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Variation in larval supply and recruitment of *Ostrea lurida* in the Coos Bay estuary, Oregon, USA

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ABSTRACT: *Ostrea lurida* is the only oyster native to the US west coast. Overharvesting and other factors have led to population declines and the extinction of some populations. Despite restoration efforts, the recovery of *O. lurida* has been weak, and the causes for limited recovery are poorly understood. To be successful, recovery efforts must consider limitations at each stage of the multiphase life cycle of *O. lurida*, including pelagic larvae and sessile juveniles and adults. In the Coos Bay estuary, Oregon, the distribution of adult oysters is relatively well known, but larval dispersal and recruitment patterns are not. Using passive larval traps and recruitment plates, we tested the hypothesis that this population is recruitment-limited through low larval availability and/or variable recruitment success within the estuary. We observed high larval availability, low recruitment, and negligible adult populations at riverine-dominated sites located in the inner bay. In contrast, polyhaline sites located in the middle region of the bay had high larval availability, high recruitment rates, and abundant adult populations. Conversely, marine-dominated sites near the mouth of the estuary had negligible larval availability, no recruitment, and adult populations were almost entirely absent. Our results indicate that a sustained population of *O. lurida* is likely feasible only in the polyhaline region of the Coos Bay estuary. Restoration and enhancement efforts designed to help recover populations of *O. lurida* should give serious consideration to early life stage characteristics including larval supplies, dispersal, and recruitment, as well as environmental conditions within the bays and estuaries.

KEY WORDS: *Ostrea lurida* · Olympia oyster · Larval supply · Recruitment · Null zone · Coos Bay estuary

INTRODUCTION

The Olympia oyster *Ostrea lurida* (Carpenter, 1864) is the only oyster native to the western coast of the US, where adults occur in protected water habitats from southeast Alaska to Baja California (Baker 1995, Polson & Zacherl 2009). Population declines caused by overexploitation (Steele 1957, Baker 1995), removal and burial of shell deposits used as substrata for settlement (Wasson 2010), habitat degradation (Kimbro et al. 2009, zu Ermgassen et al. 2012), introduction of non-native species (Bower et al. 1997, Buhle & Ruesink 2009, Trimble et al. 2009), and other factors (reviewed by Baker 1995, Pritchard et al. 2015) have caused many populations to become 'functionally extinct' (Beck et al. 2011). Some populations of *O. lurida* in the Pacific Northwest are estimated to be at only 1 to 10% of their historical abundances (Beck et al. 2011). Although restoration and enhancement efforts are currently underway in California, Oregon, Washington, and British Columbia (Canada) (Brumbaugh & Coen 2009), recovery of self-sustaining pop-

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ulations of *O. lurida* has been limited. The reasons for poor recovery of *O. lurida* populations are not well understood, and it is likely that context-dependent factors, including multiple life history stages and the biophysical characteristics of specific bays and estuaries, are important.

Olympia oysters have a complex bi-phasic life cycle that includes brooding embryos and early larvae followed by release of later-stage planktonic veliger larvae that are dispersed in the water column for 10 to 14 d (Pritchard et al. 2015). Similar to the majority of temperate nearshore benthic invertebrates, the planktonic larval stage of *O. lurida* provides an opportunity for transport and dispersal away from the sessile adult before settlement back to the bottom (Strathmann et al. 1987, Pineda 2000). Successful settlement (physical transition from the water column to the benthos), metamorphosis (ontogenetic transition from a planktonic larva to a benthic post-larva), and juvenile survival and growth lead to recruitment and incorporation of new individuals into the adult population (Pineda et al. 2009). However, for many bi-phasic species, including *O. lurida*, the processes affecting the success of each life stage are not well understood (Yoshioka 1982, Caley et al. 1996, Eckman 1996, Palmer et al. 1996, Tremblay et al. 2007, zu Ermgassen et al. 2012), and each life stage may present its own bottleneck to population growth (Gaines et al. 1985, Raimondi 1990, Minchinton & Scheibling 1991, Jenkins 2005, Shinen & Navarrete 2010). These relationships may also change over time. For example, over 90 % of the variation in adult population size of Dungeness crab *Cancer magister* can be attributed to the number of megalopae returning after off-shore development and dispersal during low recruitment years (Shanks & Roegner 2007). During high recruitment years, however, density-dependent interactions may reduce recruitment into the adult population (Shanks 2013). Thus, for studies attempting to understand factors influencing the distribution and abundance of species with planktonic and benthic stages, one must investigate all life history stages and how they are linked (Gaines & Bertness 1993).

In this study, we aimed to describe the spatial and temporal dynamics between *O. lurida* larvae and settlers along the Coos Bay estuary, and how these dynamics may be contributing to slow population recovery in an Oregon estuary. One possibility is that larval supplies or settlement may be inadequate to replace previous generations. If limitations in larval supply are the cause, it is crucial to determine whether the populations are open or closed. Open populations are characterized by larval input from distant populations. In this case, larvae should be present near the mouth of an estuary as they enter from the ocean. Alternatively, closed populations receive the majority of larvae from local populations. In this case, larvae may or may not be abundant at the mouth of the estuary, depending on the distribution and fecundity of local adults. *O. lurida* populations appear to exhibit the latter pattern in Oregon and Washington, as many populations are genetically distinct from other regions along the US west coast (Stick 2011), suggesting minimal input from or exchange with populations from the open ocean (Stick 2011, Peteiro & Shanks 2015). Consequently, effective strategies for conservation and recovery of *O. lurida* are likely needed at the local level of individual bays and estuaries along the Oregon coast.

If larval supplies and settlement are adequate for restoration, but population recovery is still slow, subsequent settler survival and growth may be insufficient due to either biotic or abiotic factors (Connell 1985, Peter-Contesse & Peabody 2005, Pineda et al. 2010). Biotic factors that may influence populations of *O. lurida* include competition with non-native species, predation, and density-dependent interactions, while abiotic factors such as desiccation and critical temperature thresholds may control reproduction, survival, or recruitment (Buhle & Ruesink 2009, Trimble et al. 2009, Wasson 2010). Temperature and salinity also influence reproductive success and survival. In the Coos Bay estuary, the critical temperature for gametogenesis for *O. lurida* is 15°C (Oates 2013); larvae are not found in this estuary when the minimum water temperature remains below 15°C, indicating that spawning may also not be initiated below this temperature (L. G. Peteiro unpubl. data). Salinity, as determined by proximity to freshwater inputs such as the Coos River or by patterns of rainfall, can also deter settlement or survival of new recruits (Hopkins 1937, Gibson 1974, Grosholz et al. 2008, Sawyer 2011).

Here, we investigated the abundance of larvae and settlers through the Coos Bay estuary, Oregon. Although the abundance and distribution of adult *O. lurida* have been described previously for the Coos Bay estuary (Groth & Rumrill 2009), contributing factors to variability in abundance, recruitment, and slow population recovery are undetermined. Extensive shell deposits in this area suggest a historically large population of *O. lurida* that probably supported tribal subsistence fisheries (S. Groth pers. obs.). Today, the estuary is inhabited by a persistent population of *O. lurida* that was likely reintroduced to the estuary inadvertently as spat on the shells of cultivated Japanese oysters *Crassostrea gigas* that were imported from Willapa Bay, Washington, for commercial aquaculture (Baker et al. 2000, Groth & Rumrill 2009, Stick 2011). This population, while probably just a fraction of its historic size (Beck et al. 2011), is relatively large compared with the populations in other Oregon estuaries. For example, scattered populations of *O. lurida* occur along ca. 32 km of the shoreline of Coos Bay, while populations occur along ca. 21 km of the shoreline of Yaquina Bay and along ca. 6 km of the shoreline of Netarts Bay, Oregon (S. S. Rumrill pers. obs.). The large size and relative success of the recovering population in Coos Bay make it a suitable location for examining how larvae and settlers contribute to the distribution of adults within the estuary.

In this study, we used passive plankton traps and recruitment plates as integrated samplers to quantify the relative larval supply and recruitment of *O. lurida* throughout the Coos Bay estuary during the reproductive seasons in 2012 and 2013. Specifically, we asked: (1) Which locations within the estuary are exposed to the highest concentration of late-stage larvae? (2) What are the spatial and temporal relationships between larval abundance and subsequent recruitment along the estuary? (3) How might the location along the temperature and salinity gradient (riverward to seaward portions of the estuary) and temporal differences in rainfall and associated salinity changes in the estuary explain larval abundance or recruitment? (4) If larvae are supplied to areas outside the distribution of adults, will larvae settle and recruitment occur if appropriate substrata are made available? We tested the hypothesis that the population of *O. lurida* in the Coos Bay estuary is limited through low larval delivery or variable recruitment success within the estuary. We predicted that recruitment regulation limits population recovery at both the riverine and marine extremes of the estuary. More specifically, we tested the hypothesis that the relationship between larval supply and recruitment will be dominated by physiological constraints in the upper estuary resulting in low recruitment (near the mouth of the Coos River) due to large variations in environmental parameters, and by supply limitations in the more marine portions of the estuary. Our study is the first investigation that we are aware of to simultaneously examine the relationships between larval supply and recruitment of *O. lurida* in the field in an Oregon estuary. The distribution of adults within the Coos Bay estuary is consistent over time (S. S. Rumrill pers. obs.), providing a unique opportunity to understand where each of the successive life stages is successful within the bay.

MATERIALS AND METHODS

The Coos Bay estuary (43.3667° N, 124.2167° W) is a large, drowned river estuary located on the southern coast of Oregon, USA. An earlier survey (conducted in 2006) of the spatial distribution of *Ostrea lurida* found numerous sites in the polyhaline region where adults were abundant, including Downtown Coos Bay (hereafter Coos Bay), Haynes Inlet, and Coalbank Slough (Fig. 1; Groth & Rumrill 2009). However, these surveys found no or very few adults at mesohaline sites near the Coos River, including Catching Slough, or at stenohaline, more marine sites within the estuary, including near the Airport and Empire (Fig. 1; Groth & Rumrill 2009).

We sampled 5 study sites in 2012 and 6 in 2013 where salinity conditions ranged from euhaline (marine-dominated) to polyhaline and mesohaline (riverine-dominated). Our sample sites included (in order from most marine to most riverine): (1) Empire, (2) Airport (2013 only), (3) Haynes Inlet, (4) Coos Bay, (5) Coalbank Slough, and (6) Catching Slough. Three sites (Coalbank Slough, Coos Bay, and Haynes Inlet) had populations of adult oysters, and 3 sites (Empire, Airport, Catching Slough) were outside the known range of adult oysters (Groth & Rumrill 2009; Table 1). We added the Airport site in 2013 to increase the spatial resolution between the Empire and Haynes Inlet sites.

Changes in the velocity of tidal currents are known to contribute to variability in larval capture efficiency and recruitment rates when using passive larval traps (see below; Butman 1986, Butman et al. 1986) and recruitment plates (Pawlik & Butman 1993, Qian et al. 2000, Larsson & Jonsson 2006). Consequently, we used numerical output from a hydrodynamic model of the Coos estuary to select study sites that experience similar current speeds. Output from the hydrodynamic model was validated in the estuary with depth-stratified measurements of current velocities generated by an acoustic Doppler current profiler (Shanks et al. 2010).

To understand how temperature may contribute to larval supply and recruitment patterns within the bay, HOBO data loggers (U24-002, Onset Computer) recorded temperature every 10 min at each study site. Temperature loggers housed inside PVC pipes were placed level with the tops of traps and plates, and were deployed into the estuarine tidal channels. Daily mean, minimum, and maximum temperatures were calculated.

To measure freshwater discharge into the estuary, we obtained precipitation data from the National

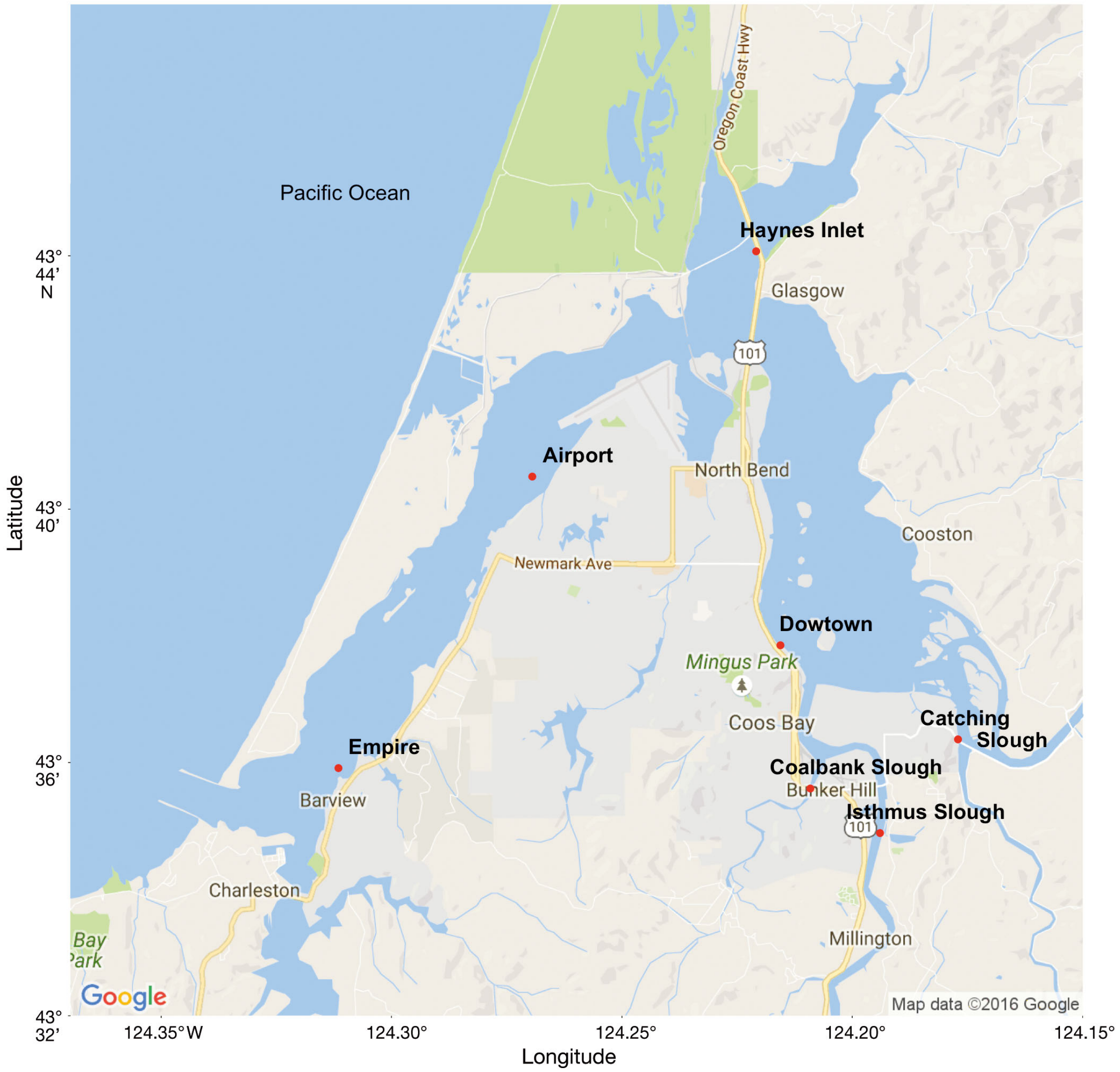

Fig. 1. The Coos Bay estuary, Oregon, USA (Kahle & Wickham 2013). Red dots indicate sampling locations

Oceanic and Atmospheric Association's National Climatic Data Center (www.ncdc.noaa.gov/) for the North Bend Southwest Oregon Regional Airport (Fig. 2). These data were plotted against recruitment in 2012 and 2013 (Fig. 3).

Larval traps have been used to gauge larval supplies in a variety of marine and estuarine habitats (Yund et al. 1991, Gaines & Bertness 1993, Todd et al. 2006). We modified the design of basic passive larval traps to increase sampling efficiency within the relatively high-velocity tidal flows observed in the Coos Bay estuary (Yund et al. 1991; Fig. 4). Use of modified traps when trying to sample the planktonic community, however, has been discouraged in the literature due to variations in capture efficiency with various shapes, sizes, and swimming abilities of zooplankton (Hargrave & Burns 1979, Butman 1986, Butman et al. 1986). The goal of our study was to effectively sample the relative abundance of a single taxon at multiple sites. Furthermore, our study sites experienced similar current velocities (Shanks et al. 2010) and any bias in sampling due to hydrodynamic factors would presumably be equal at all sites. The relative abundances of *O. lurida* larvae captured by traps are similar to those captured by plankton tows (C. E. Pritchard et al. unpubl. data), so larval trapping rates were considered to be relative to the absolute abundance of larvae within the water column. In this study, the modification of the larval traps was necessary to increase the diameter of the mouth of the trap and prevent resuspension and loss of settled materials, while keeping the cylinders of the traps relatively

Table 1. Site coordinates, descriptions, and status of adult Olympia oyster *Ostrea lurida* populations in the Coos Bay estuary, Oregon (USA), based on surveys conducted by Groth & Rumrill (2009)

Site	Latitude, Longitude	Status of adult populations	Site description
Empire	43° 21′ 32.832″ N, 124° 18′ 41.472″ W	Absent	Large flat bedrock Shallow mud Little rubble
Airport (2013 only)	43° 24′ 18.54″ N, 124° 16′ 10.02″ W	Absent	Large mudflat Little rubble, rock, or other hard substrate except for occasional clamshells Deep mud
Haynes Inlet	43° 26′ 26.52″ N, 124° 13′ 15.096″ W	Present	Intertidal slope Many rocks, rubble, and shells Deep mud and patches of eelgrass in the lowest part of the intertidal
Coos Bay	43° 22′ 42.672″ N, 124° 12′ 56.124″ W	Present	Intertidal slope Some rocks and rubble Deep mud
Coalbank Slough	43° 21′ 21.24″ N, 124° 12′ 32.76″ W	Present	Intertidal slope Some rock, cobble, shell Deep mud
Catching Slough	43° 21′ 49.176″ N, 124° 10′ 37.38″ W	Absent	Intertidal slope Some rock, cobble, and shell Deep mudflat

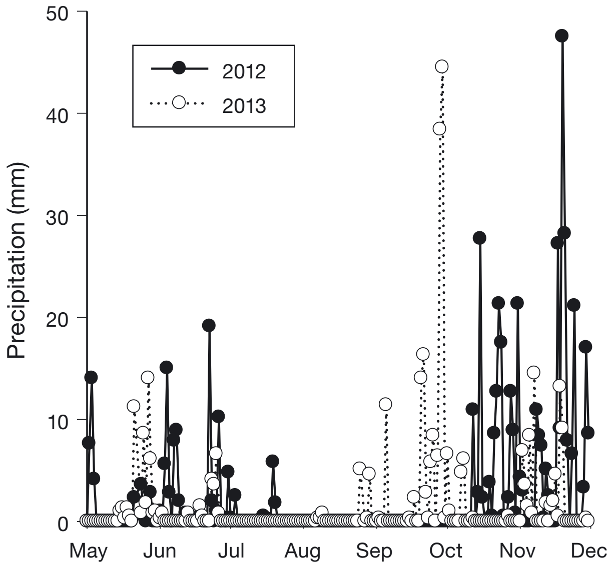

Fig. 2. Precipitation in the Coos Bay estuary in 2012 and 2013. Data from NOAA's National Climatic Data Center North Bend Southwest Oregon Regional Airport

short, and therefore appropriate for deployment in the low intertidal.

Here, we modified passive traps with a top funnel and PVC reducer to increase the trap volume. Five replicate larval traps were deployed at each study site. Traps were filled with a 10% solution of buffered formalin and filtered seawater dyed with Rose Bengal, allowing for visual confirmation of fluid retention upon trap retrieval. The Rose Bengal also dyed the organic matter, which simplified separation of organisms from sediment during analysis.

At the end of each sampling interval (~2 wk), traps were retrieved from the field and replaced with a second set of traps. The contents of each trap were sieved through 145 µm mesh and rinsed, and the plankton samples were preserved in 5% formalin-buffered seawater. Due to manpower constraints, 3 of the 5 trap samples were randomly selected for analysis. Samples were examined on an inverted microscope, and were not subsampled. Only well-developed larvae with a distinctively shaped umbo (species-specific; Fig. 5; Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m560p159_supp.pdf) were identified and counted (Loosanoff et al. 1966, Shanks 1991, P. Baker pers. comm.). D-stage larvae were excluded from abundance counts, as many species display this morphology in early ontogeny. Therefore, our estimates of larval abundance are conservative, but should still be informative about the relationships between umbo-stage larvae and settlers. In addition, in 2013, we confirmed our ability to visually identify *O. lurida* umbo larvae by molecular barcoding of the 18S gene region. All larvae (n = 24) visually identified as *O. lurida* were molecularly identified as a member of the genus *Ostrea* to 99% (C. E. Pritchard et al. unpubl.). *O. lurida* is the only known member of the species in this region.

We deployed ceramic plates adjacent to the larval traps to gauge the rate of larval settlement, metamorphosis, and recruitment. Recruitment plates (Fig. 4) were 15.2 cm^2 unglazed white ceramic tiles. The plates were bolted to the arms of PVC 'T'-shaped holders, modeled after those deployed by Seale & Zacherl (2009). The plates were oriented parallel to the benthos, and only the undersides of the plates were examined for oyster recruits. PVC holders were slipped over rebar, which had been driven into the substratum adjacent to the larval traps. The 'T's were 61 cm above the bottom and each arm was 30.5 cm

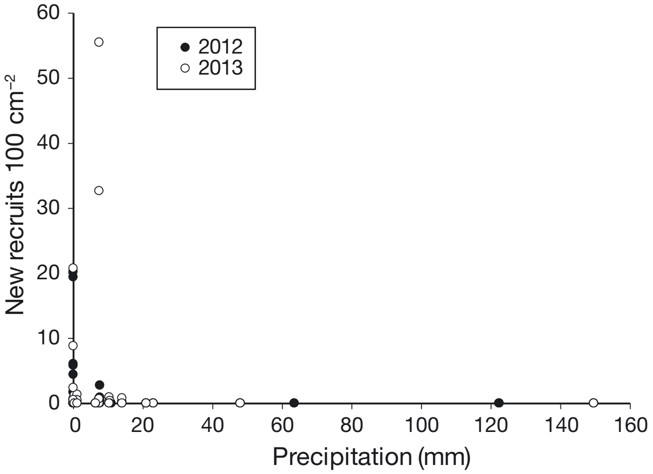

Fig. 3. Total precipitation during each sampling interval plotted against average Olympia oyster *Ostrea lurida* recruit density of that sampling interval at all sampling sites in Coos Bay estuary in 2012 and 2013

long. Plates were located at the same height above the bottom as the tops of the larval traps.

Recruitment plates (n = 8 plates per site) were collected and immediately replaced every 2 wk (simultaneously with traps), to provide continuous substrata for settlement and metamorphosis of the oyster larvae. Each plate was sub-sampled using an area grid of 15 randomly selected squares (6.45 cm^2 each), and we counted oyster settlers within a total area of 96.8 cm^2 (or 41.7 % of the total plate area). Only intact oyster recruits were counted. We relied on umbo shape, settler size, and attachment method or identification (byssal thread vs. cement; Loosanoff et al. 1966, Shanks 1991, P. Baker pers. comm.; Fig. 5). After analysis, plates were scrubbed and washed with fresh water, then allowed to generate a biofilm for at least 12 h in a flow-through seawater system before re-deployment back into the estuary for the subsequent sampling interval.

Larval traps and recruitment plates were placed in the low intertidal zone at each study site, approximately 30.5 cm below Mean Lower Low Water to ensure that traps and plates were maximally submerged while remaining accessible during monthly neap low tides. Immersion times were quantified and compared among sites with measurements of water levels recorded by automated loggers (HOBO U20-001-02-Ti, Onset Computer) placed flush with the top of the traps and recruitment plates (see below). No significant differences in immersion times were observed among the study sites (data not shown).

In 2012, sampling began mid-July and lasted through late November (sampling dates are given in

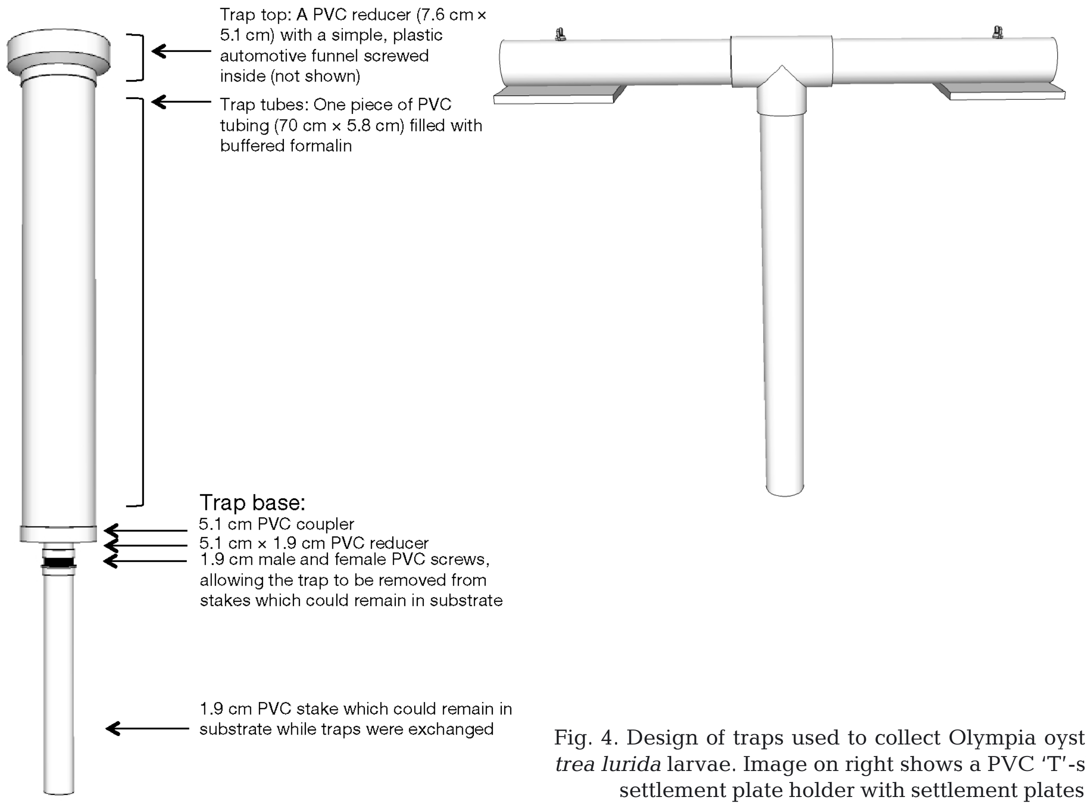

Fig. 4. Design of traps used to collect Olympia oyster *Ostrea lurida* larvae. Image on right shows a PVC 'T'-shaped settlement plate holder with settlement plates

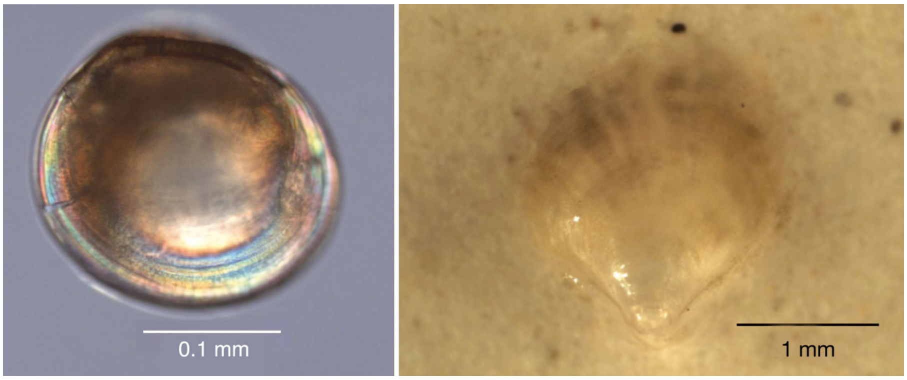

Fig. 5. (a) Young umbo-stage larva of Olympia oyster *Ostrea lurida*. (b) Settled juvenile of *O. lurida*

Table S1 in the Supplement). Evidence at the time suggested that these dates would encompass and exceed the initiation and termination of spawning, larval settlement, and recruitment of *O. lurida* larvae in the Coos Bay estuary (Sawyer 2011, L. G. Peteiro unpubl. data). However, we suspect that we missed the initiation of spawning in 2012 (see 'Results' and 'Discussion'). Therefore, informed by the results of our sampling in 2012, we sampled earlier in the year in 2013, from mid-May through mid-August.

We used least squares linear regressions (Systat Software v12) to examine the relationship between larval supply and new recruits at 3 study sites (Coalbank Slough, Coos Bay, and Haynes Inlet). Catching Slough, Empire, and Airport were all excluded due to negligible settlement at those sites and missing data in 2012 (see above). We examined 3 different relationships: larvae compared with recruits collected on the same sampling day; larvae compared with recruits collected 1 sampling period (2 wk) later; and larvae compared with recruits collected 2 sampling periods (4 wk) later (Table 2). Significance of p-values was assessed with a Bonferroni correction (α = 0.017). Larval and recruit abundances are reported as mean ± 1 SE within sampling periods (~2 wk) for each site.

RESULTS

In 2012, minimum daily temperatures above 15°C were observed from early July through mid-August at Haynes Inlet, Coos Bay, Catching Slough, and Coalbank Slough. Minimum daily temperature never reached 15°C at the Empire site (Fig. 6). In 2013, sampling began earlier in the year. Minimum daily temperatures at Haynes Inlet, Coos Bay, and Catching Slough rose above 15°C in early June and were sustained through the end of sampling in mid-August (Fig. 6). The 15°C threshold was reached later at Coalbank Slough, from mid-July through September. The minimum daily temperature rarely exceeded 15°C at either Empire or Airport.

In 2012, larval availability was highest at midbay sites, while riverine- and marine-dominated sites consistently had low larval availability (Fig. 7). Mean larval abundances were highest during the first deployment (mid-July to early August), and highest at Coos Bay and Haynes Inlet (67.7 ± 3.9 and 30.3 ± 3.2 larvae per trap, respectively). Peak abundances at Coalbank Slough occurred 2 wk later (15.7 ± 2.3 larvae per trap). Catching Slough and Empire both had very low larval abundances throughout sampling, with a maximum of 11 and 1 larvae in a single trap, respectively. Logistical difficulties prevented larval sampling at Catching Slough during most of August. Following peak abundances in early August, larval

Table 2. Correlation coefficients and p-values for regression analyses to examine the relationship between larval supply and new recruits of Olympia oysters *Ostrea lurida* at 3 study sites. **Bold** values indicate statistical significance at α = 0.017

Time lag (wk)	Site	Larva to recruit					
		2012			2013		
		r	p	n	r	p	n
0	Coalbank Slough	0.268	0.663	5	**0.931**	**0.007**	**5**
0	Haynes Inlet	0.395	0.511	5	0.806	0.053	5
0	Coos Bay	0.222	0.720	5	0.714	0.111	5
2	Coalbank Slough	0.903	0.097	4	0.008	0.989	4
2	Haynes Inlet	**0.986**	**0.014**	**4**	0.283	0.645	4
2	Coos Bay	**0.994**	**0.006**	**4**	0.318	0.602	4
4	Coalbank Slough	0.237	0.848	3	0.582	0.418	3
4	Haynes Inlet	0.744	0.466	3	0.730	0.270	3
4	Coos Bay	0.799	0.410	3	0.840	0.160	3

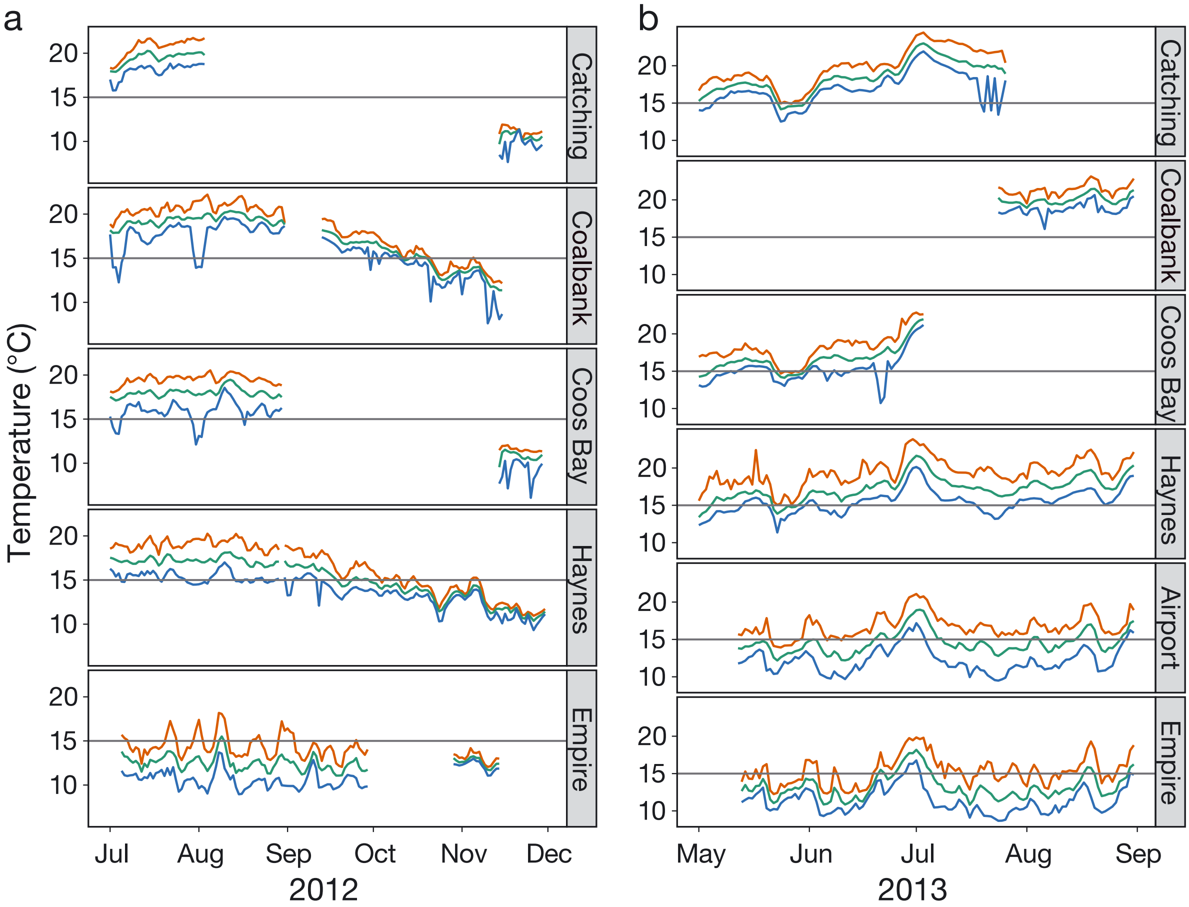

Fig. 6. Maximum, averages, and minimum temperatures at each sampling site in the Coos Bay estuary in (a) 2012 and (b) 2013. Red, green, and blue lines represent maximum, average, and minimum daily temperatures, respectively. Horizontal grey line at 15°C indicates critical spawning temperature

supply declined steadily at all sites until mid-October, when at both Coalbank Slough and Coos Bay just 1 umbo-stage larva was trapped (Fig. 7).

In 2012, recruits were observed from early August through late September, and not observed thereafter. Mean recruit abundances were also greatest at mid-bay sites, but low at both riverine- and marine-dominated sites. Mean recruitment was 3 times higher at Coos Bay than Haynes Inlet during the peak in late August (18.7 ± 2.3 and 5.7 ± 0.7 recruits 100 cm^{-2}, respectively). At Coalbank Slough and Catching Slough, recruitment was consistently low (max. 0.5 ± 0.6 and 1.7 ± 0.2 recruits 100 cm^{-2}, respectively). At Empire, no recruitment was observed throughout the 2012 study.

In 2013, larvae were not observed before mid-June, and were at low abundances until late June. Peak larval abundance in mid-July was followed by a rapid decrease in abundance at all sites through mid-August when sampling was terminated. Larval availability was again highest at midbay sites followed by riverine-dominated sites, while marine-dominated sites consistently had low larval availability. Peak larval abundances in mid-July were highest at Coos Bay (183.0 ± 14.7 larvae per trap), followed by Catching Slough (97.3 ± 42.0 larvae per trap), Coalbank Slough (117.0 ± 14.0 larvae per trap), and Haynes Inlet (44.0 ± 25.0 larvae per trap). In 2013, however, the Haynes Inlet traps were consistently disturbed (tipped or not upright), likely resulting in increased resuspension of collected materials. Therefore, these values likely underreport larval abundance. Larval abundances at Airport and Empire were consistently low throughout sampling (max. 14.0 ± 1.7 and 0.7 ± 0.3 larvae per trap, respectively).

In 2013, recruitment rates were again greatest at midbay sites, and very low at both riverine and marine-dominated sites. During peak recruitment, rates were highest at Haynes Inlet (54.5 ± 6.8 recruits 100 cm^{-2}) and Coos Bay (31.5 ± 3.9 recruits 100 cm^{-2}). Recruitment at the more riverine sites was low (1.3 ± 1.6 recruits 100 cm^{-2} at Coalbank Slough and 0.5 ±

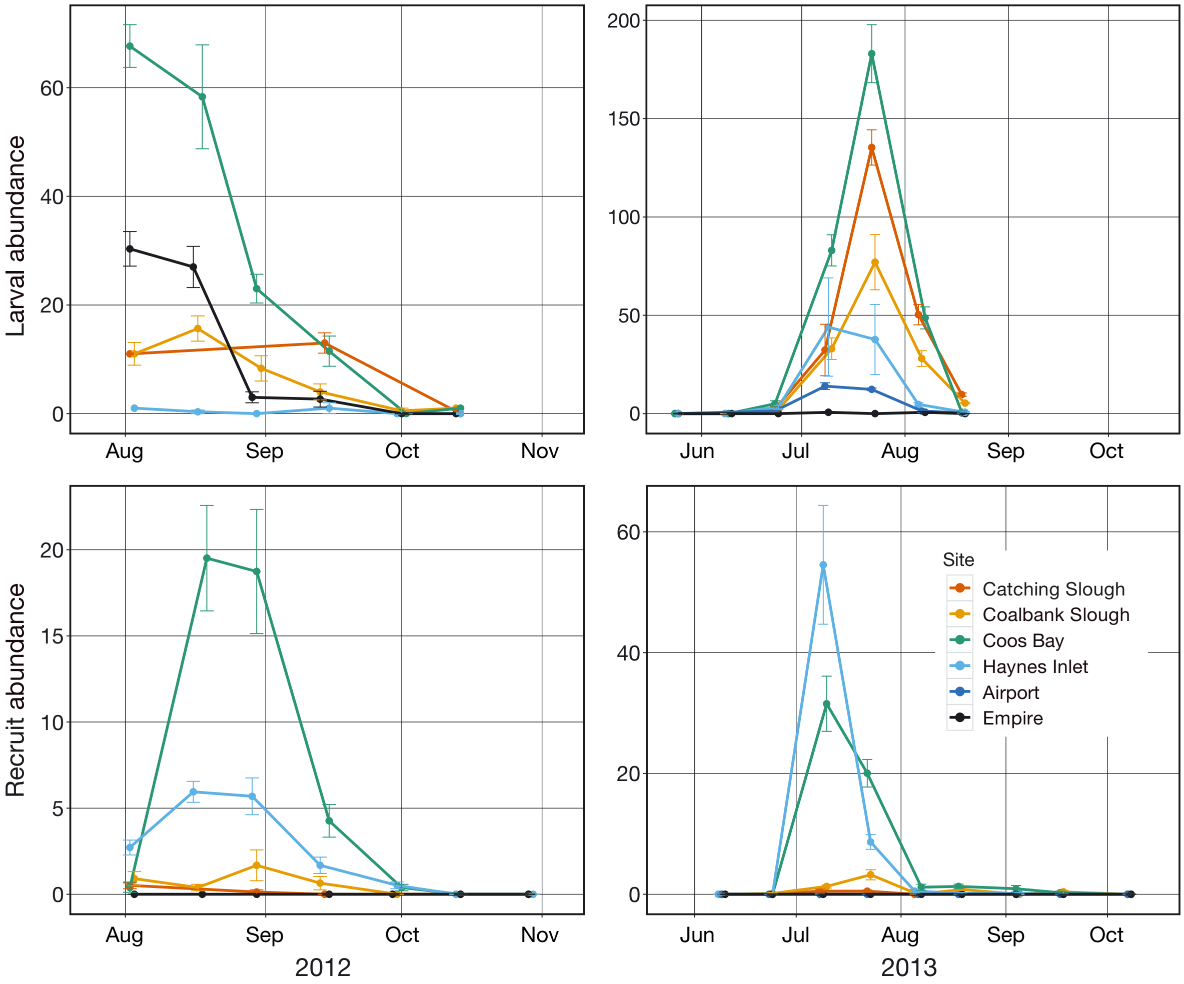

Fig. 7. Olympia oyster *Ostrea lurida* larval and recruit abundance in 2012 and 2013 at sampling sites in the Coos Bay estuary. Values are presented as means for each deployment ± SE. Symbols appearing without error bars indicate that variation was too low to generate visible SE bars

0 recruits 100 cm^{-2} at Catching Slough). No recruitment was observed at either Airport or Empire during 2013. Peak recruitment at Haynes Inlet and Coos Bay occurred between late June and early July. Peak recruitment at Coalbank Slough occurred from early to mid-July. *Ostrea lurida* recruits were present at Catching Slough from late June through mid-July.

In 2012, there were no significant relationships between larval abundance and recruits at any site within the same 2 wk sampling interval (i.e. when no time lag was applied) (Table 2). However, because *O. lurida* larvae have a pelagic larval duration of at least 7 d (reviewed by Baker 1995), recruitment recorded at the next sampling date (2 wk later) or even 2 sampling dates later (4 wk) might correlate better with larval supply in a given sampling period. The correlations between larval abundance and recruit abundance 1 sampling interval (2 wk) later were significant at Coos Bay ($r = 0.995$, $n = 4$, $p < 0.006$; Table 2) at our modified α (0.017). Although not statistically significant, correlations were also strong at Haynes Inlet ($r = 0.986$, $n = 4$, $p < 0.024$) and Coalbank Slough ($r = 0.903$, $n = 4$, $p = 0.097$). Correlations between larvae and recruits recorded 2 sampling intervals (4 wk) later were not significant at any site in 2012. In 2013, the only significant relationship between larvae and new recruits was on the same sampling date at Coalbank Slough (i.e. no lag time; Table 2) Low sample size may have prevented the significance of some correlations, although a change in environmental conditions may point to an ecological explanation. Specifically, patters of rainfall were different in 2012 and 2013 (Fig. 2). No rain fell during the period of peak recruitment in 2012, but in 2013, peak recruitment coincided with a period of moderate rainfall (Fig. 3)

DISCUSSION

During 2012 and 2013, larval abundance, recruitment, and adult populations of *Ostrea lurida* varied considerably among the different study areas in the Coos Bay estuary. *O. lurida* larvae were abundant in the inner, riverine-dominated bay sites (Catching Slough and Coalbank Slough), but neither recruits nor adults were abundant in these areas, indicating that variability in recruitment success may drive adult distribution within the riverine region of the estuary. It is curious that we observed few recruits in the shallow regions of Coalbank Slough at our sampling site, because adult oysters and settlers are typically abundant between Isthmus Slough and Coalbank Slough, and the population of adult *O. lurida* also extends into the subtidal zone a considerable distance up Isthmus Slough (Fig. 1; S. S. Rumrill pers. obs.). Freshwater input into Isthmus Slough is generally low, and the persistence of *O. lurida* and success of oyster enhancement activities here are presumably related to the availability of hard-bottom habitat and elevated salinities in this deep tidal basin (S. S. Rumrill pers. obs.).

The cause of low recruitment in Coalbank Slough is unknown, but it is likely that both Catching Slough and Coalbank Slough experience substantial freshwater inputs, large fluctuations in temperature, and other abiotic conditions that hinder successful recruitment. Laboratory and field studies suggest that low salinity decreases settlement and recruitment success (Hopkins 1937, Sawyer 2011) and causes high mortality of *O. lurida* adults (Gibson 1974, Grosholz et al. 2008). For example, the spatial distribution of *O. lurida* adults is generally limited to areas where salinities are above 20 in the Coos Bay estuary (Baker et al. 2000). Additionally, up to 100% of *O. lurida* adults died after 49 d of exposure to salinities less than 10 in a laboratory experiment, and 17% of adults died after 49 d at a salinity of 15 (Gibson 1974). Similarly, a large-scale die-off of adult *O. lurida* occurred in 2006 in San Francisco Bay, and the mass mortality event was attributed to a period of heavy rainfall and decreased salinity (Grosholz et al. 2008).

In the present study, despite sufficient larval supply, *O. lurida* recruitment was consistently low within Catching Slough, the study site located closest to the Coos River and farthest from the ocean. In contrast, both larval abundance and recruitment were relatively high in the mid-region of the bay (Coos Bay and Haynes Inlet). This may indicate that: (1) larval supplies may be adequate to facilitate successful restoration here. As adults are naturally reproducing in this region of the bay, restoration efforts will likely not be dependent on managers providing cultch. (2) Ambient environmental conditions are conducive to promoting settlement, survival, and subsequent growth into the adult population (Groth & Rumrill 2009). Conversely, at marine-dominated sites in the bay (Airport and Empire), no life stages of *O. lurida* were abundant, but the presence of single adult oysters on the docks near the Empire and Airport sites (Groth & Rumrill 2009, S. S. Rumrill pers. obs.) suggests that if given the opportunity, larvae can both settle and survive in the outer bay and live until adulthood. However, there were almost no larvae present at these sites. Thus, our results indicate that limited larval supplies may prevent the population of *O. lurida* from becoming established in the marine-dominated region of the Coos Bay estuary.

The Pacific Northwest, including the Coos Bay estuary, has a distinct wet and dry season. Spawning of *O. lurida* occurs during the dry season when river input into the estuary is low, and the estuary becomes more strongly influenced by the elevated salinities of marine waters. In addition, the estuarine basin experiences decreased flushing and longer residence times during the dry season (discussed below), which contribute to elevated temperatures in the inner estuary. *O. lurida* spawning during the dry season may indicate that survival at some life stage(s) is strongly reduced under low-salinity conditions. These seasonal dynamics contribute to substantial variability in the aquatic environment (at least in terms of temperature and salinity, but likely other factors as well) in the riverine reaches of the estuary, which recruits and adults of *O. lurida* may not tolerate well (Wasson 2010). For instance, in Elkhorn Slough, California, sites with wide ranges in water quality parameters over 5 yr (e.g. temperature, salinity, turbidity, dissolved oxygen, and chlorophyll *a* fluorescence) lacked *O. lurida* populations, while sites with smaller ranges in these parameters tended to support populations of *O. lurida* (Wasson 2010).

Variability in salinity, driven primarily by precipitation, may also explain the decoupling of larval supply from recruitment in 2013 compared to 2012. In 2012, peak recruitment of *O. lurida* occurred during a period with no precipitation, and moderate recruitment occurred during a period of moderate precipitation. In contrast, peak recruitment of *O. lurida* occurred during a period of moderate precipitation during 2013 (Fig. 3). Whether moderate precipitation (and associated lower salinity) deterred settlement or not, it is likely that freshwater inputs reduced the survival of newly settled oysters. This shift in peak recruitment from a period of no precipitation to a period of moderate precipitation could be responsible for higher post-settlement mortality and a poor relationship between supply and recruitment in 2013.

O. lurida require a minimum temperature of 15°C for successful spawning to occur (Hopkins 1937, Oates 2013). Consistent with this observation, larval supply generally followed the timeline set by a 15°C critical temperature, with a 2 wk lag (similar to the amount of time the larvae are brooded after spawning occurs). In addition, relatively high larval abundances were observed at all sites where minimum daily temperatures were elevated above 15°C (including inner and mid-bay sites), but larvae were nearly absent at sites where temperatures never reached this critical threshold (Airport, Empire). Therefore, adult oysters may be capable of spawning at sites that reached a consistent 15°C daily minimum temperature, while spawning does not occur at sites that did not reach a consistent 15°C daily minimum temperature. Therefore, water temperatures may be a crucial factor to consider for restoration efforts. For instance, if settlers recruited at Airport and Empire, spawning may not be initiated due to temperatures below the critical threshold, and thus reproductive output would be negligible, and the population would not be self-sustaining.

The mid-bay sites (Coos Bay and Haynes Inlet) had abundant larvae, recruits, and adults, as has been observed in the mid-bay of other estuaries (Kimbro 2008, Wasson 2010, Deck 2011). These locations may present the ideal balance between extremes in physical parameters such as temperature and salinity, but may also be strongly influenced by a prominent hydrodynamic pattern of the Coos Bay estuary located in the mid-bay: the null zone (Miller 1983). Specifically, the null zone is a location in an estuary where the opposing forces that characterize estuaries, namely marine inflow and riverine outflow, balance each other out, and there is little net seaward transport of inner bay waters past this zone. Water riverward of the null zone tends to be retained for relatively long periods (>2 wk, or the duration of the pelagic larval stage of *O. lurida*), but water seaward is tidally flushed almost daily (C. E. Pritchard et al. unpubl. data). Importantly, the null zone appears to be relatively stable from year to year, and is located between our Airport and Coos Bay sites (C. E. Pritchard et al. unpubl. data).

With the null zone's apparent retentive capabilities, with both physical (water quality parameters) and biological consequences (larval distributions), the physical location of *O. lurida* adults within the bay becomes quite an important consideration that likely drives larval supply, settlement, and recruitment. Multiple lines of evidence support this conclusion in the Coos Bay estuary. First, all life-stages of *O. lurida* are present in the estuary, suggesting that larvae complete their development within the bay (Peteiro & Shanks 2015). Second, *O. lurida* larvae are more abundant riverward than seaward of the null zone (this study), suggesting that the long residence times observed in the inner bay may facilitate larval retention for the duration of their development, while larvae that mix with the outer bay are lost to the ocean. Lastly, very few larvae and no recruits or adults were found on the open coast (Peteiro & Shanks 2015). Therefore, it is plausible that *O. lurida* larvae spawned upstream of the null zone have an increased probability of retention within the Coos Bay estuary (C. E. Pritchard et al. unpubl. data) in which case, they may (1) settle in the inner bay, (2) survive to become reproductive adults in the inner bay, and (3) spawn their larvae in the inner bay.

Taken in combination, these scenarios indicate that in shallow, topographically complex estuaries such as the Coos Bay estuary, it is more likely for populations to become self-sustaining in the area riverward rather than seaward of the null zone. Additionally, if high larval wastage occurs in the outer portions of the estuary, then inter-bay connectivity may be low. Indeed, Stick (2011) distinguished 5 genetically distinct regions within the oyster's distribution and determined that these genetic divergences could be observed in small geographic areas relative to the species' distribution, such as Puget Sound, suggesting that larval exchange in some areas is low enough that genetic differences can build up over time. However, larval dispersal may not always be so limited. For example, through shell elemental spectroscopy, Carson (2010) found evidence of *O. lurida* larval dispersal over 75 km along the open California coast. Despite this potential for long-distance dispersal, the concentration of larvae in the open ocean along the Oregon coast may be quite low (max. 3 m^{-3}, L. G. Peteiro unpubl. data), and further, the probability of successfully entering an estuary is also low. The hydrodynamic characteristics of each individual bay are therefore important, and need to be considered to successfully implement restoration efforts.

In summary, at least 4 factors likely influence larval abundance and recruitment of *O. lurida* in the Coos Bay estuary: (1) the larvae of *O. lurida* complete their development within the estuary; (2) larval supply is higher above the null zone (inner bay), and larvae tend to be retained above the null zone and flushed out of the estuary below the null zone (outer bay); (3)

recruitment is limiting in the uppermost reaches of the estuary perhaps due to periods of low salinity causing high recruit mortality; and (4) temperature and salinity, and their fluctuation, may influence both larval supplies and recruitment. Specifically, locations in the bay where daily minimum temperatures do not consistently reach 15°C during the spawning season for *O. lurida* are unlikely to contribute larvae to future populations.

These results have important implications for the siting, design, and evaluation of *O. lurida* restoration and enhancement efforts, which primarily involve the addition of shell or spat-on-shell to estuaries. Careful consideration should be given to the location of restoration and enhancement sites to ensure that the populations may be self-sustaining. If recruits cannot thrive at the chosen location, for instance where there may be wide variation in environmental parameters, or if natural recruitment is low due to tidal flushing or other abiotic factors (such as critical temperature thresholds), then the population is not likely to become self-sustaining. Thus, restoration sites should be focused above the null zone in the inner estuary, which will promote larval retention, but should not be located so far into the estuary that the larvae and adults experience prolonged periods of low salinity. If starting a new population, the location should be carefully assessed in terms of larval supply, recruitment, estuarine retention time, and temperature, before cultch or spat is added. Specifically, cultch or spat should be applied in areas where larvae may be retained for their entire larval duration, and variation in environmental parameters is limited (Wasson 2010), but critical temperature thresholds are reached and exposure to sustained low salinities is rare.

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