

1 **Marine ecosystem perspectives on Chinook salmon recruitment: A synthesis**  
2 **of empirical and modeling studies from the California upwelling system**

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18

19 **Abstract**

20 We review the suite of biophysical factors in the Northeast Pacific Ocean Basin and  
21 California Current shelf ecosystem that directly or indirectly relate to central  
22 California Chinook salmon (*Oncorhynchus tshawytscha*) growth and survival upon  
23 ocean entry, a critical life-history period for this population. Our synthesis provides

24 a framework for integrating ecosystem process studies with empirical hypothesis  
25 testing to benefit fisheries management. Our hypothesis includes seasonality  
26 (phenology) as a key element of early salmon growth and survival. The strength and  
27 location of the North Pacific High Pressure System in winter influences salmon  
28 growth and survival via "bottom-up" productivity and retention of key prey  
29 (euphausiid crustaceans and juvenile rockfishes, *Sebastes* spp.) in nearshore  
30 habitats prior to and during salmon emigration to sea in spring. Prey retention is  
31 associated with increased consumption of krill and juvenile rockfishes and is  
32 positively correlated with juvenile salmon body condition and ocean survival, and  
33 appears to set cohort strength and return rates. We examined these mechanistic  
34 relationships by reviewing the results of a biophysical model coupled to an  
35 individual-based model for salmon. Our review results in a final hypothesis stating  
36 that early salmon growth and survival are positively related to intensity of early-  
37 season upwelling and associated (forage) nekton production and retention on the  
38 shelf during spring and summer.

39

40 *Running page head:* Ecosystem perspective on Chinook salmon recruitment

41

42 *Keywords:* forage nekton, krill, upwelling phenology, salmon survival, California

43 Current Ecosystem, numerical ecosystem modeling

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46

47 **Introduction**

48 Quantifying the effect of ecosystem drivers on recruitment of fishes continues to be  
49 a vexing issue in fisheries science (Myers 1998, Bregnano & Fowler 2011, Haltuch &  
50 Punt 2011, Punt et al. 2013). Empirical studies of ecosystem processes, such as the  
51 controls of primary and secondary productivity, can provide a basis for quantifying  
52 direct and indirect drivers of recruitment strength through variability in trophic  
53 relationships (Hunsicker et al. 2011). Numerical ecosystem models may facilitate  
54 evaluation of expectant recruitment responses to ecosystem changes and  
55 management strategies that are not accessible using conventional empirical studies  
56 (Rose 2012, Rose et al. 2015). Moreover, integrating empirical and numerical  
57 ecosystem studies is likely to provide insight into recruitment processes (e.g., Houde  
58 2008), but in few marine ecosystems have sufficient empirical and numerical  
59 ecosystem studies been conducted to conceptualize and test synthetic hypotheses  
60 (Cury et al. 2008). In particular, this approach may be used to quantify aspects of  
61 the production, retention, and concentration of prey resources (Lasker 1975, Cury &  
62 Roy 1989) to assess impacts on fish recruitment resulting from variable overlap  
63 between the fish and their prey temporally (Cushing 1981) and spatially (Sinclair  
64 1988) during critical life stages.

65

66 Here, we synthesize ecosystem studies in the well-studied and modeled central  
67 California Current Ecosystem (CCE) to illustrate how these approaches can be  
68 integrated to better understand recruitment variability of California Central Valley  
69 Chinook salmon (*Oncorhynchus tshawytscha*), a recreationally, commercially, and

70 culturally important species of North Pacific marine ecosystems. We focus on fall-  
71 run (determined by the timing of adults return timing) Chinook salmon from the  
72 Sacramento River. Sacramento River fall-run Chinook salmon (SRFC) contribute the  
73 vast majority of Chinook salmon to the California Current Chinook salmon fishery  
74 (Lindley et al. 2009, Satterthwaite et al. 2015). The stock relies greatly on hatchery  
75 production due to river and estuary habitat loss and degradation, the impacts of  
76 water withdrawals for human uses and a large number of dams and water  
77 diversions (Lindley et al. 2009). As a result, the relationships between ocean  
78 ecosystem variability and this hatchery-dependent stock's dynamics are quite  
79 apparent (Carlson & Satterthwaite 2011, Satterthwaite & Carlson 2015).

80

81 Our conceptual model of the interacting biophysical factors affecting salmon forage  
82 and salmon productivity is founded on the work of salmon ecologists (e.g., Pearcy  
83 1992, Beamish & Mahnken 2001), fisheries oceanographers (e.g., Cury & Roy 1989,  
84 Bakun 1996), and physical oceanographers (e.g., Chelton et al. 1982, Bograd et al.  
85 2009)(Figure 1). We review the literature relevant to direct and indirect impacts of  
86 biophysical factors on the productivity of the shelf ecosystem and resulting salmon  
87 survival. We acknowledge that this synthesis is not a complete accounting of the  
88 ecosystem factors nor does it represent a prescribed chain of events that  
89 predetermine salmon productivity. What the synthesis does provide is a conceptual  
90 model of biophysical factors that current research has demonstrably linked to shelf  
91 ecosystem dynamics and Chinook salmon dynamics in CCE. Our examination of the  
92 conceptual model also provides an understanding of the consequences to the shelf

93 ecosystem resulting from variability at different spatial and temporal scales.  
94 Therefore, we focus our review on the spatiotemporal dynamics at meso (10-  
95 100km), regional (100-1000km) and basin scales in order to assess interactive  
96 effects of these scales on the central California shelf ecosystem during the period  
97 leading up to emigration of juvenile salmon. We complete our synthesis by  
98 reviewing the results of a numerical ecosystem model to examine the effect of  
99 ecosystem variability on growth of juvenile Chinook salmon during contrasting  
100 survival years. The results of the mechanistic ecosystem model are useful to  
101 evaluate the appropriateness of the conceptual model and provides a tool to assess  
102 the effect of ecosystem variability on salmon productivity.

103

104 We organize this synthesis with three overarching questions relevant to quantifying  
105 dynamics of salmon forage and salmon growth and survival early after emigration  
106 to the ocean each year, with a specific focus on seasonality (phenology) of ocean-  
107 climate conditions.

108

- 109 1. How does variability in forage availability (abundance, distribution, and  
110 species composition) affect juvenile Chinook salmon growth and survival?
- 111 2. How do regional transport and upwelling characteristics interact to retain  
112 and sustain forage on the shelf through the initial time of salmon emigration  
113 in spring?
- 114 3. How does basin-scale atmosphere/ocean variability influence development  
115 of neritic food webs upon which juvenile salmon depend?

116

117 **How does variability in forage availability affect juvenile Chinook salmon**118 **growth and survival?**

119

120 The central California region of the CCE between Point Arena (39°N) and Monterey  
121 Bay (36°N), including the Gulf of the Farallones, is a highly productive coastal  
122 ecosystem (Figure 1). The wide shelf located south of Point Reyes provides essential  
123 habitat for krill (Santora et al. 2011) and other forage nekton (Wing et al. 1998,  
124 Largier et al. 2006, Vander Woude et al. 2006)(Figure 1 and 2), as well, hosts major  
125 populations of marine birds (Ainley & Lewis 1974, Santora et al. 2012). Spring and  
126 summer in the central California region of the CCE is considered a critical period in  
127 the life history of SRFC during which the impacts of mortality can vary greatly  
128 between cohorts (Wells et al. 2012, Kilduff et al. 2014). Estimates of first-year  
129 survival from Kilduff et al. (2014) indicate a greater than 40-fold difference between  
130 the minimum of 0.07% and maximum of 3.04% (median = 0.89%) for the cohorts  
131 emigrating 1980-2006. The result is that cohort strength and return rate appear to  
132 be set shortly after emigration to sea (Wells et al. 2012, Woodson & Litvin 2015).  
133 An examination of the results reported in Kilduff et al. (2014) demonstrates the  
134 covariation between first-year Chinook salmon survival and later adult abundance  
135 (Figure 3F). Suspected agents of mortality on salmon emigrating to the region  
136 include starvation, disease and, perhaps, increased relative predation on slower  
137 growing juveniles (Emmett & Krutzikowsky 2008, Tucker et al. 2013).

138

139 Evolution of productivity on this shelf ecosystem depends upon a suite of physical  
140 and biological processes occurring at the appropriate magnitude, spatial scale, and  
141 temporal window to ensure prey availability to newly arrived Chinook salmon  
142 smolts (Figure 1) (Cushing 1981, Satterthwaite et al. 2014). The condition of the  
143 forage community on the shelf that juvenile salmon experience upon emigration is  
144 correlated to later adult abundance (Thompson et al. 2012, Wells et al. 2012). The  
145 relatively few natural origin SRFC smolts (as opposed to hatchery) enter the Gulf of  
146 the Farallones generally between March and July, with the bulk arriving to sea  
147 during April through May (Lindley et al. 2009); presumably this timing matches the  
148 peak of prey availability in spring (Quinn 2005). Spreading the time over which  
149 salmon emigrate to sea is a bet-hedging approach to increase the probability that a  
150 portion of the population will intersect an appropriate forage base and exhibit  
151 improved survival (Scheuerell et al. 2009, Satterthwaite et al. 2014). There are a  
152 number of potential forage species in Gulf of the Farallones for juvenile salmon. The  
153 four prey that dominate juvenile salmon diet (by volume) off central California are  
154 *Euphausia pacifica*, *Thysanoessa spinifera*, fish (predominantly juvenile rockfishes,  
155 *Sebastes* spp.), and crab megalopias (MacFarlane & Norton 2002, Wells et al. 2012).  
156 Growth and recruitment of juvenile Chinook salmon is related to the abundance and  
157 distribution of these forage species at the time of juvenile salmon entry into the Gulf  
158 of Farallones from San Francisco Bay (MacFarlane & Norton 2002, Wells et al. 2012)  
159 (Figure 1, Factor C1).  
160

161 Generally, krill are the primary salmon prey in early spring, followed by a shift to  
162 forage fishes in later summer as the salmon grow (MacFarlane & Norton 2002, Wells  
163 et al. 2012). Salmon body condition is significantly related to the consumption of the  
164 euphausiid *Thysanoessa spinifera* (Wells et al. 2012) and juvenile fishes (MacFarlane  
165 and Norton 2002) (Figure 1, Factor C2). *T. spinifera*, a neritic species, is abundant on  
166 the shelf and is rarely observed in substantial number off the shelf (Figure 2, D)  
167 (Santora et al. 2012). Juvenile rockfishes feed on krill and krill eggs (Reilly et al.  
168 1992), so may be related to the abundance of *T. spinifera* as well. As a result,  
169 juvenile rockfishes abundance and distribution on the shelf is positively associated  
170 with krill abundance and distribution (Wells et al 2008, Santora et al, 2014). Path  
171 analysis suggests that the role of krill on juvenile salmon recruitment is direct and  
172 also indirect through rockfish prey (Thompson et al. 2012, Sydeman et al. 2013)  
173 (Figure 1, Factors F4-F5). Therefore, it is apparent that krill availability during the  
174 spring, at the time of first ocean entry, and the forage fishes that prey on krill are  
175 critical to salmon survival and recruitment to the spawning population (Wells et al.  
176 2012)(Figure 1, Factor C4).

177

178 Body condition and growth dynamics of salmon may determine mortality (Woodson  
179 et al. 2013) (Figure 1, Factors C2, C3) and recruitment to the adult population (Wells  
180 et al. 2012). Woodson et al. (2013) demonstrated that during years characterized by  
181 poor upwelling and limited prey resources, such as early spring of 2005 (Figure 3),  
182 smaller, slower growing Chinook salmon were subjected to significantly more  
183 mortality than their larger, faster growing counterparts. As noted in Figure 3F, the

184 survival of Chinook salmon emigrating to sea during 2005 was exceptionally low, as  
185 was later adult abundance. Although untested in central California, the smaller  
186 juvenile salmon may have experienced relatively more predation (Pearcy 1992,  
187 Tucker et al. 2013)(Figure 1 C3).

188

189 **How do regional transport and upwelling characteristics interact to retain and**  
190 **sustain forage on the shelf through the initial time of salmon emigration in**  
191 **spring?**

192

193 The spatial structure of the spring community of krill and forage fish (as well as  
194 ecologically-dependent seabirds) off central California is typically defined by a suite  
195 of habitat factors including bathymetry, geographic prominences, freshwater  
196 plumes, and upwelling intensity (Santora et al. 2012)(Figure 2). Point Reyes marks  
197 the northern boundary of the Gulf of the Farallones (Figure 1) and this promontory  
198 is associated with upwelling of cool waters (Figure 2,B). Concomitant with the  
199 southwestern flow from Point Reyes is a cyclonic eddy that creates a retentive area  
200 of typically warmed water (Figure 2, B), which retains primary productivity (Figure  
201 2, C) and a number of shelf-dependent species, such as juvenile rockfishes (Figure 2,  
202 E), krill (Figure 2, D), sanddabs and squid; all significant forage for salmon (Wells et  
203 al. 2012, Thayer et al. 2014) on the shelf (Figure 2, F). At much smaller scales  
204 (<10km), Woodson and Litvin (2015) demonstrate that the presence of fronts on  
205 the shelf concentrating nutrients and secondary production are significantly  
206 correlated to forage dynamics and later salmon abundance.

207

208 Upwelling during spring and summer is largely determined by regional-scale wind  
209 patterns (Schwing et al. 2002b). Off central California, coastal winds are upwelling  
210 favorable throughout the year, but become more intense in late winter and early  
211 spring (Bograd et al. 2009). The transition of the CCE to an intense upwelling system  
212 is related to the North Pacific High (NPH) atmospheric pressure cell gaining  
213 strength and size as well as moving more northward (Schroeder et al. 2013) (Figure  
214 1, Factor P4, Figure 4). As the NPH gains strength and moves northward, the  
215 gradient between low pressure on land and higher pressure over the ocean  
216 increases which results in the strengthening of northerly coastal winds.

217

218 While increased northerly winds in the spring relates to the overall productivity of  
219 the CCE, the balance between nutrient input and advection of primary and  
220 secondary production associated with upwelling is not temporally and spatially  
221 consistent along the entire California coast. Santora et al. (2011) demonstrate that  
222 the distribution of krill abundance hotspots (determined from acoustics surveys)  
223 along the California coast is negatively related to the magnitude of northerly winds  
224 (Ekman transport) and are disassociated with strong upwelling centers. Santora et  
225 al. (2011) ascribe this relationship to the optimal environmental window theory  
226 (Cury & Roy 1989), whereby enough wind to provide upwelled nutrients is essential  
227 but as the wind increases (especially near upwelling centers; Dorman et al. 2015),  
228 offshore Ekman transport causes advection of phytoplankton and zooplankton away  
229 from the coast (Figure 1, Factors P2, F1).

230 Along the entire California coast, relevant to krill, Santora et al. (2011)  
231 demonstrated clear evidence of the descending (right) side of Cury and Roy's  
232 hypothetical dome-shaped relationship (declining localized abundance with high  
233 levels of transport), but did not provide evidence for the ascending (left) side of the  
234 dome (*see* Figure 7 in Santora et al. 2011). The limited demonstration of the  
235 ascending portion of the dome likely resulted from examination of krill in exposed  
236 regions along the California coast. Within the Gulf of the Farallones, in the lee of  
237 Point Reyes, Wells et al (2012) demonstrated that the inter-annual variability of  
238 krill abundance (derived from nets) during spring was positively related (exhibiting  
239 an asymptotic response) to the intensity of coastal upwelling winds; demonstrating  
240 the ascending side of the Cury and Roy's parabolic relationship. These findings are  
241 complementary, as they elucidate the different scale-dependent relationships that  
242 coastal forage communities have with wind conditions at regional and local scales.  
243 Similar results from an individual-based-model of krill aggregations indicate that in  
244 the more exposed area north of Point Reyes (Figure 1), the intensity of krill hotspots  
245 is reduced with increased upwelling, however, in the protected region in the Gulf of  
246 the Farallones the relationship is inverse (Dorman et al. 2015).

247

248 Garcia-Reyes et al. (2014) provide additional insight into relationships among  
249 upwelling intensity, primary productivity and krill abundance on the central  
250 California shelf (Figure 2 A,B,C,D). In agreement with Wells et al. (2012), Garcia-  
251 Reyes et al. (2014) do not show a dramatic descending side in the relationship  
252 between krill abundance and regional upwelling intensity (*see* Figure 6 in Garcia-

253 Reyes et al. 2014), suggesting more intense upwelling results in more krill on the  
254 shelf in areas protected from the direct effect of wind (Figure 2, D). However, the  
255 relationship between upwelling intensity and Chlorophyll-a concentration indicates  
256 a clear parabolic relationship, where too much upwelling may lead to increased  
257 advection of primary production away from the shelf ecosystem (see Figure 6 in  
258 Garcia-Reyes et al. 2014). As a demonstration here through an examination of 1999,  
259 a strong La Niña year, intense upwelling (Figure 3, B) and advection in the spring is  
260 associated with reduced Chlorophyll-a concentration on the shelf (Figure 3, C), yet  
261 not reduced krill (Figure 3, D). In all, upwelling intensity, when great, can have a  
262 negative impact on retention of primary production, but not necessarily krill  
263 production on a protected shelf.

264

265 There are 10 numerically-dominant juvenile rockfish species that comprise a  
266 significant proportion of the forage assemblage on the shelf in spring following  
267 winter parturition (i.e., release of larval rockfish) (Ralston et al. 2013). The  
268 abundance of juvenile rockfishes on the shelf depends largely on the balance  
269 between transport and production resulting from upwelling dynamics (Figure 1,  
270 Factors F3, F5; Figure 2, E). Off central-northern California, Ralston et al. (2013)  
271 demonstrate that high juvenile rockfish abundance in late spring is associated with  
272 strong southward (equatorward) transport in winter months (as evaluated with  
273 regional relative sea level height) while years of very low abundance correspond  
274 with stronger northward (poleward) transport in winter months. Schroeder et al.  
275 (2014) provide additional insight on the interannual variability of juvenile rockfish

276 abundance through examination of the 26.0 isopycnal depth over the rockfish  
277 spawning grounds during winter parturition. The 26.0 isopycnal depth in central  
278 California represents a region of high nutrients (Palacios et al. 2013). During  
279 upwelling and associated southward transport events the 26.0 isopycnal shoals  
280 (Collins et al. 2003, Lynn et al. 2003). Schroeder et al. (2014) conclude that high  
281 juvenile rockfish abundance in spring is associated with a shallower 26.0 isopycnal  
282 depth over the spawning ground (i.e., shelf break) in winter as a result of transport  
283 dynamics and/or better feeding conditions immediately following the release of  
284 larval rockfishes (parturition).

285

286 There is evidence that extreme events, such as the increased spring upwelling  
287 during the La Niña of 1999, resulted in relatively low abundance of rockfishes in the  
288 Gulf of the Farallones, despite average krill abundance, likely due to the intensity of  
289 advection and upwelling during the timing of the rockfish survey that year (Figure 3,  
290 B) (Schwing et al. 2000, Ralston et al. 2013, Ralston et al. 2015). In 1999, the  
291 abundance of rockfishes caught in small mesh trawl surveys in the region was below  
292 mean values (Figure 3, E), perhaps due to high offshore Ekman transport, yet this  
293 cohort has now been recognized as one of the strongest recruitment events on  
294 record for most central California coast rockfishes (Ralston et al. 2013, Thorson et  
295 al. 2013). Therefore, it is important to consider not simply the production of  
296 rockfishes as a measure of potential prey to salmon, but also to consider the degree  
297 to which that production may be advected out of the Gulf of the Farallones at the  
298 critical period for juvenile salmon growth and survival.

299

300 **How does basin-scale atmosphere/ocean variability influence development of**  
301 **neritic food webs upon which juvenile salmon depend?**

302

303 The strength of the California Current relates positively to the transport of nutrients  
304 and biotic material (plankton) from subarctic northern waters to southward coastal  
305 communities, which increases the transport of nutrients and prey between  
306 neighboring neritic communities (Chelton et al. 1982, Roesler & Chelton 1987,  
307 Sydeman et al. 2011). A demonstrated benefit of a stronger California Current is the  
308 introduction of lipid-rich copepods from the Gulf of Alaska into the northern  
309 California current. These species are associated with increased production of  
310 northern California Current Chinook and coho (*O. kisutch*) salmon through direct  
311 and indirect effects on salmon prey (Peterson & Keister 2003, Peterson & Schwing  
312 2003, Peterson 2009, Carretta et al. 2011, Keister et al. 2011). As well, the increased  
313 production associated with lipid-rich copepods may reduce the impact of  
314 competition and predation on salmon (Pearcy 1992, Emmett et al. 2006).

315

316 Conditions in the North Pacific basin during winter have dramatic effects on  
317 primary and secondary productivity of the California Current coastal ecosystem  
318 (Figure 1, Factor P1, PP1, PP2). The area (size) of the NPH and its centroid, in part,  
319 determine the coastal ecosystem state in winter and productivity of the shelf  
320 ecosystem into spring (Schroeder et al. 2013); nearer the coast, a larger NPH in  
321 winter is associated with increased primary and secondary production in the

322 following spring (Figure 4, A,B). For example, variability of forage species  
323 composition and seabird reproduction during spring and summer is related to NPH  
324 area and location during January and February. Schroeder et al. (2013) calculated a  
325 preconditioning upwelling index (pCUI; Figure 4,B) from the sum of positive  
326 upwelling events in January and February. Winter upwelling is significantly  
327 positively related to juvenile rockfish abundance and the reproductive success of  
328 seabirds off central California and, therefore is indicative of a productive shelf  
329 ecosystem in the spring (Schroeder et al. 2013; Schroeder et al. 2014) (Figure 3, E).  
330  
331 Winter upwelling may "precondition" (Logerwell et al. 2003) or jump-start  
332 ecosystem productivity by providing nutrients for an early pulse of primary  
333 production (Figure 1, Factors P3, PP1, PP2), which may in turn sustain secondary  
334 and tertiary productivity (Figure 1, Factor F2) (Feinberg & Peterson 2003, Kahru et  
335 al. 2009, Garcia-Reyes et al. 2014) on which predators depend (Schroeder et al.  
336 2009, Black et al. 2010, Black et al. 2011, Schroeder et al. 2013, Schroeder et al.  
337 2014). While coastal upwelling winds are less frequent and intense in winter than  
338 spring (as indicated in Figure 2, A and B by sea surface temperatures that are  
339 greater at Point Reyes in winter than spring), they occur over a less stratified water  
340 column along the coast (Palacios et al. 2004) allowing for easier introduction of  
341 nutrients to the shelf. In addition, increased NPH area during the winter and the  
342 southward winds it produces along the CCE (Schroeder et al. 2013) could reduce the  
343 likelihood of northward transport of plankton from the Gulf of the Farallones  
344 (Figure 1) which can be substantial during periods having frequent northward

345 winds and associated alongshore currents (Dorman et al. 2011) (Figure 1, Factors  
346 P2, F1).  
347  
348 Schroeder et al. (2014) demonstrated that krill abundance on the shelf in spring  
349 relates to shoaling of the 26.0 potential density isopycnal depth during winter; an  
350 indication of enhanced winter upwelling and southward transport. In support,  
351 Dorman et al. (2011) demonstrate that advection of krill northward out of the Gulf  
352 of the Farallones in winter determines, in part, abundance of krill on the shelf in  
353 spring (Figure 1, Factors P2, F1). The northward advection of krill from the central  
354 California shelf during the winter of 2005 was associated with reproductive failure  
355 and mortality of krill-dependent predators such as salmon (Figure 3, F) (Kilduff et  
356 al. 2014) and seabirds (Sydeman et al. 2006, Wells et al. 2008). Specifically, as  
357 spring approaches, forage species for juvenile salmon are dependent on nearshore  
358 supply of plankton resulting from the upwelling of nutrient-rich water mass  
359 characterized by the 26.0 isopycnal depth (Figure 1, Factors P4, PP3, PP4, F4, Figure  
360 3, B, C, D). Schroeder et al (2014) also demonstrated that for juvenile rockfishes,  
361 their abundance on the shelf (Figures 3, E and 2, E) is tied to a shoaling of the 26.0  
362 isopycnal depth at the shelf break during winter (Figure 1, Factors PP1, F3, F5).  
363 Once krill abundance increases on the shelf, production of a number of forage  
364 species, including juvenile rockfishes, relates to krill abundance and distribution  
365 (Wells et al. 2008, Santora et al. 2014)(Figures 3, D,E and 2, D,E).  
366

367 SRFC hatchery-origin smolts have an increased likelihood of survival to maturity  
368 when released approximately 3-4 months following the timing of the spring  
369 transition to a dominantly upwelling system (Satterthwaite et al. 2014).  
370 Presumably, following on the findings of Croll et al. (2005) and Garcia-Reyes et al.  
371 (2014), this is the time needed from initial nutrient introduction to the ocean's  
372 mixed layer to result in sustained krill density on the shelf. Furthermore, juvenile  
373 rockfishes are transported from the shelf break onto the shelf during spring where  
374 parturition occurs 3 months earlier (Ralston & Howard 1995, Schroeder et al. 2014).  
375 Once on the shelf, juvenile rockfishes rely on krill and krill eggs as prey (Figure 1,  
376 Factor F5; Figure 2, D,E) (Reilly et al. 1992). Ultimately, a robust forage base of krill  
377 (Figure 2, D) and juvenile rockfishes (Figure 2, E) may be available on the shelf for  
378 juvenile salmon (Figure 2, F) after winter seasons with an anomalously strong NPH  
379 that leads to stronger than average winter upwelling on the central CCE coast. This  
380 is provided that winter and spring upwelling are strong enough to maintain a supply  
381 of nutrients to promote primary productivity (Figure 2, C) on the shelf, reduce  
382 northward advection of krill from the shelf, and facilitate transport and retention of  
383 juvenile rockfishes on the shelf.

384

385 We provide time series to compare the difference in ecosystem indicators between  
386 contrasting years (Figures 3 and 4). The years 2001 and 2005 are highlighted here  
387 to represent a good (2001) and poor (2005) year of primary, secondary, and tertiary  
388 production on the shelf (Schwing et al. 2002a, Peterson et al. 2006, Ralston et al.  
389 2015). During 2001, the area of the NPH during winter was near the highest values

390 of the time series (1990-2010) and pCUI was equally high (Figure 4,B). Figure 3 (A  
391 through F) shows that winter and spring upwelling at 39°N, and production of  
392 Chlorophyll-a, krill, rockfishes, and salmon were also increased. Conversely, in 2005,  
393 when the area of the NPH and the pCUI were low (Figure 4, B), the conditions and  
394 forage production on the shelf were below average (Figure 3) resulting in  
395 exceptionally low survival and recruitment of Chinook salmon (Figure 3F).

396

### 397 **Numerical ecosystem modeling**

398

399 Numerical ecosystem models provide a framework, often including a number of  
400 sub-models (Rose et al. 2010), which integrate biochemical ocean processes and the  
401 response of lower and higher trophic level functional groups (Travers et al. 2007).  
402 When ecosystem modeling is linked to observations, it necessitates the  
403 incorporation of measured environmental data and evaluation of model output at  
404 each biophysical sublevel. Schroeder et al. (2014) demonstrated that a data-  
405 assimilative oceanographic model tuned to the California Current system (Moore et  
406 al. 2011) provided a reasonably accurate representation of the spatial and temporal  
407 oceanographic characteristics at a resolution sufficient for examining dynamics of  
408 juvenile forage fish and krill. Santora et al. (2013) demonstrated that a coupled  
409 physical-biochemical model (CoSiNE; Chai et al. 2002) captured the spatial  
410 variability of krill hotspots along the California coast, and temporal variability of *T.*  
411 *spinifera* within the central California shelf, and its connection to seabird  
412 reproduction and spatial distribution. Figure 5 (modified from Santora et al. 2013)

413 shows ROMS-CoSiNE successfully captured inter-annual variability of observed krill  
414 abundance and distribution on the shelf. Going up a further trophic level, Fiechter et  
415 al. (2015b) used a linked biophysical modeling system to realistically hindcast  
416 population dynamics and abundance cycles of the forage fishes sardine (*Sardinops*  
417 *sagax*) and northern anchovy (*Engraulis mordax*) in the CCE 1959-2008.

418

419 Fiechter et al. (2015a) applied a numerical ecosystem model that combines a  
420 regional ocean circulation model (Shchepetkin & McWilliams 2005, Haidvogel et al.  
421 2008), a nutrient-phytoplankton-zooplankton model (NEMURO; Kishi et al. 2007),  
422 and an individual-based-model for juvenile salmon. Model simulations examined  
423 factors that affect juvenile Chinook salmon growth during early marine residence.  
424 Specifically, Fiechter et al. (2015a) tested the hypothesis (Figure 1) that phenology  
425 and intensity of upwelling and resultant primary productivity and secondary  
426 productivity, affect salmon growth differentially between years of good and poor  
427 survival. Model results indicated that the early onset of intense upwelling is  
428 associated with increased growth of salmon. During years of improved survival  
429 (1984, 1986, and 2000) (Kilduff et al. 2014) early upwelling was more intense than  
430 years of poor survival (1989, 1990, and 2006), as indirectly demonstrated by lower  
431 modeled temperatures in late March through September. Associated with increased  
432 upwelling was greater primary productivity in March, which was sustained through  
433 September. By May, modeled zooplankton was significantly greater during good  
434 years of salmon survival relative to poor years (Figure 6, C). Salmon growth  
435 associated with the modeled years of good survival was significantly greater than

436 during years of poor survival. While we focus on the relative results, it is also worth  
437 noting that the results from the simulation are similar to observed values of salmon  
438 body condition and growth observed in juvenile Chinook salmon collected at sea  
439 (MacFarlane 2010).

440

#### 441 **Summary**

442

443 Based on our review and synthesis, we develop a conceptual model for the key  
444 biophysical processes operating at basin to meso-scales that together influence the  
445 year-to-year variations in hatchery-origin SRFC marine survival (Figure 1). A  
446 growing body of evidence suggests that variations in early marine growth and  
447 survival rates are strongly linked, and that the first few weeks at sea represents a  
448 critical period for this and many other Pacific salmon stocks. Moreover, early marine  
449 survival appears to be highly correlated with total marine survival as is apparent  
450 through examination of the covariation of early marine survival rates and later adult  
451 abundance estimates shown in Figure 3F.

452

453 At the basin scale, the strength and location of the NPH during winter preconditions  
454 the coastal ecosystem for the amount of productivity it will have during spring and  
455 summer (Schroeder et al. 2009, Black et al. 2011, Thompson et al. 2012, Schroeder  
456 et al. 2013). Preconditioning promotes the continued supply of nutrients and  
457 production of a robust forage assemblage on the shelf during winter (Wells et al.  
458 2012, Thayer et al. 2014). As spring approaches and the transition to intense

459 upwelling occurs, the strength and duration of the upwelling season will depend, in  
460 part, on the date of that transition, as moderated by the regional winds determined  
461 by location and strength of the NPH. Namely, if the ecosystem experiences more  
462 intense and consistent early upwelling (Bograd et al. 2009, Sydeman & Bograd 2009,  
463 Fiechter et al. 2015a), early and continued nutrient introduction enables  
464 development and maintenance of populations of krill, forage fish and higher trophic  
465 level predators in the Gulf of the Farallones. Otherwise, there can be a mismatch  
466 between the timing of the predator's requirements and the development of a forage  
467 base on the shelf (e.g., Sydeman et al. 2006, Ainley et al. 2009, Satterthwaite et al.  
468 2014). Relevant to salmon, the appropriate forage must be available immediately  
469 upon ocean entry in the Gulf of the Farallones (Figure 2, D, E, F), otherwise,  
470 anomalously high mortality may occur (Lindley et al. 2009, Woodson et al. 2013).

471

472 The general model of interactions acting on salmon dynamics we review is subject  
473 to vary as climate change impacts shelf ecosystems. Several studies showed that  
474 northerly alongshore winds that force coastal upwelling intensified (from the early  
475 1980s to early 2000s) along the California Current (Bakun & Parrish 1990, Schwing  
476 & Mendelssohn 1997, Garcia-Reyes & Largier 2010, Sydeman et al. 2014). However,  
477 any benefits to the ecosystem due to the increased upwelling from the intensified  
478 winds may be mitigated by increased stratification, changes in the upper ocean  
479 thermal structure, and/or changes in source water nutrient concentrations, all of  
480 which influence the biological efficacy of upwelling (Bakun et al. 2015). Further, due  
481 to basin-scale forcing, variability in coastal winds has increased (Macias et al. 2012),

482 contributing to a recent increase in the variability of production of salmon and  
483 seabirds in the region (Sydeman et al. 2013).

484

485 This work has application to management of the SRFC. A recent collapse in the SRFC  
486 stock resulted in the closure of the fishery in 2008 and 2009 with limited opening in  
487 2010. The collapse and subsequent Disaster Declaration resulted in an exhaustive  
488 search for the causes of the run failures (Lindley et al. 2009). Although a firm  
489 conclusion was elusive, there were indications that late and/or weak upwelling in  
490 the coastal ocean was the proximate cause for increased early marine mortality of  
491 juvenile salmon (Lindley et al. 2009). Our synthesis of the literature provides a  
492 detailed conceptual model for the likely causes of the collapse. As well, there is  
493 demonstrated value in using the numerical ecosystem model to anticipate future  
494 collapses under varying environmental conditions.

495

496 We largely focused on bottom-up factors related to early marine salmon growth and  
497 recruitment. A substantial amount of mortality on juvenile salmon may be due to  
498 increased predation of the slower growing, smaller members of a cohort (Cowan et  
499 al. 1996, Tucker et al. 2013). In essence, we expect top-down impacts caused by  
500 predation to be related to bottom-up determinants of juvenile salmon growth  
501 dynamics (Figure 1). The effect of these top-down impacts likely increases as  
502 alternate prey becomes more limited (LaCroix et al. 2009). Furthermore,  
503 interactions between juvenile salmon and predators can vary with changes in their

504 distributions associated with variability in ocean conditions (Pearcy 1992, Emmett  
505 et al. 2006).

506

507 Our synthesis is appropriate to a general functional understanding of the central  
508 California shelf ecosystem. The life history of many species within the greater Gulf of  
509 the Farallones region has evolved in response to winter and spring conditions that  
510 support krill and juvenile rockfishes being present on the shelf in spring and  
511 summer as a prey resource. For instance, planktivorous and piscivorous seabird  
512 species (e.g., Cassin's Auklet *Ptychoramphus aleuticus* and Common Murre *Uria*  
513 *aalge*) that nest on the Farallon Islands during the spring have lay dates that are  
514 correlated with February sea surface temperatures and northerly winds, which  
515 correspond to increased May-June forage abundance on which the nestlings can  
516 feed (Schroeder et al. 2009).

517

### 518 **Future research directions**

519

520 There are number of important issues yet to be addressed for central California  
521 Chinook salmon: (a) the impact of freshwater and estuarine conditions on condition  
522 and mortality in the ocean; (b) the impact that predators have on salmon, and (c) an  
523 evaluation of ecosystem factors contributing to mortality and maturation dynamics  
524 after the first winter at sea. Further, upon addressing these issues, we could also ask  
525 questions about the impact of salmon on the ecosystem. Such objectives should  
526 include quantifying salmon predator response to variability in salmon distribution,

527 growth and mortality. Furthermore, there should be an analysis of how all of the  
528 interacting factors (e.g., environment, forage, salmon production, and predatory  
529 responses) impact fisheries, food security, and cultures and how we may mitigate  
530 the influences of competing interests. In short, the present work is a piece of the  
531 overall requirements for defining and implementing inclusive ecosystem  
532 management objectives.

533

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545

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874 *Oncorhynchus tshawytscha* during early ocean residence. *Mar Ecol Prog Ser*  
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876

877 **Figure list**

878

879 Figure 1: A conceptual model of interacting spatial and temporal aspects related to  
880 juvenile Chinook salmon prey availability and salmon growth and survival. These  
881 factors are arranged relative to the physics (**blue**), primary production (**green**),  
882 forage (**brown**), and Chinook salmon (**purple**) responses. Upper and lower portions  
883 represent factors related to winter and spring conditions respectively. This is not a  
884 complete list of proposed ecosystem factors determining salmon growth and  
885 survival. The model is not meant as a predetermined model for salmon growth and  
886 survival but it allows for a broad examination of the system to identify factor's  
887 direct and indirect effects on salmon and forage dynamics. Monterey Bay is  
888 abbreviated to MB and Gulf of the Farallones is abbreviated to GoF. The  
889 relationships between the factors, within the ecosystem model, are supported by the  
890 literature. Factors: **P1**) Black et al. 2011, Schroeder et al. 2013, Schroeder et al.  
891 2009; **P2**) Dorman et al. 2011; **P3**) Black et al. 2011, Schroeder et al. 2011; **P4**)  
892 Bograd et al. 2009, Schroeder et al. 2013; **PP1**) Garcia-Reyes et al. 2014, Schroeder  
893 et al. 2014; **PP2**) Kahru et al. 2009; Dorman et al. 2011; **PP3**) Garcia-Reyes et al.  
894 2014; **PP4**) Kahru et al. 2009; **F1**) Dorman et al. 2011; **F2**) Feinberg & Peterson  
895 2003, Garcia-Reyes et al. 2014, Dorman et al. 2015; **F3**) Schroeder et al. 2014;  
896 Ralston et al. 2013; **F4**) Wells et al. 2008, Dorman et al. 2011, Garcia-Reyes et al.  
897 2014; **F5**) Reilly et al. 1992; **C1**) Satterthwaite et al. 2014; **C2**) MacFarlane 2010,  
898 Woodson et al. 2013b; **C3**) Woodson et al 2013b; **C4**) Kilduff et al. 2014, Lindley et

899 al. 2009, Satterthwaite et al. 2014; **Predation**) LaCroix et al. 2009, Tucker et al.  
900 2013

901

902 Figure 2: Distributions of environmental and biological values from central

903 California. A) Average sea surface temperatures in February, 2002-2013

904 (<http://coastwatch.pfeg.noaa.gov/erddap/griddap/erdBASstamday.html>). B)

905 Average sea surface temperatures in May (same source as A). C) Average

906 chlorophyll-a from SeaWiFS, May 1997-2006

907 (<http://coastwatch.pfeg.noaa.gov/erddap/griddap/erdSAchlamday.html>).

908 Biological distribution data are derived from Santora et al. 2012 and represent the

909 standardized distribution patterns for D) krill, E) juvenile rockfishes, and F) juvenile

910 Chinook salmon in May 1990-2010.

911

912 Figure 3: Environmental and biological time series from central California. We focus

913 on 1990-2010 to allow comparisons between standardized time series. Vertical blue

914 lines represent 1999, 2001, and 2005. A) Time series of upwelling in February at

915 39°N

916 (<http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling>

917 [.html](http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling)). B) Time series of upwelling in May at 39°N (same source as A). C) Time series

918 of chlorophyll-a concentrations averaged over depths 6-22 m from *in situ* collections

919 during May in central California (see Santora et al. 2012 for details). Biological time

920 series of D) krill, E) juvenile rockfishes are from Santora et al (2014). F) Black line

921 shows the adult abundance of Chinook salmon as represented by an index of adult

922 abundance lagged two years back to match timing of emigration to sea (O'Farrell et  
923 al. 2013) and the orange line shows the standardized log-transformed survival  
924 estimates of cohorts 1990-2006 from Kilduff et al. (2014).

925

926 Figure 4: The location and size of the North Pacific High pressure cell during winter  
927 relates to productivity on the shelf in the spring. A) Shows the average monthly  
928 location and size (the area encompassing the 1200 hPa isobar;  $\text{km}^2 \times 10^6$ ) of the  
929 North Pacific High, 1967-2010 (Schroeder et al. 2013). B) shows the time series  
930 1990-2010 of the area of the North Pacific High (orange) and the preconditioning  
931 upwelling index (pCUI; black) for central California (Schroeder et al. 2013). The  
932 location represented by the pCUI is shown as the inset box on plot A. Blue vertical  
933 lines represent the years 1999, 2001, and 2005.

934

935 Figure 5: A) Evaluation of the coherence between modeled meso-zooplankton (Z2;  
936  $\text{mmol-N m}^{-2}$ ), within depths of 0–100 m, and observed krill abundance (net hauls of  
937 *T. spinifera*) off central California (derived from Santora et al. 2013). The blue point  
938 represents 2006; the only over-lapping year between the analyses of Santora et al.  
939 (2013) and Fiechter et al (2015a). The data for 2006 was identified as a poor year of  
940 salmon survival and growth. B) The averaged (May; 2002-2009) spatial distribution  
941 of Z2 from the ocean-ecosystem model (CoSiNE) is coherent with observed krill  
942 distribution shown in Figure 2, D.

943

944 Figure 6: Biophysical model results taken directly from Fiechter et al. (2015a). The  
945 results demonstrate that during years of known good survival for Chinook salmon,  
946 A) cooler temperatures occurred earlier (representing upwelling), B) phytoplankton  
947 production occurred earlier and C) zooplankton was more productive and sustained  
948 (compare results to that circled in blue in Figure 5, A).  
949

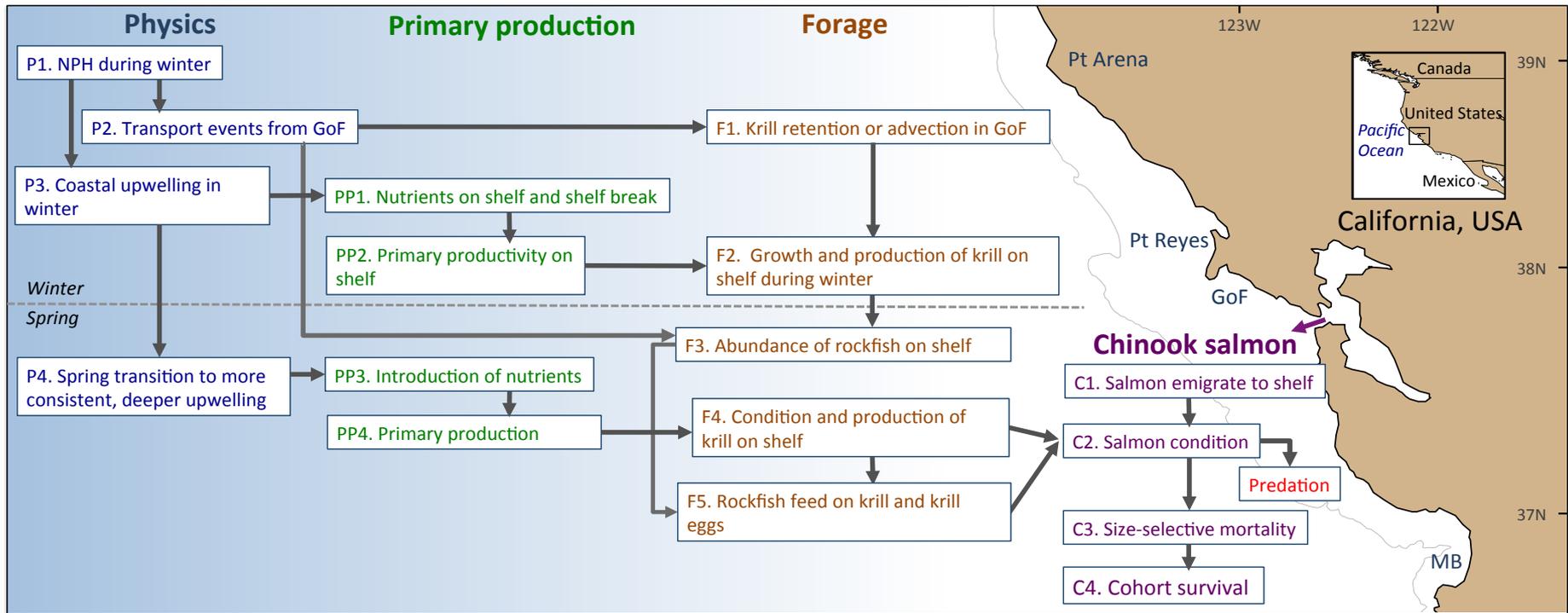


Figure 1

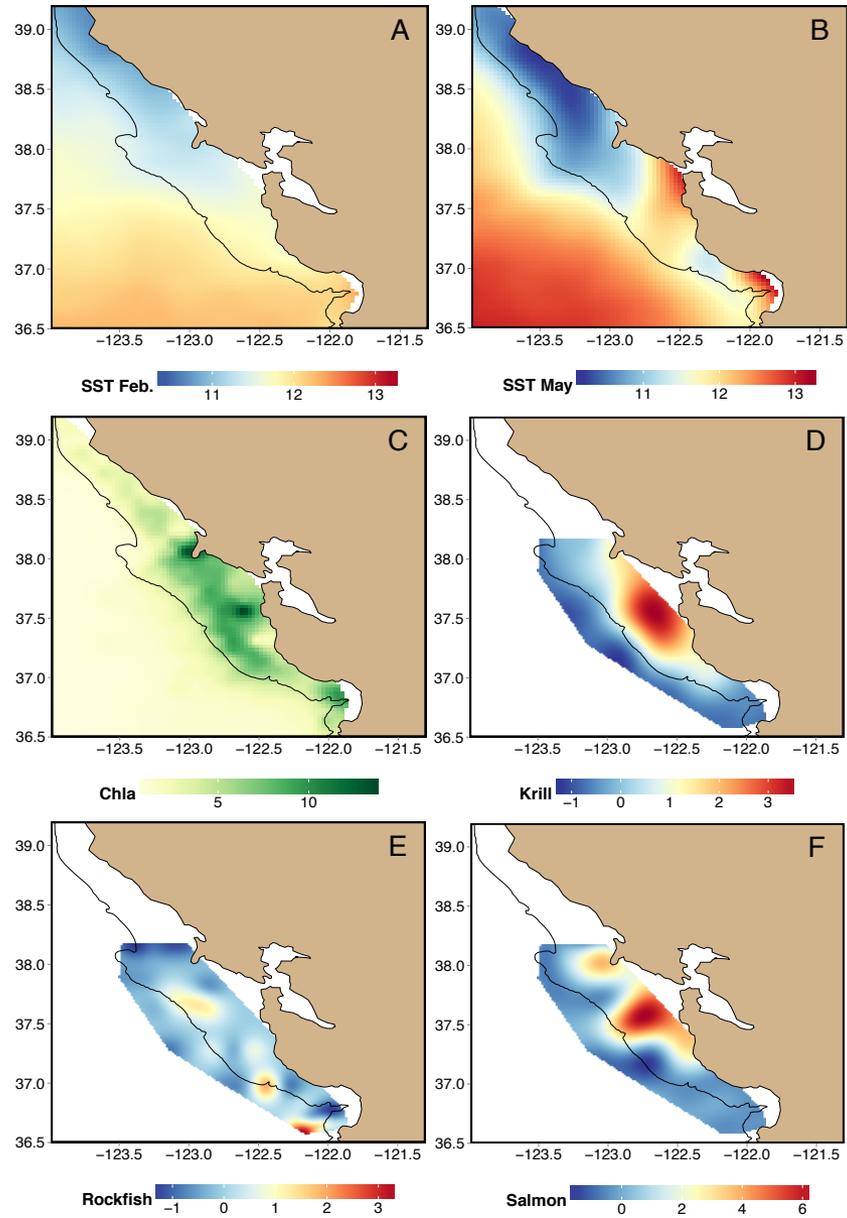


Figure 2

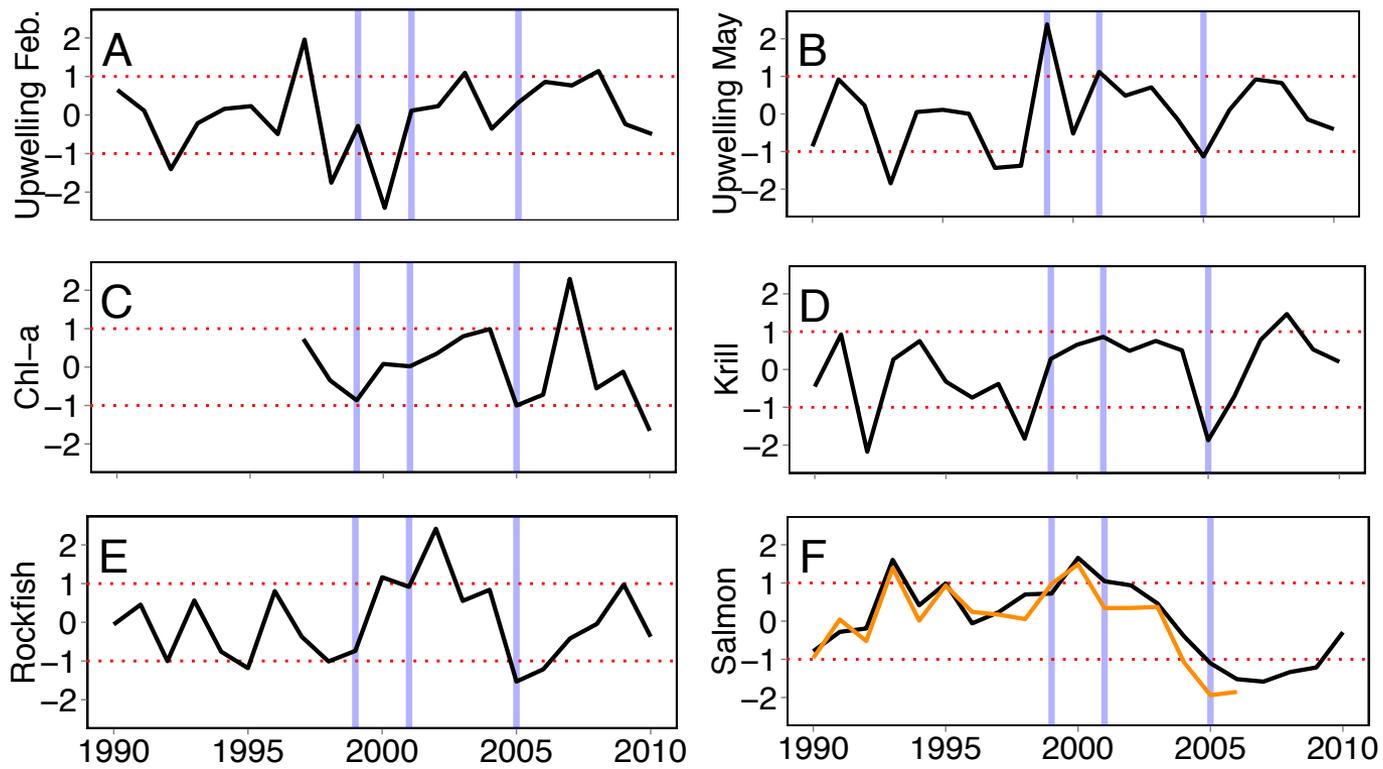


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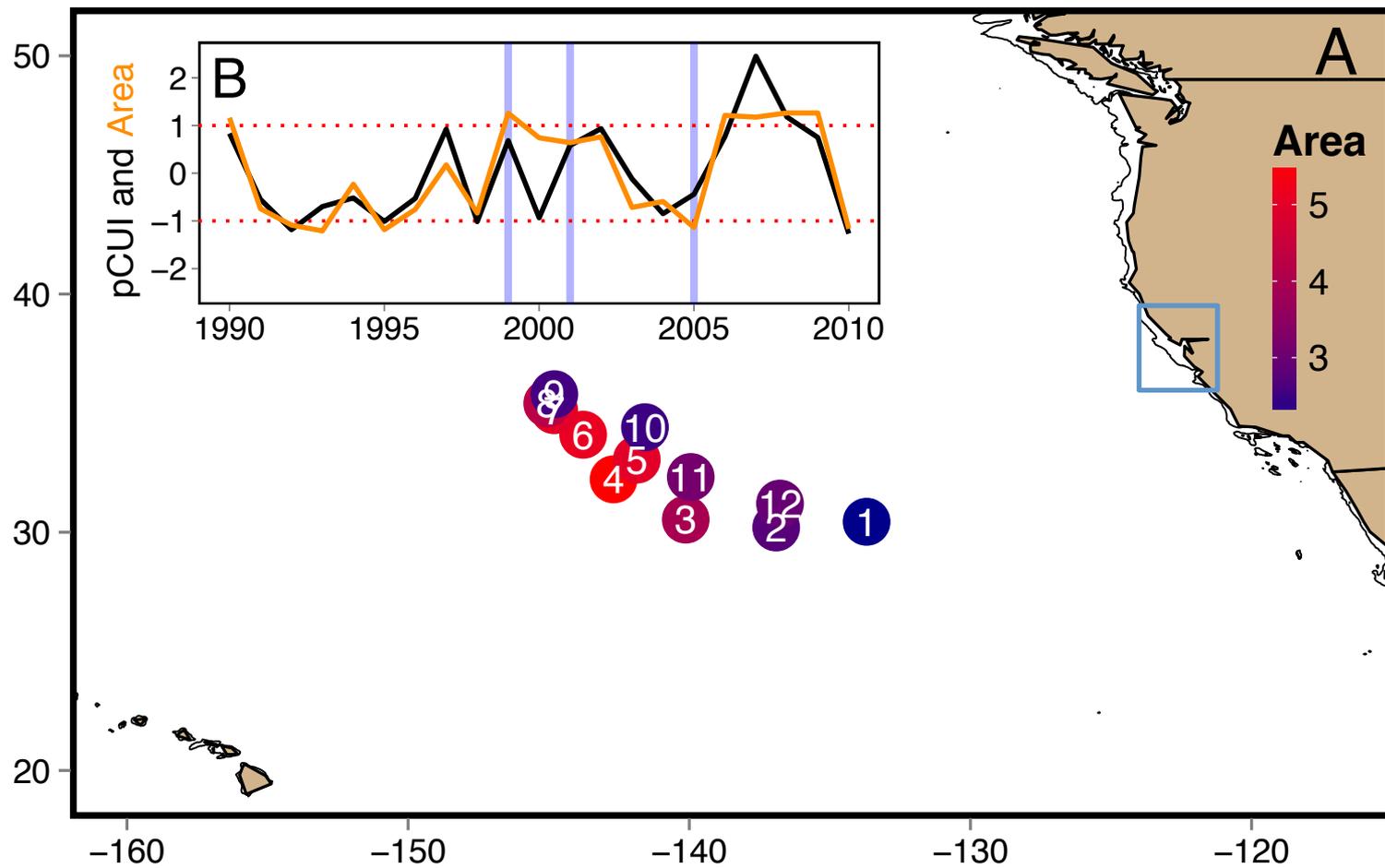


Figure 4

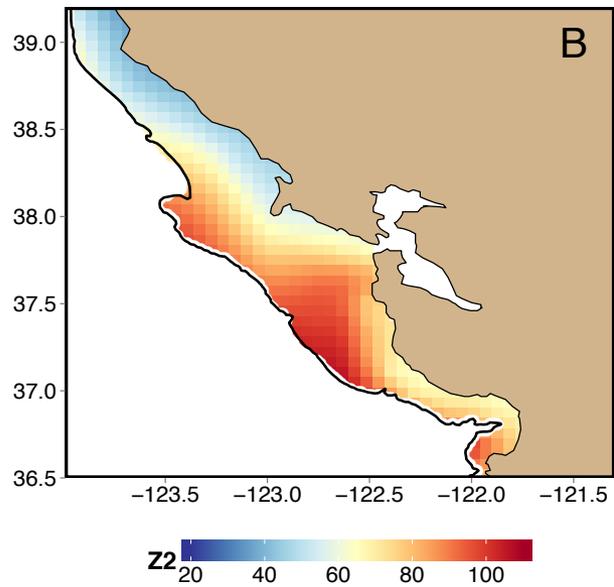
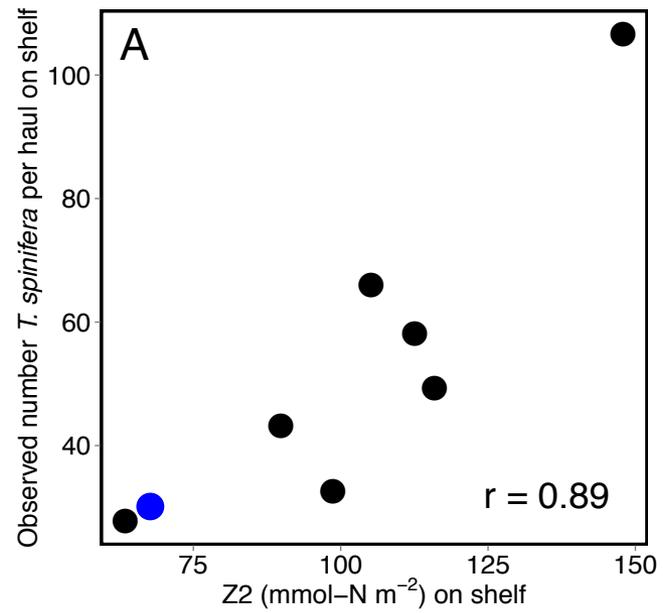


Figure 5

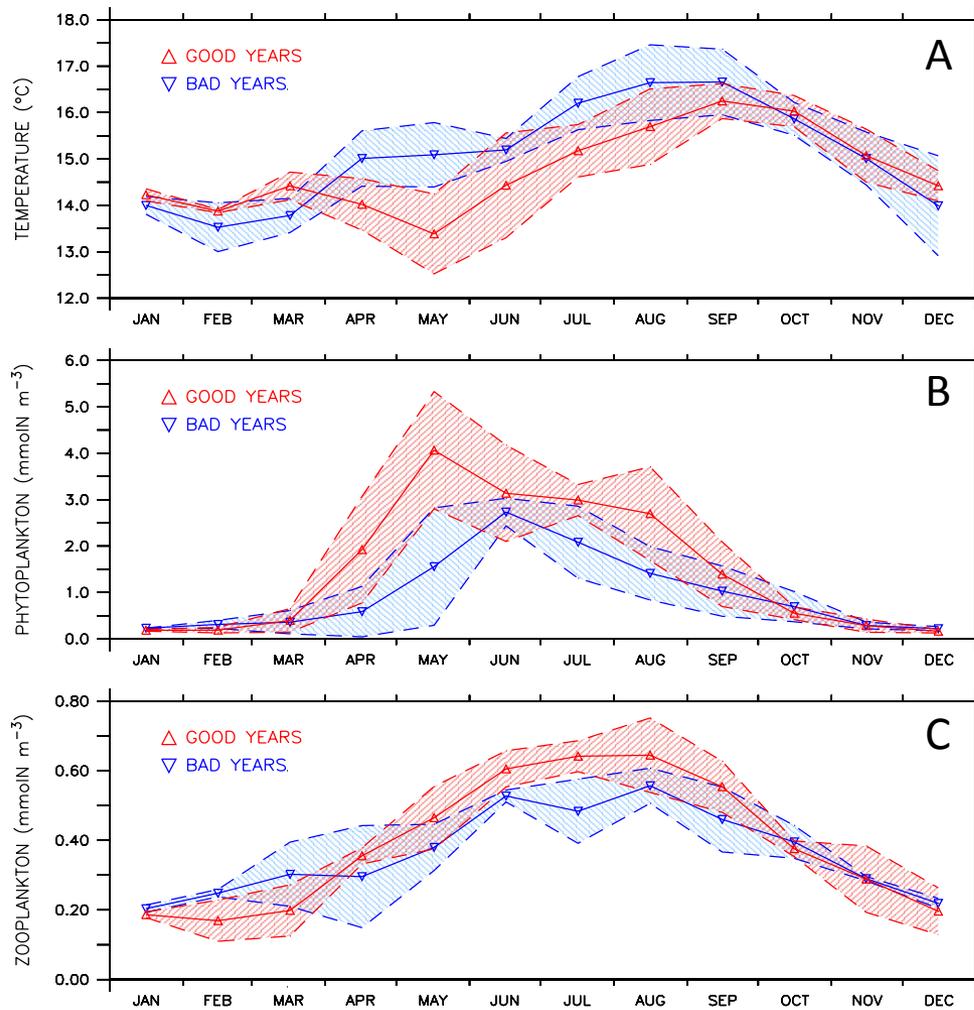


Figure 6