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Oceanographic drivers of petrale sole recruitment in the California Current Ecosystem

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Running Title: Petrale sole recruitment in the California Current Ecosystem

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41 **Abstract**

42 This paper investigates environmental drivers of US west coast petrale sole (*Eopsetta*
43 *jordani*) recruitment as an initial step towards developing an environmental recruitment index
44 that can inform the stock assessment in the absence of survey observations of age-0 and age 1-
45 fish. First, a conceptual life-history approach is used to generate life stage- and spatio-
46 temporally-specific mechanistic hypotheses regarding oceanographic variables that likely
47 influence survival at each life stage. Seven life history stages are considered, from female-
48 spawner condition through benthic recruitment as observed in the Northwest Fisheries Science
49 Center West Coast Groundfish Bottom Trawl Survey (age-2 fish). The study area encompasses
50 the region from 40-48 °N in the California Current Ecosystem. Hypotheses are tested using
51 output from a regional ocean reanalysis model outputs and model selection techniques. Four
52 oceanographic variables explained 73% of the variation in recruitment not accounted for by
53 estimates based exclusively on the spawning stock size. Recruitment deviations were (1)
54 positively correlated with degree days during the female precondition period, (2) positively
55 correlated with mixed-layer depth during the egg stage, (3) negatively correlated with cross-shelf
56 transport during the larval stage, and (4) negatively correlated with cross-shelf transport during
57 the benthic juvenile stage. While multiple mechanisms likely affect petrale sole recruitment at
58 different points during their life history, the strength of the relationship is promising for stock
59 assessment and integrated ecosystem assessment applications.

60 **Key Words:** Petrale sole, *Eopsetta jordani*, recruitment, oceanic drivers, California Current

61

62 **Introduction**

63 Petrale sole (Family: *Pleuronectidae*, *Eopsetta jordani*) has consistently been the most
64 commercially valuable flatfish targeted in the California Current Ecosystem. During the 1980s
65 through the 2000s, the petrale sole spawning biomass was around or below 10% of the
66 unexploited stock size (Haltuch et al. 2013). More recently the fishery has depended on
67 infrequent above average recruitments, generally followed by several years of low recruitments,
68 that drive fluctuations in the spawning biomass (Fig. 1) (Haltuch et al. 2013). This dependence of
69 the fishery on relatively few strong recruitment events makes understanding the drivers of petrale
70 sole recruitment a priority.

71 The horizontal-advection bottom-up forcing paradigm provided a mechanistic framework
72 for testing the hypothesis that climate-driven changes in cross-shelf and alongshore advection
73 drive petrale sole recruitment strength (Parrish et al. 1981, Di Lorenzo et al. 2013). This
74 paradigm suggested that large-scale climate forcing drives regional changes in alongshore and
75 cross-shelf ocean transport that directly impact ecosystem functions such as productivity, species
76 composition, and spatial connectivity. Oceanographic studies illustrated the influence of large-
77 scale climate drivers on mesoscale processes in the California Current Ecosystem that drive
78 cross-shelf and alongshore transport at local scales (Hickey 1979, Chelton et al. 1982, Keister et
79 al. 2011, Combes et al. 2013, Di Lorenzo et al. 2013). Variability in cross-shelf transport in the
80 California Current Ecosystem was important for understanding population and ecosystem
81 dynamics because of variable offshore and northward transport of nutrients, mass, and organisms
82 (Combes et al. 2013, Di Lorenzo et al. 2013, Jacox et al. 2016). Additionally, fish life cycles and
83 population connectivity patterns can be impacted via the transport of larvae by either coastal
84 upwelling or offshore advection of water from the poleward flowing California Undercurrent
85 (Combes et al. 2013, Di Lorenzo et al. 2013). Research has suggested that horizontal advection
86 affects density-independent survival during early life stages, specifically that offshore transport
87 of eggs and larvae results in poor recruitment (Castillo et al. 1994, Castillo 1995). Furthermore,
88 decadal-scale variability in wind-driven cross-shelf transport of early life stages of other flatfish

89 species towards favorable nursery areas influenced recruitment strength (Wilderbuer et al. 2002,
90 Hollowed et al. 2009, Wilderbuer et al. 2013). Concurrently, temperature can influence growth
91 rates of early life history stages, mediating larval vulnerability to predation and the likelihood of
92 starvation (Houde 1987, Litvak & Leggett 1992, Leggett & DeBlois 1994, Chezik et al. 2014).

93 This study leveraged recruitment estimates from an information-rich stock assessment for
94 the California Current Ecosystem petrale sole stock (Stawitz et al. 2016) to build a mechanistic
95 framework for investigating oceanographic drivers of survival using a conceptual life-history
96 approach to frame hypotheses regarding factors that affect survival at each early life history
97 stage. Petrale sole were an excellent candidate for investigations into oceanographic drivers of
98 recruitment strength for multiple reasons. First, the petrale sole data set were likely the most
99 information-rich groundfish data set due to the large amount of age and length data that spans
100 multiple generations (compared to <1 generation for most rockfishes). Next, multiple stock
101 assessment models and model sensitivity runs, and thus historical recruitment estimates,
102 produced highly similar results. Finally, previous fisheries and oceanographic research suggested
103 potential mechanisms for oceanographic drivers of petrale sole recruitment. However, prior to
104 using oceanographic recruitment drivers to forecast recruitment for either near-term tactical
105 management or long-term strategic decision-making, statistical models must be built and
106 evaluated. Our goal was to develop a statistically robust environment-recruitment relationship to
107 explain variability in recruitment (Basson 1999) for use in both near-term and long-term petrale
108 sole recruitment forecasting. We developed and tested a series of generalized linear models
109 (GLMs) to explore the influence of oceanographic drivers on petrale sole survival at different life
110 stages, from female spawner condition through benthic recruitment.

111

112 **Methods**

113 This study applied the methodology implemented by Tolimieri et al. (2018) for sablefish
114 to the U.S. west coast petrale sole stock using estimates of log recruitment deviations from the
115 petrale stock assessment (Stawitz et al. 2016) from 1981 - 2010 and model output from a
116 California Current Ecosystem configuration of the Regional Ocean Modeling System (ROMS)
117 with data assimilation (Neveu et al. 2016). While reliable recruitment estimates from the petrale
118 sole stock assessment ranged from 1945, due to earlier collections of length and age composition
119 data, through 2013, the ROMS model outputs did not span the full time series of recruitment

120 estimates. ROMS model outputs were available from 1981 through 2010. We focused on the
121 northern portion of the stock (40-48°N) because a majority of the spawning biomass and
122 spawning grounds were distributed in the north and recruitment estimates from the coast-wide
123 stock assessment model were most strongly informed by age and length composition data from
124 the north (Stawitz et al. 2016). Petrale sole stock assessments prior to 2009 were conducted
125 separately for northern and southern regions of the California Current Ecosystem (Lai et al.
126 2005). However, due to strong similarities in both spawning biomass and recruitment trends the
127 regional stock assessments were combined into a single coast-wide stock assessment during 2009
128 (Haltuch & Hicks 2009). We considered the time from female pre-spawning condition through
129 benthic recruitment (age-0 fish). This conceptual approach allowed for the generation of life-
130 stage- and spatio-temporally-specific hypotheses regarding the physical variables likely to
131 influence petrale sole survival at each life stage leading to recruitment. Hypotheses were tested
132 using linear modeling, model selection, and model validation.

133

134 *Petrале sole life history: female preconditioning to age-0 recruits*

135 The conceptual life-history approach tracked each life stage beginning with female
136 condition prior to the spawning season through recruitment at age-0 (Table 1). Research on
137 rockfishes and sablefish has shown that female condition may influence whether or not an
138 individual spawns, and the quality and number of eggs produced by female fishes (Sogard et al.
139 2008, Rodgveller et al. 2016). While petrale sole may have the potential for skip spawning,
140 currently available data are inconclusive (Pers. Comm. M. Head). Petrale sole spawn during the
141 winter, thus the summer and fall prior to spawning (May to October) were important for female
142 preconditioning.

143 Spawning occurred from November to March with a peak during December to January
144 (Cleaver 1949, Harry 1959, DiDonato & Pasquale 1970, Pedersen 1975). Petrale sole form deep
145 water spawning aggregations (270-460 m) at localized sites along the shelf break, with most
146 spawning taking place at depths ranging from 250 m to 500 m (Harry 1959, Best 1960, Gregory
147 & Jow 1976, Castillo et al. 1994, Castillo 1995, Love 1996, Moser 1996, Casillas et al. 1998).
148 Females spawn once each year and fecundity varies allometrically with fish size, with one large
149 female laying as many as 1.5 million eggs (Porter, 1964). Eggs rise to the surface between
150 November and April, remaining in surface waters for 6 to 14 days (Alderdice & Forrester 1971,

151 Hart 1973, Love 1996, Casillas et al. 1998), then sink to approximately 400 m depth before
152 hatching (Mason et al. 1983, Kendall & Matarese 1987, Hunter et al. 1989, Moser et al. 1994) as
153 yolk-sac larvae. After hatching, the larvae rise to the upper 50 m of the water column and remain
154 there for approximately five months, through the feeding larval stage (Alderdice & Forrester
155 1971, Hart 1973, Pearcy et al. 1977, Love 1996, Casillas et al. 1998). Planktonic petrale sole
156 larvae range in size from approximately 3 to 20 mm, and were found up to 150 km offshore
157 foraging upon copepod eggs and nauplii (Hart 1973, MBC Applied Environmental Sciences
158 1987, Moser 1996, Casillas et al. 1998). At about 2.2 cm in length petrale sole larvae settle to the
159 benthos as age-0 recruits on the inner continental shelf (Pearcy et al. 1977). Benthic juveniles
160 inhabit sandy or sand-mud bottoms (Eschmeyer et al. 1983, MBC Applied Environmental
161 Sciences 1987)-, ranging in size from approximately 2.2 cm to the size at maturity. Fifty percent
162 of the population was mature at approximately 38 cm and 41 cm for males and females,
163 respectively (Casillas et al. 1998). Specific nursery areas for juvenile petrale sole have not been
164 identified. Due to a lack of sampling of newly settled petrale sole, this study evaluated two
165 alternative hypotheses regarding settlement depths, from 50 m to 150 m depth and from 150 m to
166 500 m depth.

167 In northern and central California petrale sole were found primarily on the middle and
168 outer continental shelf (Allen et al. 2006). Pacific Fisheries Information Network (PacFIN)
169 fishery logbook data showed that a majority of the adult petrale sole catch off the U.S. West
170 Coast takes place between 70 and 220 m during March through October, and between 290 and
171 440 m from November through February.

172 Juveniles show little coast-wide or bathymetric movement, while studies suggested that
173 adults generally move inshore, and northward to the continental shelf feeding grounds during the
174 spring and summer and offshore and southward to deep water spawning grounds during the fall
175 and winter (Hart 1973, MBC Applied Environmental Sciences 1987, Horton 1989, Love 1996).

177 *Regional Ocean Modeling System (ROMS)*

178 Predictors considered here were physical oceanographic parameters including
179 temperature, long-shore and cross-shelf currents and mixed layer depth (Table 1). Variables
180 were obtained from a California Current Ecosystem configuration of the Regional Ocean
181 Modeling System (ROMS) of the California Current Ecosystem with 4-Dimensional Variational

182 (4D-Var) data assimilation (Neveu et al. 2016). The ROMS model domain covered the region
183 30-48°N and from the coast to 134°W at 0.1° (~10 km) horizontal resolution, with 42 terrain-
184 following vertical levels. For the 1980-2010 California Current Ecosystem reanalysis used for
185 this study, satellite observations (SST, SSH) and in situ data (temperature and salinity
186 measurements from ships, floats, moorings) are assimilated into the model to improve its
187 representation of the true ocean state. This reanalysis has been used extensively to study physical
188 and biogeochemical dynamics in the California Current Ecosystem (Jacox et al. 2014, Jacox et
189 al. 2015a, Jacox et al. 2015b), and to develop models of marine species recruitment (Tolimieri et
190 al. 2018) and distribution (e.g., Brodie et al. 2018). All ROMS outputs for the study region were
191 obtained as 4-day averages, and then either averaged or summed over the appropriate life-history
192 time period (as defined in **Error! Reference source not found.**) within each of the 30 years
193 (1980 to 2010) for each time series in the analysis. Specific hypotheses for each predictor below
194 are described below.

195 Oceanographic data were scarcer at depth than at the surface. As a result, the ROMS
196 output that assimilates available data was less constrained by observations at the subsurface than
197 at the surface. Therefore, the ROMS output likely deviates from nature more at the subsurface
198 than at the surface. However, the paucity of subsurface data was the motivation for using model
199 output in this study; the model output was useful despite the inability to validate the subsurface
200 model transport. Data assimilation was used to improve models that already capture the
201 California Current Ecosystem dynamics without data assimilation. The fidelity of this model to
202 nature has been documented extensively for applications with and without data assimilation (e.g.,
203 Veneziani et al. 2009, Jacox et al. 2015a). The model was forced by realistic winds, surface heat
204 fluxes, and lateral boundary conditions, which drive realistic physical variability even in the
205 absence of data assimilation. Assimilated data, even if only available at the surface, can
206 influence the subsurface dynamics. For example, assimilating sea surface height measurements
207 constrains the geostrophic flow and therefore transport at the both the surface and subsurface.
208 The impact of assimilated data on different metrics of the California Current Ecosystem
209 circulation is discussed in detail in Moore et al. (2017).

210

211 *Hypotheses and additional data sources*

212 We developed 18 *a priori*, life-stage-specific and space-specific (considering time, depth,
213 and longitude) hypotheses for environmental covariates that may drive variation in petrale sole
214 recruitment (**Error! Reference source not found.**). Hypotheses for age-0 benthic juveniles
215 were tested using two depth ranges given the uncertainty and lack of literature regarding the
216 depth range of newly settled to age-2 juvenile petrale sole. Given the 18 hypotheses, three of
217 which had two covariates, 21 total predictors were tested. Each hypothesis tested had specific
218 temporal, longitudinal, and depth ranges (**Error! Reference source not found.**).

219 Only hypotheses that had ROMS model outputs available were tested (Table 1), thus
220 excluding potential hypotheses such as food availability for larvae and pelagic juveniles
221 (McFarlane & Beamish 1992), which remain untestable due to insufficient data. This study did
222 not test mechanisms with potential indirect effects on survival at each life stage such as drivers
223 of food availability (e.g. upwelling). However, some of these effects are implicit in the transport
224 and temperature indices that are included (e.g., upwelling cools surface waters and drivers
225 offshore transport).

226

227 *Temperature*

228 Temperature may affect recruitment through multiple mechanisms. During spawner
229 preconditioning (Table 1, hypothesis 1, hereafter, H1) warmer temperatures may increase energy
230 demands (H1), forcing female petrale sole to allocate less energy to reproduction by reducing
231 egg production or aborting spawning. Temperature may also act as a spawning cue (H2 and H3),
232 or affect growth, development, survival, and susceptibility to predation of eggs and pelagic
233 larvae through multiple mechanisms, among which we cannot distinguish (H7, H10, H13, and
234 H16). For example, warmer temperatures allow for faster growth and may help larvae to
235 transition through developmental stages (e.g., egg stage) or outgrow potential predators (e.g.,
236 stage duration or 'bigger-is-better' hypotheses; Houde 1987, 1997), but warm waters may also
237 increase energy demands making larvae more susceptible to starvation, especially if warmer
238 waters bring poor feeding conditions. In most cases, temperature data was included as degree
239 days (cumulative temperature above a threshold value, Chezik et al. 2014). There is limited
240 information on the effects of temperature on the development of petrale eggs and larvae.

241 Alderdice and Forrester (1971) saw slight curvature and an increase in the rate of development
242 from 4 – 8.5°C. Therefore, we set the cumulative threshold to 3.5°C in this study.

243

244 *Transport*

245 Transport to or away from appropriate settlement habitat can strongly affect larval supply
246 and settlement of marine species with pelagic eggs and larvae (Montgomery et al. 2001,
247 Schirripa & Colbert 2006). Transport to settlement habitat was characterized by estimates of
248 mean long-shore (LST: H5, H9, H11, H14 and H17) and cross-shelf transport (CST: H6, H8,
249 H12, H15 & H18) at specific depths and times for each petrale sole life-history stage.

250 Petrale sole spawn at depth but eggs rise in the water column. The mixed-layer depth
251 (MLD) may influence how high eggs rise in the water column, thereby affecting transport (H4)
252 (Sundby 1991, Hinckley et al. 1996) and available food resources post-egg hatch (Cushing
253 1982). Therefore, the mean MLD from November to April, when eggs are in the water column,
254 was included.

255

256 *Preliminary Analyses*

257 The correlations among predictor variables and individual linear and quadratic
258 regressions for each predictor against recruitment deviations were calculated (Tables S1 and S2)
259 and evaluated prior to model fitting and selection. Strongly correlated predictors (Table S1, $r >$
260 0.70), were not permitted in the same model (Dormann et al. 2013). Quadratic terms were
261 included in the main modeling exercise, in addition to linear terms, if the individual quadratic
262 model fit better than the individual linear model (Akiake's Information Criterion, AIC, was <2.0
263 that of the linear model, see Table S1, Burnham & Anderson 1998). Based on preliminary
264 analyses, a quadratic term for degree-days during the egg stage (DD_{egg}) and degree-days during
265 the larval stage (DD_{larv}) were included as potential predictors in the final model selection.

266

267 *Recruitment deviations*

268 Model estimates of petrale sole recruitment were taken from the most recent stock-
269 assessment (Fig. 1c here, Fig. C in Johnson et al. 2016, Stawitz et al. 2016). Specifically, the
270 model-estimated log deviations where the deviations were the annual deviations from log-mean
271 recruitment were used. Mean recruitment was a function of the assumed Beverton-Holt stock-

272 recruitment relationship, aging error assumptions, and the data included in the stock assessment
273 model.

274

275 *Model selection*

276 A series of generalized linear models (GLMs) were run including all possible
277 permutations of the 21 covariates (n = 11611 models) excluding highly correlated terms ($|r| > 0.7$)
278 from the same model. Each covariate matched a specific hypothesis in Table 1. The number of
279 predictors in a candidate model was limited to five (one covariate per six data points in the time
280 series) to prevent over-fitting. The potentially quadratic predictors were allowed to enter the
281 models as linear, or linear + quadratic forms. The best-fit models were selected using $\Delta AICc$
282 values, retaining models with $\Delta AICc < 2.0$ (Burnham & Anderson 1998).

283

284 *Model validation and testing*

285 Performance of the best fit model was evaluated using

286 (1) resampling with replacement of recruitment deviations to estimate r^2 values using
287 100 randomized data sets; (2) bootstrapping whole years with replacement to estimate bias and
288 calculate standard error of the parameter estimates; (3) annual jackknife resampling to determine
289 the effect of any single year on the r^2 ; (4) resampling annual recruitment deviations from a log-
290 normal distribution using the annual mean and standard deviation estimated from the assessment
291 (Fig. 1c here, Stawitz et al. 2016, Fig c.), then recalculating recruitment residuals and refitting
292 the model 1000 times; (5) refitting the model using data for 1981-2005 and predicting
293 recruitments deviations for 2006-2010; (6) jackknife resampling to re-run the entire model fitting
294 and comparison exercise, to determine if removal of any individual year would change the
295 selected oceanographic variables; and (7) the entire model fitting exercise was re-run 100 times
296 using the re-sampled petrale recruitment deviations with error (from Step 4 above), comparing
297 $AICc$ selected models from each run. Finally, (8) we used jackknife resampling but fit only the
298 years 1981-2005, compared the resulting models to the best-fit model above, and used the 1981-
299 2005 model to predict recruitment deviations for 2006-2010.

300

301 **Results**

302 There were six candidate models with a $\Delta AICc < 2.0$. All of these models had the same
303 three core terms (**Error! Reference source not found.**): degree days during the female
304 preconditioning stage (DDpre), mixed-layer depth during the egg stage (MLDegg), and cross-
305 shelf transport during the larval stage (CSTlarv) (Fig. 2). Two of these models (Model 1 and
306 Model 2) included four total predictors, while the remaining models included five. The fourth
307 terms for Model 1 and Model 2 were highly correlated and essentially indistinguishable: cross-
308 shelf transport during the benthic juvenile stage (CSTbjuv.a) and long-shore transport during the
309 same stage (LSTbjuv.a)(Fig. 2). We chose Model 1 as the best-fit model because it had the
310 lowest AICc, highest weight, and fewest parameters. However, we note that CSTbjuv.a and
311 LSTbjuv.a are highly correlated with several other variables and distinguishing between them
312 was not possible.

313 Predictions of recruitment deviations from the best-fit model closely followed those
314 estimated within the stock assessment ($r^2 = 0.73$, Fig. 3a). Analysis of partial residuals showed
315 that recruitment deviations were positively correlated with degree days during the female
316 preconditioning period and mixed-layer depth during the egg stages. Recruitment deviations
317 were negatively correlated with cross-shelf transport during both the larval stage and benthic
318 juvenile stages (Fig. 4, **Error! Reference source not found.**). Standardized coefficients
319 suggested roughly similar effects of the three core variables on recruitment deviations with
320 cross-shelf transport during the benthic juvenile stage having the smallest effect (**Error!**
321 **Reference source not found.**). Including only the three core terms in the model resulted in a
322 moderate decrease in fit ($r^2 = 0.64$, Table S3).

323 There was weak correlation among the covariates in the best-fit model with the highest
324 being -0.58 for the correlation between mixed-depth layer and cross-shelf transport during the
325 benthic juvenile stage (**Error! Reference source not found.**). The variance inflation factor
326 values (VIF), which measure how much the variance of the estimated regression coefficients are
327 inflated as compared to when the predictor variables are not linearly related, were low (**Error!**
328 **Reference source not found.**). The diagnostics for the best-fit model show good model fit (Figs.
329 4 and S1) with residuals that did not show signs of autocorrelation (Fig. S2).

330

331 *Model testing and validation: core-fit model*

332 Randomly resampling the recruitment deviations (bootstrap with replacement) gave a
333 median expected $r^2 = 0.14$ (95% C.I. = 0.02-0.33) for the core model suggesting that the
334 observed value of $r^2 = 0.73$ was unlikely to be observed at random.

335 Removing individual years and refitting the best-fit model (jackknifing) had little impact
336 on the model fit (Figs. 3 & 5, median $r^2 = 0.73$ (95% C.I. = 0.70-0.76). Predicting the missing
337 year from any iteration produced estimates very similar to those for the full model (Fig. 3a). The
338 years that showed the highest impact on the model's ability to explain the data were 1991
339 (increased to $r^2 = 0.77$) and 2008 (decreased to $r^2 = 0.69$) (Figure 5).

340 Resampling annual recruitment deviations with error produced a modest decline in model
341 performance (median $r^2 = 0.0.62$ (95% C.I. = 0.48-0.75). This suggests that uncertainty in the
342 time-series of recruitment deviations (given the current assessment parameters) results in a
343 somewhat lower ability to explain the variability in recruitment.

344 Using the jackknife resampling and re-running the entire model fitting process produced
345 results consistent with the primary analysis (Table 5). Degree days during preconditioning,
346 mixed-layer depth, and cross-shelf transport during the larval stage appeared in all models, while
347 cross-shelf transport and long-shore transport during the benthic juvenile stage alternated in
348 appearance.

349 Resampling the recruitment deviations (with error) and re-running the entire model fitting
350 exercise 100 times was generally consistent with the core model from the primary analysis
351 (Table 6). The three core terms appeared in the majority of models and years.

352 Finally, jackknife resampling and re-running the entire model fitting process for the 1981
353 – 2005 data supported the inclusion of the three core terms, which appeared in all best-fit models
354 given the exclusion of a given year (Table 7). The only exception was cross-shelf transport
355 during the larval stage, which appeared in 24 out of 25 years. Predicting recruitment deviations
356 for 1981-2005 generally did a good job of predicting recruitment deviations ($r^2 = 0.61$, Fig. 3b).
357 This three-term model did not predict the high recruitment deviations in 2006-2008 when used to
358 forecast recruitment (Fig. 3b) but did forecast increases in recruitment for these years and closely
359 forecast recruitment deviations for 2009 and 2010. Thus Model 1 appears to be an effective yet
360 conservative predictor.

361

362 **Discussion**

363 The four oceanographic variables in the best-fit model explained 73% of the variation in
364 petrale sole recruitment not accounted for by estimates based exclusively on the spawning stock
365 size. Recruitment deviations were positively correlated with: (1) degree days at the female
366 preconditioning stage and (2) mixed-layer depth at the egg stage, but negatively correlated with
367 (3) cross-shelf transport during the larval stage and (4) cross-shelf transport during the benthic
368 juvenile stage. These results suggest that petrale sole recruitments were a product of multiple
369 mechanisms acting at different early life history life stages (Fig. 6). Notably, although the time
370 spans and depth ranges for each life stage were different, both the core model relationships for
371 petrale sole and the best fit model from a similar study for California Current sablefish
372 (Tolimieri et al. 2018) share some of the same linear covariates that suggested spawner condition
373 and horizontal transport impact recruitment success for both species.

374 The best-fit model (Model 1) fit the recruitment deviations from the stock-recruitment
375 relationship well. During the spawner preconditioning stage degree days from May through
376 October impacted subsequent recruitments, with better recruitment when females experienced
377 warmer conditions prior to spawning. Some species like Atlantic cod (Pedersen & Jobling 1989)
378 and bullhead (Abdoli et al. 2005) showed positive correlations between growth or egg production
379 and water temperature. Presumably warmer water temperatures allowed for higher metabolism
380 and more rapid conversion of energy into eggs resulting in higher growth and fecundity given
381 sufficient food resources. Earlier work by Castillo et al. 1994 also concluded that warmer
382 water temperatures were associated with increased egg and larval survival, which may be
383 influenced by increased egg production.

384 During the egg stage, mixed layer depth from November through April was an important
385 driver of recruitment. Specifically, water below the MLD was denser than that above, thus
386 petrale sole eggs that are positively buoyant at spawning depths below the MLD were neutrally
387 buoyant at or above the MLD (Alderdice and Forrester 1971). The vertical distribution of fish
388 eggs in the water column affected horizontal transport of eggs and larvae (Sundby 1991,
389 Hinckley et al. 1996). A shallower MLD may allow eggs to rise and be transported into more
390 productive waters, resulting in higher larval survival due to better feeding conditions (Cushing
391 1982).

392 At both the larval (from December through May) and benthic juvenile (from April to
393 October) stages, cross shelf transport was an important driver of recruitment. Similarly, Castillo
394 et al (1994) found that winter horizontal transport played an important role in determining petrale
395 sole year class strength, describing over half recruitment variability estimated at that time.
396 Stronger cross-shelf transport from deep water spawning locations to shallower continental shelf
397 waters transported and retained individuals in near-shore settlement habitat, resulting in higher
398 recruitment and reduced advection of larvae and juveniles off-shore, potentially important for
399 match-mismatch dynamics with prey resources (Peck et al. 2012).

400 Hypotheses regarding recruitment drivers at other life stages including spawning, the
401 sinking egg stage, and pelagic juvenile stage were not included in the core model. However, the
402 AICc selected suite of models (Table 2) includes additional covariates that appear to be
403 occasional recruitment drivers including long-shore transport during the surface egg and benthic
404 juvenile stages, and degree days during the surface egg and larval stages. The cross-shore and
405 long-shore transport at the benthic juvenile stages, as well as degree days at the surface egg and
406 larval stages were highly correlated (Table S1). Including these additional covariates explained
407 up to about 75% of the variability in petrale sole recruitment deviations. However, model
408 diagnostics for these models were poor, indicating that they were likely overfitting the data. The
409 negative relationship with cross-shore transport and the positive relationship with long-shore
410 transport during the benthic juvenile stage may indicate that if benthic juveniles were transported
411 offshore and to the south then recruitment is lower, possibly due to relatively poor food resources
412 in this region. The positive relationship with warm conditions during the surface egg and larval
413 stages may indicate faster development in warmer waters, thus decreased predation pressure
414 (Chavez et al. 2003, Harvey 2005, Peterson 2009, Sydeman et al. 2011).

415 The multiple model validation methods applied to these data suggest that the core model
416 predictions were robust. Recruitment residuals from the Beverton-Holt stock recruitment
417 relationship, based on the 2015 petrale sole stock assessment fell within the core model 95%
418 confidence interval during 24 years, below during 3 years (1986, 2001, and 2005), and above
419 during 3 years (1989, 1990, and 2008) (Fig. 3a). The years in which recruitment residuals fell
420 outside of the predicted 95% confidence interval did not clearly align with large-scale climate
421 oscillations in the north Pacific, such as the El Niño – Southern Oscillation (ENSO). The core
422 model predictions from a leave-one-year-out jackknife analysis provided predictions within the

423 95% confidence limits of the fitted core model for all years, 1981 through 2010 (Fig. 3a). Core
424 model predictions that used the available data through 2005 then predicting 2006-2010 resulted
425 in under predicting three out of five years that were among the largest recruitment deviations in
426 the time series (Fig. 3b). These under predictions were likely due to increases in the spawning
427 biomass at the end of the time series that were removed from the 1981 through 2005 training
428 data set.

429 This study provides the basis for understanding and forecasting the implications of
430 climate change and climate variability on petrale sole recruitment within the stock assessment
431 process, ecosystem assessments, and MSEs (e.g., Hollowed et al. 2009). The stock assessment
432 uses the Northwest Fisheries Science Center West Coast Groundfish Bottom Trawl Survey data,
433 which initially samples petrale sole as age-2 fishes. However, petrale sole are not 50% selected
434 until approximately age-6 (Stawitz et al. 2016). The ability to predict recruitment more than one
435 year ahead would allow the stock assessment to provide better catch advice based on improved
436 estimates of the recruitments likely to be entering the fishery in the near term, prior these
437 recruitments being well sampled by the survey (Kaplan et al. 2016, Siedlecki et al. 2016).
438 Annually updating environmental predictors to inform recruitment forecasting based on both
439 observed oceanographic conditions and potentially sub-annual forecasts of environmental
440 conditions (Siedlecki et al. 2016, Jacox et al. 2017) could provide leading environmental
441 indicators of recruitment for managers and fishers. Additionally, long-term stock productivity
442 projections based on oceanographic output from global climate models or regional ocean models
443 could be useful for fishery stakeholders and for evaluating the robustness of harvest control rules
444 (HCRs) to changes in long-term stock productivity evaluation via Management Strategy
445 Evaluation (MSE). Of course, given concerns about nonstationarity in environment-recruitment
446 relationships (Myers 1998), periodic re-evaluations any environmental drivers of recruitment are
447 necessary, and are dependent upon the continuation of both oceanographic and biological
448 monitoring programs.

449 This work can also inform the selection of historical environmental data sets for
450 hindcasting petrale sole recruitment in the absence of age and length composition data, rather
451 than assuming some level of average recruitment into the past based on more recently observed
452 recruitment variability. Using environmental indicators of what early recruitment might have
453 been could reduce stock assessment uncertainty and provide better estimates of management

454 reference points. Stock assessments estimate age-0 recruitment conditioned on the available data,
455 a majority of which may come from only one environmental regime. Using stock-recruitment
456 data from only one environmental regime may result in over- or underestimating past
457 recruitment, producing bias in the calculation of fishery reference points, particularly in the
458 California Current Ecosystem where many age and length time series are short relative to the
459 timescales of low frequency environmental variability (e.g., the Pacific Decadal Oscillation,
460 Berger 2019).

461 Transitioning the environmental drivers of petrale sole recruitment from this research to
462 an operational product for both stock assessments and ecosystem assessments for fishery
463 managers ideally requires the extension of ocean reanalyses both forward and backwards in time,
464 this study uses data from 1980 through 2010. Alternatively, more easily available observational
465 data sets could serve as proxies for the selected covariates. Finally, if available, skillful, short-
466 term oceanographic model forecasts of relevant oceanographic covariates could be used to
467 inform recruitment estimation prior to survey data availability.

468

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476

477 **Author Contributions**

478 M.A.H. and N.T. conceived the study. L.Q., M.A.H, and N.T. developed the conceptual life
479 history model. N.T. and M.A.H. developed and undertook statistical analyses. M.G.J. provided
480 the oceanographic expertise and ROMs model outputs for the study. M.A.H. and N.T. drafted the
481 manuscript with input and revisions from all authors.

482

483 **Conflict of Interest**

484 The authors do not have any conflicts of interest, commercial or otherwise, that have influenced
485 the findings of this research.

486

487 **Data Availability Statement**

488 The data associated with this manuscript is available through the NOAA Northwest Fisheries
489 Science Center, Fishery Resource Analysis and Monitoring Division.

490

491

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Life Stage	Year	Stage Duration	Stage Depth	Ho Number	Hypothesis	ROMS Covariates (40° N – 48° N)
<i>Preconditioning</i>	Year 0,		Bottom		Higher bottom water temperatures increases food demand resulting in lower egg production, egg quality, or probability of spawning and lowers recruitment (likely a bell-shaped relationship)	Mean bottom water temperature (°C, 4d)
	May-Oct		depths of 50 - 200 m	1		
<i>Spawning</i>	Year 1,		Bottom		Bottom water temperature acts as a spawning cue with fish less likely to spawn at high temperature resulting in lower recruitment	Mean bottom water temperature (°C, 4d)
	Nov - Mar		depths of 250 - 500 m	2		
<i>Egg, surface</i>	Year 1, Nov-Apr	6-14 days	Bottom		Water column temperature acts as a spawning cue with fish less likely to spawn at high temperature resulting in lower recruitment	Mean water column temperature (°C, 4d)
			depths of 250 - 500 m	3		
			Water column from surface to MLD	4	Eggs are buoyant so Mixed Layer Depth limits how far they rise in the water column affecting later transport	Mean mixed layer depth (m)
<i>Egg, surface</i>	Year 1, Nov-Apr	6-14 days	Water column from surface to MLD	5	Transport in the water column above the MLD to settlement habitat affects recruitment	Mean long-shore transport between the surface and MLD (m/s, 4d cumulative)
			Water column from surface to MLD	6	Transport in the water column above the MLD to settlement habitat affects recruitment (aka Advection reduces recruitment while retention	Mean cross-shelf transport between the surface and MLD (m/s, 4d cumulative)

			MLD		enhances recruitment)	
<i>Egg, sinking</i>	Year 1, Nov- Apr	6-14 days	Water column from surface to MLD	7	Growth/Predation hypothesis: growth rate is faster in warm water leading to reduced time vulnerable to predators	Degree days in the water column calculated from mean water column temperature between the surface and MLD (days, 4d)
			Water column from MLD to 400 m	8	Transport in the water column to settlement habitat affects recruitment (aka Advection reduces recruitment while retention enhances recruitment)	Mean long-shore transport from the MLD to 400m (m/s, 4d cumulative)
			Water column from MLD to 400 m	9	Transport in the water column to settlement habitat affects recruitment	Mean cross-shelf transport from the MLD to 400 m (m/s, 4d cumulative)
<i>Larvae (both yolk sac and feeding)</i>	Year 1, Dec- May	~ 5 months for all pelagic stages	Water column from MLD to 400 m	10	Growth/Predation hypothesis: growth rate is faster in warm water leading to reduced time vulnerable to predators	Degree days in the water column calculated from mean water column temperature between the MLD and 400 m (days, 4d)
			Water column from 0 - 50 m	11	North to south transport in the water column brings northern zooplankton and leads to higher survival and recruitment	Mean long-shore transport in the water column at 50-150 km offshore (m/s, 4d cumulative)

<i>Pelagic juveniles (feeding pelagics)</i>	Year 1, Mar - June	~ 5 months for all pelagic stages	Water column from 0 - 50 m	12	Transport in the water column to settlement habitat affects recruitment (aka Advection reduces recruitment while retention enhances recruitment)	Mean cross-shelf transport in the water column at 50-150 km offshore (m/s, 4d cumulative)	
			Water column from 0 - 50 m	13	Growth/Predation hypothesis: growth rate is faster in warm water leading to reduced time vulnerable to predators	Degree days in the water column calculated from mean water column temperature at 50 - 150 km offshore (days, 4d)	
			Water column from 0- 150 m	14	North to south transport brings northern zooplankton and leads to higher survival and recruitment, Transport to settlement habitat affects recruitment	Mean long-shore transport in the water column at 80-120 km offshore (m/s, 4d cumulative)	
	<i>Benthic Juvenile (Age-0)</i>	Year 1, Apr - Oct		Water column from 0- 150 m	15	Transport in the water column to settlement habitat affects recruitment (aka Advection reduces recruitment while retention enhances recruitment)	Mean cross-shelf transport in the water column at 80-120 km offshore (m/s, 4d cumulative)
				Water column from 0- 150 m	16	Growth/Predation hypothesis: growth rate is faster in warm water leading to reduced time vulnerable to predators	Degree days in the water column calculated from mean water column temperature at 80- 120 km offshore (days, 4d)
				Bottom depths from 50-150 m AND 150-500 m	17	Bottom water transport to settlement habitat affects recruitment (Advection reduces recruitment while retention enhances recruitment)	Mean long-shore transport at bottom depths of 50-150 m and 150 - 500 m (m/s, 4d cumulative); Two depth ranges are considered due to uncertainty regarding juvenile distributions

Bottom depths from 50-150 m AND 150-500 m	18	Bottom water transport to settlement habitat affects recruitment (aka Advection reduces recruitment while retention enhances recruitment)	Mean cross-shelf transport at bottom depths of 50-150 m and 150 - 500 m (m/s, 4d cumulative); Two depth ranges are considered due to uncertainty regarding juvenile distributions
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Model	Intercept	DDpre	MLDegg	CSTlarv	CSTbjuv.a	LSTbjuv.a	DDegg1	DDLarv	LSTegg	R ²	AICc	ΔAICc	Weight
Model.1	-3.779	0.012	0.041	-41.815	-38.526					0.73	-0.38	0	0.32
Model.2	-4.043	0.012	0.040	-39.178		11.778				0.72	0.82	1.19	0.17
Model.3	-4.272	0.012	0.038	-47.960	-43.688		0.003			0.75	1.3	1.67	0.14
Model.4	-4.459	0.013	0.041	-47.763	-44.831			0.002		0.75	1.38	1.76	0.13
Model.5	-3.632	0.012	0.038	-39.673	-43.993				-1.640	0.74	1.49	1.87	0.12
Model.6	-4.737	0.012	0.036	-46.850		14.671	0.004			0.74	1.62	2.00	0.12

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Predictor	Coefficient	Bias	SE	Standardized	Std	Std SE
				Coefficient	Bias	
Intercept	-3.779	-0.010	0.499	0.006	0.002	0.038
DDpre	0.012	0.000	0.002	0.237	-0.005	0.040
MLDegg	0.041	0.001	0.008	0.212	0.006	0.047
CSTlarv	-41.815	-0.119	7.801	-0.292	0.001	0.055
CSTbjuv.a	-38.526	1.392	15.075	-0.153	0.008	0.062

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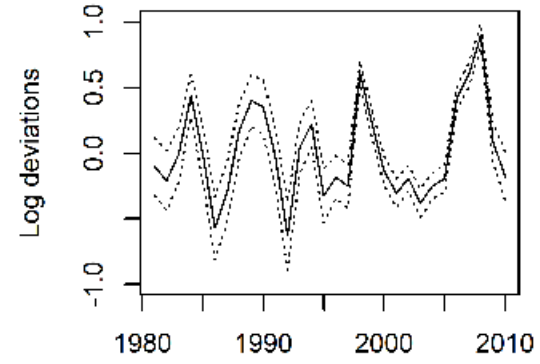
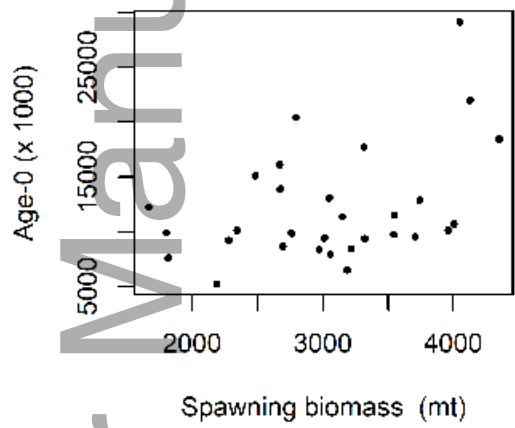
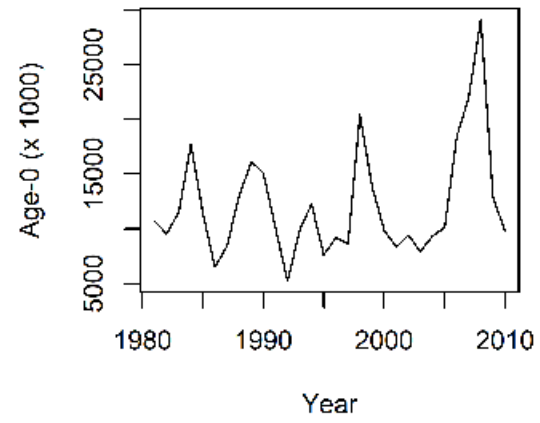
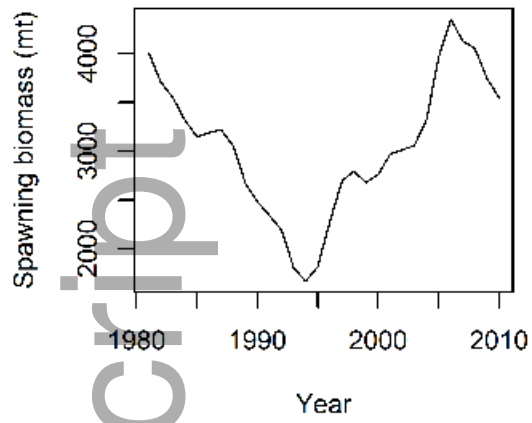
Parameter	DDpre	MLDegg	CSTlarv	VIF
DDpre	--			1.48
MLDegg	0.13	--		1.91
CSTlarv	0.31	0.54	--	1.65
CSTbjuv.a	0.28	-0.58	-0.38	2.02

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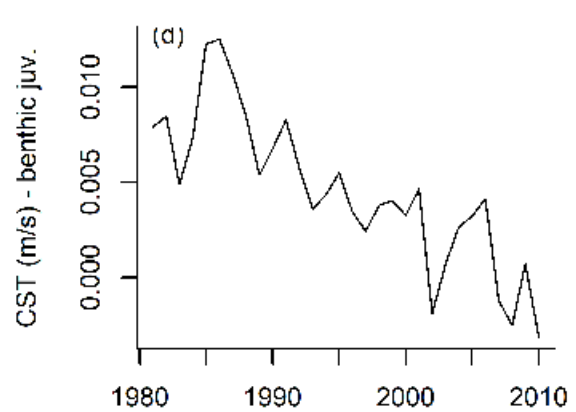
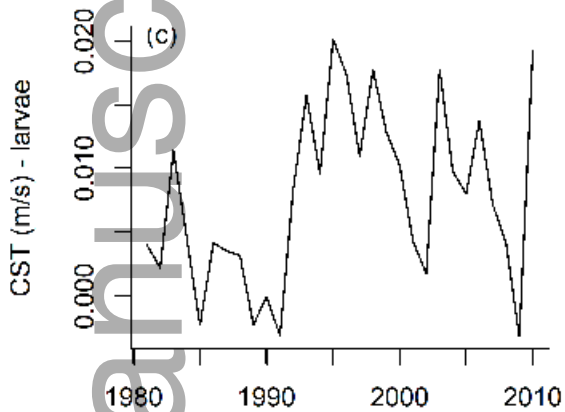
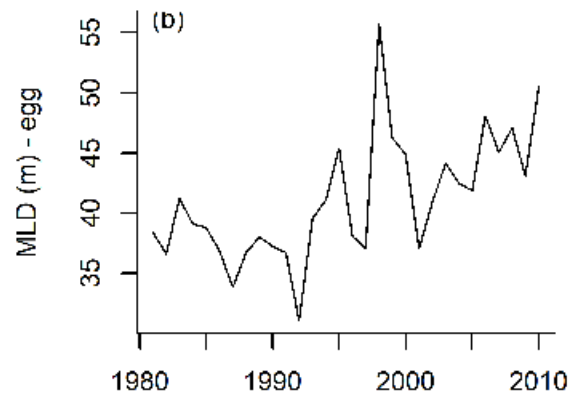
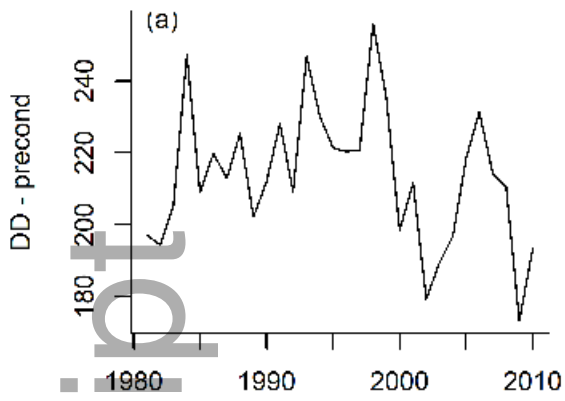
ROMS predictor	Times included
CSTbjuv.a	29
CSTbjuv.b	4
CSTegg1	0
CSTegg2	0
CSTlarv	66
CSTpjuv	0
DDegg1	3
DDegg1 ²	0
DDegg2	0
DDlarv	0
DDlarv ²	0
DDpjuv	0
DDpre	66
LSTbjuv.a	28
LSTbjuv.b	4
LSTegg	0
LSTegg2	0
LSTlarv	0
LSTpjuv	0
MLDegg	66
Tpre.a	0
Tpre.b	0
Total models	66

ROMS	Number of jackknives	Number of models
CSTbjuv.a	56	88
CSTbjuv.b	21	24
CSTegg1	13	21
CSTegg2	12	17
CSTlarv	81	161
CSTpjuv	29	50
DDegg1	13	23
DDegg2	7	10
DDlarv	3	4
DDpjuv	0	0
DDpre	100	218
DDegg1 ²	1	3
DDlarv ²	0	0
LSTbjuv.a	35	42
LSTbjuv.b	31	36
LSTegg	11	19
LSTegg2	18	29
LSTlarv	5	5
LSTpjuv	11	20
MLDegg	81	164
Tpre.a	4	6
Tpre.b	4	6
Total	100	227

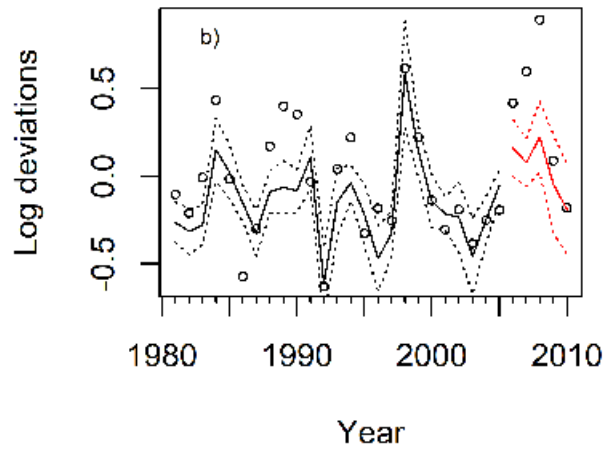
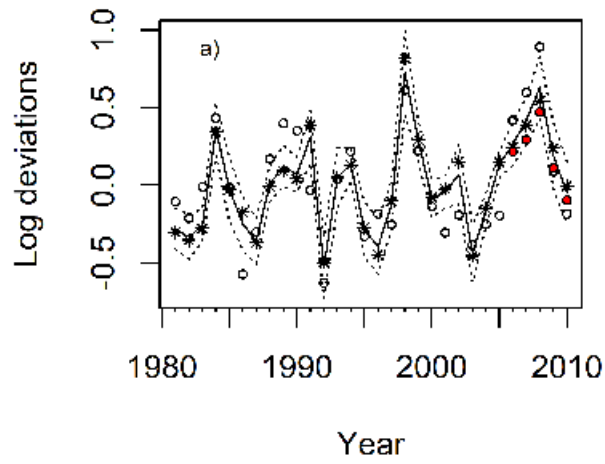
ROMS parameter	Time included
CSTbjuv.a	0
CSTbjuv.b	0
CSTegg1	0
CSTegg2	1
CSTlarv	24
CSTpjuv	1
DDegg1	0
DDegg1 ²	0
DDegg2	0
DDlarv	0
DDlarv ²	0
DDpjuv	0
DDpre	25
LSTbjuv.a	0
LSTbjuv.b	0
LSTegg	1
LSTegg2	0
LSTlarv	0
LSTpjuv	0
MLDegg	25
Tpre.a	0
Tpre.b	0



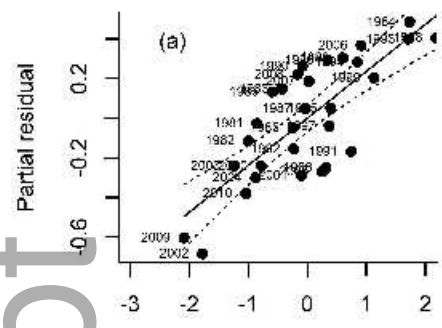
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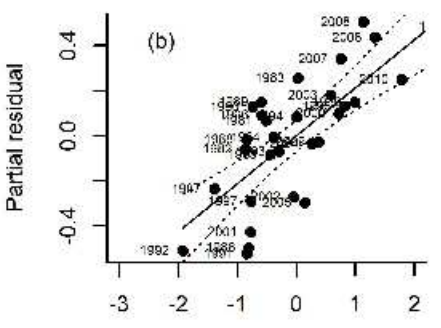
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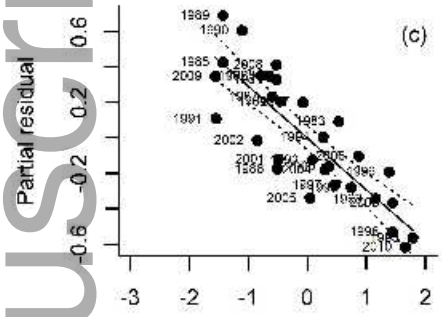
fog_12459_f3.tif



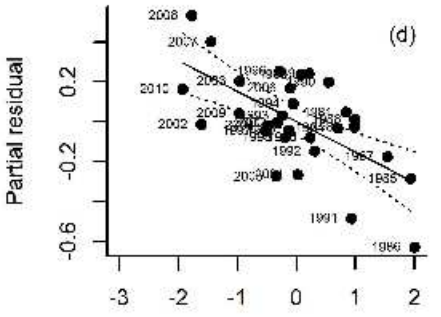
Degree days - precond

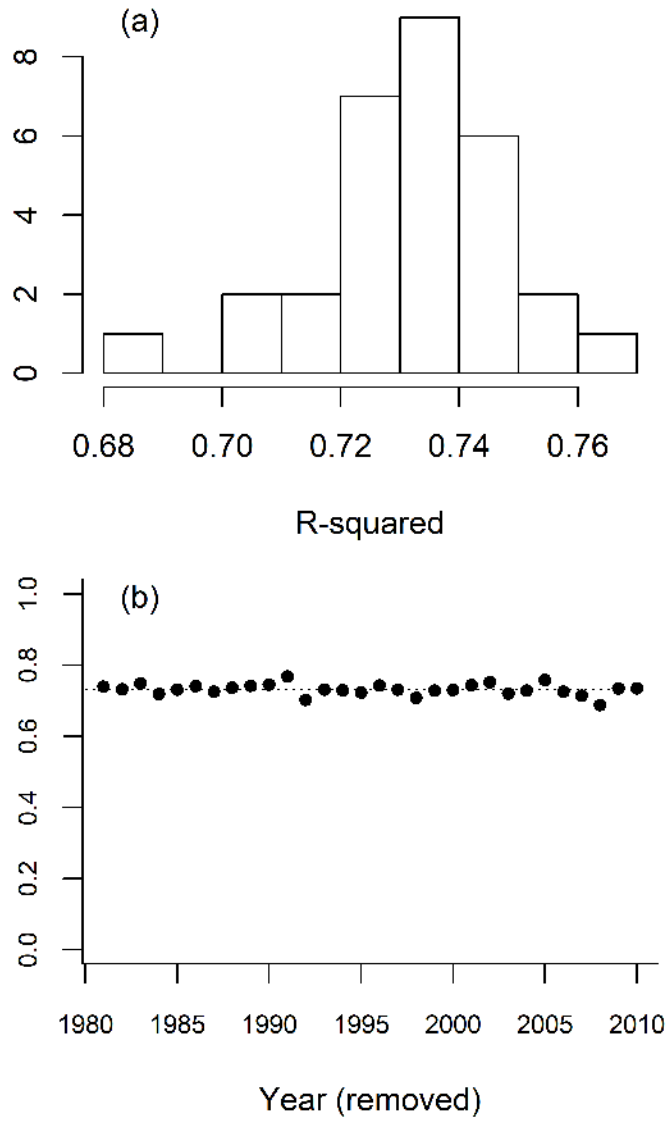


Mixed-layer depth - egg

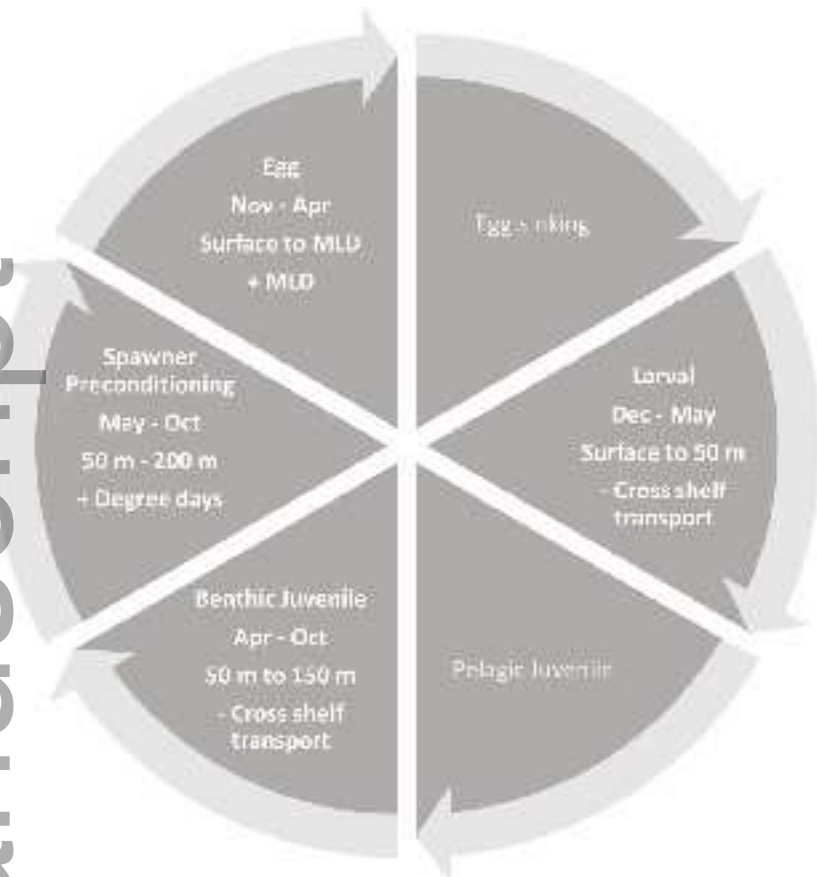


Cross-shelf transport (m/s) - larvae





fog_12459_f5.tif



fog_12459_f6.tiff