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Title: **Coast-wide recruitment dynamics of Olympia oysters reveal limited synchrony and multiple predictors of failure**

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## Abstract

2 Recruitment of new propagules into a population can be a critical determinant of adult  
density. We examined recruitment dynamics in the Olympia oyster (*Ostrea lurida*), a species  
4 occurring almost entirely in estuaries. We investigated spatial scales of interannual synchrony  
across 37 sites in eight estuaries along 2500 km of Pacific North American coastline, predicting  
6 that high vs. low recruitment years would coincide among neighboring estuaries due to shared  
exposure to regional oceanographic factors. Such synchrony in recruitment has been found for  
8 many marine species and some migratory estuarine species, but has never been examined across  
estuaries in a species that can complete its entire life cycle within the same estuary. To inform  
10 ongoing restoration efforts for Olympia oysters, which have declined in abundance in many  
estuaries, we also investigated predictors of recruitment failure. We found striking contrasts in  
12 absolute recruitment rate and frequency of recruitment failure among sites, estuaries, and years.  
Although we found a positive relationship between upwelling and recruitment, there was little  
14 evidence of synchrony in recruitment among estuaries along the coast, and only limited  
synchrony of sites within estuaries, suggesting recruitment rates are affected more strongly by  
16 local dynamics within estuaries than by regional oceanographic factors operating at scales  
encompassing multiple estuaries. This highlights the importance of local wetland and watershed  
18 management for the demography of oysters, and perhaps other species that can complete their  
entire life cycle within estuaries. Estuaries with more homogeneous environmental conditions  
20 had greater synchrony among sites, and this led to the potential for estuary-wide failure when all  
sites had no recruitment in the same year. Environmental heterogeneity within estuaries may thus  
22 buffer against estuary-wide recruitment failure, analogous to the portfolio effect for diversity.  
Recruitment failure was correlated with lower summer water temperature, higher winter salinity,  
24 and shorter residence time, all indicators of stronger marine influence on estuaries. Recruitment  
failure was also more common in estuaries with limited networks of nearby adult oysters. Large  
26 existing oyster networks are thus of high conservation value, while estuaries that lack them  
would benefit from restoration efforts to increase the extent and connectivity of sites supporting  
28 oysters.

30 **Key words:** Biogeography, Bivalves, Conservation, Population cycles, Population ecology,  
Regional studies, Restoration

## Introduction

34 Understanding recruitment dynamics is essential for conservation or restoration of  
organisms with a complex life cycle, such as sessile marine invertebrates with mobile larvae  
36 (Roughgarden et al. 1988). The term “supply-side ecology” was coined to emphasize the  
importance of recruitment for population and community processes (Lewin 1986), building on a  
38 long history of interest in the larval stage in marine species (Young 1990, Grosberg and Levitan  
1992). Indeed, recruitment of new propagules into a population can be a critical determinant of  
40 adult population densities, especially if adult densities and intraspecific competition are low  
(Roughgarden et al. 1988). Recruitment variability in marine organisms has consequences for  
42 adult size structure and demography (Underwood and Fairweather 1989), and for population  
limitation or regulation (Caley et al. 1996). The causes of recruitment variability across both time  
44 and space have been explored in marine species, with patterns of sea surface temperature (SST)  
and processes such as nearshore upwelling figuring prominently as drivers of recruitment for  
46 some coastal species (Connolly and Roughgarden 1998, Diehl et al. 2007, Broitman et al. 2008).  
However, local dynamics can also be important, and larvae may be retained near the adults that  
48 produced them through larval behaviors interacting with hydrography as well as coastal  
geomorphology (Morgan et al. 2002, Shanks et al. 2009, Morgan et al. 2009, Byers et al. 2015,  
50 Nickols et al. 2015).

Recruitment can link spatially separated sites, and understanding the scale of linkages  
52 among separate populations is a fundamental issue in ecology (Roughgarden et al. 1988,  
Strathmann et al. 2002, Navarrete et al. 2008, D’Aloia et al. 2015). Separate populations can  
54 undergo similar dynamics across a large area, for instance if they all respond similarly to climatic  
drivers that occur across a broad geographic range. This regional synchrony, typically declining  
56 with distance, is called the Moran effect, after pioneering studies of lynx population synchrony  
across Canada (Moran 1953). Shared regional oceanographic factors, such as wave strength and  
58 nutrient concentrations, underlie synchrony in biomass of giant kelp (*Macrocystis pyrifera*)  
populations along the California coast (Cavanaugh et al. 2013). Myers et al. (1997) found strong  
60 synchrony in recruitment of 11 marine fish species, which declined on average around 500 km,  
and was attributed to climate forcing affecting factors such as SST or wind patterns. Stachura et  
62 al. (2014) found evidence for synchrony in 52 fisheries species within large marine regions in the

northeast Pacific, attributable to oceanographic factors including sea surface height.

64 Oceanographic processes can also underlie larval delivery; for instance, an investigation of  
common barnacles and mussels along the West West Coast of North America found that  
66 different biogeographic regions had similarities in seasonal timing of recruitment peaks, and that  
recruitment was positively associated with SST (Broitman et al. 2008). Likewise, an  
68 investigation of barnacles and mussels along the California-Oregon coast and central Chilean  
coast found regional coherence in temporal patterns of recruitment at a scale around 250km  
70 (Navarrete et al. 2008). A study of mussels (*Mytilus* spp.) and oysters (*Crassostrea gigas*) along  
thousands of kilometers of coastal European waters showed strong synchrony in peaks of larval  
72 abundance within a single year (Philippart et al. 2012). However, other evidence regarding  
recruitment synchrony in coastal species is mixed. Among 15 invertebrate species observed on  
74 recruitment plates in Chile, synchrony occurred in only four species, specifically barnacles and  
mussels with high recruitment rates, and sites were synchronous only within about 30 km (Lagos  
76 et al. 2007). For marine species with dispersive larvae, a Moran effect could arise not only due to  
regional factors that influence larval delivery, but also from population connectivity. Particularly  
78 successful production of larvae at one site could provide a batch of propagules that recruit across  
a wider area, illustrating the key importance of understanding the scale of linkages among  
80 separate populations (Roughgarden et al. 1988, Hughes et al. 2002).

There have been far fewer investigations of synchrony among species in estuaries than on the  
82 open coast. Since estuaries are influenced by riverine inputs and the surrounding watersheds, as  
well as by oceanic inputs, recruitment to sites in different estuaries along the coast might display  
84 less synchrony than to sites along the open coast. However, species within estuaries can also be  
strongly influenced by regional oceanographic or meteorological drivers (Cloern et al. 2010,  
86 Hughes et al. 2015) that can override local influences. For example, abundance of juvenile  
eastern oysters (*Crassostrea virginica*) within the large Chesapeake Bay estuary is strongly  
88 influenced by regional weather, with more production in years with less rain (Kimmel et al.  
2014). In addition to sites among different estuaries potentially facing similar oceanic or weather  
90 influences across estuaries, they may also be linked by dispersal of mobile stages that could face  
shared oceanic conditions while outside the estuary. For example, Pyper et al. (1999) found  
92 sockeye salmon (*Oncorhynchus nerka*) had a similar length by age relationship across years  
when caught in different streams across Alaska and British Columbia, due to shared offshore

94 history, with SST the likely driver of growth differences offshore between years. Taylor et al.  
102 (2010) examined 23 years of southern flounder (*Paralichthys lethostigma*) juvenile recruitment  
96 data for 105 estuarine sites in North Carolina, and identified substantial synchrony attributed to  
weather affecting hydrodynamics, which drove larval transport into estuaries. These studies  
98 focused on species that spend a significant portion of their life history outside estuaries, in the  
ocean. No study that we are aware of examines potential synchrony among estuaries in a species  
100 that can complete the entire life cycle in estuaries.

The oyster native to the West Coast of North America, the Olympia oyster (*Ostrea lurida*), is  
102 almost entirely found in estuarine ecosystems, and all larval stages as well as adult stages are  
known to occur within estuaries (Peteiro and Shanks 2015). The known distribution of this  
104 species is from British Columbia, Canada (Polson and Zacherl 2009) to Guerrero Negro, Baja  
California, Mexico (Raith et al. 2015). The Olympia oyster has undergone dramatic declines in  
106 many estuaries, due to overharvesting, habitat degradation, and introduced competitors and  
predators (Baker 1995, zu Ermgassen et al. 2012, and Pritchard et al. 2015). Recruitment is  
108 considered a key limiting factor for adult densities, and restoration projects have focused on  
providing additional hard substrates to enhance recruitment in systems where substrates large  
110 enough to prevent burial by sediments are limited (Pritchard et al. 2015, Zacherl et al. 2015).

We examined the spatial scale of interannual recruitment synchrony in the Olympia oyster  
112 along the West Coast of North America from southern California, U.S.A. to British Columbia,  
Canada, testing for synchrony within and among estuaries, and determining whether synchrony  
114 declines with distance. We hypothesized that high vs. low recruitment years would be shared  
among estuaries because many of these estuaries are very marine-influenced, and broad  
116 oceanographic effects such as upwelling strength, El Niño-Southern Oscillation (ENSO) or the  
Pacific Decadal Oscillation (PDO) could be shared across neighboring systems. Similar  
118 responses to oceanographic drivers could lead to shared peaks in larval production or settlement  
within separate estuaries. Another source of synchrony among neighboring estuaries might be a  
120 shared larval pool (Carson 2010), though larval retention within the area of production is  
considered the rule for many estuaries (Pritchard et al. 2015). We thus expected synchrony  
122 among estuaries to decline rapidly with distance, as has often been shown for marine species  
(Myers et al. 1997, Cavanaugh et al. 2013). We also expected to find some within-estuary

124 synchrony, especially in small or strongly marine-influenced systems with similar environmental  
conditions among sites.

126 We were further interested in characterizing factors that influence recruitment failure across  
estuaries, since recruitment may be an important determinant of adult densities and certainly is  
128 critical for restoration efforts for Olympia oysters, which typically rely on natural larval pools  
rather than hatchery-reared spat. We compared recruitment rates and consistency in recruitment  
130 across estuaries, and identified locations with recruitment failure at the site level and whole-  
estuary level. We hypothesized that strongly marine-influenced systems might have more  
132 recruitment failure because of unfavorably cold temperatures and lack of larval retention. We  
predicted that recruitment failure would be greater in estuaries with low chlorophyll *a*  
134 concentrations, indicating food limitation. We also hypothesized that large estuaries might have  
less recruitment failure than small estuaries, because they are more likely to harbor large oyster  
136 abundances and have heterogeneity in conditions such that larvae could be successfully produced  
somewhere in the estuary in any year, supplying the rest of the system. Finally, we hypothesized  
138 that sites with more abundant adults in the vicinity, and estuaries with large networks of nearby  
adult oyster sites would be less prone to failure than ones with small networks, again due to both  
140 larger population size and buffering against failure by having suitable conditions for larval  
production in at least some portions of the network.

142

## Methods

### 144 *Characterization of recruitment across estuaries*

To examine recruitment dynamics across as much of the range of the Olympia oyster as  
146 possible, we solicited data from researchers along the West Coast of North America and included  
data sets with at least three years of recruitment data from at least one site in an estuary. Our  
148 exhaustive search yielded eight estuaries where such monitoring data were available. These  
estuaries span 2500 km of coastline along much of the range of the species (Fig. 1). Estuaries are  
150 generally small and rare along the West Coast, so these eight represent an appreciable subset of  
estuarine habitat along the coast. Varying numbers of sites were assessed within the estuaries,  
152 ranging from one to nine, for a total of 37 sites. All sites had adult oysters present. Locations of  
sampling sites are shown in Appendix S1: Fig. S1. To compare a consistent time period across  
154 estuaries, we limited our analysis to 2006-2014, even though data from one or more earlier years



was available from six sites in four estuaries. Only Newport Bay, CA had data for all sites in every one of these nine years. Three to eight years of data were available for other sites.

We defined recruitment as the addition of new individuals into the population, resulting from larval settlement on hard substrates. For each site and year, we estimated the recruitment rate as the number of new oysters that appeared on deployed substrates per m<sup>2</sup> per year. Recruitment was assessed using different methods across the eight estuaries (Appendix S1: Table S1), with differing sensitivity to detection of early post-settlement mortality. Given the differences in measuring absolute recruitment rate across sites, we focused instead on relative measures to allow for comparisons of high vs. low recruitment years across sites. For univariate analyses, we converted recruitment to a percentage of the best year for each site. We used this to calculate the average recruitment percentage relative to the maximum for each site, and to calculate the percentage of years in which there was zero recruitment at each site. For Netarts Bay, which only provided presence/absence data, we considered years with recruitment 100% and years without 0%. We also calculated the coefficient of variation (CV=standard deviation/mean) for recruitment at each site. We examined the relationship between these different metrics with linear regressions, first taking the natural log of the absolute recruitment rate because San Francisco Bay values were extreme outliers with untransformed data.

#### *Testing for synchrony*

We characterized synchrony using recruitment data expressed as a percentage of the maximum value for each site. We defined a high recruitment year as one in which recruitment was >70% of the maximum for that site, and a low recruitment year as one in which recruitment was <30% of the maximum. We tallied what percentage of sites (of those where data were collected) in each year that had a high vs. low recruitment year by these criteria. As our quantification of synchrony at the site level, we then calculated the percentage of years (out of nine total) in which >75% of sites had either a high or low recruitment year.

To examine synchrony among estuaries, we conducted the same analyses as above for one single site per estuary. For those estuaries with multiple sites, we chose the site with the greatest absolute recruitment rate (marked by an asterisk in Fig. 2). The underlying rationale was that these sites represented the best comparison to single-site estuaries, in which cursory surveys informed selection of a monitoring site most likely to have high recruitment.

186 To examine synchrony within estuaries, we used the same metric described above,  
quantifying the percentage of sites within estuaries that were synchronous per year, and the  
188 percent of years that showed synchrony. As another indicator of synchrony, we calculated the  
CV of the raw recruitment density across all sites per year within an estuary, and then averaged  
190 this across all years. To test for the role of environmental heterogeneity in synchrony, we  
calculated a regression of the CV of average winter salinity (as an indicator of freshwater input)  
192 across all sites within an estuary vs. the percentage of sites per year that were synchronous in  
recruitment at that estuary.

194 To further explore patterns of synchrony among estuaries, we used non-metric  
multidimensional scaling (nMDS) in Primer v. 7.0 (Clarke and Warwick 2014). We created a  
196 Bray-Curtis similarity matrix using recruitment expressed as percent of maximum for each site,  
as described above. While this procedure is typically used to examine similarity among sites  
198 based on abundance of species, in this case we used it to examine similarity in recruitment by  
year (i.e., years are used like species in a community analysis). We qualitatively explored  
200 synchrony within and among estuaries with an nMDS plot representing all 37 sites. To test for  
synchrony among estuaries, we carried out an analysis of similarity (ANOSIM), omitting Fidalgo  
202 Bay and Netarts Bay, which had no replication (only a single site per estuary). Finally, we  
compared the Bray-Curtis similarity for sites within and among estuaries, using an independent  
204 samples t-test. We used the mean Bray-Curtis similarity value for each combination of sites for  
each estuary-estuary pair ( $n = 27$ ) and each site-site pair for within estuaries ( $n = 6$ ), respectively.

206 To examine patterns of synchrony as a function of distance, we estimated linear  
(Euclidean) distances among each of the 37 sites (see Appendix S1) and conducted regressions  
208 of distance by Bray-Curtis similarity. We recognize that oceanographic currents complicate such  
distance estimates (White et al. 2010), but previous studies have successfully identified  
210 synchrony relationships for marine species using Euclidean distances (e.g. Myers et al. 1997).  
We also examined three common oceanographic indices for their potential relationship with  
212 recruitment, because this could drive synchrony among sites: we conducted regressions of  
recruitment vs. ENSO, PDO and upwelling (see Appendix S1 for details).

214 To compare the role of temporal vs. spatial drivers of variation in recruitment, we used a  
Generalized Linear Mixed Effects Model (GLMM) to quantify the relative strength of effect of  
216 year (continuous random factor), site (random factor), and year\*site interaction on recruitment.

We used data from the two estuaries (Elkhorn Slough and Newport Bay) with the most years of data (2007-2014) and the most consistently sampled sites. We calculated the percent of variance for each factor to identify the key factors explaining patterns in recruitment for each estuary, respectively. We developed models using the glmer function with a Poisson distribution and log-link using the lme4 package (Bates et al. 2016) in R 3.2.3 (R Core Team 2015).

### *Predictors of recruitment failure*

We examined nine variables that might influence frequency of recruitment failure (described in detail in Appendix S1). Two of these were related to oyster population size: number of adult oysters near the recruitment monitoring site, and total size of the network of sites with adult oysters in the estuary. For both, our hypothesis was that increasing oyster numbers or network size would decrease frequency of recruitment failure. The other seven variables were environmental attributes of the sites or estuary. We quantified freshwater inputs, salinity, water temperature and residence time as proxies for marine influence to test the hypothesis that more marine-influenced estuaries (which typically have less freshwater inputs, higher winter salinities, lower summer temperatures, and shorter summer residence times) have more frequent recruitment failure. We used the CV of winter salinity across sites within each of the six estuaries with multiple sites to test the hypothesis that environmental heterogeneity reduces recruitment failure. We also examined estuary size, again with the hypothesis that larger estuaries may have more heterogeneous conditions that buffer against estuary-wide failure. To determine whether recruitment failure might be linked to food limitation, we also characterized chlorophyll *a* concentrations. We carried out regressions with each of these nine potential drivers as independent variables and frequency of recruitment failure as the dependent variable, using a simple linear regression unless the distribution of data better fit a logarithmic regression.

To further explore patterns of recruitment failure among estuaries, we used non-metric multidimensional scaling (nMDS) in Primer v. 7.0 (Clarke and Warwick 2014). Using the same two oyster and seven environmental variables as in the regressions, we conducted an ordination of estuaries with vs. without estuary-wide recruitment failure, used ANOSIM to determine whether the separation between these groups was significant, and SIMPER (similarity percentages) to determine which parameters contributed most to the separation.

248 **Results**

*Characterization of recruitment across estuaries*

250 Absolute recruitment rates varied tremendously across sites and over time (Fig. 2). The  
lowest recruitment rate observed was at Schooner Cove in the Strait of Georgia with an average  
252 rate of one oyster per m<sup>2</sup> per year, while the highest rate was at China Camp in San Francisco  
Bay, with an average of 125,526 oysters per m<sup>2</sup> per year. Some of these differences may be due  
254 to methodological differences in sampling, but great contrasts were observed even among sites  
sampled with similar methods, such as those in San Francisco Bay and Newport Bay (Appendix  
256 S1: Table S1).

Relative recruitment was low at most sites in most years; across our 37 sites, average  
258 recruitment was 36% of the maximum at that site (Fig. 2). In other words, variability was high  
and most years had much less recruitment than the peak year. Relative recruitment was not a  
260 function of absolute recruitment (linear regression  $R^2 = 0.02$ ,  $F_{1,34} = 0.83$ ,  $P = 0.36$ ). The CV  
ranged from 0.48 to 2.39 (Fig. 2), with an average of 1.25 across all sites. The CV declined with  
262 absolute recruitment rate, but the relationship was not strong (linear regression  $R^2 = 0.15$ ,  $F_{1,34} =$   
 $5.8$ ,  $P = 0.02$ ).

264 Recruitment failure was common at the site level; 20 of 37 sites had at least one year with  
no recruitment whatsoever. Average frequency of a year of zero recruitment was 20% across all  
266 sites. At one estuary, Elkhorn Slough, we quantitatively documented estuary-wide recruitment  
failure: in three of eight years, all five monitored sites had zero recruitment. Such estuary-wide  
268 failure did not occur at any of the other five estuaries with data from multiple sites during our  
study period, but qualitative surveys pre-dating our study period revealed estuary-wide failure at  
270 Tomales Bay in 2003-2005 (E. Grosholz, pers. obsv.). Quantitative data were only available for  
one site at Netarts Bay and Fidalgo Bay, but we conducted rapid assessments of other areas and  
272 observed zero recruitment throughout those estuaries in the years where zero recruitment was  
documented at the quantitative monitoring site (D. Vander Schaaf, pers. obsv. for Netarts; P.  
274 Dinnel pers. obsv. for Fidalgo). Thus, four of the eight studied estuaries have experienced  
estuary-wide recruitment failure.

276

*Testing for synchrony*

278 Among estuaries

When we examined patterns of synchrony among all sites along the entire coast, we  
280 found that our conditions for synchrony were met in only one year, 2006, when 88% of reporting  
sites had a low recruitment year (<30% of maximum recruitment documented for that site). In no  
282 other year did 75% or more sites share a high vs. low recruitment year. This lack of synchrony is  
evident from visual inspection of the recruitment patterns across sites (Fig. 2).

When we examined only one site per estuary (using the site with the highest recruitment  
284 for those with data for multiple sites), we found evidence for synchrony in three of nine  
monitoring years: in 2006, 100% of estuaries reporting data (5/5) had a low recruitment year; in  
286 2008, 75% (3/4 estuaries) did, and in 2010, 80% (4/5 estuaries) did.

Our multivariate analysis (Fig. 3, Appendix S1: Table S2) revealed few close associations  
288 among estuaries, further highlighting the lack of synchrony in recruitment. ANOSIM indicated  
that estuaries were a significant factor explaining variation in recruitment (global  $R = 0.447$ ,  $P =$   
290  $0.001$ ). Of 14 possible pairwise comparisons among estuaries, nine showed significant ( $P < 0.05$ )  
differences in recruitment patterns across years, i.e., lack of synchrony. Three pairs of estuaries  
292 showed marginally significant ( $P = 0.05-0.15$ ) differences. Two pairs (Elkhorn Slough and  
Tomales Bay; San Francisco Bay and Strait of Georgia) had no indication of significant  
294 differences ( $P > 0.5$ ), suggesting possible synchrony of these pairs.

Our regression analysis of synchrony by distance at the estuary scale revealed no  
296 significant patterns ( $R^2 = 0.020$ ,  $F_{1,25} = 0.507$ ,  $P = 0.483$ ): nearby estuaries did not show more  
synchrony with each other than farther ones. Our examination of the potential role of  
298 oceanographic drivers in leading to synchrony among sites revealed no significant relationships  
between recruitment and ENSO or PDO across estuaries. However, we detected a small but  
300 significant positive correlation between standardized upwelling indices and recruitment among  
estuaries ( $R^2 = 0.15$ ,  $F_{1,41} = 6.98$ ,  $P = 0.012$ ) (Fig. 4).

#### 304 Within estuaries

Synchrony within estuaries was strong at Willapa Bay and Elkhorn Slough: these had a  
306 high percentage of synchronous sites per year and a low CV of recruitment (Table 1). San  
Francisco Bay and Newport Bay had the lowest percentage of synchronous sites, while San  
308 Francisco Bay and Strait of Georgia had the highest CV of recruitment. Synchrony was generally  
greater at estuaries with less variable salinity conditions. We found a suggestive but non-

310 significant relationship between the percentage of sites that are synchronous per year and the CV  
of salinity across sites (linear regression  $R^2 = 0.38$ ,  $F_{1,4} = 2.5$ ,  $P = 0.19$ ).

312 The multivariate analysis also detected contrasting patterns across estuaries. Inspection of  
the nMDS ordination (Fig. 3) reveals that sites at some estuaries (e.g., Elkhorn Slough, Willapa  
314 Bay) cluster together, meaning they have similar relative recruitment each year, while sites at  
other estuaries (e.g., San Francisco Bay) show substantial spread, indicating dissimilarity in  
316 recruitment each year, or lack of synchrony. Overall, an independent samples t-test of Bray-  
Curtis similarity revealed significantly greater similarity for sites within estuaries compared to  
318 among (Appendix S1: Fig. S2;  $t = 3.335$ ,  $df = 32$ ,  $P = 0.002$ ).

With data from all sites included in a single analysis, we found no significant patterns in  
320 synchrony-by-distance within estuaries ( $R^2 = 0.140$ ,  $F_{1,4} = 0.652$ ,  $P = 0.465$ ). Furthermore, when  
each estuary was examined separately (Appendix S1: Fig. S3), we found no relationship of  
322 synchrony with distance (all  $P > 0.05$ ).

#### 324 Temporal synchrony vs. spatial variance

Our analysis of temporal synchrony vs. spatial variance with GLMM showed contrasting  
326 patterns at the two estuaries we examined (Appendix S1: Table S3, Fig. S4). At Elkhorn Slough,  
year explained the majority of the variation in recruitment (88.2%), which is consistent with the  
328 high synchrony among sites reported above. At Newport Bay, site (48.9%) and the year\*site  
interaction (47.3%) explained more variation than year (3.8%), consistent with the low  
330 synchrony among sites reported above.

#### 332 *Predictors of recruitment failure*

Of the nine variables we examined, four had a significant relationship with frequency of  
334 recruitment failure when analyzed with regressions (Table 2). Size of the network of sites  
containing oysters was strongly inversely correlated with frequency of recruitment failure: the  
336 larger the network, the rarer recruitment failure (Fig. 5A,  $R^2 = 0.95$ ,  $F_{1,6} = 121.8$ ,  $P < 0.0001$ ).  
The CV of winter salinity also showed a strong negative relationship: the greater the variation,  
338 the less recruitment failure (Fig. 5B,  $R^2 = 0.86$ ,  $F_{1,4} = 24.3$ ,  $P = 0.008$ ). Winter salinity had a  
weaker positive relationship; the higher the salinity, the more frequent recruitment failure (Fig.  
340 5C,  $R^2 = 0.24$ ,  $F_{1,35} = 11.1$ ,  $P = 0.002$ ). Breeding period temperature showed a weak negative

relationship with frequency of recruitment failure; the higher the summer temperatures, the less  
342 recruitment failure (Fig. 5D,  $R^2 = 0.12$ ,  $F_{1,35} = 4.9$ ,  $P = 0.03$ ). Two other variables showed a  
marginally significant negative relationship with recruitment failure; freshwater inputs ( $R^2 =$   
344  $0.52$ ,  $F_{1,6} = 4.13$ ,  $P = 0.09$ ) and estuary size ( $R^2 = 0.36$ ,  $F_{1,6} = 3.3$ ,  $P = 0.12$ ). The other three  
variables, chlorophyll *a* concentration, summer residence time, and number of nearby adult  
346 oysters showed no significant relationship with recruitment failure ( $R^2 < 0.1$ ,  $P > 0.15$ ).

The multivariate analysis of the same nine variables revealed distinct separation between  
348 estuaries with and without periodic estuary-wide recruitment failure (Fig. 6); ANOSIM  $R = 0.48$ ,  
 $P = 0.03$ . A SIMPER analysis indicated that the top contributors to this separation were length of  
350 the oyster network, winter salinity, residence time, summer temperature, estuary size and  
freshwater input (Table 3). Together these variables explained 80% of the separation between  
352 estuaries with and without recruitment failure.

## 354 Discussion

### *Striking spatial and temporal variation in recruitment*

356 In our investigation of *Olympia* oysters along 2500 km of coastline, we found great  
contrasts in absolute recruitment rate and recruitment failure rate among sites, estuaries, and  
358 years. Variability in recruitment of marine organisms is to be expected, given type III  
survivorship curves in which small changes in larval mortality dramatically alter settlement  
360 densities (Strathmann 1985, Cushing 1990, Rumrill 1990) and transport processes vary with  
weather events (Roughgarden et al. 1988, Rumrill 1990). Datasets that provide many years of  
362 recruitment data across a large geographic area are rare, but the high variance we observed may  
be common for marine species. Broitman et al. (2008) examined three species of common  
364 mussels and barnacles across eight years and 1750 km of the West Coast of North America and  
found many orders of magnitude of variation in recruitment between different sites and years. In  
366 our study, the relative role of spatial vs. temporal variation differed across estuaries: at Elkhorn  
Slough, year explained more variation than site, while at Newport Bay, site and the site\*year  
368 interaction explained more variation than year.

Understanding spatial and temporal patterns of recruitment is important for management  
370 of this species that was once common, but now is quite rare in many estuaries, and is facing a  
variety of threats (Pritchard et al. 2015, Wasson et al. 2015). Sites that have high and regular

372 recruitment should be conservation priorities, and if they have limited hard substrate, might also  
be preferred sites for population enhancement through substrate addition. Conversely those  
374 estuaries with frequent recruitment failure may need restoration intervention to prevent local  
extinction from repeated failure. For instance, Elkhorn Slough seems at risk of local extinction  
376 due to frequent years of zero recruitment with the longest such period being three consecutive  
years 2013–2015 (Wasson, unpublished data). In the next large estuary to the south, Morro Bay,  
378 Olympia oysters went locally extinct in the 1900s (Polson and Zacherl 2009), so this risk is real.

### 380 *Lack of synchrony among estuaries: importance of local dynamics*

The spatial scale of synchrony among populations has been a fundamental question in  
382 ecology for many decades (e.g., Moran 1953, Bjørnstad et al. 1999). To our knowledge, ours is  
the first investigation of potential synchrony in interannual recruitment among estuaries for  
384 species that can complete their entire life cycle in the estuary. A few years (2006, 2008, 2010)  
had low recruitment at most sites, which could be evidence of a Moran effect, but there were no  
386 years with high recruitment at the majority of sites. We conclude that shared response to broad  
regional oceanographic factors is not a major driver of recruitment variation among estuaries,  
388 which is consistent with ENSO and PDO indices displaying no significant statistical  
relationships with recruitment. We did find a positive relationship of recruitment with upwelling,  
390 but this did not translate into synchrony, perhaps because upwelling varies in strength and timing  
in different regions, and because the relationship was fairly weak ( $R^2 = 0.15$ ). Only two estuaries  
392 were within the same upwelling region (Tomales Bay, San Francisco Bay), and they did not  
show synchrony, with recruitment at these estuaries more affected by other factors, and quite  
394 variable within each estuary. Our lack of synchrony related to oceanographic drivers contrasts  
with open coast studies that found that regional patterns of sea surface temperature, as well as  
396 regional processes such as upwelling, ENSO, and PDO, can sometimes predict variation in  
recruitment in open coast communities (Connolly and Roughgarden 1998, Botsford 2001,  
398 Broitman et al. 2008). Estuarine communities can also respond to oceanographic drivers and  
regional factors (Peterson et al. 1992, Cloern et al. 2010, Hughes et al. 2015). We thus expected  
400 to detect synchrony, at least among populations within the same bioregion, as has been  
demonstrated for marine fish and invertebrates (Myers et al. 1997, Stachura et al., Lagos et al.  
402 2007, Philippart et al. 2012) and estuarine fish (Taylor et al. 2010). However, those species share



an obligate oceanic life-history stage with the potential to experience similar conditions while at  
404 sea.

Lack of recruitment synchrony among oyster populations may be due to multiple factors,  
406 but one possible cause is the lack of an obligate oceanic phase in the life cycle. The larval period  
of oysters (one to a few weeks) is potentially long enough to allow for dispersal among estuaries,  
408 and such exchange has been documented for nearby estuaries in southern California (Carson  
2010). However, various lines of evidence suggest larval retention is more typical of Olympia  
410 oysters, at least for more isolated estuaries (Peteiro and Shanks 2015, Pritchard et al. 2015).  
Recruitment is highest in areas where retention is likely; mid to upper estuarine areas generally  
412 have higher recruitment than estuarine mouths (Kimbrow et al. 2009, Pritchard et al. 2015). Larvae  
at multiple stages of development are often captured within the upper portion of an estuary  
414 (Rimler 2014, Peteiro and Shanks 2015), while few larvae are present in the outer portion or  
offshore (Pritchard et al. 2015). Furthermore, while 16S and mitochondrial genetic markers (i.e.,  
416 COI, COIII) indicate that Olympia oysters are connected at sites across their range on  
evolutionary timescales (Polson et al. 2009), they show genetic differentiation in relatively more  
418 variable microsatellite markers among some estuaries, and even within large estuaries such as  
Puget Sound and San Francisco Bay (Stick 2011, Linnenbrink 2016), though sites in southern  
420 California lack such differentiation (Linnenbrink 2016), consistent with Carson (2010). So, with  
the exception of southern California, Olympia oysters among different estuaries may not  
422 constitute a classic open metapopulation with a shared larval pool, as may be the case for some  
open coast species (Roughgarden and Iwasa 1986). The spatial scale of connectivity among  
424 marine populations varies tremendously, depending on life history and oceanographic factors,  
but even for many coastal species is often only 10s to 100s of km (Cowen et al. 2006), lower  
426 than the distance between many of the estuaries in our study. Numerous mechanisms can  
promote larval retention (Cowen et al. 2000, Nickols et al. 2015), and in such cases, synchrony  
428 due to a shared larval pool across sites would not occur.

Even without a shared larval pool experiencing similar offshore conditions, oyster  
430 populations in different estuaries might still show synchrony in high vs. low recruitment years.  
This could occur if larval production or settlement success within the estuary was strongly  
432 affected by oceanic influences that vary across a larger region. Our results showed no strong  
synchrony among estuaries and no synchrony-by-distance relationship suggesting that local

434 forcing factors outweigh broad-scale oceanographic factors. Estuaries are of course affected by  
their watersheds as well as the ocean (e.g., Ruesink et al. 2015), and the lack of synchrony  
436 among estuaries or even among sites within large estuaries such as San Francisco Bay could  
reflect such local factors. Given locally influenced dynamics, wetland management and policies  
438 that affect the watershed could exert a strong influence on oyster recruitment. Local management  
may thus affect estuarine residents much more than migratory estuarine species or species along  
440 the open coast, which are often strongly affected by oceanography.

#### 442 *Synchrony within estuaries*

Recruitment at sites within estuaries showed strong synchrony at two of the studied  
444 estuaries (Willapa Bay and Elkhorn Slough) and weak synchrony at two estuaries (San Francisco  
Bay and Newport Bay), with intermediate synchrony at the other two estuaries. In general, it  
446 appears that synchrony is greater in estuaries with environmental homogeneity, as indicated by  
similar salinity conditions. This can be illustrated by comparing two small California estuaries.  
448 Elkhorn Slough is very marine-influenced, with strong tidal currents resulting from an artificial  
harbor mouth to the estuary, while most freshwater inputs to the estuary have been diverted for  
450 agriculture (Caffrey et al. 2002). Sites in the estuary have similar salinity conditions and also  
strong synchrony. This estuary frequently has years with zero recruitment at all sites. In contrast,  
452 Newport Bay is marine-influenced at the mouth, but receives substantial year-round freshwater  
inputs from municipal sources at the head of this small estuary (Pednekar et al. 2005). Sites in  
454 this estuary have quite different water quality conditions and flushing time scales (Pednekar et al.  
2005), and are not synchronous: a high-recruitment year in the upper estuary may be a low-  
456 recruitment year towards the mouth, and vice versa, leading to the strong site\*year interactions  
we detected (Appendix S1: Table S4, Fig. S3). This lack of synchrony means that all sites do not  
458 share poor recruitment simultaneously, which provides buffering against estuary-wide  
reproductive failure.

460 The finding that heterogeneity prevents estuary-wide recruitment failure is analogous to  
tenets of metapopulation theory, where synchronous populations are at risk of extinction while  
462 asynchronous ones persist (Hanski and Gilpin 1997). Our oyster populations within estuaries do  
not necessarily fit the definition of a metapopulation, because sites are not very isolated and may  
464 not have separate dynamics, but the same concept of risk associated with synchrony applies. Our

finding is also related to the concept of the biological portfolio effect (developed from portfolio theory of economics), where species or genetic diversity is linked to ecological stability, while shared variation within the portfolio leads to greater risk and lower returns (Figge 2004, Schindler et al. 2010). We are thus extending the portfolio concept to environmental heterogeneity, inferring that this may lead to greater stability in oyster populations than does homogeneity.

#### *Predictors of recruitment failure*

We documented frequent recruitment failure for Olympia oysters: 20 of 37 sites had zero recruitment in some years. Moreover, at the scale of the whole estuary, complete reproductive failure at all sites in a given year occurs periodically at four of eight of our studied estuaries. Estuary-wide recruitment failure was also reported previously for Coos Bay and attributed to lack of larval supply, since no larvae were found in the water column during sampling in this year (Rimler 2014). The frequency of recruitment failure may be due to the strong reduction in population sizes relative to historic levels (zu Ermgassen et al. 2012); recruitment failure was perhaps rarer historically and prehistorically when populations were larger. For restoration practitioners, our results have practical implications: for many sites, there is a reasonable chance that there will be no recruitment the first year new substrates are deployed to enhance populations.

Our analysis of oyster population attributes revealed that the size of networks of nearby oyster sites was a strong predictor of estuary-wide recruitment failure – much more so than size of the estuary itself, which only showed a weak relationship with recruitment failure. Large estuaries like San Francisco Bay have large networks of nearby oyster sites within the estuary. However, one of our very small estuaries, Newport Bay, also had a large network of nearby oyster sites, extending outside the estuary to other small embayments to the north and south. In years of low larval production within Newport Bay, it is possible that recruitment occurs there from larval subsidies in other parts of the network, as has been shown for estuaries further south in California (Carson 2010). In contrast to size of the network of oyster sites in or around the estuary, the number of adult oysters within the immediate vicinity of the recruitment monitoring site did not show a relationship with recruitment failure. This lack of an effect of local adult

abundance is consistent with documentation of larvae recruiting tens of kilometers away from  
496 where they were produced (Carson 2010).

498 Recruitment failure also appears to be related to strong marine influence. The frequency  
of recruitment failure increases with decreasing summer water temperatures and increasing  
500 winter salinity, both of which are associated with strong marine influence in estuaries. Several  
possible mechanisms could connect marine influence to failed recruitment. The onset and  
intensity of reproduction by adults is related to local temperature increases (Coe 1931, Hopkins  
502 1936, Seale and Zacherl 2009, Oates 2013, Peteiro and Shanks 2015), so colder marine waters  
might decrease larval production. Strong marine influence also increases the risk of loss of  
504 larvae, as these may be swept out to sea rather than retained in the estuary (Pritchard et al. 2015).  
Strong tidal energy is favorable for recruitment and adults of eastern oysters (Byers et al. 2015),  
506 but may pose a threat to much rarer Olympia oysters, which are largely limited to isolated  
estuaries. Olympia oyster larvae undergo vertical migrations, staying near the bottom on ebbing  
508 tides, a behavior that enhances larval retention; however, strong tidal currents overwhelm these  
behaviors (Peteiro and Shanks 2015). Residence time was identified in the multivariate analysis  
510 as an important contributor to the separation of estuaries with and without recruitment failure –  
three of four estuaries with estuary-wide recruitment failure typically have very short residence  
512 times, less than two weeks. While residence time did not correlate with frequency of recruitment  
failure at the site level (because some sites with recruitment failure had long residence times), at  
514 all eight of the estuaries in this study there is generally near-zero recruitment in the most marine-  
influenced sites near the estuarine mouth (all authors, pers. obsv.). Thus a strong marine  
516 influence exerts a negative effect on oyster recruitment, and perhaps also recruitment of other  
estuarine resident species dependent on warmer waters or larval retention.

518 In contrast, we found that estuary-wide recruitment failure was reduced at estuaries with  
stronger freshwater inputs, where there was more variation among sites within the estuary in  
520 salinity. Again, this may be an example of a sort of environmental portfolio effect, as discussed  
above for synchrony – estuaries with spatial variability in conditions may be buffered against  
522 synchronous failure of all sites, because some have appropriate conditions for larval production  
even if others do not. What exactly those conditions are remains to be elucidated. While it has  
524 been suggested that high chlorophyll *a* concentrations are related to Olympia oyster reproduction  
(Oates 2013), we found no relationship between chlorophyll *a* concentrations and recruitment

526 failure. Some estuaries that never have estuary-wide failure, such as San Francisco Bay, have  
quite high chlorophyll *a* concentrations, but others, such as Newport Bay and Willapa Bay, have  
528 rather low concentrations.

After evaluating numerous oyster and environmental variables, we thus conclude that  
530 large oyster networks spanning heterogeneous environmental conditions, including sites that are  
not heavily marine-influenced, can buffer against recruitment failure. Such networks could be  
532 incorporated into restoration planning and design. Restoration success is likely to be highest at  
sites that are part of a larger network spanning a range of conditions, either within a large estuary  
534 such as San Francisco Bay or among nearby neighboring estuaries such as in southern California.  
At estuaries that currently lack a large network, management efforts could attempt to  
536 strategically restore one. For the more abundant and widespread eastern oyster (*Crassostrea*  
*virginica*), a recent study showed that marine reserves need to be large enough to allow for larval  
538 retention and/or close enough together (<40 km) to allow for larval transport (Puckett et al.  
2014). Conservation of oysters thus depends on connectivity, as has been found for many other  
540 species, and future studies could apply formal network measures and models (Rayfield et al.  
2011) to the strategic design of Olympia oyster restoration plans.

542

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**Table 1. Synchrony within estuaries.** <sup>1</sup>The percent of sites within each estuary that were synchronous (all with >70% or <30% of maximum recruitment for each site), averaged across all monitored years. <sup>2</sup>The CV of recruitment for each year across all sites, averaged across years for each estuary. <sup>3</sup>The CV of winter salinity across sites within estuaries, presented as a factor related to synchrony. Boldface values are the ones indicative of greatest synchrony and least variation in salinity among sites within estuaries.

<i>Estuary</i>	<i>% sites synchronous per year<sup>1</sup></i>	<i>CV of recruitment<sup>2</sup></i>	<i>CV of winter salinity<sup>3</sup></i>
Strait of Georgia	75%	1.59	0.11
Willapa Bay	<b>94%</b>	<b>0.77</b>	<b>0.08</b>
Tomales Bay	75%	1.32	<b>0.07</b>
San Francisco Bay	67%	1.39	0.13
Elkhorn Slough	<b>90%</b>	<b>0.78</b>	<b>0.04</b>
Newport Bay	52%	1.01	0.10

**Table 2. Predictors of recruitment failure.** Summary of analyses examining the relationship of two oyster variables and seven environmental variables with recruitment failure. <sup>1</sup>The relationship is negative if increasing values of the variable lead to decreasing recruitment failure. <sup>2</sup>Regressions examined the relationship between the variables and the percent of years where recruitment failure occurred. \*\*\* P < 0.01; \*\* P < 0.05; \* P < 0.15. <sup>3</sup>For the multivariate analysis, a SIMPER was conducted to identify the factors that contribute the most to separating estuaries that do vs. do not experience estuary-wide recruitment failure. The percent contribution of the top six contributing variables is shown. CV of winter salinity was not included in the analysis because estimates were not available for the two estuaries where only a single site was monitored, and SIMPER cannot accommodate missing data.

	<i>Relationship with recruitment failure<sup>1</sup></i>	<i>Regressions<sup>2</sup></i>	<i>Multivariate analysis<sup>3</sup></i>
<b><i>Oyster variables</i></b>			

Network size	-	***	17%
Number of nearby adults		n.s	n.s
<i>Environmental variables</i>			
Winter salinity	+	***	14%
CV of winter salinity	-	***	n.a.
Freshwater inputs	-	*	11%
Summer temperature	-	**	13%
Chlorophyll <i>a</i>		n.s.	n.s.
Residence time	-	n.s.	13%
Estuary size	-	*	12%

### Figure Legends

**Figure 1. Location of the eight focal estuaries in this study.**

**Figure 2. Summary of recruitment among sites and estuaries.** For each site, recruitment is expressed as a percent relative to the best year; every site thus has one year with 100% (color-coded green). Sites marked with asterisk had highest absolute recruitment per estuary for multi-site estuaries, and were used for estuary comparisons. Recruitment by year is rounded to nearest percent except for 0%, where decimal is included to distinguish years with very low but non-zero recruitment.

**Figure 3. Multivariate analysis of similarity in recruitment synchrony among sites and estuaries.** A non-metric multi-dimensional scaling plot is shown, based on similarity in percent recruitment (relative to the maximum at each site) for each shared year. Site numbers correspond to Figure 2.

**Figure 4. Linear relationship between upwelling and recruitment.** Standardized upwelling scores were calculated from the nearest upwelling station to each estuary correlated with recruitment. Each point represents the mean of all sites within each estuary for each year. Shaded area represents 95% confidence interval.

**Figure 5. Predictors of recruitment failure.** A and B are logarithmic regressions using estuary as replicate (B has multi-site estuaries only); C and D are linear regressions and use site as replicate.

**Figure 6. Multivariate analysis separation among estuaries with and without years with estuary-wide recruitment failure.** A non-metric multi-dimensional scaling plot is shown based on similarity in two oyster and seven environmental variables.

**Figure 1.**

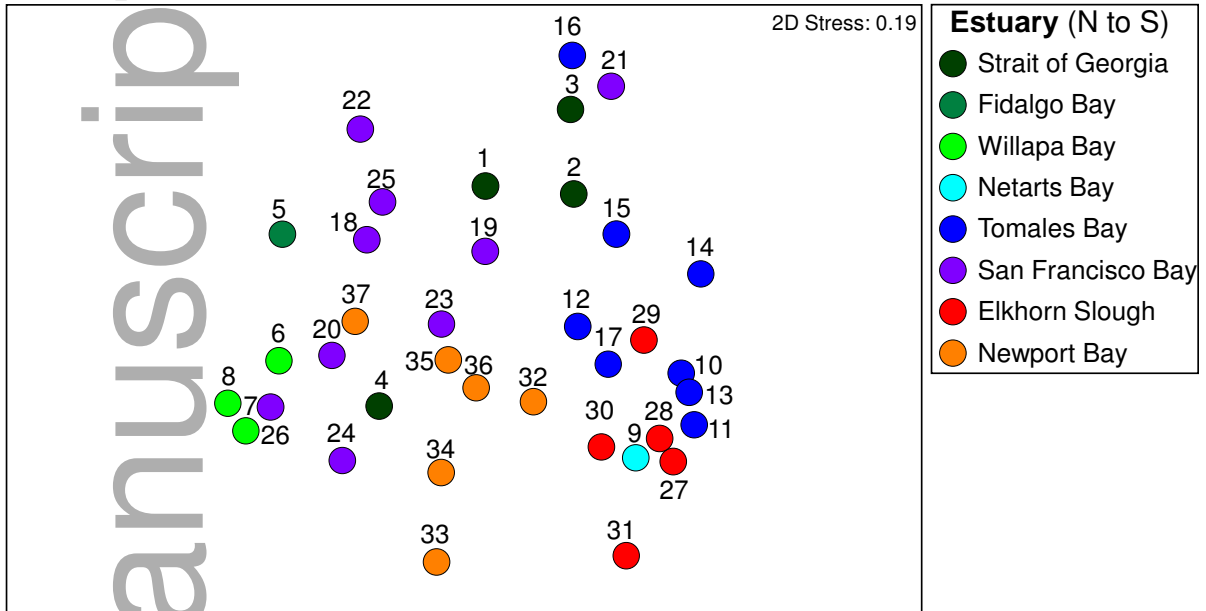


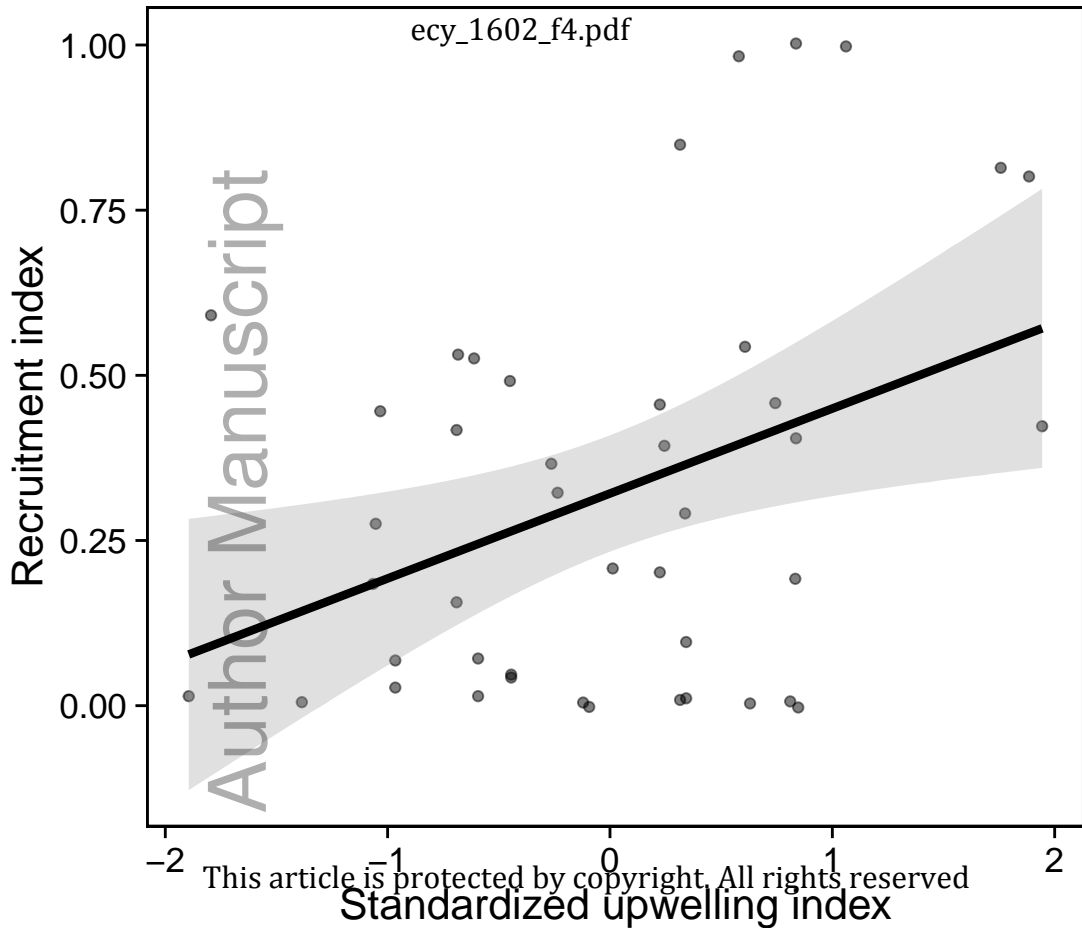
Figure 2.

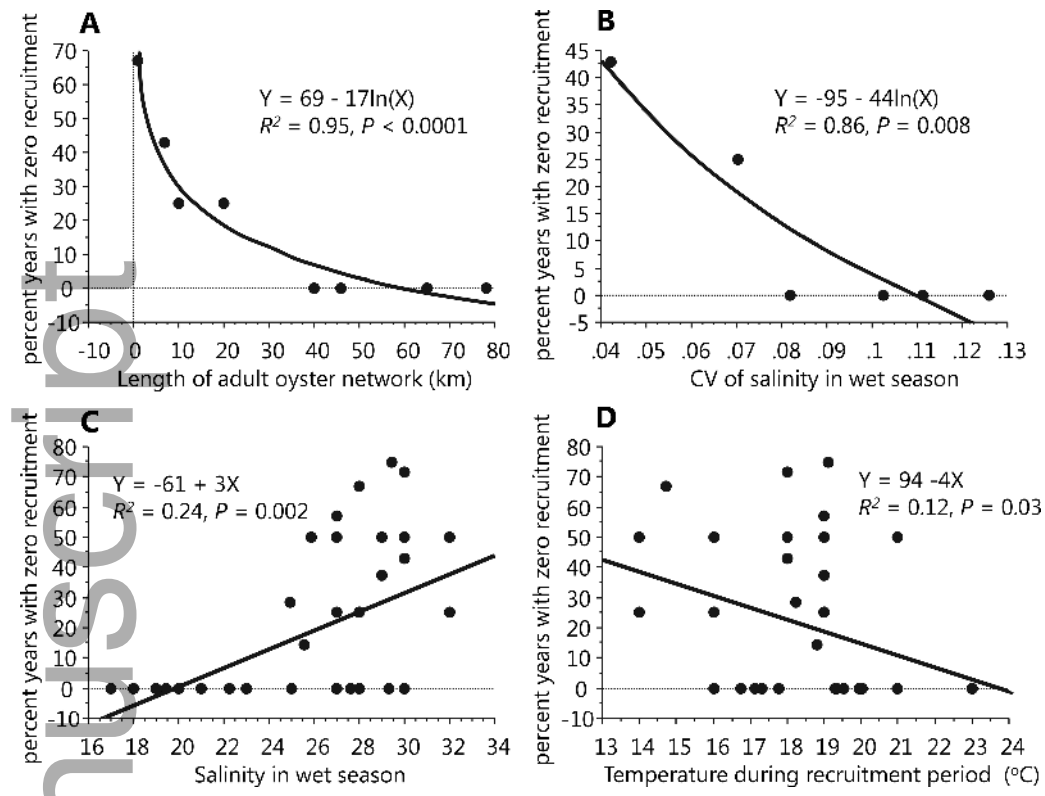
Estuary	Site name	Site #	Recruitment percent relative to best year									Average recruitment rate (#/m2/yr)	Average recruitment as % of maximum	CV of recruitment	% of years with 0 recruitment
			2006	2007	2008	2009	2010	2011	2012	2013	2014				
Strait of Georgia	Union Bay	1						100%	16%	29%		2	48%	0.94	0%
	Schooner Cove	2						100%	23%	9%		1	44%	1.12	0%
	Nanaimo	3						100%	2%	7%		5	36%	1.52	0%
	*Ladysmith Harbour	4						10%	53%	100%		98	54%	0.83	0%
Fidalgo Bay	Trestle Plot B	5	2%	0.0%	0.0%	100%		2%	7%	41%	35%	96	23%	1.50	25%
Willapa Bay	*Mill Channel	6	18%				1%	14%	3%	100%	76%	2965	35%	1.19	0%
	Station 3	7	5%				0.4%	3%	3%	100%	19%	1937	22%	1.79	0%
	Long Island Slough	8	3%				2%	3%	1%	100%	16%	922	21%	1.89	0%
Netarts Bay	Netarts Bay	9	0.0%	100%	0.0%	0.0%	0.0%		100%						67%
Tomales Bay	E1	10	0.0%	100%	13%	13%						29	31%	1.47	25%
	W1	11	0.0%	100%	0.0%	12%						29	28%	1.73	50%
	E2	12	23%	100%	43%	32%						270	49%	0.71	0%
	W2	13	0.0%	100%	0.0%	19%						19	30%	1.60	50%
	*E3	14	0.0%	100%	82%	3%						574	46%	1.13	25%
	W3	15	0.0%	74%	100%	44%						264	54%	0.79	25%
	E4	16	0.5%	0.0%	100%	0.0%						315	25%	1.99	50%
	W4	17	16%	100%	30%	9%						395	39%	1.08	0%
San Francisco Bay	*China Camp	18					100%	18%	26%	42%	30%	125526	43%	0.76	0%
	Loch Lomond	19					100%	94%	58%	44%	13%	29452	62%	0.58	0%
	Point Orient	20	0.0%	0.0%	1%	35%	76%		48%	100%		3934	37%	1.08	29%
	Ferry Point	21	0.0%	0.0%	100%	16%						136	29%	1.66	50%
	Tiburon	22	0.0%	0.0%	0.0%	100%						2	25%	2.00	75%
	Brickyard	23					21%	84%	76%	100%	46%	4597	65%	0.48	0%
	Berkeley	24	0.1%		4%	3%	30%	2%	45%	100%		2647	26%	1.41	0%
	Alameda	25	29%	7%	14%	100%						103	38%	1.14	0%
	Oyster Point	26	0.0%	0.0%	0.1%	1%	28%		20%	100%		42400	21%	1.71	14%
Elkhorn Slough	North Azevedo	27		100%		0.0%	0.0%	2%	96%	0.0%	0.0%	160	28%	1.68	57%
	Kirby	28		100%	2%	2%	0.0%	14%	62%	0.0%	0.0%	101	23%	1.67	38%
	Whistlestop	29		100%	0.0%	27%	0.0%	83%	54%	0.0%	0.0%	64	33%	1.25	50%
	*Hummingbird	30		92%		100%	0.0%	0.5%	89%	0.0%	0.0%	334	40%	1.25	43%
	South Marsh	31			0.0%	9%	0.0%	0.0%	100%	0.0%	0.0%	35	16%	2.39	71%
Newport Bay	Rocky Point	32	83%	100%	49%	28%	37%	6%	45%	34%	26%	5104	46%	0.64	0%
	Coney Island	33	100%	18%	12%	14%	12%	5%	15%	19%	7%	2900	22%	1.32	0%
	Newport Wall	34	100%	33%	18%	25%	18%	10%	24%	42%	18%	2599	32%	0.84	0%
	Balboa Island	35	23%	52%	27%	79%	44%	23%	100%	80%	86%	1012	57%	0.52	0%
	*15th Street	36	18%	35%	6%	37%	16%	42%	100%	43%	43%	6410	38%	0.71	0%
	Public Dock	37	2%	16%	6%	50%	65%	26%	38%	100%	89%	624	44%	0.82	0%
<b>Average</b>			<b>17%</b>	<b>57%</b>	<b>24%</b>	<b>32%</b>	<b>26%</b>	<b>32%</b>	<b>46%</b>	<b>52%</b>	<b>28%</b>	<b>6557</b>	<b>36%</b>	<b>1.25</b>	<b>20%</b>



Figure 3.

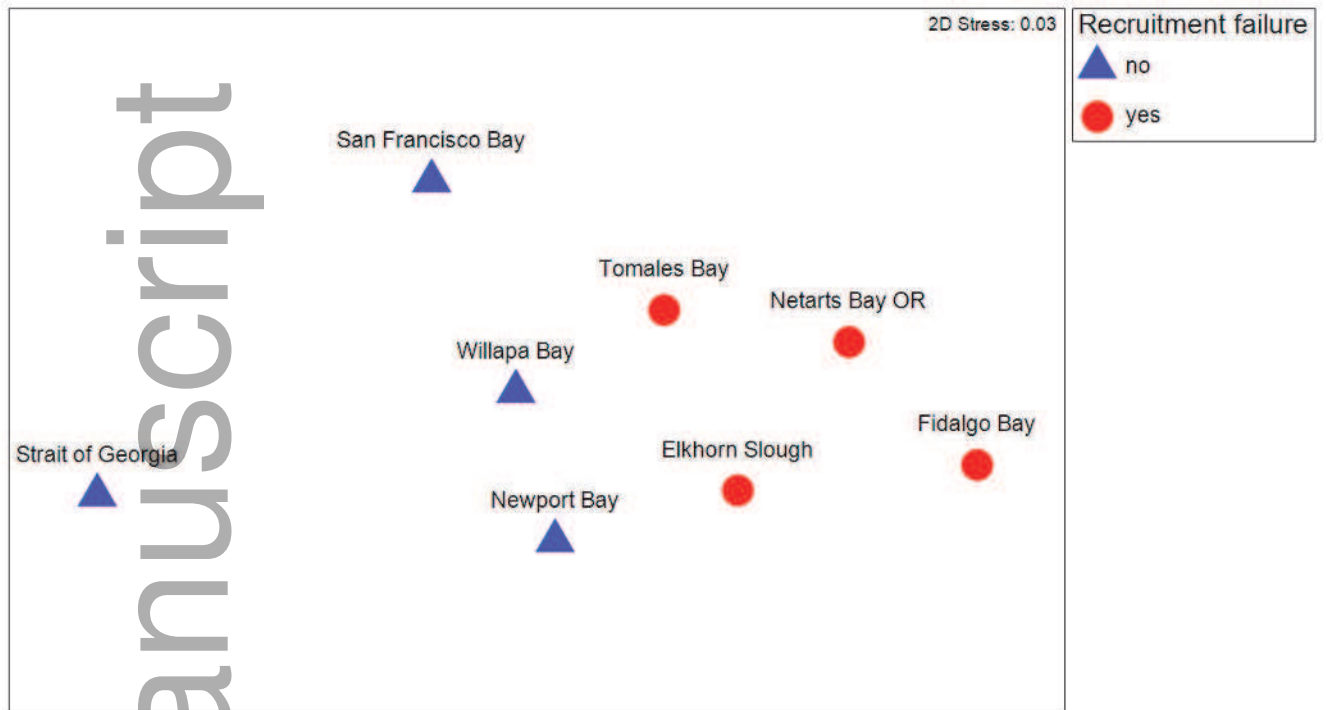






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Figure 6.



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