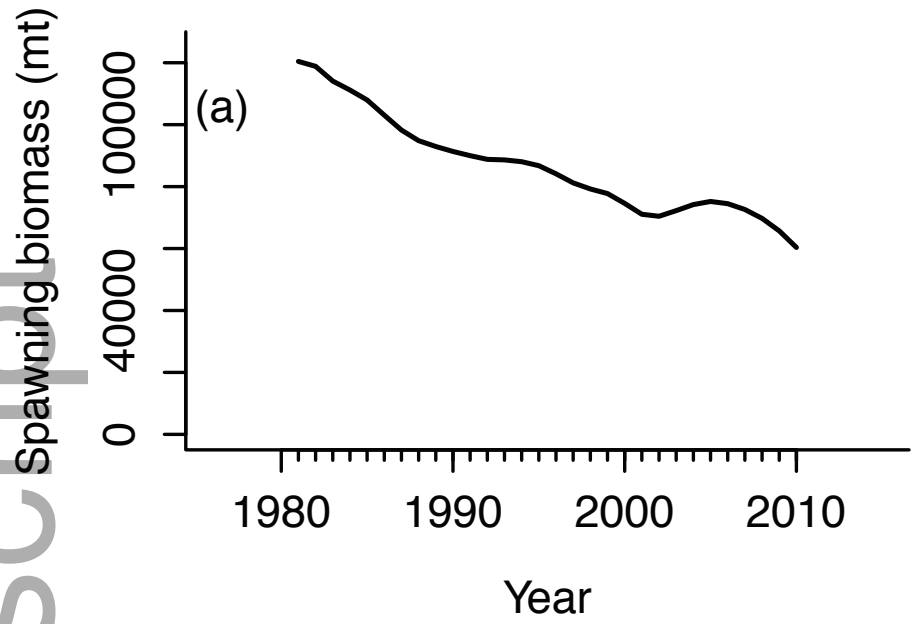
	Coefficient	Bias	S.E.	Standardized Coefficient	Bias	S.E.
Intercept	6973.8	-888.9	18216.9	-1534.3	38.1	1288.1
DD <sub>pre</sub>	-523.2	8.2	147.4	-6149.0	103.1	1753.2
CST <sub>egg</sub>	112489.8	3344.9	26593.2	6607.4	107.3	1641.2
DD <sub>egg</sub>	1308.52	12.8	250.1	11126.9	-91.2	2100.1
LST <sub>yolk</sub>	44813.1	209.9	15348.5	4920.7	-48.4	1669.3
DD <sub>larvae</sub>	-231.3	-9.3	84.3	-5012.8	-134.7	1987.8

Table 4 Correlations among variables included in the best-fit model. VIF = generalized variance inflation factor. DD = degree days CST = cross-shelf transport, LST = long-shore transport, pre= preconditioning, egg = egg stage, yolk = yolk-sack larvae, larvae = larval stage.

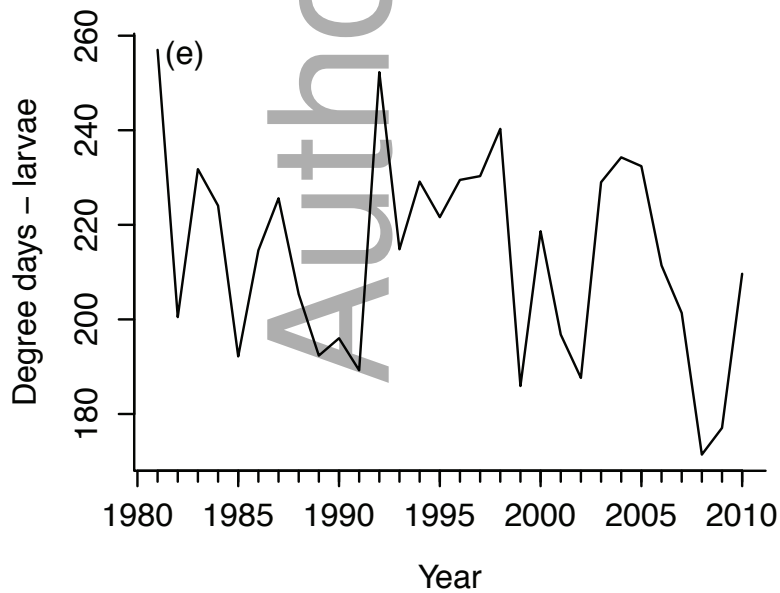
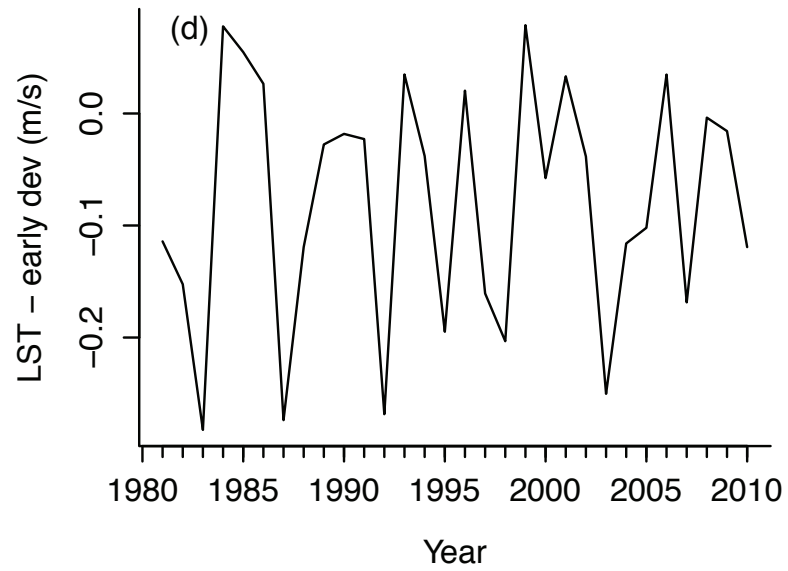
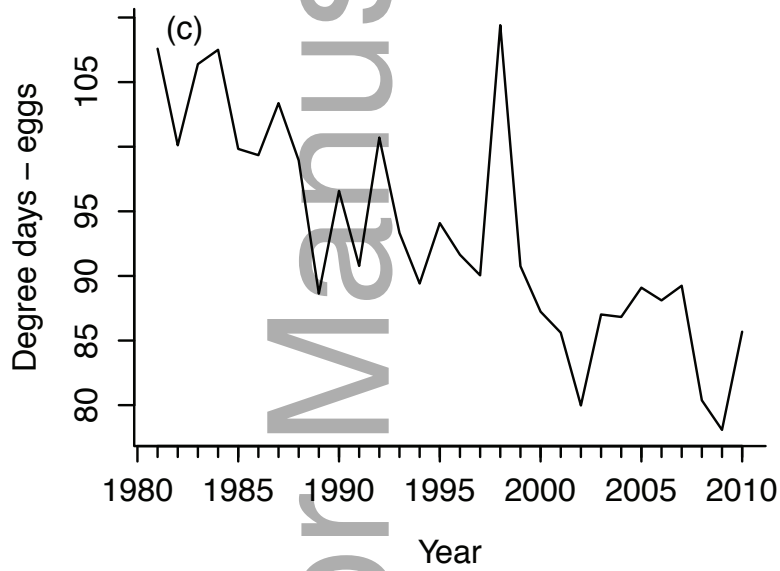
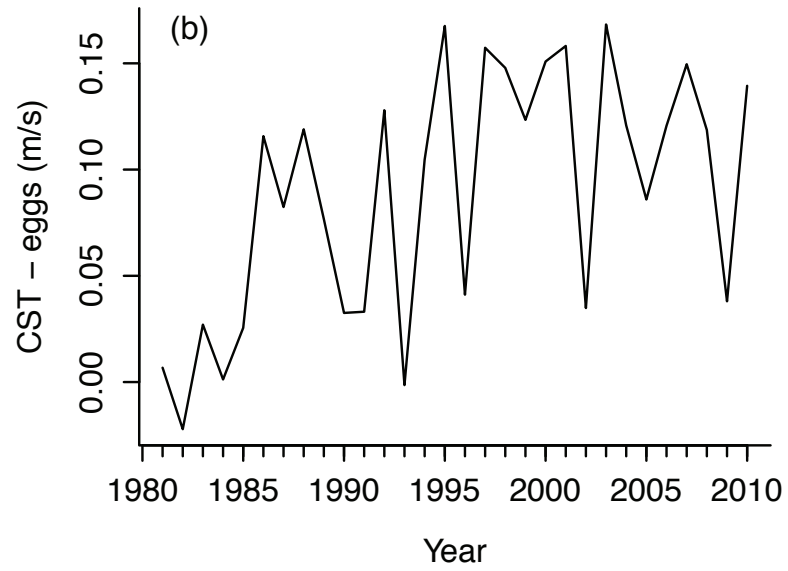
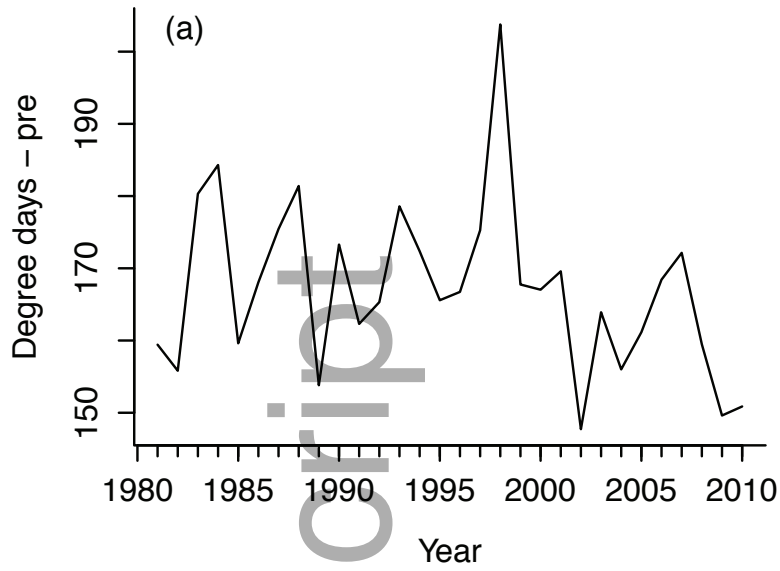
	DD <sub>pre</sub>	CST <sub>egg</sub>	DD <sub>egg</sub>	LST <sub>yolk</sub>	VIF
DD <sub>pre</sub>	--				2.17
CST <sub>egg</sub>	0.08	--			1.87
DD <sub>egg</sub>	0.62	-0.43	--		3.38
LST <sub>yolk</sub>	-0.17	0.23	-0.30	--	1.63
DD <sub>larvae</sub>	0.38	-0.14	0.55	-0.54	1.92

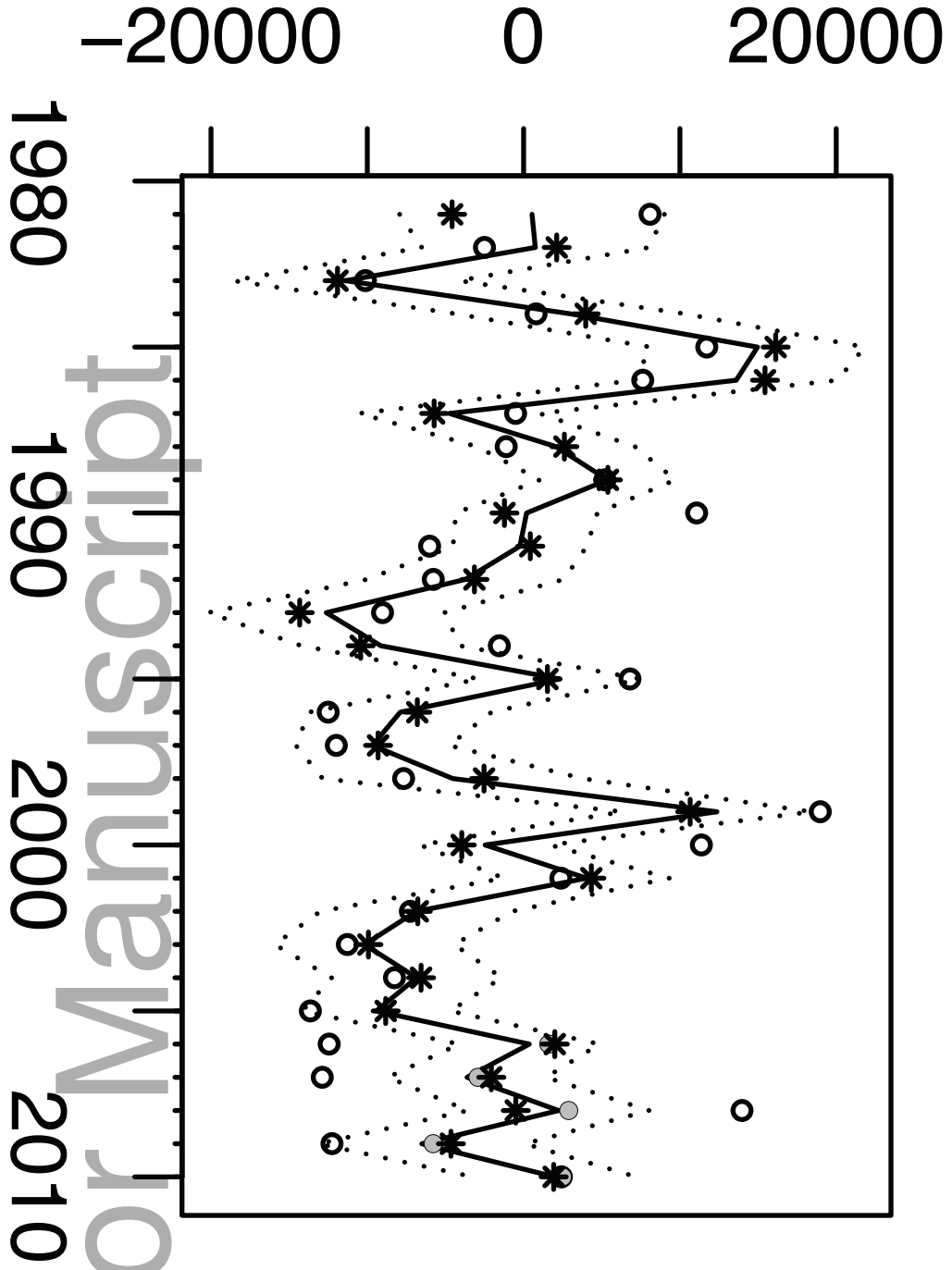
Table 5. Best-fit models from jackknife refits of the entire model-fitting process. Removing the years 1984, 1987, 1989 and 1991 changed the best-fit model in those iterations. All other years produced models with the same covariates as in the main model.

Main model	Year removed			
	1984	1987	1989	1991
DD <sub>pre</sub>	Prey <sub>Hake</sub>	DD <sub>spawn</sub>	Prey <sub>Hake</sub>	Prey <sub>Hake</sub>
CST <sub>egg</sub>	CST <sub>larv</sub>	LST <sub>yolk</sub>	DD <sub>egg</sub>	DD <sub>egg</sub>
DD <sub>egg</sub>	LST <sub>pjuv</sub>	CST <sub>pjuv</sub>	LST <sub>pjuv</sub>	LST <sub>yolk</sub>
LST <sub>yolk</sub>	SSH <sup>2</sup>	LST <sub>bjuv</sub>	DD <sub>bjuv</sub>	LST <sub>pjuv</sub>
DD <sub>larv</sub>		FWI <sub>bjuv</sub>	SSH	SSH

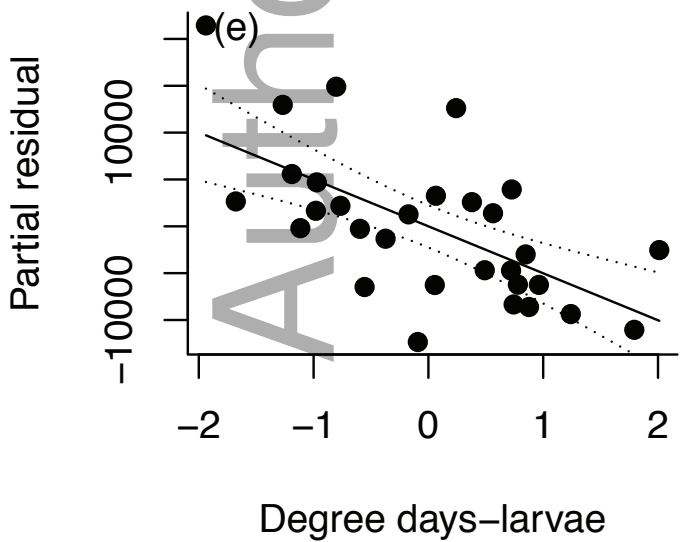
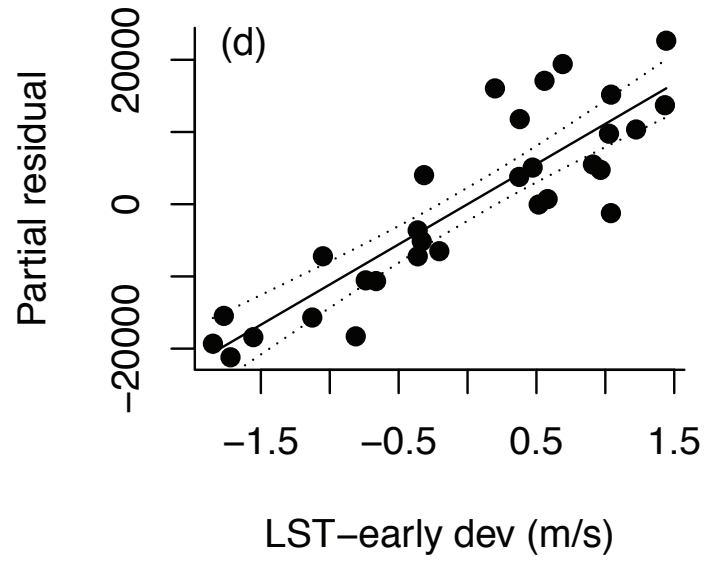
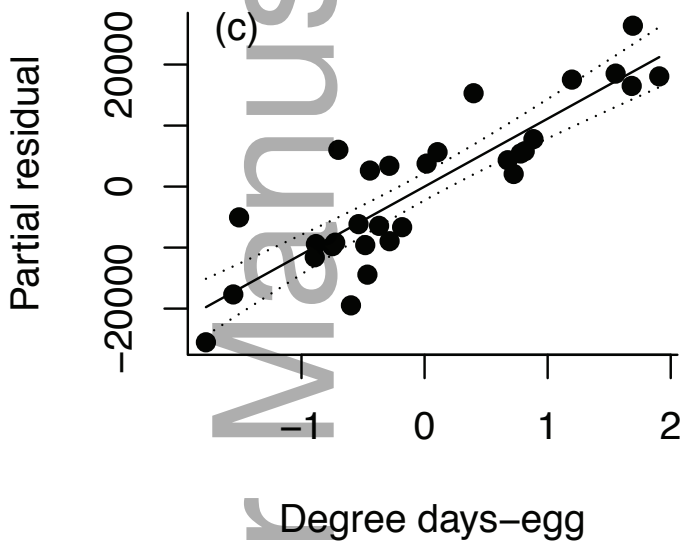
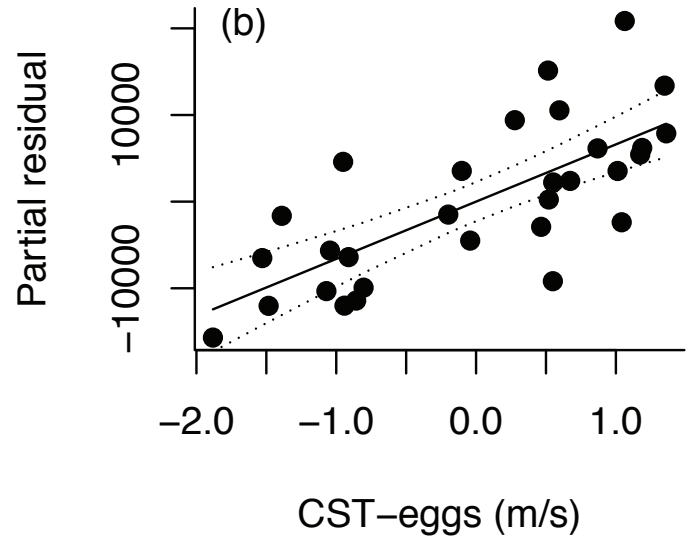
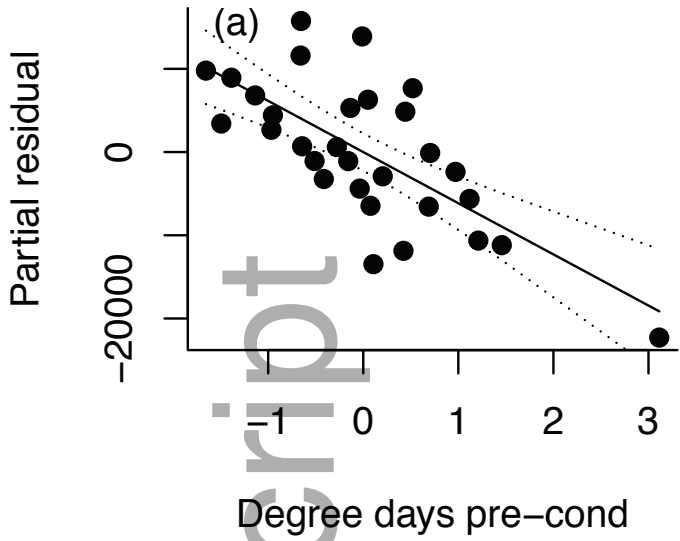


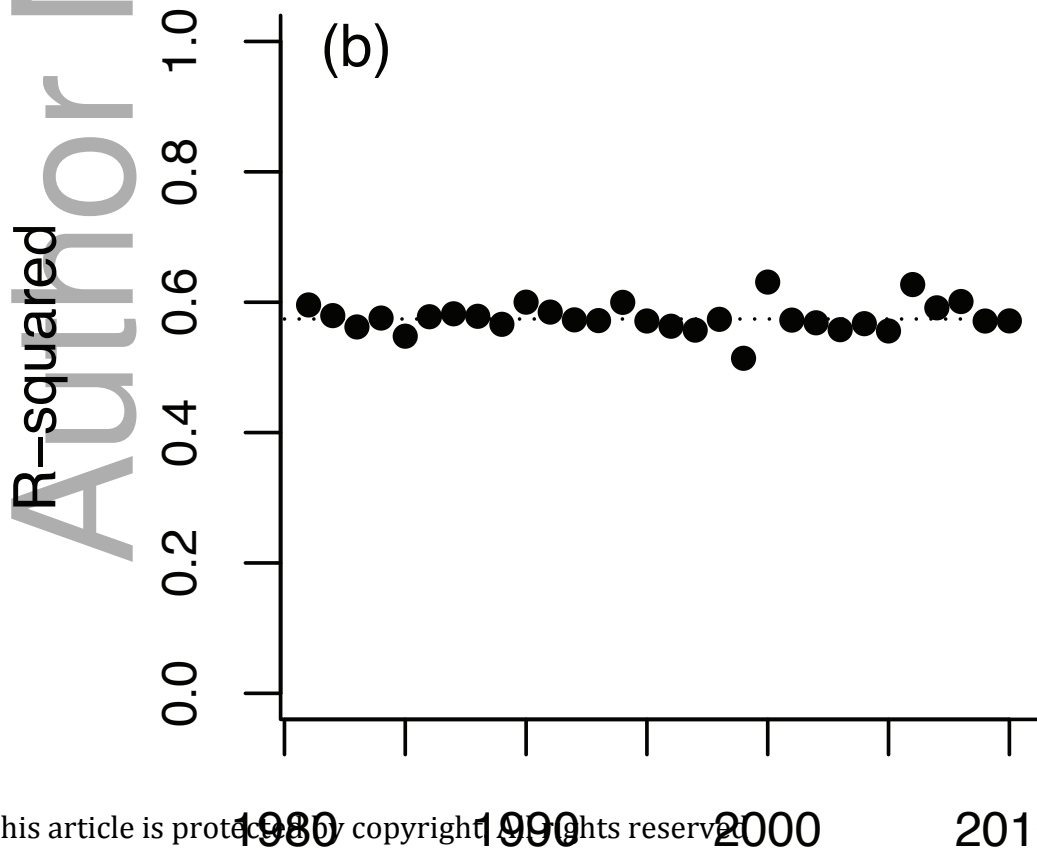
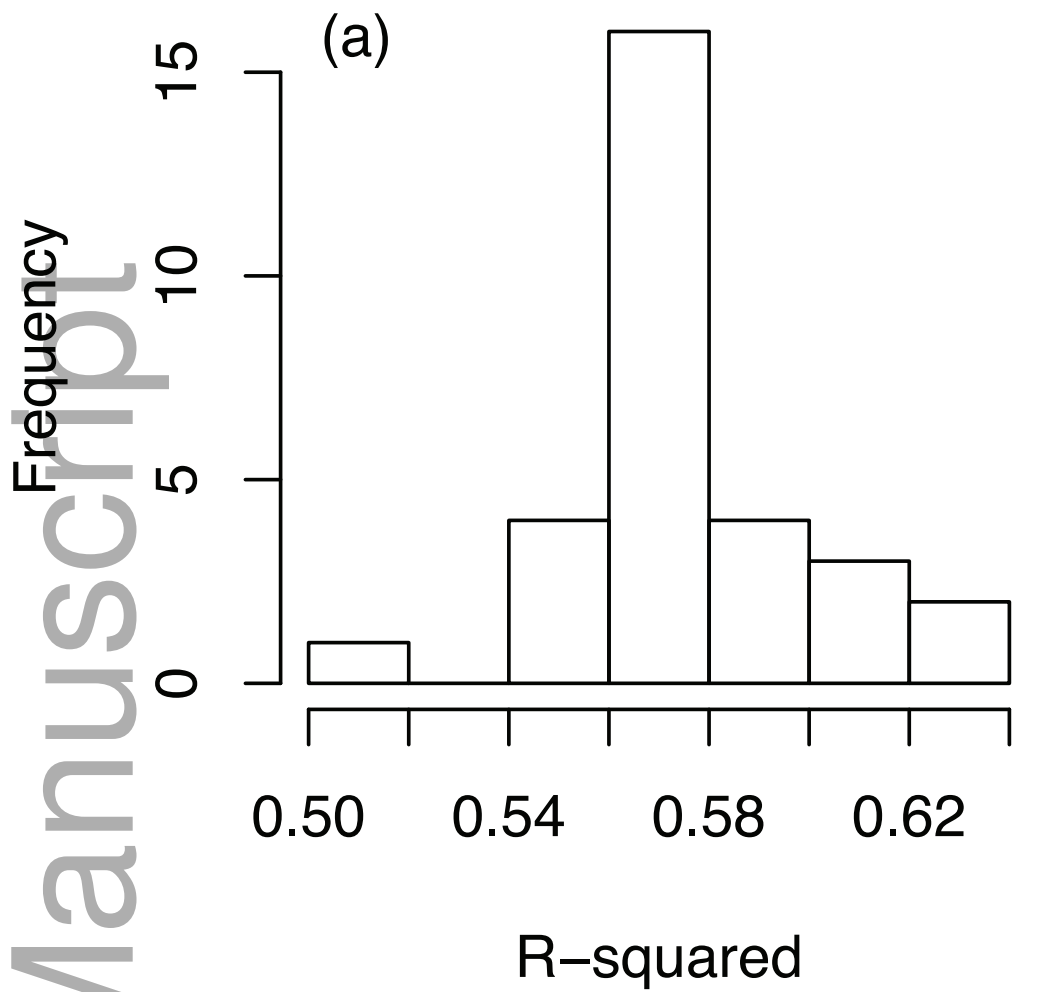






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**Female preconditioning (50-1200 m)**

(-)  $DD_{pre}$

Cold water is associated with higher system productivity and lower metabolic costs making more energy available for reproduction

**Eggs (300-825 m)**

(+)  $CST_{egg}$

Onshore transport maintains larvae near settlement habitat

(+)  $DD_{egg}$

Faster development in warm water

**Early development larvae (yolk-sack) (1000-1200 m)**

(+)  $LST_{yolk}$

Transport to the north results in better feeding later on northern zooplankton

**Pelagic larvae (surface waters)**

(-)  $DD_{larv}$

Cold water is associated with higher system productivity and lower chance of starvation