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**Phenological and distributional shifts in ichthyoplankton associated with recent warming in the northeast Pacific Ocean**

Running head: Phenology shifts in Pacific Ocean fish

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ABSTRACT: Understanding changes in the migratory and reproductive phenology of fish stocks in relation to climate change is critical for accurate ecosystem-based fisheries management. Relocation and changes in timing of reproduction can have dramatic effects upon the success of fish populations and throughout the food web. During anomalously warm conditions (1-4° C above normal) in the northeast Pacific Ocean during 2015-2016, we documented shifts in timing and spawning location of several pelagic fish stocks based on larval fish samples. Total larval concentrations in the northern California Current (NCC) during winter (January-March) 2015 and 2016 were the highest observed since annual collections first occurred in 1998, primarily due to increased abundances of *Engraulis mordax* (northern anchovy) and *Sardinops sagax* (Pacific sardine) larvae, which are normally summer spawning species in this region. *Sardinops sagax* and *Merluccius productus* (Pacific hake) exhibited an unprecedented early and northward spawning expansion during 2015-16. Additionally, spawning duration was greatly increased for *E. mordax*, as the presence of larvae was observed throughout the majority of 2015-16, indicating prolonged and nearly continuous spawning of adults throughout the warm period. Larvae from all three of these species have never before been collected in the NCC as early in the year. Additionally, other southern species were collected in the NCC during this period. This suggests that the spawning phenology and distribution of several ecologically and commercially important fish species dramatically and rapidly changed in response to the warming conditions occurring in 2014-2016, and could be an indication of future conditions under projected climate change. Changes in spawning timing and poleward migration of fish populations due to warmer ocean conditions or global climate change will negatively impact areas that were historically dependent on these fish, and change the food web structure of the areas that the fish move into with unforeseen consequences.

## INTRODUCTION

61 Global climate change is expected to occur over the next few centuries and lead to  
62 unprecedented effects in both terrestrial and aquatic ecosystems (Walther et al., 2002;  
63 Parmesan, 2006; Doney et al., 2012), many of which have already been observed  
64 (Parmesan & Yohe, 2003; Poloczanska et al., 2013, 2016). Among the many  
65 perturbations (e.g., warming, acidification, deoxygenation, sea-level rise) expected to  
66 occur in marine systems with climate change, the effects of temperature on the  
67 distribution and physiology of marine organisms is expected to be the most pervasive  
68 (Doney et al., 2012). Although global temperatures are expected to rise by several  
69 degrees in the next century, these effects are not uniform throughout the world's oceans  
70 (Wang et al., 2010), with the California Current upwelling system off the west coast of  
71 North America expected to show highly variable responses (Wang et al., 2010; Sydeman  
72 et al., 2014; García-Reyes et al., 2015).

73 Based on projected model outputs under different climate scenarios, the  
74 California Current is expected to show changes in fish distributions (Hsieh et al., 2009;  
75 Cheung et al., 2015) and carrying capacity (Woodworth-Jefcoats et al., 2013, 2016). In  
76 addition to shifts in distribution that result in habitat changes, changes to the seasonal  
77 timing of events (phenology) such as plankton blooms and fish spawning events are  
78 likely to occur. Larval fish appear to be sensitive indicators of climate change, reflecting  
79 advancement of spring spawning at approximate rates of 11 days per decade  
80 (Poloczanska et al., 2013). The only study to date which examined changes in the  
81 phenology of larval fishes from the southern California Current in response to climate  
82 change found evidence for both earlier and delayed timing of larval occurrence, which  
83 “were more closely associated with a trend toward earlier warming of surface waters  
84 rather than decadal climate cycles” (Asch, 2015).

85 Larval-stage fish dynamics are important for understanding various aspects of  
86 marine ecosystems. This information can be used as indicators of spawning locations and  
87 seasonality, spawning stock biomass (Lasker, 1985; Hunter & Lo, 1993; Ralston et al.,  
88 2003), future recruitment potential of fish stocks (Houde, 2008; Hsieh et al., 2006), and  
89 trophic interactions between zooplankton and piscivore communities (Young & Davis,  
90 1990; Auth, 2003; Daly et al., 2013). Because larval-stage dynamics are influenced by  
91 local and basin-scale environmental forcing factors both in the northern California  
92 Current (NCC; Auth, 2008, 2011; Brodeur et al., 2008; Auth et al., 2011) and elsewhere

93 in the northeastern Pacific Ocean (Hsieh et al., 2005; Boeing & Duffy-Anderson, 2008;  
94 Doyle et al., 2009), they are particularly suitable as indicators of changes in ocean and  
95 climate conditions in the region (Brodeur et al., 2006, 2008; Guan et al., 2017).

96 Ichthyoplankton communities have been relatively well-studied in the NCC  
97 region over the last 30 years (Auth & Brodeur, 2013), during which time episodic  
98 anomalies in those communities have been documented resulting from several El Niño  
99 events and other environmental fluctuations. For example, Brodeur et al. (2008)  
100 examined larvae collected biweekly-monthly in 1997-2006 at two nearshore stations off  
101 the central Oregon coast and found the lowest mean concentration of the time-series for  
102 total larvae during the 1997-98 El Niño. However, Auth et al. (2015) found anomalously  
103 high concentrations and both shoreward and northward displacement of fish larvae during  
104 the 2010 El Niño.

105 Anomalously warm (1-4 °C above normal) ocean conditions occurred in the  
106 northeastern Pacific Ocean from late 2014 through late 2015 (Di Lorenzo & Mantua,  
107 2016; Peterson et al., 2016). This warming, commonly referred to as the ‘warm blob’,  
108 was the result of reduced cyclonic storms in the Gulf of Alaska which reduced oceanic  
109 mixing, and subsequent cooling, of the upper ocean (Bond et al. 2015). This was  
110 followed by the strongest tropical El Niño event ever recorded (Jacox et al., 2016), that  
111 lasted into early summer 2016 and resulted in continued elevated water temperatures (Di  
112 Lorenzo & Mantua, 2016; McClatchie et al., 2016). These events culminated in  
113 prolonged anomalously warm ocean conditions that exceeded the duration and magnitude  
114 of other warming events occurring over the past two decades such as the 1997-98 El  
115 Niño. This prolonged warming resulted in significant changes to marine communities  
116 throughout the pelagic food-web of the California Current (Leising et al., 2015; Cavole et  
117 al., 2016; Di Lorenzo & Mantua, 2016; McClatchie et al., 2016; Peterson et al., 2016).

118 The purpose of this study is to examine how the anomalous ocean conditions  
119 resulting from the 2015-16 warm-water phenomenon affected the larval assemblage  
120 structure, diversity, concentration, distribution, and phenology of commercially and  
121 ecologically important fish stocks in the NCC. To compare this recent event to other  
122 climatic events, we analyzed larvae collected during winter of 2015-16 in relation to a  
123 long time-series of similar winter collections that occurred in 1998-2014. To determine  
124 whether larval fish exhibited shifts in phenological timing or cross-shelf distributions, we

125 also examined biweekly-monthly year-round collections from near-shore stations, as well  
126 as cross-shelf to oceanic samples from quarterly surveys, conducted in 2015-16 off the  
127 central coast of Oregon. We focused our analyses on *Engraulis mordax* (northern  
128 anchovy) and *Sardinops sagax* (Pacific sardine) larvae, and to a lesser extent larval  
129 *Merluccius productus* (Pacific hake), and related variations in their concentration patterns  
130 to local (i.e., temperature and salinity) and basin-scale (i.e., Pacific Decadal Oscillation  
131 [PDO] and Oceanic Niño Index [ONI]) environmental variables. By comparing our  
132 findings with previous studies, we hope to show how increasingly dynamic and  
133 prolonged environmental fluctuations may impact fish stocks in the California Current  
134 ecosystem in the future.

## 135 136 137 **MATERIALS AND METHODS**

### 138 139 **Sampling procedures**

140  
141 A total of 188 ichthyoplankton samples were collected during 31 cruises from  
142 stations spaced 7-46 km apart along a single transect (Newport Hydrographic [NH] line;  
143 44.6° N) extending 2-364 km off the central Oregon coast (Appendix 1, Fig. 1). From  
144 this set of samples, we extracted overlapping subsets (i.e., winter, near-shore, and cross-  
145 shelf) according to a design structured to address specific hypotheses. Winter samples  
146 were collected at six stations spaced ~9 km apart located 2-46 km offshore (NH 1-25)  
147 during January-March 2015-16 on a ~biweekly basis (only one set of samples was  
148 collected in January and February 2016). These samples were compared with data from  
149 similar collections made in 1998-2010, as described in Auth et al. (2015) and updated  
150 (2011-14) and summarized in the National Oceanic and Atmospheric Administration  
151 (NOAA) Northwest Fisheries Science Center's (NWFSC) winter ichthyoplankton index  
152 for the forecasting of adult returns of coho (*Oncorhynchus kisutch*) and Chinook (*O.*  
153 *tshawytscha*) salmon in the Pacific Northwestern United States  
154 (<https://www.nwfsc.noaa.gov/research/divisions/fe/estuarine/oeip/g-forecast.cfm>, 2017).  
155 In order to understand high-frequency patterns in larval dynamics, near-shore samples  
156 were collected at four stations spaced ~9 km apart located 2-28 km offshore (NH 1-15)

157 monthly from January 2015 to December 2016 (no samples were collected in December  
158 2015). To investigate cross-shelf patterns across seasons, samples were collected at 10  
159 stations spaced 7-37 km apart located 2-155 km offshore (NH 1-85) ~quarterly from  
160 March 2015 to December 2016. However, in April 2015 and February 2016, sampling  
161 was conducted at 15 and 13 stations, respectively, extending 2-364 km offshore (NH 1-  
162 200), while in December 2016, sampling was conducted at only six stations extending 2-  
163 46 km offshore (NH 1-25). Not all samples from each sampling subset were distinct, as  
164 samples collected from some cruises were analyzed as part of multiple, overlapping  
165 sampling subsets. Sampling was done at different times during both day and night, and  
166 not all stations were sampled during each cruise due to weather or equipment issues.

167 Samples were collected using a 60-cm diameter bongo with paired 333- $\mu$ m mesh  
168 nets. The bongo was fished as a continuous oblique tow within the upper ~30 m of the  
169 water column at stations NH 1-25 and within the upper ~100 m at stations NH 35-200, at  
170 a line retrieval rate of ~30 m min<sup>-1</sup> and a ship speed of 1 to 1.5 m s<sup>-1</sup>. The length of tow-  
171 wire out and ship and retrieval speeds were continually adjusted during each tow to  
172 ensure a wire angle of 45° in order to maintain an effective mouth opening of 0.28 m<sup>2</sup>  
173 throughout the tow. A depth recorder and flowmeter were placed within the net to  
174 determine the tow depth and volume of water filtered. Mean water-volume filtered was  
175 45.19 (SE = 0.96) and 138.16 m<sup>3</sup> (SE = 5.05) for the 30-m and 100-m tows, respectively.

176 Ichthyoplankton samples were preserved in a 10% buffered-formalin seawater  
177 solution at sea. Fish larvae from each sample were counted and identified to the lowest  
178 taxonomic level possible in the laboratory using a dissecting microscope. The lesser of  
179 either all larvae or a random subsample of 30 individuals from each taxon in each sample  
180 were measured to the nearest 0.1 mm standard length (SL), or notocord length (NL) for  
181 preflexon larvae, using either an ocular micrometer mounted on the sorting microscope or  
182 Leica Application Suite 4.5.0 imaging software (Leica Microsystems Ltd. 2014). Most  
183 larval osmerids (smelts), *Sebastes* spp. (rockfishes), *Sebastolobus* spp. (thornyheads), and  
184 *Citharichthys* spp. (sanddabs) collected were not identifiable to species based on  
185 meristics and pigmentation patterns, so these taxa were analyzed at the family or generic  
186 level. However, the majority of individuals classified as *Citharichthys* spp. are either *C.*  
187 *sordidus* (Pacific sanddab) or *C. stigmaeus* (speckled sanddab) based on the larger,

188 identifiable individuals collected and dominance of these species in the NCC  
189 ichthyoplankton (Matarese et al., 2003).

190

191

### **Environmental Data**

192

193 Local changes in hydrography were determined at each station from water-  
194 column profiles of temperature and salinity collected with a SBE25 CTD (Sea-bird  
195 electronics). Temperature and salinity from two stations, NH 5 located in 60 m of water  
196 and NH 25 located in 300 m of water, were chosen to represent fluctuations on the shelf  
197 and shelf slope. To show the winter annual deviations throughout the water column,  
198 anomalies of temperature and salinity were obtained by subtracting the January-March  
199 climatology (1996-2015) from the annual January-March mean. Monthly-averaged sea-  
200 surface temperature in 1998-2016 (SST, °C; <http://www.ndbc.noaa.gov/>, 2017) recorded  
201 from the National Oceanic and Atmospheric Administration's (NOAA) Stonewall Banks  
202 buoy located 20 nm (37 km) west of Newport, Oregon (44.64°N, 124.50°W) was  
203 calculated to show seasonal and annual water temperature differences in 2015-16 relative  
204 to the monthly means over the past two decades. Low-frequency, basin-scale fluctuations  
205 in the north Pacific Ocean and at the equator were indexed using the PDO  
206 (<http://research.jisao.washington.edu/pdo/PDO.latest.txt>, 2017) and ONI  
207 ([http://www.cpc.ncep.noaa.gov/products/analysis\\_monitoring/ensostuff/ensoyears.shtml](http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml),  
208 2017).

209

210

### **Data analyses**

211

212 Larval concentrations were expressed as the number of individuals per 1000 m<sup>3</sup>.  
213 Mean concentrations were often log<sub>10</sub>(N + 0.1)-transformed to facilitate the display of  
214 data over a wide range of values. Weighted mean (based on concentration) lengths  
215 (WML) of important larval species were calculated for each sample, and after testing for  
216 and finding no significant cross-shelf differences in WMLs for any of the primary larval  
217 species examined, monthly means were calculated based on all sampled stations from all  
218 sampling subsets. Length distributions were expanded to concentrations per 1000 m<sup>3</sup> at

219 size for each sampling date when sufficient larvae were present to facilitate the creation  
220 of length-frequency (LF) plots.

221 For all analyses limited to the winter sampling subset, monthly means of the 10  
222 most abundant larval taxa in the time-series were calculated then annual mean  
223 concentrations were plotted. Additionally, taxonomic evenness, diversity, and  
224 distinctness were determined for each tow ( $n = 267$ ) on all identifiable larval fish taxa ( $n$   
225  $= 77$ ). Taxonomic evenness was calculated using Pielou's evenness index ( $J'$ ), which has  
226 output values ranging from 0 to 1, with higher values indicating that all fish taxa are  
227 characterized in the same relative concentrations (Krebs, 1989). Taxonomic diversity  
228 was calculated based on the Shannon-Weiner diversity index ( $H'$ ), with higher values  
229 representing greater diversity (Shannon & Weaver, 1949). Lastly, taxonomic distinctness  
230 ( $\Delta^*$ ) was utilized as an index of biodiversity based on taxonomic or phylogenetic  
231 relatedness patterns within a community (Clarke & Warwick, 2001). Taxonomic  
232 distinctness assesses the average 'distance apart' of any species in a tow based on a  
233 Linnaean tree which was developed from the 77 fish taxa of our study (Clarke &  
234 Warwick, 2001). Data from the taxonomic evenness, diversity, and distinctness analyses  
235 were pooled across tows within a year and were averaged for annual mean estimates of  
236 diversity along with standard errors. Tows where no larvae were collected were not  
237 included in the analyses because  $J'$ ,  $H'$ , and  $\Delta^*$  cannot be calculated. Software utilized to  
238 calculate the evenness, diversity, and distinctness indices were performed using PRIMER  
239 7 statistical software (Clarke & Gorley, 2015).

240 To determine the similarity in the winter larval fish community over time,  
241 hierarchical two-way cluster analysis was used to identify taxa assemblages over the  
242 time-series from 1998 to 2016. To eliminate the effect of rare taxa on the analysis, only  
243 those taxa that occurred in at least 5% of the samples were used, leaving 25 larval taxa.  
244 Larval fish concentrations were averaged monthly and 4<sup>th</sup>-root transformed prior to  
245 analysis. The two-way cluster was constructed with the Bray-Curtis distance measure  
246 and a flexible beta ( $\beta = -0.25$ ) clustering algorithm. A non-parametric multi-response  
247 permutation procedure (MRPP) was used on larval fish concentrations for each tow ( $n =$   
248  $267$ ) to test the hypothesis that there was no difference in the larval community between  
249 all pairs of sampling years (1998-2016). Results from the paired tests were used to  
250 calculate the percent of the years that were significantly different for each year. Fish taxa



251 primarily responsible for significant differences between years were identified using  
252 indicator species analysis (ISA). The ISA measured the fidelity of fish taxa within a  
253 particular year in relation to their concentrations in all other years, and a measure of  
254 statistical significance is generated as well as an indicator value (IV) index. The IV index  
255 is a combination of both taxa specificity (concentration) and fidelity (frequency of  
256 occurrence in a year), and its value is not influenced by the concentration of other taxa  
257 (Dufrene & Legendre, 1997). The hierarchical two-way cluster, MRPP, and ISA were  
258 performed using PC-ORD 6 statistical software (McCune & Grace, 2002).

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260

261

## RESULTS

262

263

### Hydrography

264

265 The PDO changed from negative to positive in January 2014, followed soon after  
266 by a similar change in sign by the ONI (Fig. 2). Both indices remained strongly positive  
267 through the early summer of 2016, matching magnitudes that occurred during the strong  
268 El Niño events of 1982-83 and 1997-98. The local response is reflected in strongly  
269 positive winter temperature anomalies throughout the water column at NH 5 and over the  
270 upper 80 m at NH 25. These warm anomaly patterns are similar to those observed during  
271 the 1997-98 El Niño, except the entire water column warmed at NH25 in 1997-98 (Fig.  
272 3a,b). Salinity values at both stations in 2015-16 were approximately average relative to  
273 the 1997-2016 time-series. In January 2015-December 2016, monthly-averaged SST at  
274 NH 20 was consistently higher (mean monthly difference = +1.1 °C) than the 19-y mean,  
275 although it was  $\leq 1$  °C lower in June 2015 and August 2016 (Appendix 2).

276

277

### Larval collections, concentrations, and distributions

278

279 Mean concentrations of the 10 dominant larval fish taxa (comprising 95% of the  
280 total mean larval concentration) collected in winter of both 2015 and 2016 were higher  
281 than in any other year in the 19-y time-series (Fig. 4). Larval *Engraulis mordax* and  
282 *Sardinops sagax* dominated the ichthyoplankton in winter 2015, and both species were in

283 the top four most dominant taxa in winter 2016. *Engraulis mordax* larvae were found  
284 only once before in the 19-y time-series: in relatively low concentrations (mean = 16.3  
285 1000 m<sup>-3</sup> [SE = 6.3]) in March 1998. *Sardinops sagax* larvae were never before collected  
286 during winter. *Engraulis mordax* larvae were collected as early as 4 February in 2015  
287 and 8 January in 2016, while *S. sagax* larvae were collected as early as 18 February in  
288 2015 and 15 February in 2016.

289 ■ *Sardinops sagax* larvae were collected in the near-shore samples from February to  
290 May in 2015 and March to May in 2016, with maximum mean concentrations in March  
291 of both years (Fig. 5). *Engraulis mordax* larvae were collected in the near-shore samples  
292 from February to June and in September-October in 2015, and January to August and  
293 November-December in 2016, with maximum mean concentrations in April of both years  
294 (Fig. 5). Together, these two species accounted for 76% of the total larval mean  
295 concentration from the near-shore samples in January 2015-December 2016, and 83% of  
296 the February-May larvae collected in both 2015 and 2016.

297 The cross-shelf sampling subset showed that *E. mordax* and *S. sagax* larvae were  
298 not just collected in near-shore samples, but were found across the shelf in March and  
299 April 2015 and May 2016 (Appendix 3a,b,c). In March 2015, *E. mordax* larvae were  
300 collected at every cross-shelf station except for NH 35 and 85, but were most  
301 concentrated at NH 1-25. However, *S. sagax* larvae were not collected at the  
302 intermediate cross-shelf stations (NH 5-25), but were found at the most near-shore station  
303 (NH 1) and three of the four offshore stations (NH 35-65). In April 2015, *E. mordax*  
304 larvae were collected at every cross-shelf station from NH 1-150, with the highest and  
305 most even concentrations at NH 1-65, while *S. sagax* larvae were highly concentrated at  
306 NH 1, but were found at low concentrations at only two other, far-offshore stations: NH  
307 65 and 105. The following year, in May 2016, *E. mordax* larvae were evenly distributed  
308 at every cross-shelf station from NH 1-85, while *S. sagax* were mostly evenly distributed  
309 at every offshore station from NH 20-85, with a maximum concentration at the shelf  
310 break (NH 35). No *E. mordax* larvae were collected at the offshore (NH > 15) stations in  
311 either August 2015 or February 2016, but were collected at relatively low concentrations  
312 at two offshore stations in August 2016 (NH 35 and 45; mean = 14.1 1000 m<sup>-3</sup> [SD =  
313 4.2]). *Sardinops sagax* larvae were found at relatively low concentrations at three  
314 offshore stations in August 2015 (NH 20, 65, 85; mean = 19.6 1000 m<sup>-3</sup> [SD = 7.5]), at

315 one offshore station in February 2016 (NH 85; concentration = 7.8 1000 m<sup>-3</sup>), and at the  
316 same two offshore stations as *E. mordax* in August 2016: NH 35 (concentration = 11.4  
317 1000 m<sup>-3</sup>) and 45 (concentration = 134.4 1000 m<sup>-3</sup>). No *E. mordax* or *S. sagax* larvae  
318 were collected at any cross-shelf station in November 2015 or October and December  
319 2016.

320

321

### Larval size distributions

322

323 In 2015, WMLs for both *E. mordax* and *S. sagax* larvae initially increased, then  
324 decreased, before increasing again (Appendix 4). In 2016, WML for *E. mordax* larvae  
325 was relatively even from January to March, increased in April, decreased in May, then  
326 increased to even levels in June-July, before increasing even further in August (Appendix  
327 4). After not being found in the ichthyoplankton in September and October, recently  
328 hatched *E. mordax* larvae were again collected in November and December 2016 at  
329 WMLs of 3.1 and 3.3 (SE = 0.07) mm, respectively. *Sardinops sagax* larval lengths  
330 increased from February to March 2016, then remained relatively even through May,  
331 before increasing again in August (Appendix 4). There were no significant cross-shelf  
332 differences in WMLs for any of the three larval species examined.

333

334 LF plots showed clear signs of continuous spawning for both *E. mordax* and *S.*  
*sagax* during each of the biweekly-monthly cruises in February-May 2015-16, as evident  
335 in the large number of recently-spawned (<5 mm) larvae collected during each cruise  
336 (Appendix 5a,b). Survival of multiple larval cohorts was also evident by the  
337 multimodality and/or presence of larger larvae in the LF plots for *E. mordax* in 2015 and  
338 2016 and for *S. sagax* in 2015, although no evidence was found for multiple cohort  
339 survival of larval *S. sagax* in March-May 2016.

340

341

### Unusual larval occurrences

342

343 We observed several unusual patterns of abundance in the ichthyoplankton  
344 collected during winter 2015-16. Osmerids and *Ammodytes personatus* (Pacific sand  
345 lance), which normally are two of the dominant taxa found in the winter ichthyoplankton  
346 and are morphologically and ecologically similar larvae to *E. mordax* and *S. sagax*, were

347 found in relatively low concentrations in both 2015 and 2016. Conversely, *Psettichthys*  
348 *melanostictus* (sand sole) and *Isopsetta isolepis* (butter sole) larvae were found in two out  
349 of the four highest concentrations of the 19-y winter time-series in 2015 and 2016, with  
350 the anomalously warm years of 2002 and 2010 comprising the other two highest years.  
351 In addition, *Citharichthys* spp. larvae were collected in the highest concentrations in 2015  
352 and 2016 of the winter time-series, while *Ronquilus jordani* (northern ronquil) larvae  
353 were collected in the highest concentrations in 2016.

354 Several larval taxa normally found offshore were found nearshore in winter 2015-  
355 16, likely due to the relaxed upwelling associated with the warming phenomena.  
356 *Cololabis saira* (Pacific saury) and *Lipolagus ochotensis* (eared blacksmelt) were both  
357 collected for the first time in the 19-y time-series: *C. saira* in March 2015 at NH 10, and  
358 *L. ochotensis* in March 2015 at NH 20 and in March 2016 at NH 25. Larval *Microstomus*  
359 *pacificus* (Dover sole) were found as far inshore as NH 5 in March 2016 and at NH 25 in  
360 March 2015, while larval *Sebastes* spp., another taxa with an offshore distribution,  
361 were found pervasively at NH 1-25 in February-March 2015 and 2016 at the highest  
362 concentrations ever observed in the 19-y winter time-series.

363 We also observed two novel species of larval fish during this study. A single  
364 recently-hatched (2.6 mm) *Peprilus simillimus* (Pacific pompano) larva, a species that  
365 normally spawns in the southern California Current in spring-summer, was collected at  
366 NH 15 in December 2016, and represents the first confirmed occurrence of a larva for  
367 this species off Oregon in at least the last 19 y. We also observed the presence of  
368 *Merluccius productus* larvae, a normally southern-spawning species, in high  
369 concentrations (mean = 1920.1 [SE = 784.4]; maximum = 3918.3 1000 m<sup>-3</sup>) at all far-  
370 offshore stations between NH 35 and 105 in February 2016: the only time that we  
371 collected this species in all of the sampling conducted during this study, and the earliest  
372 in the year and in the highest concentrations that have ever been observed in the NCC  
373 (Auth & Brodeur, 2013). The WML for larval *M. productus* in February 2016 was 4.8  
374 mm (SE = 0.1), with a range of 2.8-7.2 mm (SL), which suggested that they were all  
375 recently hatched.

376

377

### Community analysis

378

379 Taxonomic diversity and distinctness was above average in winter 2015-16  
380 relative to the 19-y time-series, while evenness was slightly below average (Fig. 6).  
381 Diversity in 2016 was the third highest of the time-series, behind the El Niño years of  
382 1998 and 2010, while 2015 was the fifth highest. Taxonomic distinctness was virtually  
383 the same in 2015 and 2016, ranking third highest in the time-series behind 2000 and  
384 1998. Likewise, evenness values in 2015 and 2016 were almost identical, ranking third  
385 lowest behind 2011 and 2000.

386 The dendrogram resulting from the two-way cluster analysis using the 19-y time-  
387 series from the winter data revealed several notable temporal and taxonomic groupings  
388 (Fig. 7). February and March of 2015 and 2016 clustered close together and separated  
389 out from the rest of the sampling periods, although their closest temporal grouping was  
390 February and March of 2010: another anomalously warm period in the NCC. Larval *E.*  
391 *mordax* and *S. sagax* similarly clustered close together and separated from the rest of the  
392 taxonomic groups, and were strongly associated with the February-March 2015-16  
393 temporal grouping. However, January of 2015 and 2016 clustered together with other  
394 years. The results from the MRPP analysis support those from the cluster analysis,  
395 showing that 2015 and 2016 were the only years in the time-series that were significantly  
396 different from every other year, while 2010 was significantly different from 94.4% of the  
397 other years (Appendix 6). The ISA analysis revealed nine significant indicator taxa in the  
398 winter time-series, with four being from 2015-16 (Appendix 7). Most notably, *E. mordax*  
399 and *Sebastolobus* spp. larvae were indicative of 2016, while *S. sagax* and *Citharichthys*  
400 spp. were indicative of 2015. These four significant indicator species also exhibited the  
401 highest IVs.

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## DISCUSSION

405 Dramatic and prolonged changes in the ocean temperature patterns reported here  
406 and elsewhere (Bond et al., 2015; Peterson et al., 2016) in the north Pacific Ocean  
407 resulted in widespread ecosystem anomalies in the northern California Current (Leising  
408 et al., 2015; Di Lorenzo & Mantua, 2016; McClatchie et al., 2016; Peterson et al., In  
409 revision). An unusual weather pattern in the north Pacific resulting in extremely elevated  
410 surface and water-column temperature anomalies ('warm blob') was followed by a large

411 El Niño pattern, which was reflected in high PDO and ONI values in the NCC, leading to  
412 a multi-year marine heatwave unprecedented in the historical record (Di Lorenzo &  
413 Mantua, 2016). Although equatorial conditions in early summer 2016 reverted back to El  
414 Niño/Southern Oscillation (ENSO) neutral conditions (NOAA Earth System Research  
415 Laboratory, <http://www.esrl.noaa.gov/psd/enso/mei/>, 2017), the return of warm ocean  
416 temperature anomalies in the NCC was observed in late summer 2016 but dissipated in  
417 the coastal region by the fall that same year (Gentemann et al., 2017).

418 The year-round presence of warm water (11-15 °C) off the Oregon coast in 2015-  
419 16 created habitat favorable for winter spawning of several fish species that generally  
420 spawn off southern California during this time, or off of Oregon only during the summer  
421 when temperatures are at their seasonal maxima, and thus over short temporal periods.  
422 Takasuka et al. (2008) showed that the optimal temperature range for spawning of  
423 northeastern Pacific *Engraulis mordax* ranged between 11 and 16 °C. Historically, there  
424 were three populations of *E. mordax* in the California Current: two in California and one  
425 off central-northern Oregon in the Columbia River plume (Huppert et al., 1980;  
426 Richardson, 1981; Parnel et al., 2008); although more recent data suggest that spawning  
427 has been occurring in southern-central Oregon waters at least since 2013 (Auth &  
428 Brodeur, Unpub. Data). While the more southern populations have an early and  
429 protracted reproductive season, the Columbia River population typically has a later and  
430 relatively narrow window for spawning from late-May to early August (Brodeur et al.,  
431 2008; Parnel et al., 2008; Auth, 2011). It is beyond the scope of this study to discern if  
432 the individuals that spawned in the NCC in 2015-16 were migrants from southern areas,  
433 but there is little evidence for this (Davison et al., 2017). For *Sardinops sagax*, Takasuka  
434 et al. (2008) showed that the optimal temperature range for spawning ranged between  
435 ~13 and ~25 °C. However, in the present study, the highest concentrations of *S. sagax*  
436 larvae were found during February-May of both 2015 and 2016, when SST was 11-13 °C:  
437 below the 13 °C lower threshold previously documented by Takasuka et al. (2008).  
438 These temperature thresholds generally limit spawning of *S. sagax* to the area south of  
439 Point Conception off southern California during most years, although the spawning  
440 population is noted to shift northward during positive ENSO years (Fiedler et al., 1986;  
441 Auth, 2008; Sadrozinski, 2008).

442 *Engraulis mordax*, and to a lesser extent *S. sagax*, demonstrated multiple  
443 spawnings throughout most of each year in 2015-16 off Oregon, with the presence of  
444 newly-hatched larvae occurring over several successive monthly cruises starting in  
445 February 2015. Although no *E. mordax* or *S. sagax* larvae were collected in January  
446 2015, *E. mordax* larvae as large as 5.3 mm NL were collected on 4 February 2015 and *S.*  
447 *sagax* larvae as large as 11.2 mm SL were collected on 18 February 2015, while hatch  
448 sizes for these species are 2.5 and 3.5 mm NL, respectively (Matarese et al., 2003),  
449 indicating that spawning for both species occurred at least as early as January in 2015.  
450 The reason that only a relatively few *E. mordax*, and no *S. sagax*, larvae were collected in  
451 June-July and in September-October in 2015-16 may be because we only sampled  
452 nearshore (NH 1-15) in those months (except for October 2016 when sampling was  
453 conducted at NH 1-200), and these larvae were probably located farther offshore. In a  
454 separate study conducted off the Oregon coast in June 2015 and 2016 (McClatchie et al.,  
455 2016; Auth & Brodeur, Unpub. Data), *S. sagax* larvae were found in moderate  
456 concentrations at NH 20 but absent at NH 15 and 45 in both years, while *E. mordax*  
457 larvae were found at relatively high concentrations at NH 20 and 45 in both years, but at  
458 NH 15 were absent in 2015 and at a low concentration in 2016.

459 Unlike *E. mordax* and *S. sagax*, *Merluccius productus* spawn in relatively deep  
460 water (50-100 m), where they inhabit cooler waters (10.3 °C) as early-stage larvae,  
461 eventually rising above the thermocline to warmer surface temperatures (11-11.3 °C;  
462 Moser et al., 1997). The normal spawning area for this species is considered to be off  
463 southern and Baja California, although spawning has been observed to shift northward  
464 during warm years (Horne & Smith, 1997; Ressler et al., 2007; Auth, 2008; Sadrozinski,  
465 2008). We found *M. productus* larvae only during one sampling cruise (14-17 February  
466 2016), but we were not able to sample in offshore waters (>46 km from shore) along the  
467 NH line often in the winter months. However, larvae as large as 7.2 mm NL were  
468 collected, while hatch size for this species is 2.4 mm NL (Matarese et al., 2003),  
469 indicating that spawning occurred at least as early as January 2016. Although we did not  
470 find *M. productus* larvae in the NCC in winter 2015 during the local 'warm blob', we did  
471 find them in large numbers in winter 2016 during the El Niño, which may be indicative  
472 of migration of southern stocks northward resulting from El Niño effects in the south, and  
473 not just early spawning in response to local warming conditions in the north like *E.*

474 *mordax* and *S. sagax*. It is also possible that *M. productus* spawned somewhere north of  
475 their usual spawning grounds in 2015, but it may have been somewhat south of our  
476 sampling, and stronger than average northward-flowing currents in winter 2016  
477 compared to winter 2015 transported the larvae to our study region (Peterson et al., In  
478 revision).

479 Previous studies have documented some anomalous distributions in early-life  
480 stages of *E. mordax* and *M. productus*. During the 1983 El Niño, Brodeur et al. (1985)  
481 observed shoreward displacement and increased abundance of larval taxa that generally  
482 occur offshore, especially *E. mordax* which are normally found in warm, offshore,  
483 Columbia River plume waters (Richardson, 1973; Auth, 2009). They also observed a  
484 shift in the timing of spawning of *E. mordax*, collecting larvae continuously in April-  
485 September 1983, when the normal spawning period for this species is June-July in the  
486 NCC (Auth, 2011). Doyle (1995) also found *E. mordax* eggs and larvae as early as April  
487 in 1983 over a much broader area, along with unusual occurrences of eggs and larvae of  
488 species such as *M. productus* during spring of 1983 and 1984. The only other time *E.*  
489 *mordax* larvae were found in winter during the present study's 1998-2016 time-series was  
490 in March of 1998: a strong El Niño year. In 2004-05, when anomalously elevated sea-  
491 surface temperatures and decreased upwelling unrelated to ENSO occurred in the NCC,  
492 Brodeur et al. (2006) observed high concentrations of larval and age-0 *M. productus* in  
493 the NCC region from Oregon to British Columbia, which represents a significant  
494 northward shift in their spawning distribution since they normally spawn in the southern  
495 California Bight. They also observed a shoreward displacement of *E. mordax* larvae.  
496 These northward and shoreward shifts in spawning distributions during the present warm  
497 event are similar to those observed during the 1983 El Niño (Brodeur et al. 1985). Auth  
498 et al. (2015) also found anomalously high concentrations and both shoreward and  
499 northward displacement of fish larvae during the 2010 El Niño. However, none of these  
500 or any other studies (see Auth & Brodeur, 2013 for references) have documented such a  
501 widespread and early spawning of *E. mordax*, *S. sagax*, and *M. productus* in the NCC as  
502 we found in the present study.

503 Although we do not have direct corroborative evidence of adult spawners shifting  
504 their distributions north during our surveys, findings from other studies indicate the  
505 winter/spring presence of adult *E. mordax* and *S. sagax* well north of their normal



506 distribution in surveys conducted by NOAA's Southwest Fisheries Science Center  
507 (SWFSC; Leising et al., 2015; McClatchie et al., 2016). Similarly, a Northwest Fisheries  
508 Science Center (NWFSC) 2016 winter spawning survey of *M. productus* found  
509 developing adults as far north as the NH line off Oregon (S. Parker-Stetter, NOAA  
510 NWFSC, Pers. Comm.). Although warm periods such as El Niño events have been  
511 shown to produce less productive zooplankton communities in the NCC potentially  
512 leading to less productive systems as a whole (Fisher et al., 2015), periods of elevated  
513 water temperature such as were present in 2015-16 have generally seen increased  
514 spawning and larval production in pelagic fish communities in the California Current  
515 (Hsieh et al., 2005; Auth, 2008; Daly et al., 2013; Auth et al., 2015). This may be a result  
516 of faster gonadal development and growth of adults at higher temperatures (Greve et al.,  
517 2005). In any case, adult *E. mordax* and *S. sagax* apparently found adequate prey  
518 resources to continue the energetically-expensive serial spawning that they exhibited in  
519 the NCC throughout most of the year in 2015-16.

520 Shifts in spawning phenologies have been observed in the north Atlantic Ocean  
521 (Greve et al., 2005; Genner et al., 2010) and in the north Pacific Ocean off California  
522 (Asch, 2015) as well. In an analysis of multi-decadal larval densities for 43 species off  
523 southern California, Asch (2015) found earlier phenologies for many species including  
524 *M. productus*, *E. mordax*, and *S. sagax*, although the variability in the latter two species  
525 was high so that they did not show a significant trend (see online supplementary material  
526 [http://www.pnas.org/content/suppl/2015/07/09/1421946112.DCSupplemental/pnas.  
201421946SI.pdf](http://www.pnas.org/content/suppl/2015/07/09/1421946112.DCSupplemental/pnas.201421946SI.pdf), 2017). These changes were correlated with long-term changes in sea  
528 surface temperature, likely mediated through trends in PDO and ENSO conditions, but  
529 also may be attributed to other factors such as zooplankton biomass (Asch 2015).

530 Pelagic spawning fishes are known to have limited temperature dependencies for  
531 spawning initiation, but other physical (e.g., currents, stratification) and biological (e.g.,  
532 prey and predator distributions) factors may also affect spawning timing and habitats. In  
533 particular, spawning cycles have evolved to coincide with the availability of the proper  
534 food resources for larvae (Platt et al., 2003), and disruption of the temporal overlap  
535 between larvae and their food may lead to poor survival. In contrast to many demersal  
536 spawners, the three species of interest here are iteroparous and capable of multiple  
537 spawning events within a season, thus generating a higher probability of a temporal

538 match between food production and at least one of the spawning events. Length-  
539 frequency plots show multiple *E. mordax* and *S. sagax* cohorts surviving at least between  
540 biweekly-monthly surveys in February-May 2015-16, and an increase in WML is  
541 evidence for larval growth and survival through the summer. In addition, juvenile  
542 pelagic fish surveys have collected age-0 individuals of all three species off both Oregon  
543 and especially Washington during June of 2015 and 2016, which were absent in previous  
544 years (Auth & Brodeur, Unpub. Data), indicating a northward shift in their spawning  
545 habitat and providing evidence of successful recruitment of these early-spawned larvae at  
546 least to the juvenile stage. Providing that there is not a mismatch between the earlier-  
547 spawned fish larvae and their prey (Asch, 2015), warmer temperatures in the larval  
548 habitat would be expected to increase the growth rate of larvae (Takahashi et al., 2012),  
549 decreasing their vulnerability window to size-selective predation.

550 Our results indicate that the spawning and nursery habitats of *E. mordax*, *S.*  
551 *sagax*, and *M. productus* may have shifted north by 500-1000 km from their usual winter  
552 habitats as a result of recent oceanic warming, with important ecological ramifications for  
553 the entire food web. *Engraulis mordax* spawning biomass has been steadily decreasing  
554 off southern California in recent years (MacCall et al., 2016), and this, along with  
555 declines in *S. sagax* and other pelagic forage species, may have led to precipitous  
556 declines in sea lion survival off California (McClatchie et al., 2016). In the NCC, growth  
557 and survival of juvenile salmon is dependent on the availability and type of fish prey  
558 available to them in spring and summer (Daly et al., 2017). In 2015 and 2016, there were  
559 anomalously high amounts of *E. mordax* juveniles in the stomachs of out-migrating  
560 Columbia River Chinook salmon (*Oncorhynchus tshawytscha*) (Daly et al., 2017). In  
561 addition, juvenile *S. sagax* were consumed by juvenile coho (*Oncorhynchus kisutch*) and  
562 Chinook salmon in May and June of 2016 (Daly & Brodeur, Unpub. Data). This is  
563 further evidence of early-spawned larval *E. mordax* and *S. sagax* recruitment to the  
564 juvenile stage in 2015 and 2016, making them available as prey for juvenile salmon  
565 which could influence their growth and survival to adults.

566 Changes in spawning timing and poleward migration of fish populations due to  
567 warmer ocean conditions or global climate change will negatively impact areas that were  
568 historically dependent on these fish, as well as change the structure of the areas that the  
569 fish move into (Cheung et al., 2015; Asch, 2015). If the unprecedented ocean warming

570 and/or more frequent and prolonged temperature surges such as has been occurring over  
571 the last two years continues, the northward migration of spawning stocks (Last et al.,  
572 2011), increased larval species richness (Koslow et al., 2017), and disruption to the food  
573 web may become the new normal in the NCC with unforeseen consequences.

574 As is often the case with ecosystem change, some species may benefit from  
575 changes in distribution and timing of prey whereas others may not be able to adapt and  
576 subsequently decline (Cavole et al., 2016). Similar northward shifts in pelagic fish  
577 species due to climate change have occurred in European waters with important  
578 implications for ecosystems in those regions (Beare et al., 2004; Alheit et al., 2012;  
579 Montero-Serra et al., 2015). Changing ocean conditions can be incorporated within in-  
580 season forecasting models (Kaplan et al., 2016) to inform fisheries management. We  
581 know from past work that the ecosystem recovery time is strongly related to the intensity  
582 and duration of warm events (Fisher et al., 2015). However, it is unknown whether the  
583 ‘warm blob’ or El Niño will persist for the next year, or whether the system will  
584 transition to cooler and/or La Niña conditions with a different fish community as in 2011  
585 (Auth et al., 2015), or if the phenological changes documented in this study will persist  
586 regardless of future oceanographic fluctuations. Only through continued, regular, cross-  
587 shelf surveys will we be able to answer these questions, or discern the signals of future  
588 anomalies and their relationship to global climate change.

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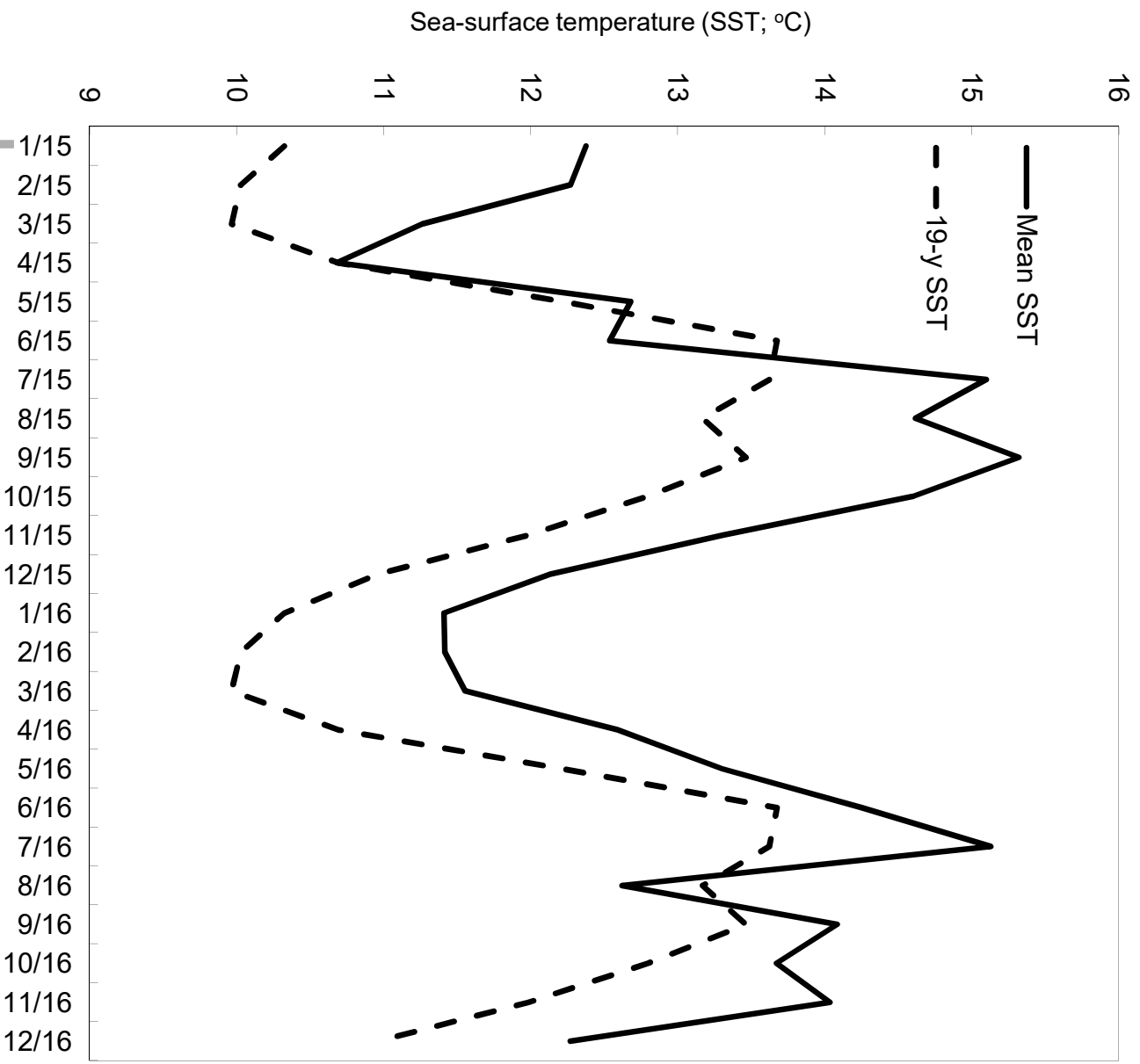
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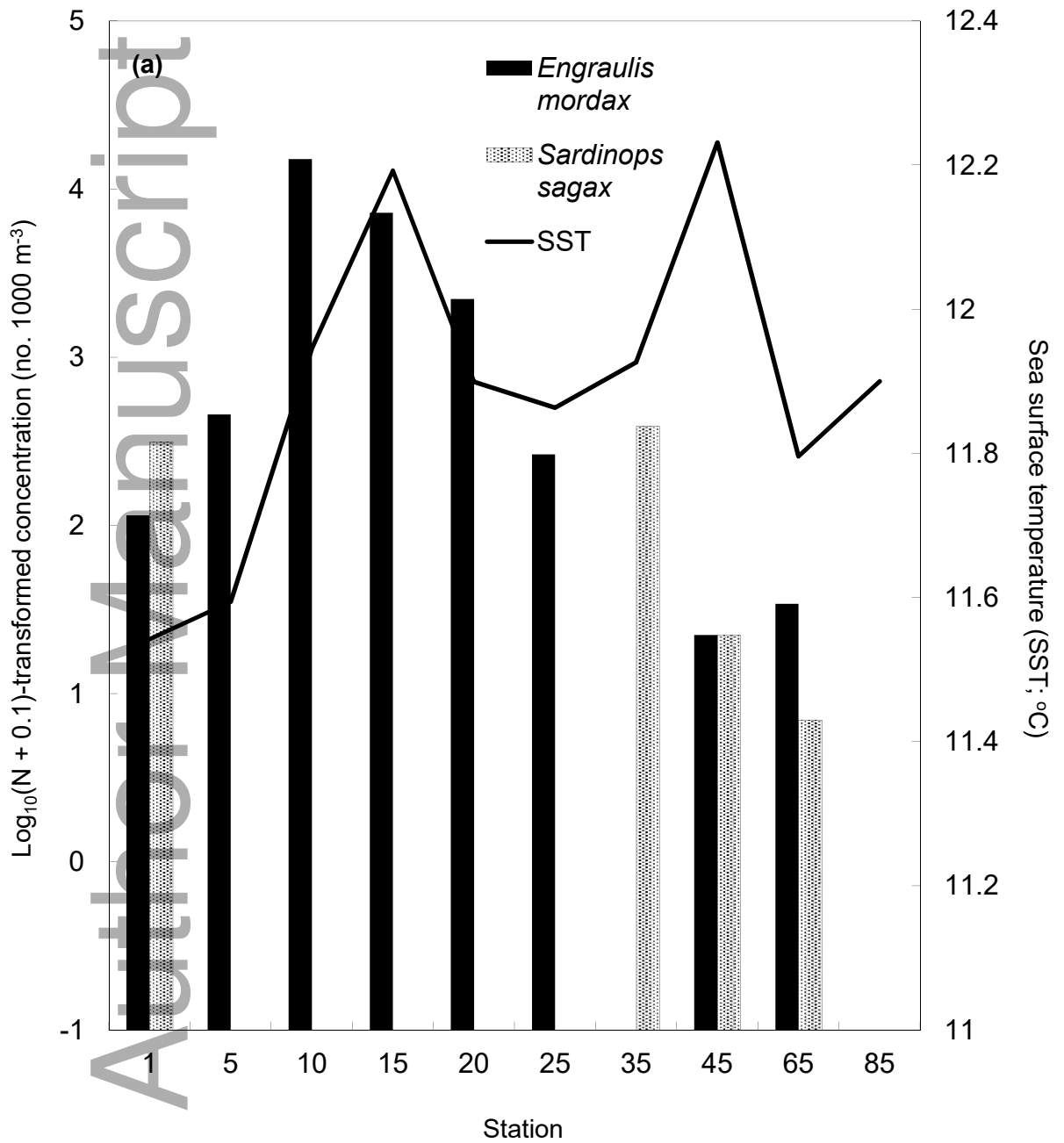
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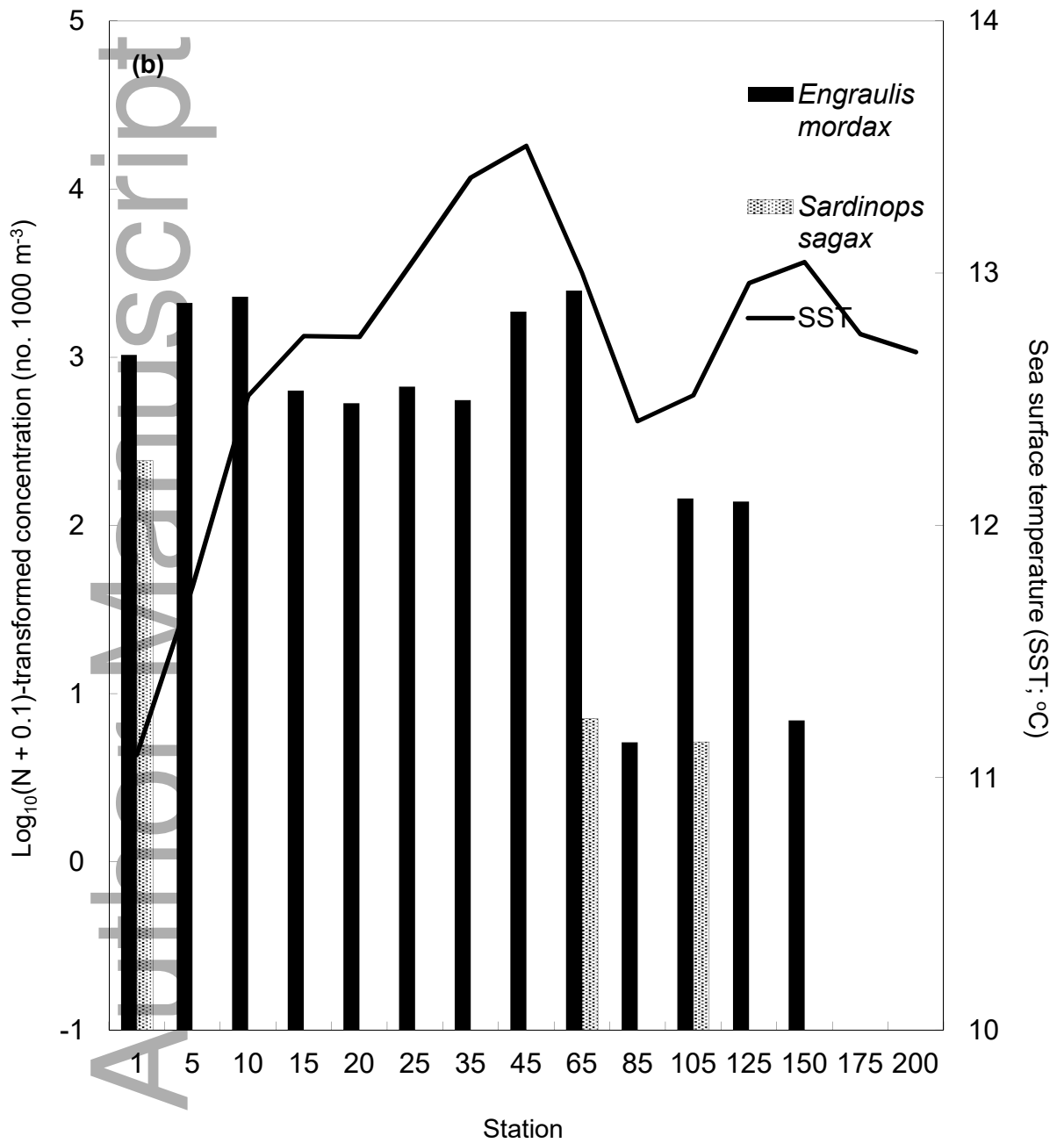
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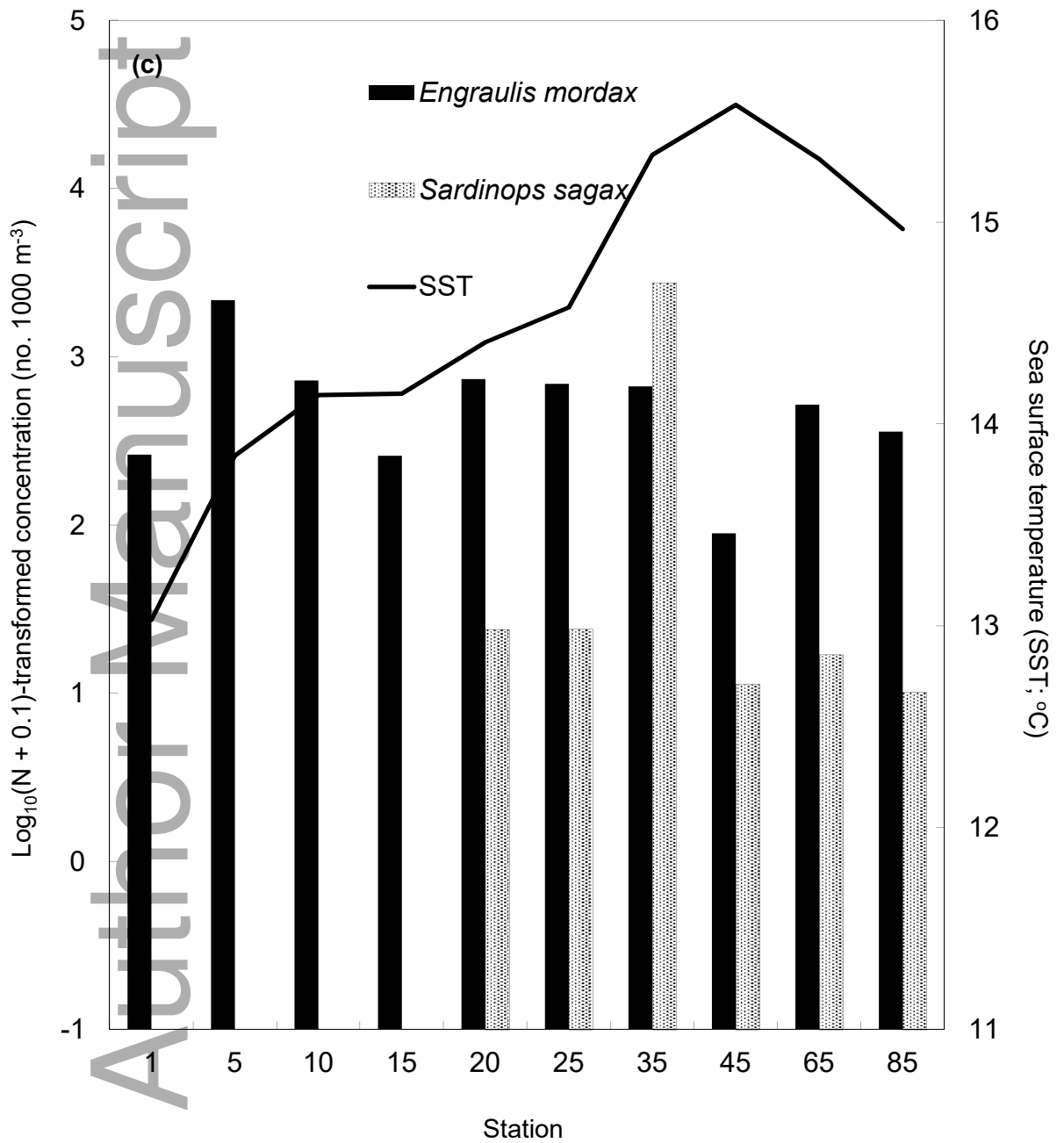
Appendix 1. Dates, stations sampled along the Newport Hydrographic (NH) line, and associated sampling regimes for each of the 31 cruises conducted for this study.

Year	Month	Day	Stations sampled	Sampling regime
2015	1	6	1, 5, 10, 15, 20, 25	Winter, Near-shore
2015	1	21	1, 5, 10, 15, 20, 25	Winter, Near-shore
2015	2	4	1, 5, 10	Winter, Near-shore
2015	2	18	1, 5, 10, 15, 20, 25	Winter, Near-shore
2015	3	4-5	1, 5, 10, 15, 20, 25, 35, 45, 65, 85	Winter, Near-shore, Cross-shelf
2015	3	26	1, 5, 10, 15, 20, 25	Winter, Near-shore
2015	4	7	1, 5, 10, 15	Near-shore
2015	4	27-29	1, 5, 10, 15, 20, 25, 35, 45, 65, 85, 105, 125, 150, 175, 200	Near-shore, Cross-shelf
2015	5	19	1, 5, 10, 15	Near-shore
2015	6	10	1, 5, 10, 15	Near-shore
2015	7	15	1, 5	Near-shore
2015	8	10	1, 5, 15	Near-shore
2015	8	26-27	1, 5, 10, 15, 20, 25, 35, 45, 65, 85	Near-shore, Cross-shelf
2015	9	29	1, 5, 10, 15	Near-shore
2015	10	13	1, 5, 10, 15	Near-shore
2015	11	3-4	1, 5, 10, 15, 20, 25, 35, 45, 65, 85	Near-shore, Cross-shelf
2016	1	8	1, 5	Winter, Near-shore
2016	2	14-17	1, 5, 10, 15, 20, 25, 35, 45, 65, 85, 150, 200	Winter, Near-shore, Cross-shelf
2016	3	11	1, 5, 10, 15	Winter, Near-shore
2016	3	26	1, 5, 10, 15, 20, 25	Winter, Near-shore
2016	4	18	1, 5, 10	Near-shore
2016	5	12	1, 5, 10, 15	Near-shore
2016	5	24-25	1, 5, 10, 15, 20, 25, 35, 45, 65, 85	Near-shore, Cross-shelf
2016	6	12	1, 5, 10, 15	Near-shore
2016	7	7	1, 5, 10, 15	Near-shore
2016	8	1	1, 5, 10, 15	Near-shore
2016	8	21-23	1, 5, 10, 15, 20, 25, 35, 45, 65, 85	Near-shore, Cross-shelf
2016	9	20	1, 5, 10, 15	Near-shore
2016	10	10-12	1, 5, 10, 15, 20, 25, 35, 45, 65, 85, 105, 125, 150, 175, 200	Near-shore, Cross-shelf
2016	11	18	5, 10	Near-shore
2016	12	6	1, 5, 10, 15, 20, 25	Near-shore, Cross-shelf

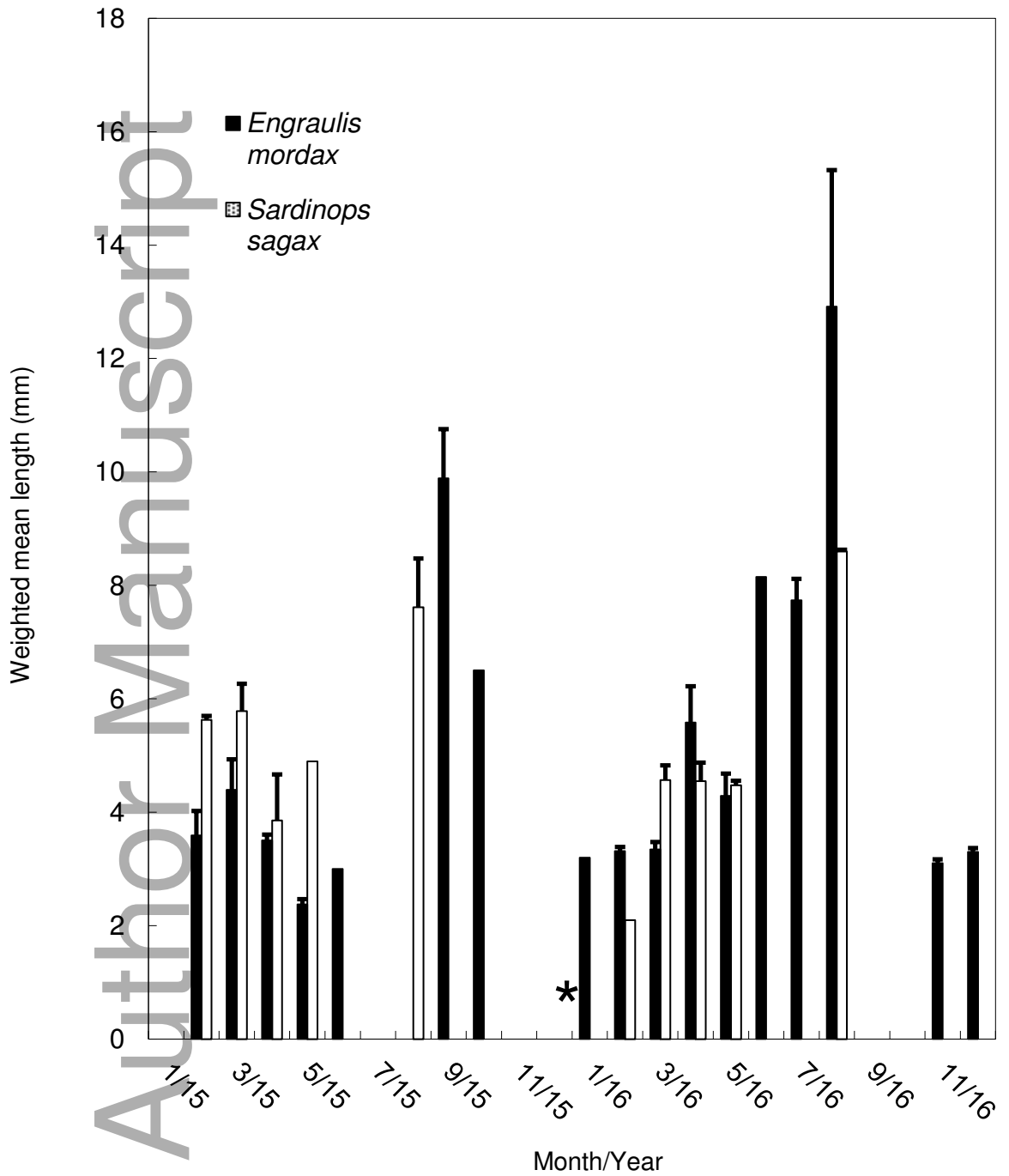








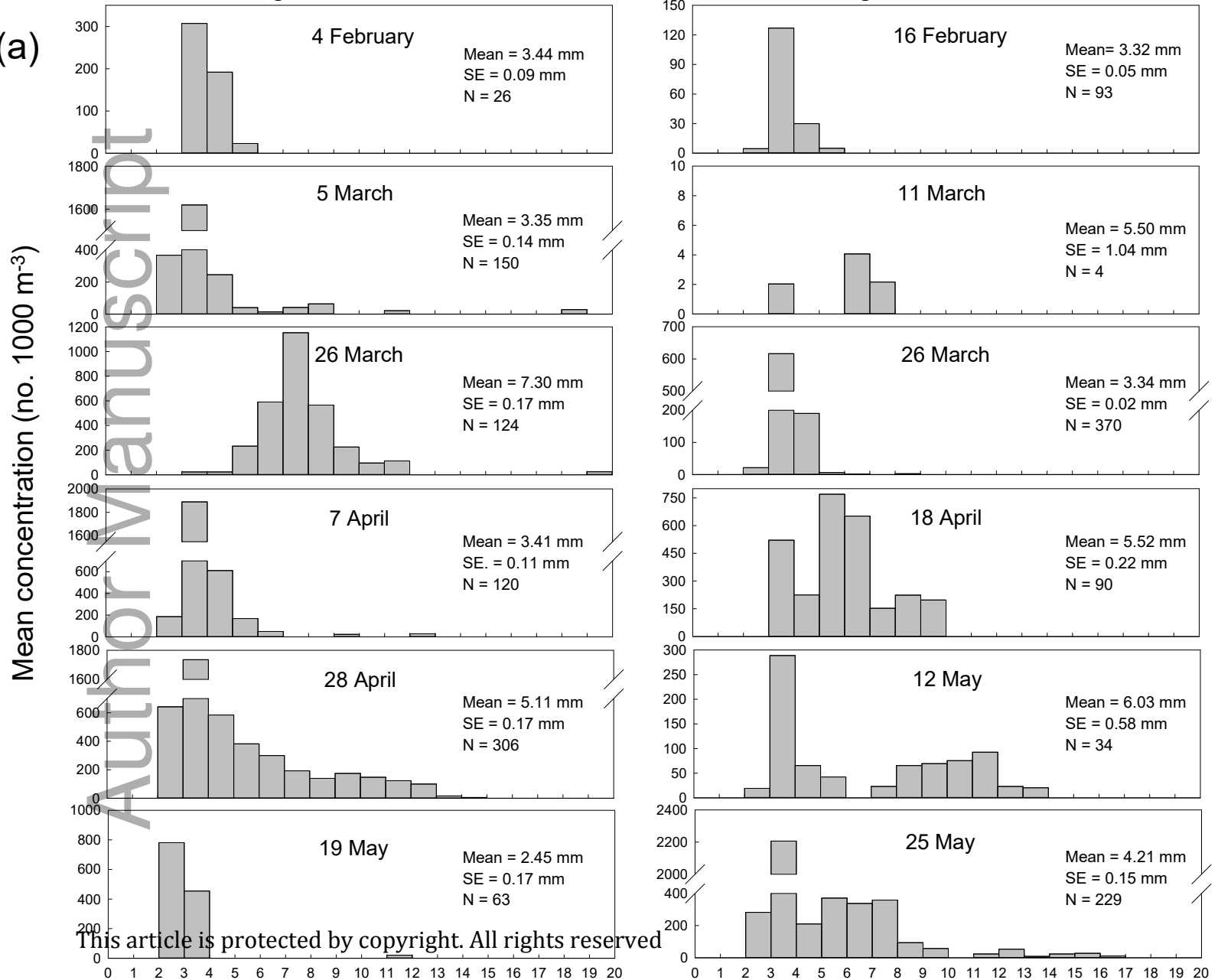




*Engraulis mordax* 2015

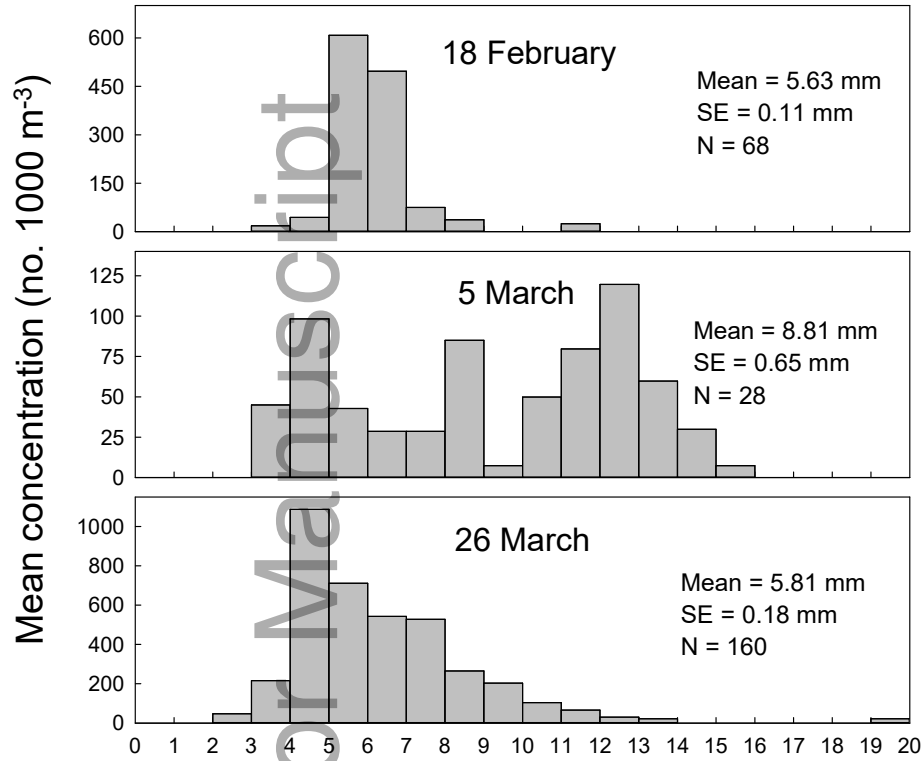
*Engraulis mordax* 2016

(a)

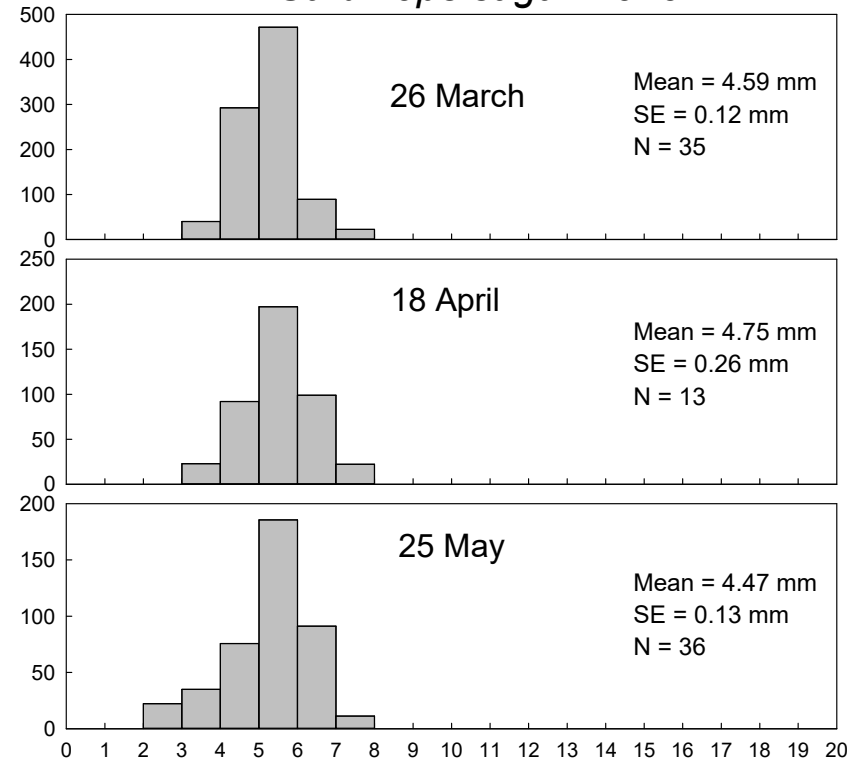


(b)

*Sardinops sagax* 2015



*Sardinops sagax* 2016



Appendix 6. Results of the multi-response permutation procedure (MRPP) analysis for the 25 most dominant taxa collected from stations NH 1-25 during winter (January-March) 1998-2016.

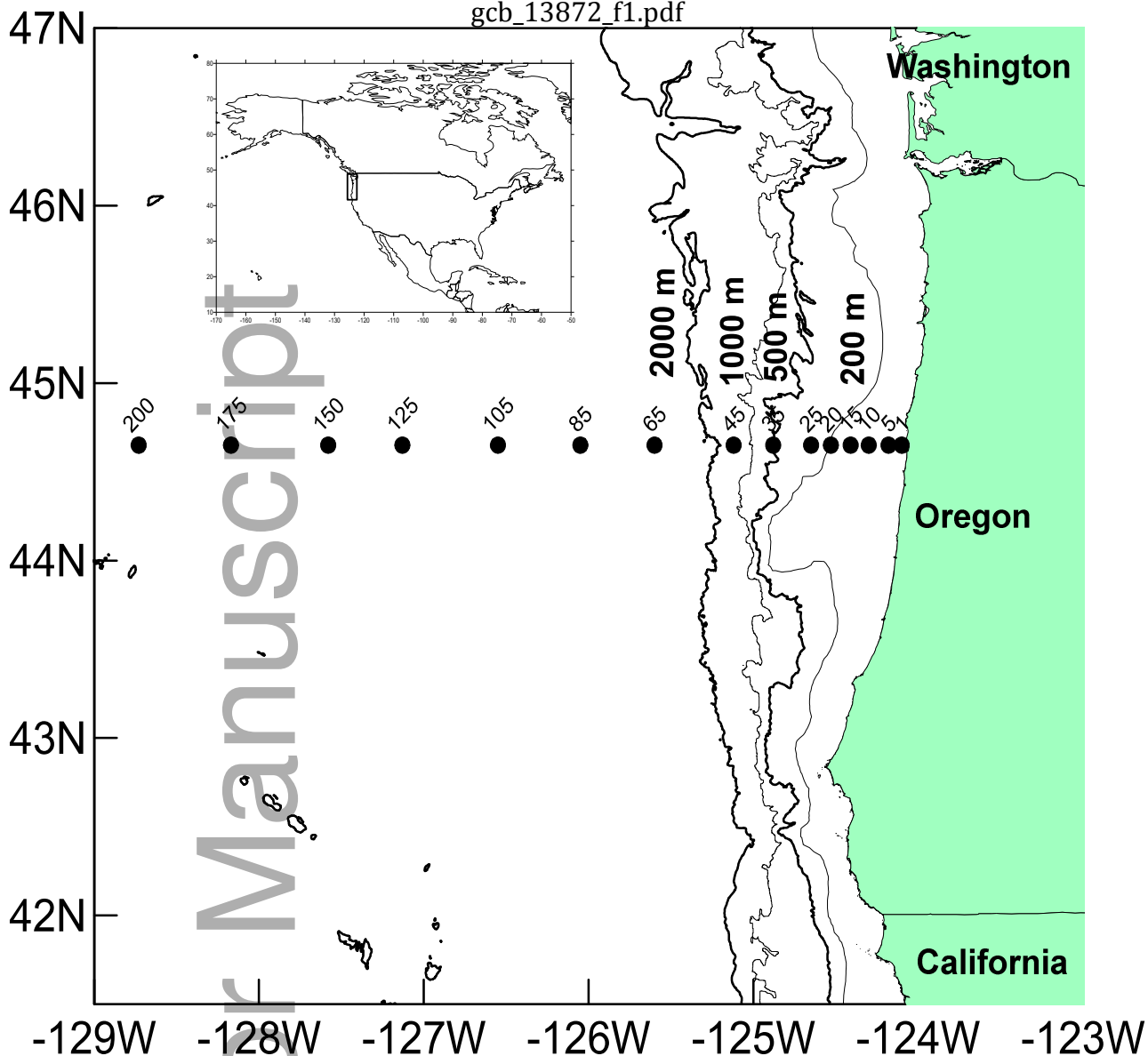
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Year	Pairs significantly different	% significantly different
1998	16	88.9
1999	5	27.8
2000	12	66.7
2001	9	50.0
2002	12	66.7
2003	11	61.1
2004	6	33.3
2005	10	55.6
2006	8	44.4
2007	14	77.8
2008	4	22.2
2009	11	61.1
2010	17	94.4
2011	12	66.7
2012	8	44.4
2013	7	38.9
2014	8	44.4
2015	18	100.0
2016	18	100.0

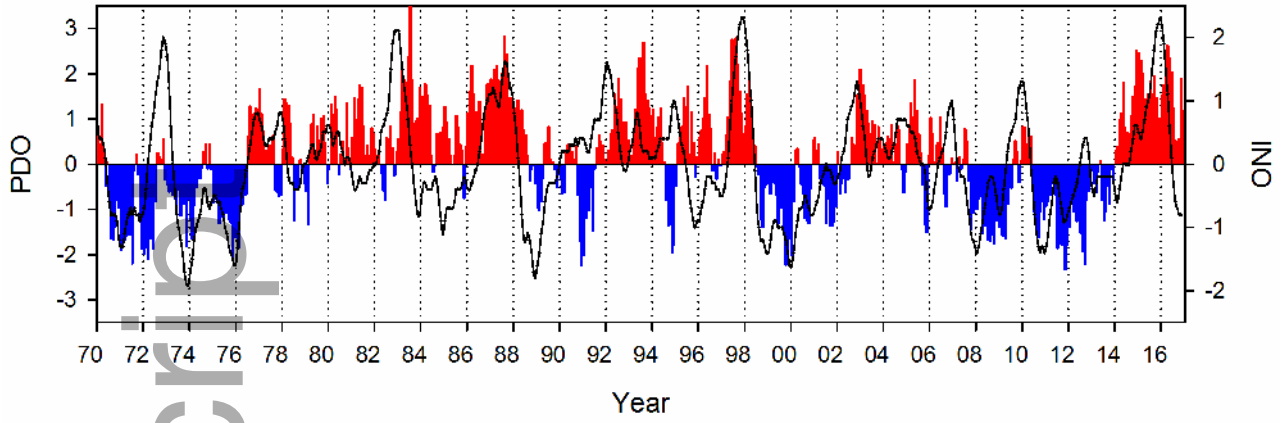
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Appendix 7. Results of the indicator species analysis (ISA) with indicator year, value (IV), mean, standard deviation (SD), and p-value (p) for the 25 most dominant taxa collected from stations NH 1-25 during winter (January-March) 1998-2016. \* = statistically significant ( $p < 0.05$ ).

Scientific name	Common name	Year	IV	Mean	SD	p
<i>Engraulis mordax</i>	Northern anchovy	2016	25.6	5.5	2.93	0.0018*
<i>Sebastes</i> spp.	Thornyheads	2016	24.9	5.0	2.92	0.0018*
<i>Sardinops sagax</i>	Pacific sardine	2015	25.7	5.1	3.23	0.0022*
<i>Citharichthys</i> spp.	Pacific or speckled sanddab	2015	16.6	6.1	2.18	0.0046*
<i>Microgadus proximus</i>	Pacific tomcod	2002	14.0	5.1	2.76	0.0138*
<i>Isopsetta isolepis</i>	Butter sole	2010	12.4	5.8	2.18	0.0208*
<i>Ammodytes personatus</i>	Pacific sand lance	2000	12.6	6.0	2.31	0.0212*
<i>Lyopsetta exilis</i>	Slender sole	2002	12.9	4.9	2.88	0.0334*
<i>Liparis fucensis</i>	Slipskin snailfish	1999	11.1	4.9	2.87	0.0448*
<i>Ophiodon elongatus</i>	Lingcod	2008	10.8	5.0	2.93	0.0506
Osmeridae	Smelts	2010	9.8	6.1	2.17	0.0618
<i>Hemilepidotus spinosus</i>	Brown Irish lord	1999	9.3	5.2	2.60	0.0644
<i>Ronquilus jordani</i>	Northern ronquil	1999	8.5	5.0	3.16	0.0824
<i>Stenobranchius leucopsarus</i>	Northern lampfish	2010	8.7	6.3	2.04	0.1046
<i>Sebastes</i> spp.	Rockfishes	2010	8.5	6.9	1.39	0.1342
<i>Psettichthys melanostictus</i>	Sand sole	1998	8.2	6.1	2.13	0.1428
<i>Glyptocephalus zachirus</i>	Rex sole	2010	6.4	5.5	2.48	0.2927
<i>Arteidius harringtoni</i>	Scalyhead sculpin	2002	5.1	5.3	2.66	0.3903
<i>Hemilepidotus hemilepidotus</i>	Red Irish lord	2011	4.8	4.9	3.11	0.4075
<i>Leptocottus armatus</i>	Pacific staghorn sculpin	2001	4.3	5.0	3.05	0.4923
<i>Hexagrammos decagrammus</i>	Kelp greenling	2014	4.2	4.9	2.74	0.5277
<i>Arteidius fenestralis</i>	Padded sculpin	2002	4.1	5.0	2.91	0.5399
<i>Parophrys vetulus</i>	English sole	2011	6.4	6.9	1.53	0.5773
<i>Scorpaenichthys marmoratus</i>	Cabezon	2006	3.6	5.0	2.92	0.7021
<i>Anoplarchus purpurescens</i>	High cockscomb	2000	2.5	4.9	2.96	0.8930

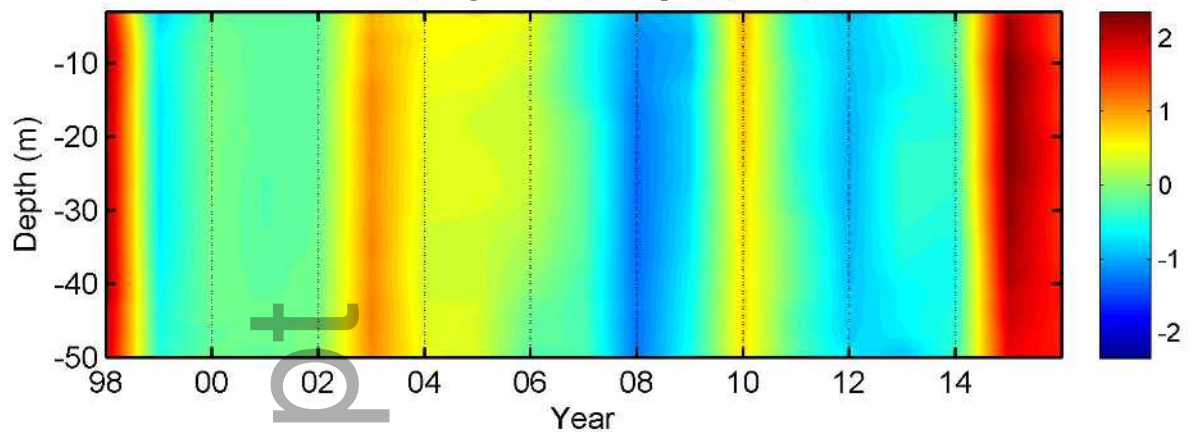


Station	Distance from shore (km)	Depth (m)
1	2	33
5	9	55
10	18	79
15	28	92
20	37	145
25	46	283
35	65	518
45	84	830
65	120	2880
85	155	2903
105	182	2885
125	238	2906
150	274	2910
175	320	2871
200	364	2868

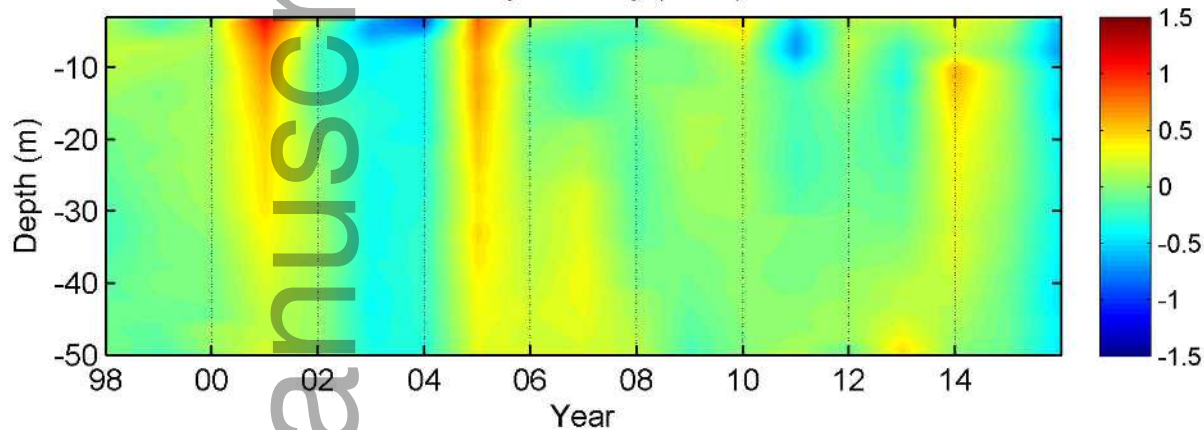


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(a)

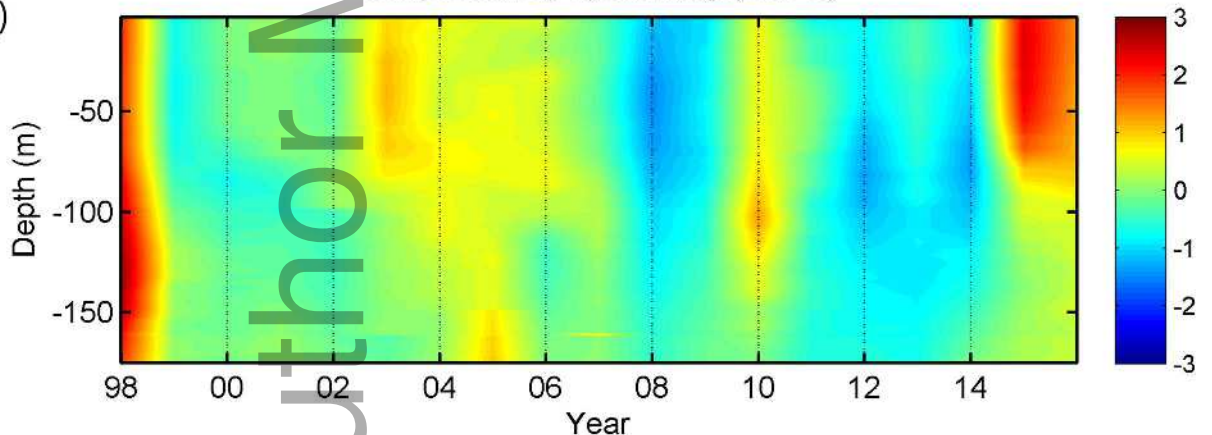


Salinity anomaly (NH 5)

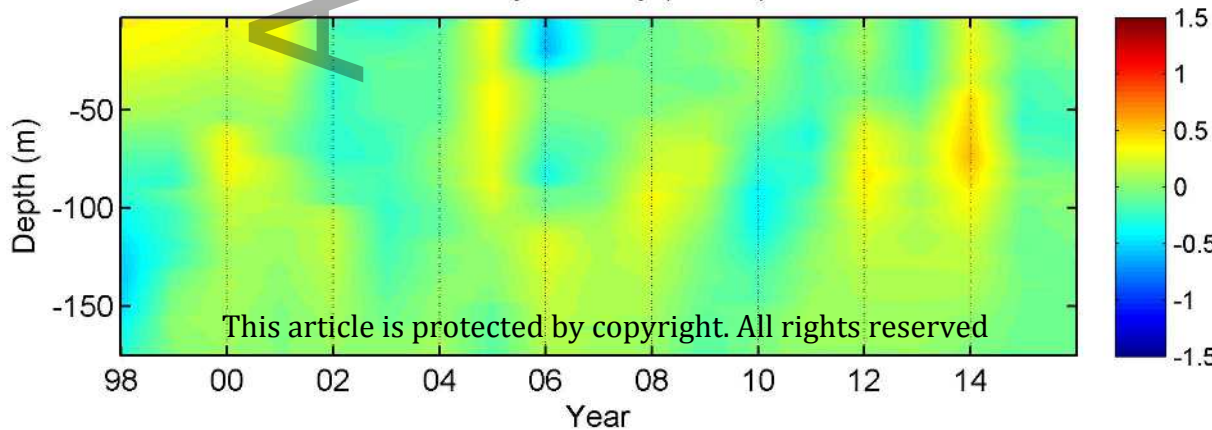


(b)

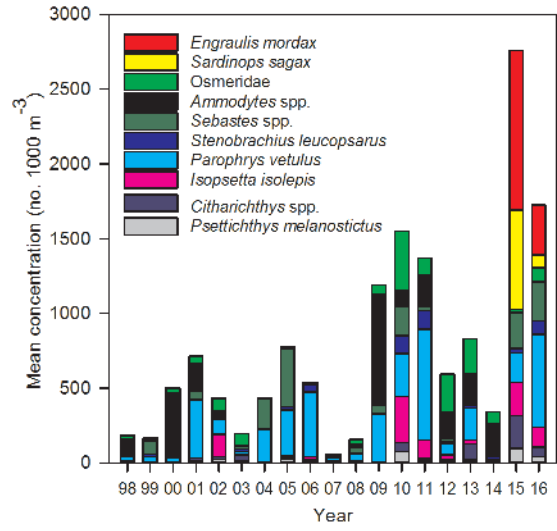
Temperature ( $^{\circ}\text{C}$ ) anomaly (NH 25)



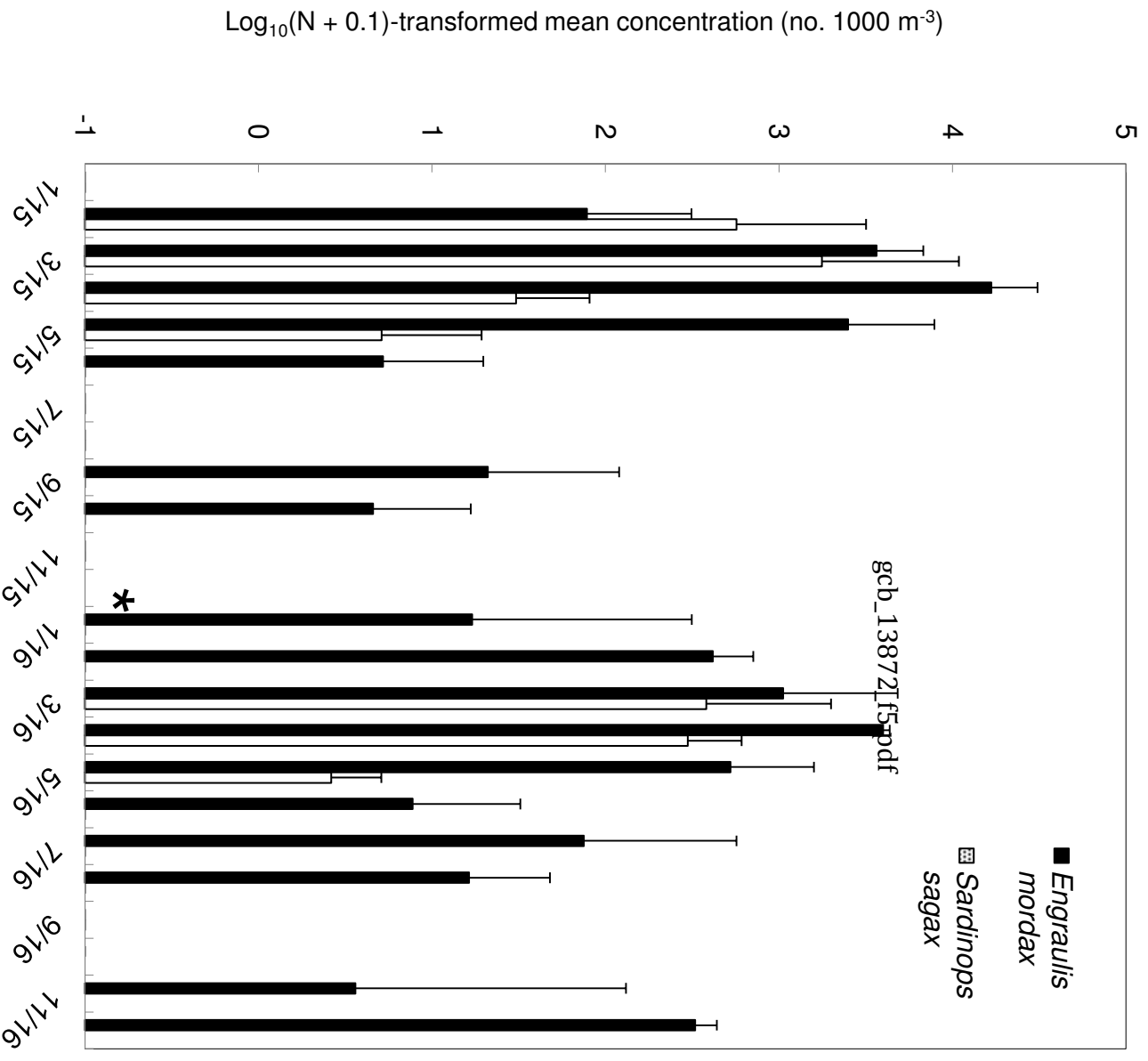
Salinity anomaly (NH 25)

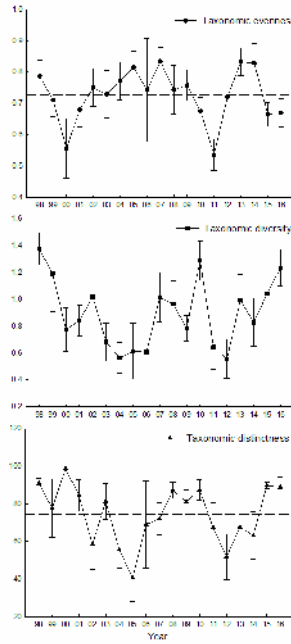






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