LARVAL SUPPLY, SETTLEMENT, AND POST-SETTLEMENT PERFORMANCE AS DETERMINANTS OF THE SPATIAL DISTRIBUTION OF OLYMPIA OYSTERS (*OSTREA LURIDA*) IN COOS BAY, OR

by

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THESIS ABSTRACT

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Title: Larval Supply, Settlement, and Post-Settlement Performance as Determinants of the Spatial Distribution of Olympia Oysters (*Ostrea lurida*) in Coos Bay, OR

The Olympia oyster, *Ostrea lurida,* was overharvested in the early 20th century and is now the focus of restoration efforts in estuaries along the west coast of North America. These efforts would be aided by a better understanding of patterns of larval abundance, settlement behavior, and post-settlement performance of oysters in estuaries throughout its range. In Coos Bay, Oregon, all three of these components of the oyster life cycle were investigated at multiple sites. Like adult oysters, larvae were restricted to the upper portion of the bay, although larvae were supplied to sites in the upper bay where settlement was low. Settlement and post-settlement growth was highest at sites of high adult density. These results indicate that in *O. lurida,* as in many other marine invertebrates, the adult population is subject to bottlenecks at the larval and juvenile stages that can vary spatially.

This thesis contains previously unpublished co-authored material.

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This thesis is dedicated to my family, who always expected the best of me, and to the wonderful friends and mentors I met at the Oregon Institute of Marine Biology.

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CHAPTER I

GENERAL INTRODUCTION

Ostrea lurida, the Olympia oyster, is the only oyster native to the west coast of North America north of central Baja California (Polson *et al.,* 2009). It was synonymized with *Ostrea conchaphila* by Harry (1985) but recent molecular work confirmed the original taxonomic distinction between a southern species (*O. conchaphila*) and a northern species (*O. lurida*) (Polson et al., 2009). It is typically found in the mesohaline portion of estuaries and tidal bays (Baker et al., 2000; Peter-Contesse and Peabody, 2005) and is more tolerant of full strength seawater than it is of freshwater (Gibson, 1974). It is intolerant of freezing temperatures and requires a temperature of 13-16˚C to reproduce (Peter-Contesse and Peabody, 2005).

Oysters of the genus *Ostrea* brood their larvae, unlike those of *Crassostrea* and *Saccostrea* which broadcast release eggs and sperm. Broadcast spawning is the ancestral condition, and brooding has apparently evolved once and has been retained by all descendant lineages (Ó Foighil and Taylor, 2000). Larvae are planktotrophic, swimming and eating with a ciliated velum. Like other bivalves, when larvae of *O. lurida* are first released, at 165-189 µm long, they lack a distinctive umbo shape and resemble the letter "D;" therefore, they are known as D-stage veligers (Strathmann, 1987). When larvae of *O. lurida* reach about 205 µm, they develop a knob-shaped umbo which can be distinguished from the larva of *C. gigas* by the relatively obtuse angle of its slope (Brink, 2001). Settlement occurs when the veligers are about 300 µm long (Strathmann 1987) and is aided by the larval foot, an organ that is resorbed in oysters, along with the velum, during metamorphosis as the animal cements itself to the substratum (Coon et al., 1985).

Like many native oysters, populations of *O. lurida* have declined significantly within the past century. A variety of stressors have been blamed for worldwide native oyster loss, including degradation of estuarine habitat, pollution, overharvesting, introduced diseases, introduced predators, parasites, and competition from in situ aquaculture of the commercially important non-native species *Crassostrea gigas* (Groth and Rumrill 2009, Jackson *et al*., 2001, Lenihan and Peterson 2004). In the case of *O. lurida,* overharvesting for a post-Gold Rush market in the late 19th and early 20th centuries decimated populations along the species range. Remnant populations persist in a number of estuaries from British Columbia to Mexico, but the number and extent of populations are believed to be nowhere near their historical abundance (Polson and Zacherl 2009, Gillespie 2009). There is little information available to quantify that historical abundance (Brumbaugh and Coen, 2009). Modern-day blocks to success of *O. lurida* vary by estuary, but habitat loss, lack of suitable substrata, non-native oyster drills, and pollution have all been implicated (Barrett, 1963; Grosholz et al., 2008; Harris, 2004).

In Coos Bay, Oregon, evidence from dredge spoils and shell mounds indicates that a population of *Ostrea lurida* was present historically but was wiped out by a tsunami or earthquake before the arrival of Europeans to the area (Baker 2000, Groth and Rumrill 2009). While an intentional reintroduction in Coos Bay failed in 1917, individuals were discovered in Coos Bay in the late 1980's (Baker et al., 2000). Since then the population has remained patchy but persistent, even expanding slightly at the edges of its range. Genetic analysis suggests that the current Coos Bay population consists of individuals derived from those in Willipa Bay, WA that may have been transported to Coos Bay on the shells of *C. gigas* brought to the estuary for commercial purposes (Stick, 2011).

Recently, researchers have taken an interest in restoring populations of *Ostrea lurida*. Re-establishing this species is likely to be beneficial in a number of ways. While the benefits of a large population of *O. lurida* are likely overstated in the case of water quality (Ermgassen et al., 2013) other environmental benefits are clear. Because oysters settle gregariously, they tend to form relatively large patches of hard substrata in the otherwise soft-bottom environment of the estuary. This creates a unique habitat for a number of sessile species. Fish, too, find refuge in oyster beds. Dense oyster beds and reefs can even alter the flow of the estuary itself, dissipating wind and wave energy near shorelines (Ruesink *et al.*, 2005, Jackson *et al.,* 2001).

This species is also of economic and cultural significance. Native species, especially in urbanized settings like estuaries, carry a special cultural value (Garibaldi and Turner, 2003). Indigenous peoples harvested *O. lurida* for thousands of years before the West Coast was colonized (Groth and Rumrill, 2009), and its culinary value is still recognized today. A thriving, self-sustaining oyster population in Coos Bay could be harvested recreationally and even commercially. Currently, *O. lurida* is not harvested outside of Washington, so such a fishery would be unique and a potential attraction for tourists to visit southwestern Oregon.

This thesis is part of a larger project aimed at assessing the reproduction and population dynamics of *O. lurida* in Coos Bay, with the ultimate goal of informing future restoration efforts. As part of this project, the gonad structure and gametogenesis of the

Coos Bay population of *O. lurida* was analyzed over the course of a year (Oates 2012), and larval supply was measured throughout the bay (Pritchard 2013). This thesis contributes information about the later portion of the life cycle of *O. lurida*: settlement and post-settlement performance.

Chapter II is co-authored with Catharine Pritchard and describes the relationship between settlement and supply at five to six sites throughout the bay for two consecutive years. In Chapter III, post-settlement mortality and growth of two size classes of oyster were measured at two to four sites throughout the bay for six months. Combined, these studies sought to identify the population bottleneck, or bottlenecks, that determine the spatial distribution of the adult population of *O. lurida* in Coos Bay. Seasonality of larval abundance, settlement, and post-settlement growth were also elucidated, and are compared with patterns observed in other estuaries. This information can be used to pinpoint the best possible restoration sites within Coos Bay and inform restoration of *O. lurida* elsewhere; it is also a useful addition to the body of knowledge concerning marine invertebrate population dynamics.

CHAPTER II

LARVAL SUPPLY AND SETTLEMENT OF *OSTREA LURIDA* IN COOS BAY, OR

Catherine E. Pritchard and I developed and carried out much of the experimental protocol of this chapter together. Ms. Pritchard was responsible for the construction and maintenance of larval traps and for the analysis of their contents, while I was responsible for the construction and maintenance of settlement plate equipment and for the analysis of settlement. The larval data and some of the figures were supplied by Ms. Pritchard; the settlement data, most of the figures, and all of the text in this chapter is my own.

INTRODUCTION

Approximately 70% of temperate nearshore benthic invertebrates produce eggs and larvae which temporarily inhabit the pelagic environment before settlement (Pineda, 2000). This planktonic stage results in dispersal and together with settlement shapes, in large part, the spatial and temporal distribution of such species. Larvae must contend with, or take advantage of, water movement that sweeps them to or away from suitable habitat. Successful settlement also depends on a variety of biotic and abiotic factors including hydrodynamics, behavior, substrate suitability, predation, and mortality (Connell, 1985). Many studies have sought to understand the relationship between larval availability and settlement in structuring intertidal communities (Dudas et al., 2009; Gaines et al., 1985; Jenkins, 2005; Jonsson et al., 2004; Minchinton and Scheibling, 1991; Pineda et al., 2010; Raimondi, 1990; Satumanatpan and Keough, 2001; Shinen and Navarrete, 2010). The results of these studies have been mixed, emphasizing the need to assess these factors on a case-by-case basis. In some cases, settlement choice was a greater factor than larval supply in determining adult distribution patterns (Jenkins, 2005, Shinen and Navarrete, 2010), in others, larval supply was more important (Gaines et al., 1985, Minchinton and Scheibling, 1991, Raimondi, 1990). Such information is important for the protection and management of benthic marine species, whether for the purpose of designing marine reserves, managing fisheries (Pineda, 2000), predicting the spread of invasive species (Bohn et al., 2013) or mitigating the effects of estuarine habitat loss.

The Olympia oyster, *Ostrea lurida,* provides an opportunity to study the relationship between larval supply and settlement and how this relationship may structure the population within an estuary. While larvae can go offshore and populate other estuaries (Carson, 2010), open-coast populations are very rare (Coe 1932) and self-recruitment within an estuary seems to be the major method of sustaining populations (Carson, 2010; Stick, 2011). Recent work found larvae of all ages within the Coos ay estuary, and found that larvae occupy deeper portions of the water column during falling tides when currents are relatively weak, suggesting the larvae of this species have some ability to vertically migrate; together, these results suggest that these larvae are not advected offshore and then returned to the estuary (Garcia-Peitero, L. *unpub.*). Therefore, in this species, the effects of large-scale offshore water movement are muted and within-estuary hydrodynamics prevail, followed by behavior and biotic processes like predation and mortality (Pineda, 2000).

O. lurida is also a worthwhile study organism because it is the target of restoration efforts up and down the west coast of North America, including Coos Bay. It has never fully recovered from overharvest for a post-Gold Rush market, even though it has not been routinely commercially harvested in nearly a century. Habitat degradation, limitation of substrata, invasive predators, and parasites are likely to blame, although factors vary among estuaries (Gillespie, 2009; Grosholz et al., 2008; Meyer et al., 2010; Wasson, 2010; White et al., 2009). The history of *O. lurida* in Coos Bay differs from the history of this species in other estuaries. It was not present in Coos Bay from about 1700, after a major siltation event likely caused by a tsunami, to the 1980's (Baker et al., 2000). It was likely introduced to the bay as spat on the shells of Pacific oysters, *Crassostrea gigas,* imported for commercial use (Groth and Rumrill, 2009). *C. gigas* is still grown in Coos Bay commercially, but does not appear to compete for space with the native oyster: the population of *C. gigas* is not self-sustaining in this estuary because water temperature rarely exceeds its spawning threshold (however, larvae and spat of *C. gigas* are occasionally reported; see Results below). Despite its unusual origin, the Coos Bay population is of interest to those wishing to increase the numbers of *O. lurida* in general (see Chapter I).

Efforts to encourage a healthy oyster population, whether for restoration or commercial purposes, often require importing seed from hatcheries or other estuaries. This is an expensive, labor-intensive strategy. Encouraging a self-sustaining population is much more efficient than re-seeding oyster beds in the event of reproductive failure. If larvae are present in the water column near a site of interest, and if they settle successfully at this site, then adding substrate in the form of shell or rock may be enough to increase the population. In order to find such sites in Coos Bay, we quantified larval supply and settlement at several sites through the estuary in 2012 and again in 2013.

MATERIALS AND METHODS

Site selection

Coos Bay is a drowned river-mouth estuary located on the southern coast of Oregon, USA. Except for occasional individuals found on hard substrate in the lower estuary, such as the Charleston docks, the population of *O. lurida* is confined to the upper, mesohaline portion of the estuary (Baker et al., 2000; Groth and Rumrill, 2009 and see Figure 1). Individuals are typically found attached to hard substrata in the middle and lower intertidal of mudflats and areas with rip-rap, such as the runway of the Southwest Oregon Regional Airport (S. Rumrill, pers. comm.). They are also present subtidally in the upper arm of the bay, with increasing density up-estuary (Baker et al., 2000).

We measured larval supply and what we called "settlement" of *O. lurida* at five sites in 2012 and six sites in 2013. "Settlement" is defined here as the observation of recently settled oysters, or new recruits, present on plates at the time of collection after two weeks in the field; in other words, we measured individuals that settled and then survived for up to two weeks. We chose sites along a salinity gradient from marine-dominated to river-dominated: Empire (43.35912°N, 124.31152°W); Airport, added in 2013 (43.40515°N, 124.26945°W); Haynes Inlet (43.44070°N, 124.22086°W); Downtown Coos Bay (43.37852°N, 124.21559°W); Coalbank Slough (43.35590°N, 124.2091°W); and Catching Slough (43.36366°N, 124.17705°W) (Figure 1). Haynes Inlet, Downtown Coos Bay, and Coalbank Slough are all within the known distribution of the species and adults were present at all three sites. Empire and Catching Slough are both outside the adult distribution of the species. The site we called "Airport" is a mudflat close to the Southwest Oregon Regional Airport, which is just outside the lowermost portion of the oyster's distribution; no adults were present at this site. However, adults of *O. lurida* are known to occur in the rip-rap along the airport runway, about 1 km north of our study site. The sites varied to some degree in terms of available substrata: Haynes Inlet, Downtown Coos Bay, and Coalbank Slough were a mixture of rubble and mud; Empire was dominated by bedrock; Airport was primarily mud with occasional shells, and Catching Slough was primarily muddy with some shell. While we did not quantify substrate at each site, we can provide estimates of substrate availability at each site for comparison purposes. At Empire, most of the intertidal is characterized by large flat bedrock rather than cobble, and the mud present is relatively shallow. Little of the rubble associated with adults of *O. lurida* is present at this site. The Airport site is a large mudflat lacking rubble, rock, or other hard substrate except for occasional clamshells. The mud here is fairly deep. At Haynes Inlet, much of the mudflat is covered in rocks, rubble, and shell of varying sizes, to which adults of *O. lurida* are often attached singly or in clumps. This type of hard substrate gives way to soft mud and patches of eelgrass in the lowest part of the intertidal. The substrate at Downtown Coos Bay is similar to what is found at Haynes Inlet, although less extensive. Less of the shoreline at Downtown Coos Bay is covered with rock and cobble than the shoreline at Haynes Inlet, and the mud is especially deep at this site. The intertidal at Coalbank Slough is a mix of rock, cobble, shell, and soft, deep mud, with the density of rock and cobble comparable to that at Haynes Inlet. Lastly, at Catching Slough, some rock, cobble, and shell can be found but the site is primarily a relatively deep mudflat.

At Catching Slough, our equipment was knocked over after our first collection date; we were also concerned for our own safety when accessing the equipment at that

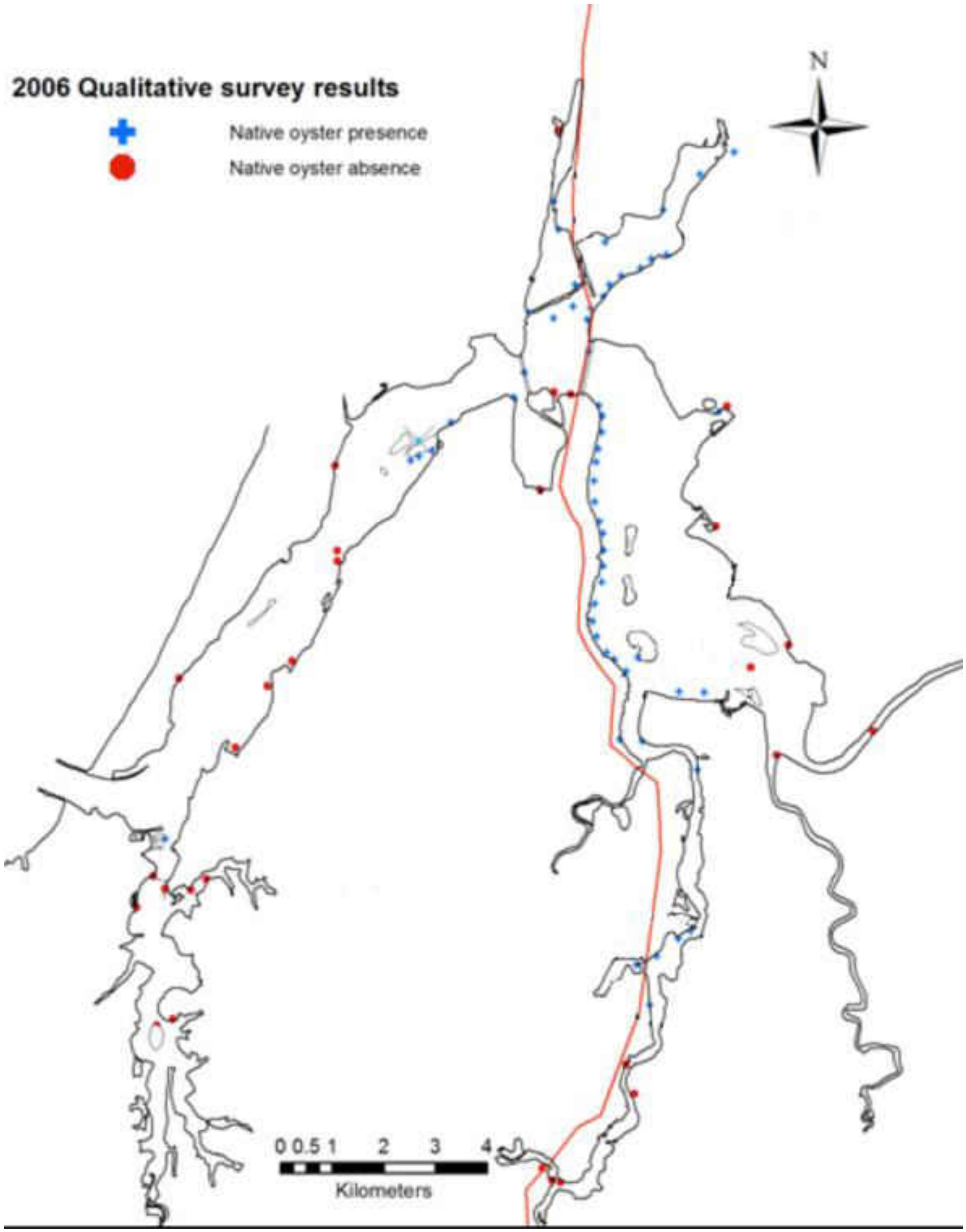

Figure 1. Distribution of adults of *Ostrea lurida* in Coos Bay (adapted from Groth and Rumrill, 2009). Blue dots indicate oyster presence and red dots oyster absence (dots are based on surveys in 2006 as reported in Groth and Rumrill 2009). Black circles indicate sampling sites for the present study. Red line indicates US Highway 101.

spot, so we moved everything from the rocky slope on the north side of the Catching Slough Bridge to the mudflat just underneath it, on the west side of the bridge. At each site, we sampled in the low intertidal, approx. 30.5 cm below MLLW (referenced to Downtown Coos Bay) so that our equipment would be accessible at the lowest tides of the month but submerged as much as possible. We sampled approximately every two weeks during spring tides. In 2012, we deployed sampling equipment in July and first collected it in early August; our last collection date was in November. This was about the same time frame when previous researchers observed larvae and new recruits of *O. lurida* in Coos Bay (Garcia-Peitero *unpublished*; Sawyer, 2011). However, our first trap sample in August 2012 contained more larvae than samples taken at later dates, so we suspected that we missed the beginning of the spawning season. Therefore, we began sampling in May the following year. Due to time constraints imposed by staggered graduation schedules, we stopped sampling larval supply in August 2013, but continued to sample settlement through November (see Appendix A for collection dates).

Trap design and larval identification

We used passive larval traps to sample the plankton for larval supply of *O. lurida*. This was for two reasons: 1) Like settlement plates, traps sample plankton continuously for the entire length of time they are deployed, and 2) traps could be placed in the intertidal alongside settlement plates. Larval traps have previously been deployed successfully in the intertidal (Gaines and Bertness, 1993; Todd, 2003). We modified the basic trap design (Yund et al., 1991) to ensure trap efficiency in the high-velocity tidal flows observed in Coos Bay. Each trap was composed of a funnel (7 cm x 5 cm PVC reducer and funnel), a PVC tube (61 cm x 5 cm), and a base (Figure 2). The base of the trap consisted of five separate parts: a 5 cm PVC coupler, a 5 cm x 2 cm PVC reducer, 2 cm male and female PVC screws, and a 2 cm diameter PVC stake. We used 5 replicate tubes per site, although occasionally the traps would be knocked over or lost, reducing our number of replicates. The stakes were pounded into the substrate until the reducer was flush with the substrate, and the traps were screwed into the stake so that they could be removed without removing the stake from the substrate. Each trap was filled prior to deployment with a solution of 10% formalin buffered with borax and filtered seawater. The solution was dyed with Rose Bengal, which turns organic matter pink—this helped when larvae was sorted from sediment during analysis of trap contents. The dye also allowed for visual confirmation that the fluid was retained in the trap during deployment.

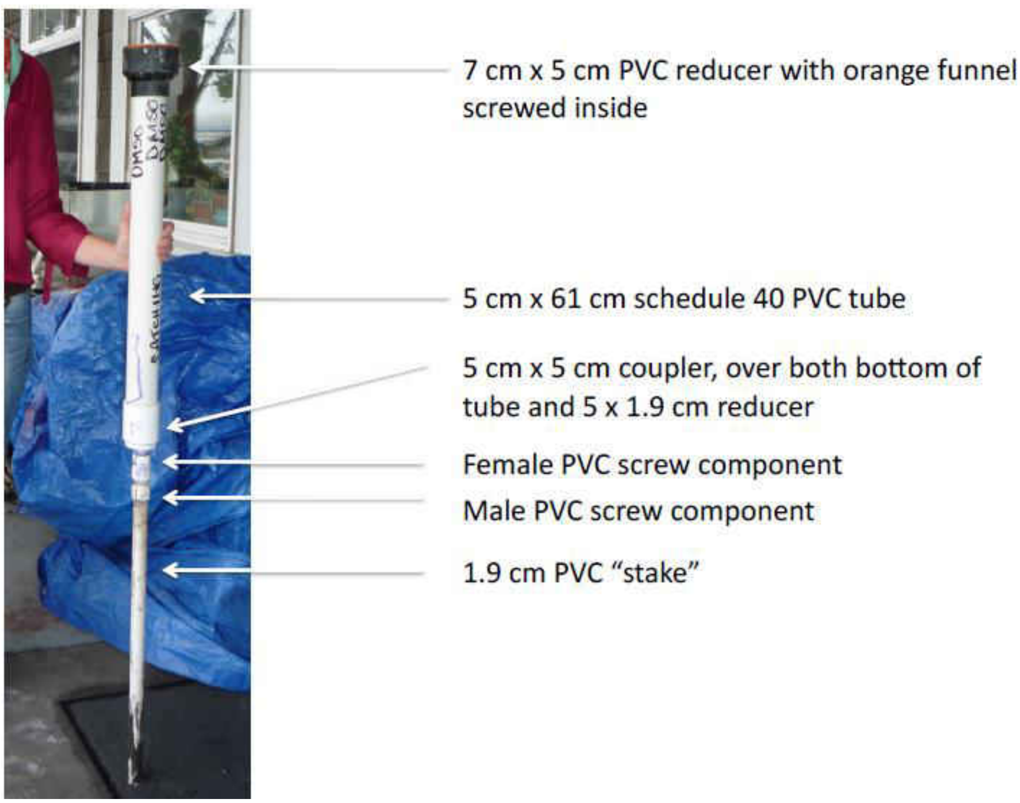

Figure 2. Larval trap.

On each collection date, traps in the field were exchanged for a second set and the field traps were taken back to the lab for analysis. The contents were poured through a 145 µm sieve and each trap was rinsed well to ensure collection of all particles. The contents in the sieve were then rinsed and preserved in 5% formalin-buffered seawater. Samples were examined on an inverted microscope, and the whole sample was inspected. Larvae of *O. lurida* were divided into categories: 1) D-stage, or larvae that had not yet formed a knob-shaped umbo and 2) umbo-stage, or older larvae that had already developed the umbo (Loosanoff et al., 1966; Shanks, 1991). While D-stage bivalves in general are difficult to identify, D-stage of *O. lurida* were distinguishable from other D-stage bivalves by their relatively smooth, round shape (Figure 3). In 2013, our identifications of both D-stage and umbo-stage *O. lurida* were confirmed by sequencing the 18S gene region of larval bivalves captured in plankton tows (Pritchard, 2013.)

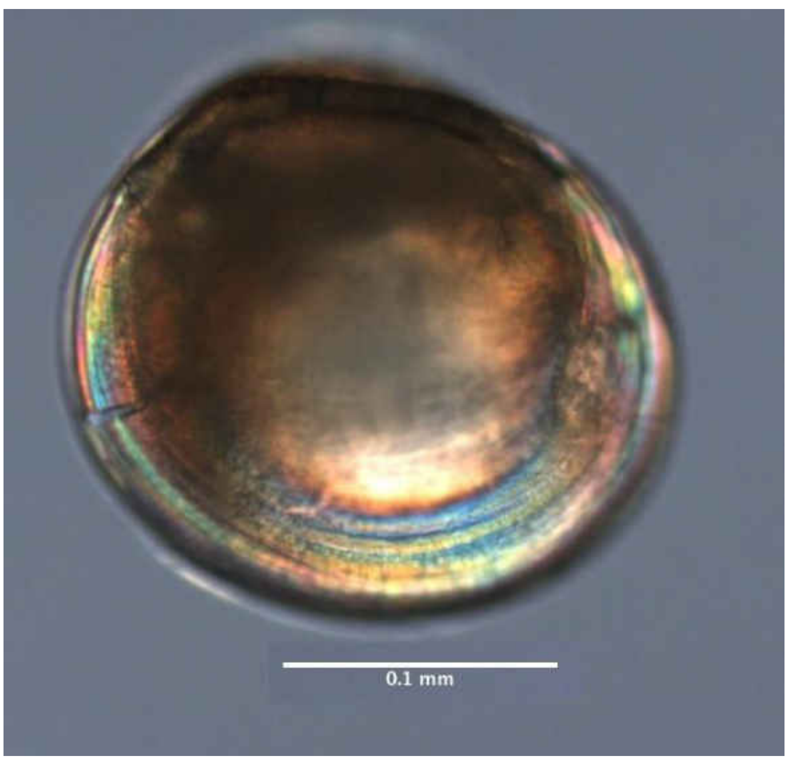

Figure 3. D-stage larva of *Ostrea lurida*

Settlement plate design and new recruit identification

Settlement plates were square, 15.24 cm^2, unglazed, off-white ceramic tiles, which had been previously used in settlement studies of *O. lurida* in Yaquina Bay (C. Eardley, *pers. comm.*). The plates were bolted to PVC "T" shaped holders, which held one plate per arm of the T, as in Seale and Zacherl (2009). Each arm was 30 cm long, and the vertical portion was 61 cm long. The vertical portion of each T was reinforced with rebar, which was pounded into the substrate at each site (Figure 4). We used four replicate T's at each site, each holding two plates, for a total of eight replicate plates per site. Each plate was parallel to the substratum, and only the underside of each plate was examined for new recruits. The T's were placed next to, rather than "in front of" the traps (relative to the flood/ebb currents) in order to minimize the possibility of formalin leaking onto the plates. The distance between each trap and its adjacent T was between 0.5 and 1 m. The T's were positioned so that the plates would be roughly level with the tops of the traps, within about 30 cm.

Like the traps and on the same sampling schedule, the plates were replaced with a second set upon collection; the T's remained in the field and the plates were exchanged by unscrewing one set from the arms of the T's and replacing them with the second set. In order to develop a biofilm that might enhance settlement, plates were always soaked for a minimum of 12 hours in running seawater in the lab before deployment. Field-collected plates were brought back to the lab and held in running seawater until they could be counted. Each plate was subsampled. To subsample, a plastic grid was laid over the plate and 15 squares, each 6.45 cm^2, were chosen using a random number generator.

About 42% of each plate (96.8 cm^2 of 232.26 cm^2 total area) was inspected. Plates were examined using a dissecting microscope and epiluminescent lights. Only intact oysters were counted. Identification of bivalve recruits was based on size, attachment method (byssal thread vs. cement), and overall shape. Only intact oysters were counted, and identification to species was based on umbo shape (Loosanoff et al., 1966, Baker *pers. comm.*) By this criterion, new recruits of *Crassostrea gigas* were observed on the first set of plates collected after deployment in 2012, on August 2 and 3. No *C. gigas* were observed thereafter in 2012 or ever in 2013 (see Introduction). After analysis, plates were carefully scrubbed and rinsed with freshwater. Once all plates from all sites were counted, scrubbed, and rinsed, they were all placed in running seawater at the same time until the next deployment date.

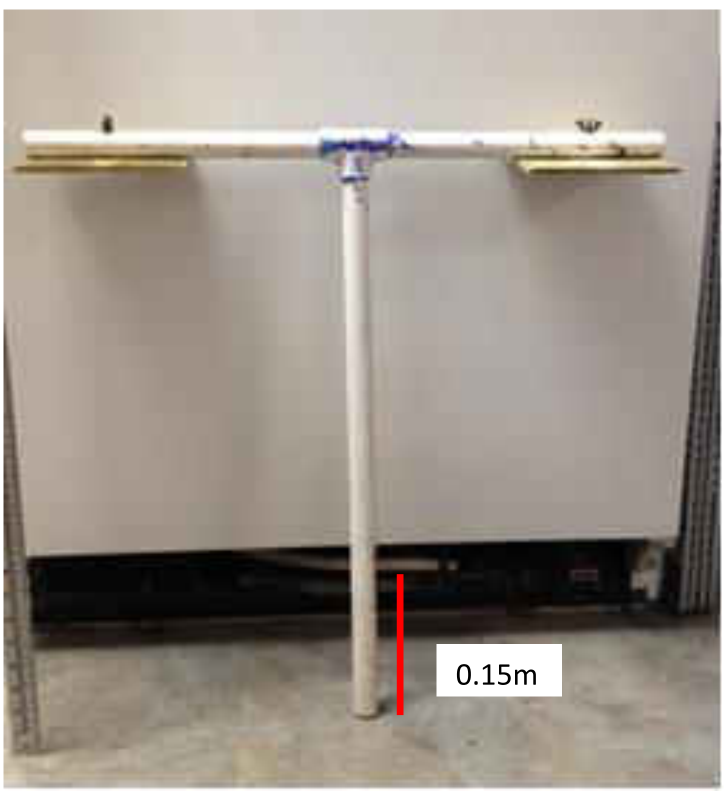

Figure 4. PVC “T” settlement plate holder with settlement plates.

To examine the relationship between larval supply and new recruits, least squares linear regressions were run at three sites: Coalbank Slough, Downtown Coos Bay, and Haynes Inlet. In 2012, Catching Slough was excluded because of missing data, and Empire was excluded because there was no settlement. In 2013, Catching Slough, Empire, and Airport were all excluded due to negligible or no settlement.

Physical data

HOBO data loggers (Onset Computer Corp.) recorded temperature and conductivity (U24-002) and water level (U20-001-01-Ti) every ten minutes. Water level loggers were used to compare emersion times across sites. The loggers were mounted inside PVC pipes in which holes had been drilled to allow for water to flow in and out of the pipe. Later, we attached rebar to the pipe. We pounded the pipe or the attached rebar into the substrate at each site adjacent to the sampling apparatus within 0.5 and 1 m. We were careful to align the position of the logger inside the pipe so that it was approximately level with the tops of the traps and with the plates, or about 0.61 m off the ground. One temperature/conductivity logger was placed at each site, but as we were in possession of only three water level loggers, we were not able to measure water level simultaneously at all sites. Instead, we kept one water level logger at Hayes Inlet continuously, and moved the other two from site to site so that at least one month of data was available for each of the other sites. These loggers record pressure. Immersion (logger covered by water) and emersion (logger exposed to air) were inferred from the data by noting each data point for which the loggers recorded a pressure below 102 kPa, or a value approximately equal to atmospheric pressure. These values were assumed to record logger emersion. All values greater than 102 kPa were assumed to record logger immersion. The fraction of time loggers were emersed out of the total time the loggers were in the field was then calculated for each site. The logger at Coalbank Slough appears to have failed since the data do not reflect a tidal cycle. To estimate emersion time at this site, we measured tidal height relative to MLLW at our Coalbank Slough site and used this information along with tide height predictions from the program JTides (v 5.2), which gives a tide height value every ten minutes, to calculate time when equipment would have been emersed or immersed. Ideally, we would have cross-checked this method with the logger method at a site with both types of data available; however, time constraints and tide schedule prevented this.

Salinity and temperature data are reported in Appendix B. These values are minimum, maximum, and mean of the data points logged (one data point per ten minutes) within each two-week time interval. The mean daily range, or mean of the means of the difference between maximum and minimum temperature recorded each day (from midnight to midnight) within each two-week time interval, is also reported. We did not exclude temperature data during periods when loggers were likely exposed to air, so the temperature data discussed below and presented in the Appendix includes temperatures when the equipment was exposed. Outlier salinity data was removed from analysis, because it may have represented logger error. The salinity data from the temperature/conductivity logger is compromised because the loggers were inaccurate in environments that experienced large fluctuations in salinity, which we discovered when the loggers were recalled by Onset Computer Corp. in April 2013. Because the error is non-linear, no correction can be applied and as a result, our salinity data should be evaluated with caution.

RESULTS

Temperature

In general, *O. lurida* spawns at water temperatures between 13 and 16˚C (Peter-Contesse and Peabody, 2005), but in Coos Bay specifically it spawns at water temperatures above 15˚C (Oates 2013). In 2012, average temperature only exceeded the 15˚C spawning threshold once at Empire, in early August (see Appendix B for temperature and salinity values). At Downtown Coos Bay and Haynes Inlet, the average temperature was greater than 15˚C from the beginning of our sampling period until mid-September. At Coalbank Slough and Catching Slough, average temperature was above 15˚C until early October.

In 2013, average temperature exceeded 15˚C briefly in early August at Empire and in early July at Airport. Average temperature was above 15˚C at Downtown Coos Bay from the beginning of sampling through early July, after which the logger at this site malfunctioned. Average temperature at Haynes Inlet reached 15˚C in early July and stayed above that threshold until early September. Like Downtown, logger malfunction at Coalbank Slough and Catching Slough resulted in lost data. At Coalbank Slough, data are only available from late August and early September, and at Catching Slough, data are only available from the beginning of sampling through mid-July. During these periods, average temperature was consistently above 15 ˚C.

We present temperature data that includes periods when equipment was likely exposed to air, although critical spawning temperatures refer to water temperature, because aerial exposure time appears to have been minimal (see below);

Water level

Water level data are available from Haynes Inlet for the entirety of our sampling period, but data from the other sites are only available for portions of the sampling period because we were only in possession of three loggers (see Methods). The logger at Coalbank Slough appears to have malfunctioned, since the data do not indicate a tidal cycle. Over the periods a logger was recording at each site, our equipment was emersed, or exposed to air, 1.1% of the time at Empire, 1.6% of the time at Airport, 1.7% of the time at Haynes Inlet, 3.4% of the time at Downtown Coos Bay, and 1.5% of the time at Catching Slough. According to the rough approximation of emersion time at Coalbank Slough, our equipment at this site was exposed 0.3% of the time (Table 1).

Emersion time was very similar at Empire, Airport, and Haynes Inlet. At Downtown Coos Bay, our equipment was emersed slightly more often than at any other site. Most dissimilar was the emersion time at Coalbank Slough, which was an order of magnitude less than at the other sites. The following data are larval and recruit counts divided by estimated immersion time; both raw and adjusted data are in Appendix A.

Table 1. Proportion of time equipment was immersed and emersed at each site.

	Empire	Airport	Haynes Inlet	Downtown	Coalbank	Catching
Proportion of time immersed	0.989	0.984	0.983	0.966	0.997	0.985
Proportion of time emersed	0.011	0.016	0.017	0.034	0.003	0.015

2012 Larval supply of *O. lurida*

We observed the highest numbers of larvae on our first two collection dates, in early and mid-August, after which larval abundance steadily decreased (Figure 5 and Appendix A). Very few larvae were observed after mid-September, and none after October 1st.

Both D-stage and umbo-stage larvae were most abundant at Downtown Coos Bay, with a peak of 147±29.4D-stage larvae per trap and 70.1±8umbo-stage larvae per trap. They were also relatively abundant at Coalbank Slough, with a peak of 78.2±35.4 D-stage larvae per trap and 15.7±4.6 umbo-stage larvae per trap, and less abundant at Haynes Inlet, with a peak of 60.3±10.7 D-stage larvae per trap and 30.8±6.3 umbo-stage larvae per trap. Few larvae of either kind were observed at Empire. Data on Catching Slough larvae are not available for mid-August and late-August intervals (see Methods). Data from early August and mid-September indicate low larval supply at this site, except for a slight increase to 13.2±3.8 umbo stage larvae per trap in mid-September.

2013 Larval supply of *O. lurida*

In 2013, both D-stage and umbo-stage larvae peaked in late July (Figure 6). D-stage larvae were present in highest numbers at Downtown Coos Bay, Catching Slough, and Coalbank Slough. Umbo-stage larvae were present in highest numbers at Downtown Coos Bay, with relatively high numbers of umbo-stage larvae at Catching Slough and Coalbank Slough on this date.

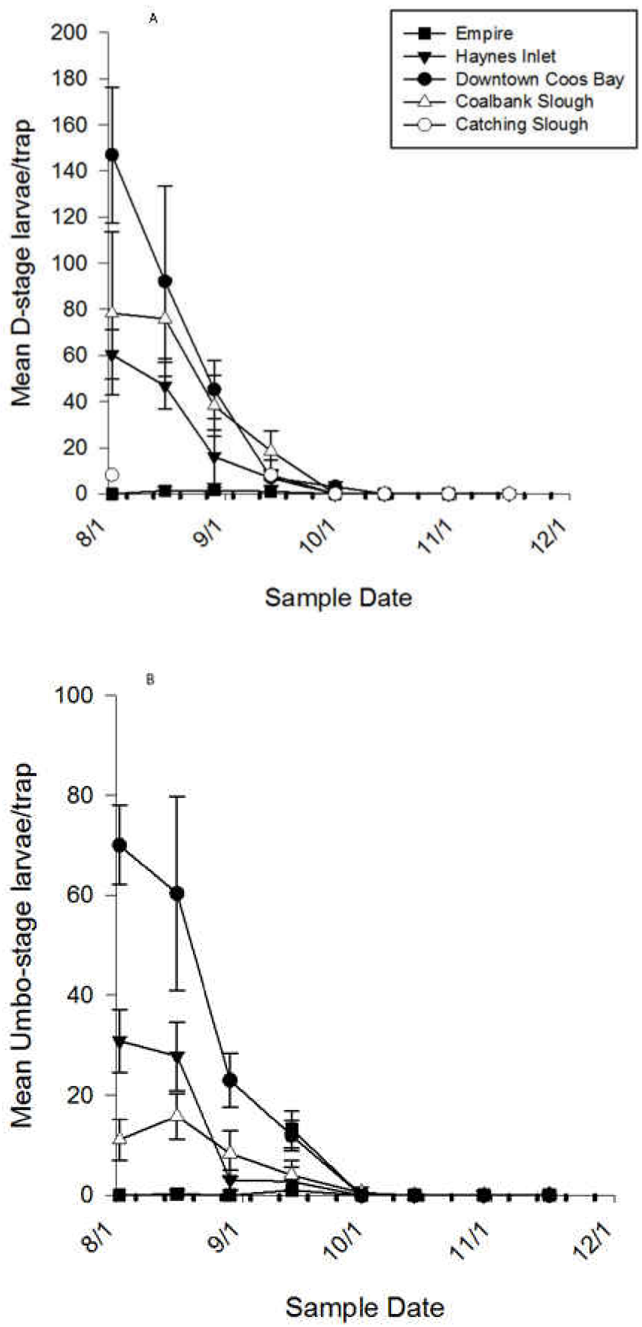

Figure 5. Abundance of A) D-stage and B) umbo-stage larvae in 2012. Larval counts are adjusted for approximate immersion times. Errors bars are 95% confidence intervals.

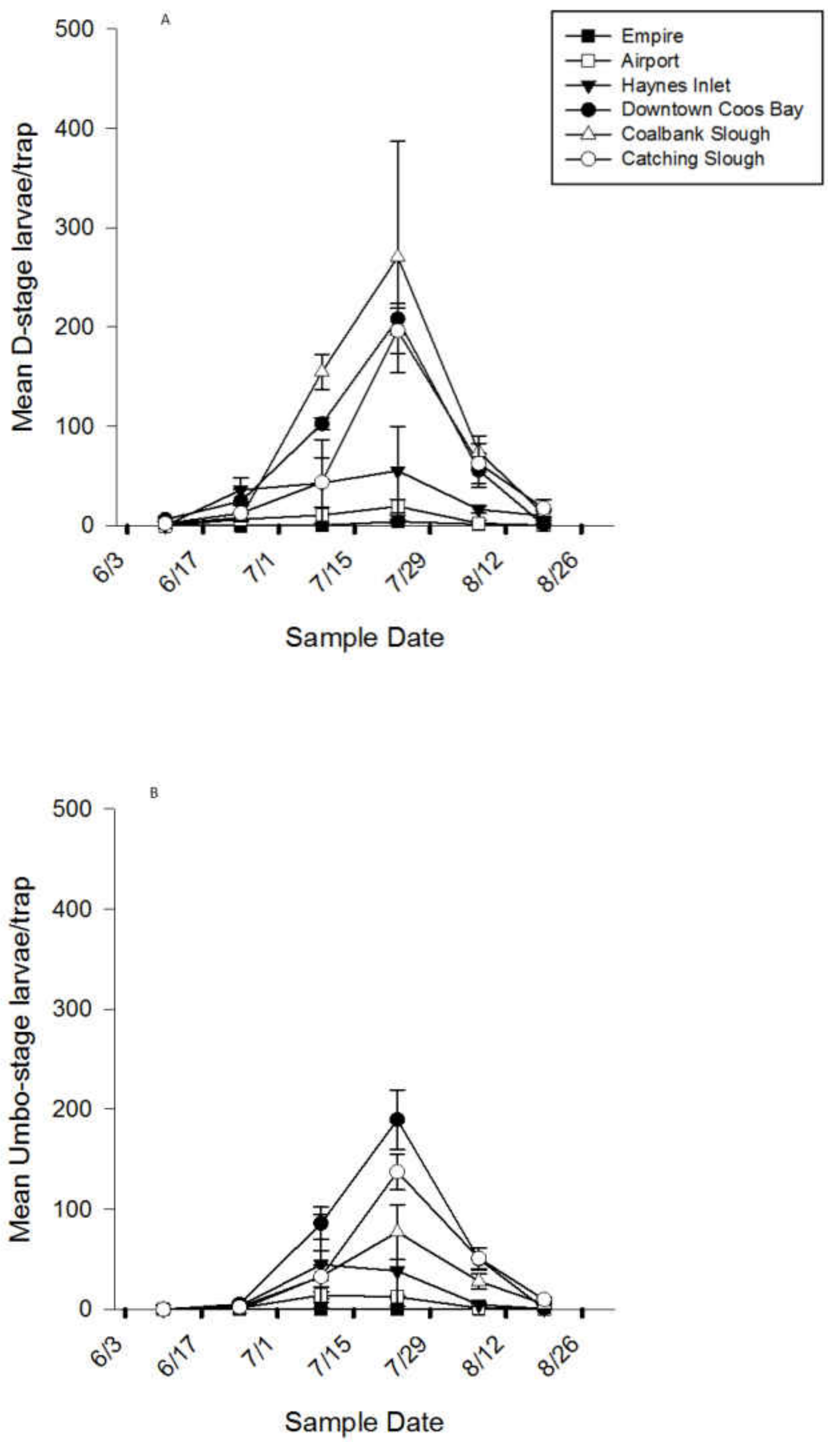

Figure 6. Abundance of A) D-stage and B) Umbo-stage larvae in 2013. Larval counts are adjusted for approximate immersion times. Errors bars are 95% confidence intervals.

2012 Settlement

Settlement was observed from early August through October 1st (Figure 7A). Settlement peaked in mid- to late August at both Downtown Coos Bay and Haynes Inlet. At Coalbank Slough, settlement was consistently low, with a peak occurring in late August. Data from mid-August are missing from Catching Slough (see Methods) but data from early and late August indicate very low settlement. At Empire, no new recruits were ever observed.

2013 Settlement

In 2013, new recruits were observed from late June through mid-September, although the bulk of settlement occurred from early July through early September (Figure 7B). There was a large settlement peak in early July. Average settlement was higher at Haynes Inlet than at Downtown Coos Bay, but the difference between the two sites was not significant (F=0.573, p=0.571). Like in 2012, settlement was consistently low at Coalbank Slough and settlement also peaked slightly later at this site, in late July rather than early July. Settlement was brief and low at Catching Slough. Finally, no recruits were observed at Empire or at the newly added Airport site.

Settlement vs. larval supply, 2012

Least-squares linear regressions of both D-stage and umbo-stage larval abundance against number of new recruits on the same date were not significant (Figure 8A, 9A, Table 2 Because larvae of *O. lurida* have a pelagic larval duration of 7-23 days

(Strathmann, 1987), settlement recorded two or even four weeks later might correlate better with larval supply of a given sampling period. Indeed, linear regressions between numbers of umbo-stage larvae and numbers of new recruits two weeks (one sampling interval) later were significant at Haynes Inlet and Downtown Coos Bay even when a Bonferonni correction was applied (α=0.05/3 or 0.017) and with the small sample size of 4 (Figure 9B; Table 2). The correlation (R=0.903) of umbo-stage larvae against lagged recruits at Coalbank Slough is not significant, but this is likely a result of small sample size: this relationship would be significant if there were six data points instead of just four. Small sample size may also account for the non-significance of D-stage larvae against lagged settlement at Downtown Coos Bay and Haynes Inlet despite the apparent correlation (R=0.983 and 0.934). Regressions between larvae and recruits recorded four weeks (two sampling intervals) later were not significant. (Figure 8C, 9C).

Settlement vs. larval supply, 2013

Regressions comparing larval supply with settlement in 2013 produced very different results from those in 2012 (Figures 10 and 11.) Catching Slough, Empire, and Airport were excluded from these analyses due to low or no settlement. The only significant relationships were those between D-stage and umbo-stage larvae and new recruits of the same sampling date and only at Coalbank Slough (Figure 10A, 11A) at α= 0.017 and n=5; again, low sample size may prevent the significance of some correlations, such as D-stage and umbo-stage larvae and new recruits without lag at the other two sites (Table 2).

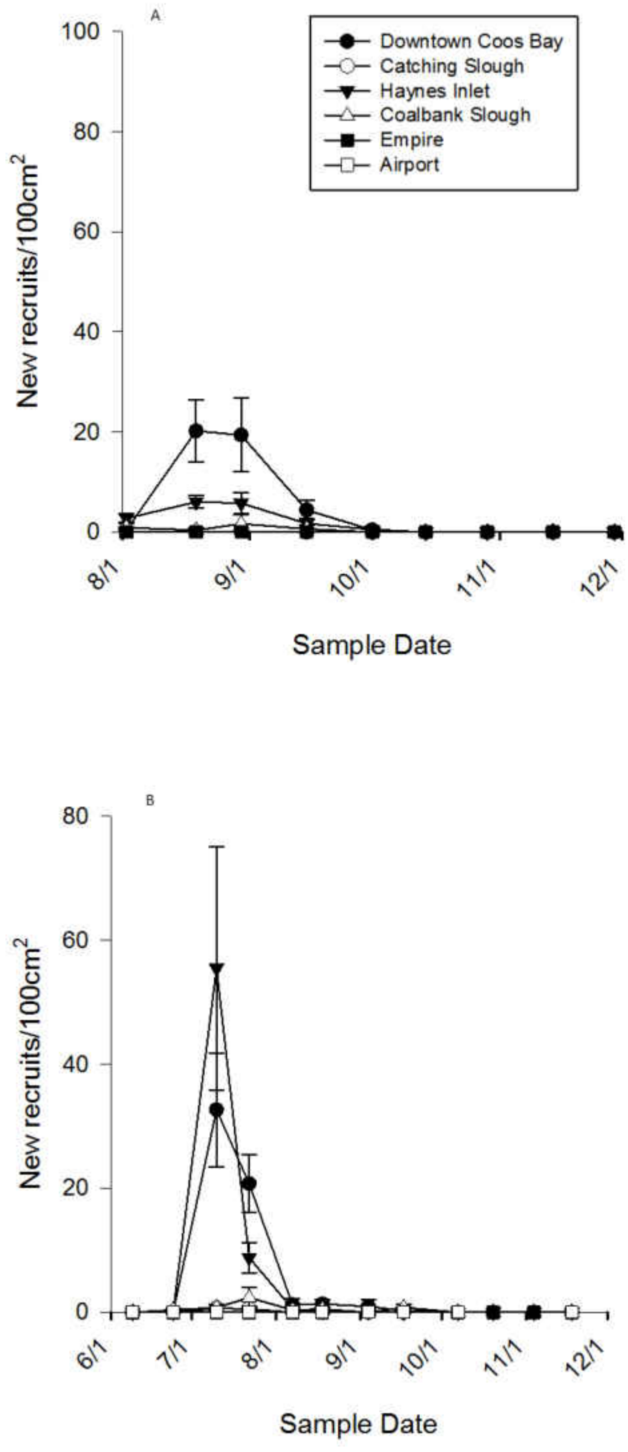

Figure 7. Settlement in A) 2012 and B) 2013. Recruit counts are adjusted for approximate immersion times. Errors bars are 95% confidence intervals.

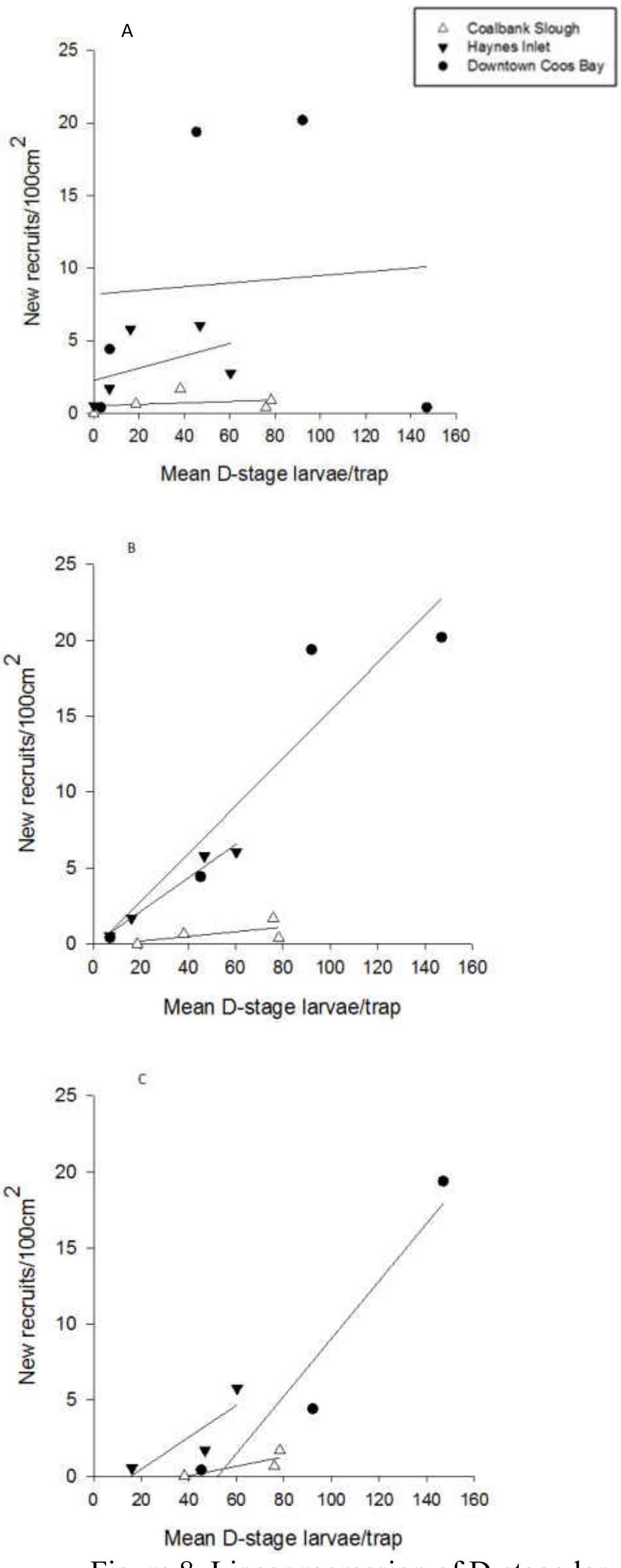

Figure 8. Linear regression of D-stage larvae and new recruits (adjusted for immersion times) in 2012 with A) no lag B) two-week lag and C) four week lag.

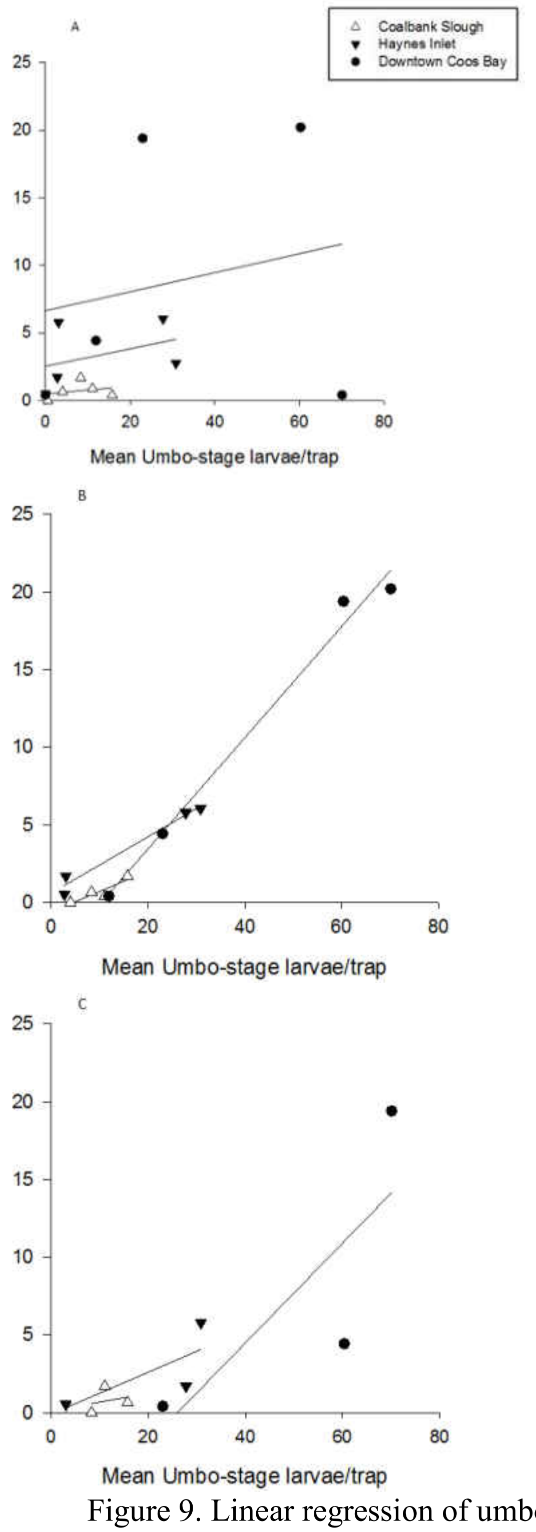

Figure 9. Linear regression of umbo- stage larvae and new recruits (adjusted for immersion times) in 2012 with A) no lag B) two-week lag and C) four week lag.

Table 2. Correlation coefficients and p-values for all regression analyses.

Year	Lag?	Site	D-stage larvae	Umbo-stage larvae
2012	No lag	Coalbank Slough	R= 0.269; p=0.661	R=0.266; p=0.666
2012	No lag	Haynes Inlet	R= 0.451; p=0.446	R=0.395; p=0.511
2012	No lag	Downtown Coos Bay	R=0.078; p=0.901	R=0.215; p=0.729
2012	Two-week lag	Coalbank Slough	R=0.626; p=0.374	R=0.903; p=0.097
2012	Two-week lag	Haynes Inlet	R=0.983; p=0.017	R=0.986; p=0.014
2012	Two-week lag	Downtown Coos Bay	R=0.934; p=0.066	R=0.994; p=0.006
2012	Four-week lag	Coalbank Slough	R=0.824; p=0.383	R=0.237; p=0.848
2012	Four-week lag	Haynes Inlet	R=0.863; p=0.337	R=0.744; p=0.466
2012	Four-week lag	Downtown Coos Bay	R=0.962; p=0.176	R=0.797; p=0.413
2013	No lag	Coalbank Slough	R=0.911; p=0.011	R=0.931; p=0.007
2013	No lag	Haynes Inlet	R=0.482; p=0.333	R=0.806; p=0.053
2013	No lag	Downtown Coos Bay	R=0.728; p=0.101	R=0.714; p=0.111
2013	Two-week lag	Coalbank Slough	R=0.179; p=0.773	R=0.008; p=0.989
2013	Two-week lag	Haynes Inlet	R=0.213; p=0.731	R=0.283; p=0.645
2013	Two-week lag	Downtown Coos Bay	R=0.318; p=0.602	R=0.318; p=0.602
2013	Four-week lag	Coalbank Slough	R=0.615; p=0.385	R=0.582; p=0.418
2013	Four-week lag	Haynes Inlet	R=0.971; p=0.029	R=0.730; p=0.270
2013	Four-week lag	Downtown Coos Bay	R=0.859; p=0.141	R=0.840; p=0.160

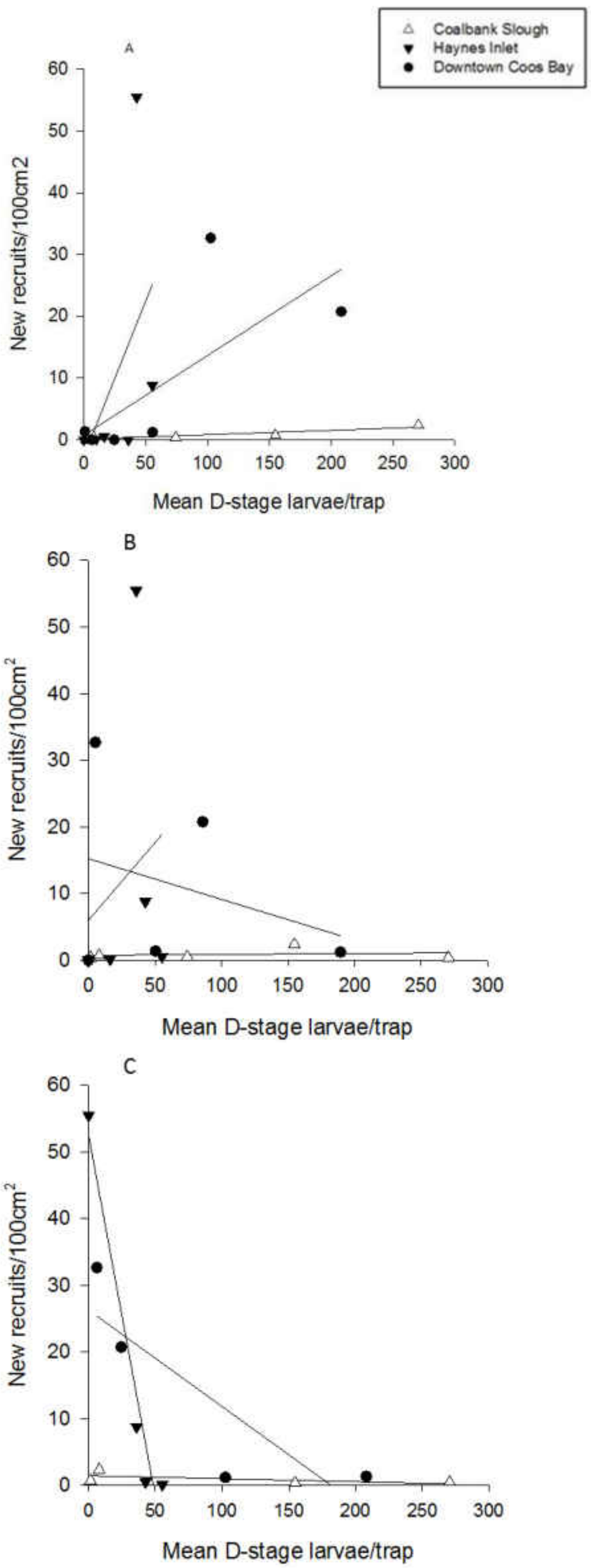

Figure 10. Linear regressions of D-stage larvae and new recruits (adjusted for immersion times) in 2013. A) No lag B) Two-week lag C) Four-week lag

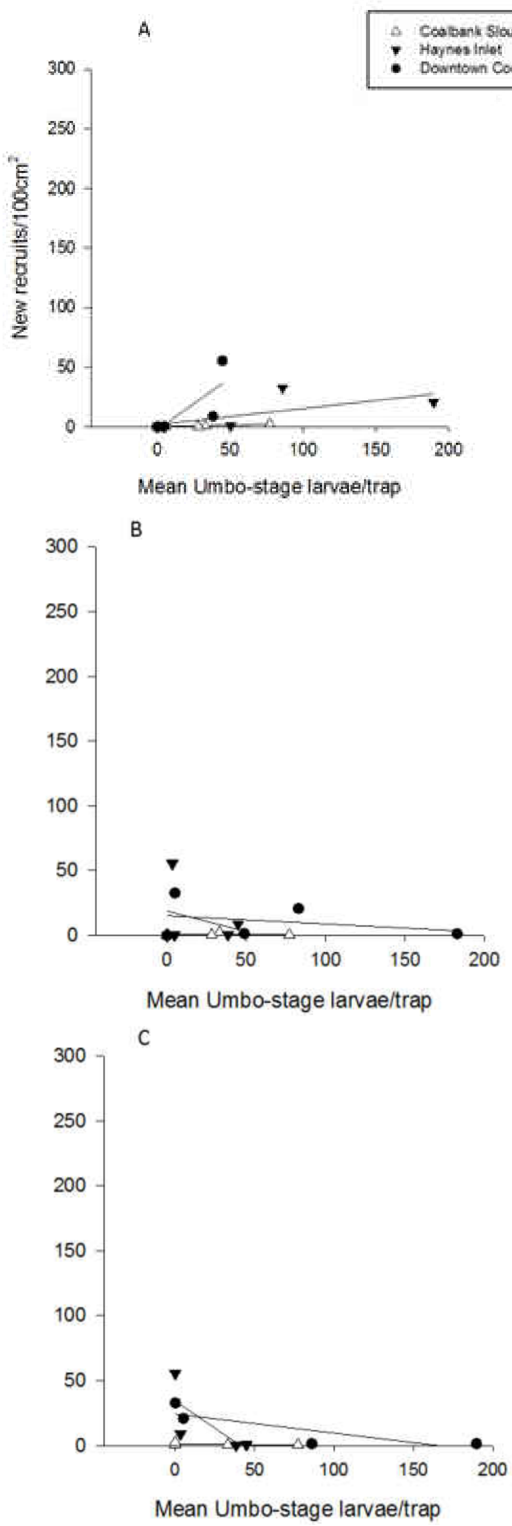

Figure 11. Linear regressions of umbo-stage larvae and new recruits (adjusted for immersion times) in 2013. A) No lag B) Two week lag C) Four week lag

DISCUSSION

Timing of larval occurrence and settlement of *O. lurida* in Coos Bay

Larvae of *O. lurida* were present from early August through late September in 2012 and peaked in early August. However, since the peak in larval supply occurred during our first sampling interval, the actual peak may have happened before we began sampling that year. This suspicion is reinforced by the fact that the 2012 “peak” consisted of many fewer larvae than the 2013 peak. For example, we collected a mean of 70.1±8 umbo-stage larvae on our first sampling date in Downtown Coos Bay in 2012 and a mean of 189.4±29.9 umbo-stage larvae at that site during our peak sampling interval in 2013. Therefore, the actual peak in larval abundance in 2012 may have occurred before we started sampling in 2012.

In 2013, we observed larvae of *O. lurida* in the water column from early June through our last sampling date in mid-August with a peak in mid-July. While it appears that larval presence may have occurred earlier in the year in 2013 than in 2012, this observation might actually be an artifact of changing our sampling dates. Our first collection date was in early June rather than early August, and our last collection date was in mid-August rather than late November. We found that younger larvae were distributed temporally in much the same way as older larvae.

In 2010, larvae of *O. lurida* were found in weekly plankton tows in Coos Bay from late July, about six weeks after sampling began, through early October, when sampling ended. Larval presence peaked twice: once in mid-August and again in mid-September (Garcia-Peteiro, *unpublished*).

In this study, only recruits of *O. lurida* that survived to be counted on a sampling date were included in our assessment of "settlement". "Settlement" can refer to the behavior of a competent larva when it contacts appropriate substrate or to the observation of survival of post-larvae for some period of time. Because we cannot tease apart settlement as behavior from settlement as survival of post-larvae within our two week sampling period, we refer to the individuals we counted on plates as "new recruits." These recruits could have settled that day or could have settled up to two weeks prior; indeed, spat size ranged from less than 300 μm to over 1 millimeter, although individuals at either extreme were less common than oysters somewhere in the middle of that range. Since high mortality has been observed in young oyster settlers, particularly in the first week after settlement (Roegner and Mann, 1995, Michener and Kenny, 1991) it is possible that we missed at least some of the oysters that settled during each interval.

The timing of settlement in Coos Bay appears to vary from year to year. In 2010, shell bags hung off a dock near our Downtown Coos Bay site collected new recruits from mid-August through early December and peaked in October (Sawyer, 2011). In 2012, settlement on plates in the low intertidal occurred from early August through early October and peaked in mid- to late August (Figure 7A). In 2013, settlement at these same sites occurred from early July to early September and peaked in early July (Figure 7B). To summarize, the settlement period of *O. lurida* in Coos Bay has been observed to start as early as July and to end as late as December, with a peak in settlement occurring in July, August, or October of different years.

Settlement in summer to early fall of *O. lurida* observed in Coos Bay is generally consistent with observations of settlement of *O. lurida* from other estuaries [it should be noted, however, that these studies sampled at different frequencies, which can affect settlement patterns (Michener and Kenny, 1991; Pineda, 2000)]. Our observations of a slight variation in timing of settlement between years are also consistent with variations seen in multi-year studies in other estuaries. In Puget Sound, settlement varied between years and with location but generally occurred between June and October and peaked multiple times every summer (Hopkins, 1937). In Tomales Bay, CA, settlement occurred between August and November and peaked in September one year and August the next year (Deck, 2011). Other sites in California seem to depart from the summer and fall pattern. On the Scripps Institute pier in La Jolla, CA, an anomalous open coast population of *O. lurida* settled from April to November (Coe, 1932). In one estuary in Southern California, settlement occurred from May to June and peaked in June; in a slightly more southern estuary, settlement occurred from June to February, again with a peak in June (Seale and Zacherl, 2009). Natural recruitment was observed from December to February one year in San Francisco Bay (Grosholz et al., 2008). We saw only one peak in settlement, which, as described above, has been the case for some researchers in other estuaries but not for all.

There is also evidence that the population in Coos Bay occasionally experiences reproductive failure. In 2011, plankton tows failed to capture larvae of *O. lurida* although similar tows, by the same scientist, in 2010 had captured these larvae at densities up to $50/m^3$ (Garcia-Peitero, L. *pers. comm.*). Settlement, too, may have been a failure that year. In 2011, I made an attempt to quantify settlement using the same methods of a previous researcher in 2010 (Sawyer 2011). Settlement was assessed on shell bags hung off a dock in Downtown Coos Bay every two weeks from September through December but no settlement was observed during that period. It is worth noting that in 2013, settlement had ended by September, so it is conceivable that sampling began too late in 2011 for settlement to be observed. However, the fact that plankton sampling in 2011 returned no larvae of *O. lurida* lends support to the hypothesis that there was a reproductive failure for this species in Coos Bay in 2011. Unusually low settlement seasons have been reported in California (Deck, 2011; Grosholz et al., 2008).

Magnitude of settlement

We observed a greater density of spat during periods of peak settlement than what was observed by researchers in California observed: 20.2/100 cm^2 in 2012 and 55.5/100 cm^2 in 2013, compared with 11/100 cm^2 (Seale and Zacherl, 2009), 15/100 cm^2 (Deck, 2011), and 10/100 cm^2 (Grosholz et al., 2008). Of course, these measurements were all taken at different tidal heights, at different sampling intervals, and with different settlement materials. It is even more difficult to compare our results with those of Hopkins (1937) in Puget Sound, because he used bags of shell to collect spat rather than tiles. He reported a maximum of 372 spat on one side of one shell. We can only make a very rough estimation: if we assume he used *C. gigas* shells measuring on average about 25.4x12.7 cm, that would be 115 spat per 100 sq cm, a higher density than we observed on our tiles.

Location of larvae and new recruits of *O. lurida* in Coos Bay

Two of our field sites were included in surveys of adults in 1996-97 and 2006: Haynes Inlet and Downtown Coos Bay. Oysters were more dense at Downtown Coos Bay

(6.7 individuals/m^2 in 96-97 and 61.3 individuals/m^2 in 2006) than at any other site surveyed (Baker et al., 2000; Groth and Rumrill, 2009). Our results suggest that this high density may be due to high larval supply (Figures 5 and 6) as well as high settlement (Figure 7) although it could also be the result of more available hard substrata, higher post-settlement survival, or better growth (see Chapter III). Also, in 2012, a significant linear relationship was found between larvae and recruits lagged two weeks at this site so that there was one recruit for every 2.8 umbo-stage larvae—a relatively high proportion (see below).

Adult *O. lurida* at Haynes Inlet were less dense than at Downtown Coos Bay when surveyed in 96-97 and 2006 (0.7 individuals/m^2 in 96-97 in 96-97 and 4.7 individuals/m^2 in 2006). Our results suggest that, in addition to fewer available larvae, this difference in density may be due to fewer recruits per larvae. There was a significant linear relationship between umbo-stage larvae and recruits lagged two weeks in 2012 such that there was only one recruit for every 5.5 umbo-stage larvae.

Coalbank Slough was not surveyed as part of these previous studies (Baker et al., 2000; Groth and Rumrill, 2009), although adult *O. lurida* are present at this site. Larvae of *O. lurida* were relatively abundant here but settlement was low. Additionally, the ratio of recruits to larvae was very low. In 2013, there was a significant relationship at this site between both D-stage and umbo-stage larvae and recruits of the same sampling date, such that there was only one recruit for every 138.31 D-stage larvae and 37.88 umbo-stage larvae.

No adult *O. lurida* were present at Catching Slough, but this was not due to low larval supply. Larval supply at this site was relatively high in 2013 (Figure 6) but settlement was vanishingly low (Figure 7). Low substratum availability would be a reasonable hypothesis as to why there are no adults at this site despite high larval supply, but the fact that larvae failed to settle when given artificial hard substrata in the form of tiles, and/or died within the first two weeks of settlement, implies that recruitment limitation, rather than substratum limitation, is the impediment to adults living in this area.

There were no adult *O. lurida* present at either Empire or Airport, and larvae are apparently not supplied in large numbers to these sites. This result provides evidence for the existence of a “null zone” in the bay located near the McCullough Bridge. In estuaries, “the null zone” refers to a portion of the estuary upwards of which estuarine water is retained during the relatively dry summer. Lack of freshwater input increases residence times in estuaries, so that the water mass from the head of the estuary does not exit the estuary on the falling tide. Since larvae are spawned in the summer, this phenomenon may prevent dispersal of larvae spawned up-estuary past the null zone (Largier et al., 1997, Pritchard 2013). However, the presence of adult oysters on the runway of the Southwest Oregon Regional Airport and on the docks in Charleston, both locations that are down-estuary from the proposed location of the summer null zone, suggests that this explanation is only part of the story. How adults came to occupy these locations, how the timing of the reproductive cycle of adults at these lower estuary sites compares to adults in other parts of the estuary, and where their larvae are transported, is not known and could be the subject of future investigations.

Change in relationship of larval supply to settlement

The significant linear relationships between larval supply and settlement found at several sites in 2012 did not occur in 2013. Sample size was greater by one data point in 2013, and yet correlation coefficient (R) values were much lower. This decoupling of settlement from larval supply could have been caused by a decrease in settlement success, an increase in post-settlement mortality, or a combination of the two. While recruitment events may look "chaotic" and with respect to larval supply, this "chaos" may actually reflect ignorance of environmental factors at play (Yoshioka, 1982, 1986). Settlement in this species can be affected by a number of factors including substrate type and salinity (Sawyer, 2011). We can rule out the influence of substratum type as we used the same settlement material both years. We cannot, however, rule out change in salinity between the two years. While our salinity data are unreliable due to logger error, we can use precipitation data as a proxy for salinity: higher precipitation would increase freshwater input, which would lower the salinity of the bay. In 2013, high precipitation occurred earlier in the year than in 2012 (Figure 12). Sawyer (2011) found a decrease in settlement with decreasing salinity in the lab, and Hopkins (1937) found that higher settlement was correlated with higher salinity (but did not separate higher salinity from other factors like pH, current speed, and tide). However, Sawyer (2011) also observed settlement in the field during periods of relatively high precipitation that would likely be correlated with low salinity (Figure 13), which suggests that settlement is not necessarily deterred by periods of low salinity.

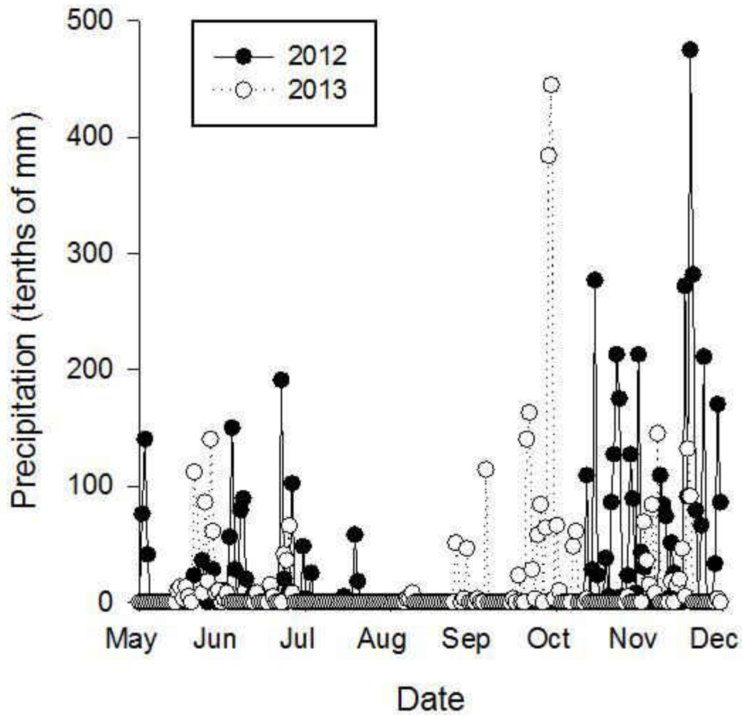

Figure 12. Precipitation in 2012 and 2013. Data from NOAA's National Climatic Data Center North Bend Southwest Oregon Regional Airport

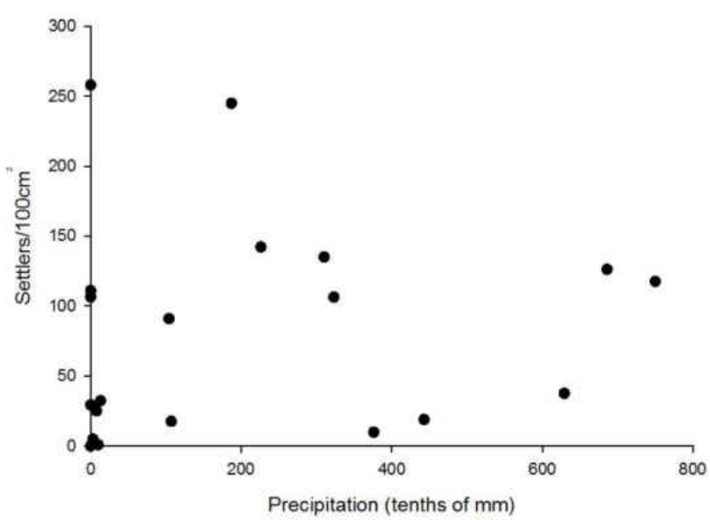

Figure 13. Precipitation vs. recruits, 2010. With data from Sawyer (2011)

Lower salinity has been correlated with poor survival in *O. lurida.* In a laboratory experiment, 100% of adult *O. lurida* died after 49 days at salinities less than 10; 17% died after 49 days at a salinity of 15 (Gibson, 1974). Additionally, a large-scale die-off of adult *O. lurida* in 2006 in San Francisco Bay was attributed to a period of heavy rainfall and decreased salinity (Grosholz et al., 2008). The estuarine distribution of adults of *O. lurida* also suggests that lower salinity is not tolerated by this species, as adults are not generally found at salinities under 20 (Baker et al., 2000). In 2012, in our study, peak settlement occurred during a period with no precipitation, and moderate settlement occurred during a period of moderate precipitation (Figure 14). In 2013, in contrast, peak settlement occurred during a period of moderate precipitation (Figure 15). Whether moderate precipitation (and associated lower salinity) deterred settlement or not, it likely inhibited the survival of newly settled oysters. This shift in peak settlement 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 settlement in 2013.

The high spatial and temporal variability observed in this study is in accordance with observations of populations of *O. lurida* in other estuaries. Larval supply varied in terms of both magnitude and location between years. Settlement magnitude also varied, although the two sites where settlement was greatest were consistently Haynes Inlet and Downtown Coos Bay. Settlement can drain larval supply (Gaines 1985) but because the provenance of these larvae is unknown—were they released at Haynes Inlet, Downtown Coos Bay, Coalbank Slough, or elsewhere?—the effect of settlement as a drain on larval supply here is unknown. Using laser ablation inductively coupled mass spectrometry to match veligers to a place of origin was used successfully in San Diego (Carson, 2010). Perhaps this technique could be used in a future study in Coos Bay.

Because we found high settlement at sites of high adult density, we hypothesize that restoration efforts would best focus on locations where adult densities are already high. Locations without adult oysters or with very few adult oysters should be carefully assessed in terms of larval supply, settlement, estuarine retention time, and temperature before addition of cultch or spat is undertaken.

In addition to providing valuable information for those interested in restoring *O. lurida* in Coos Bay and elsewhere along the west coast of North America, we have also contributed new information to the field of marine invertebrate population dynamics. The majority of such studies focus on barnacles, which have a very different life history than *O. lurida*. *O. lurida* is a brooded, planktotrophic veliger that metamorphoses at settlement and whose dispersal outside of estuaries is limited. As in barnacles, we found that assessing larval abundance separately from settlement provided a more thorough understanding of the factors controlling the adult population of *O. lurida.*

BRIDGE

Chapter II quantified larval supply and settlement and explored the relationship between these two stages in the life cycle of *Ostrea lurida*. Chapter III will measure survival and growth of oysters after settlement. These three stages in the oyster life cycle—larva, settler, and recently metamorphosed juvenile—present three potential bottlenecks to a self-sustaining adult population at any given location. Larvae may not be supplied to an area, as was the case for Empire and Airport; they may arrive but fail to

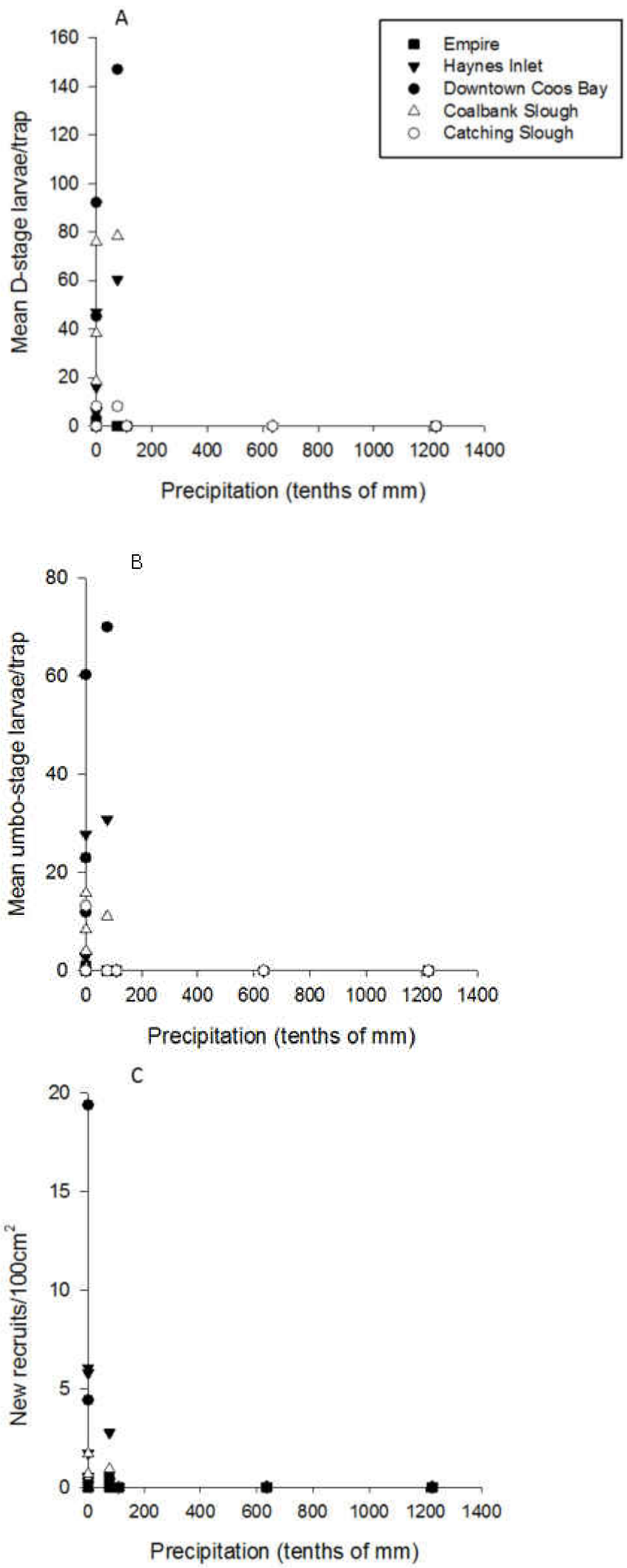

Figure 14. Precipitation vs. A) D-stage larvae, B) umbo-stage larvae, and C) new recruits (adjusted for immersion times). 2012.

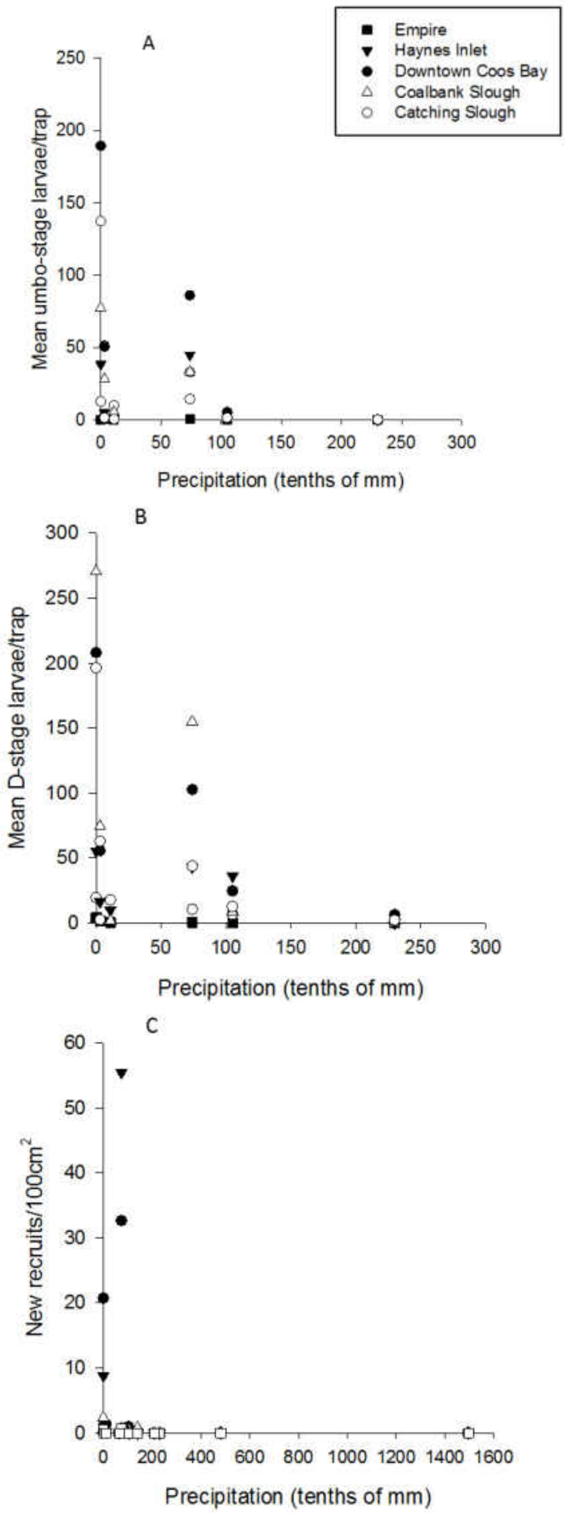

Figure 15. Precipitation vs. A) D-stage larvae, B) umbo-stage larvae, and C) new recruits (adjusted for immersion times). 2013. Larval data in 2013 are missing during the period of peak precipitation.

settle, or die immediately after settlement, as was the case at Catching Slough and, to a degree, Coalbank Slough; or they may arrive, settle, and survive for a period of time, but die before reaching sexual maturity. Oyster mortality and growth was measured during the winter, when oysters pause gametogenesis, and into the spring and summer, when gametogenesis accelerates (Oates 2013).

CHAPTER III

POST-SETTLEMENT PERFORMANCE OF OLYMPIA OYSTERS (*OSTREA LURIDA*) IN COOS BAY, OR

INTRODUCTION

Like many marine invertebrates, the oyster *Ostrea lurida* has a pelagic larval stage and benthic juvenile and adult stages. In its benthic stage, it is sessile: therefore, habitat selection at settlement is a critical factor in the individual's future success (Larsson and Jonsson, 2006). Once an individual has settled, its performance as a juvenile—its survival and growth—determines whether and when it will become a reproductively active member of the population. Settling in an area where conditions are favorable is necessary for oysters to survive the period between settlement and sexual maturity, since very young animals are often more vulnerable to both biotic and abiotic factors (Gosselin, L.A. and Qian, P., 1996, 1997; Griffiths and Gosselin, 2008; Howard and Goldberg, 2001). Furthermore, settling in area where the individual is likely not just to survive but also to grow can determine when the animal reaches sexual maturity. Fast-growing individuals of this species can reproduce within the same season they are born, while slower-growing oysters typically reach sexual maturity the following year (Coe, 1932).

For these reasons, understanding the post-settlement performance of this species is a crucial step in elucidating the determinants of its spatial distribution. Such information is valuable for researchers who hope to restore this species in estuaries on the west coast of North America, where it is native. *O. lurida* has never fully recovered from a period of overharvest in the late 19th century. In Coos Bay, Oregon, an inadvertentlyintroduced population has been growing since at least the 1980's (Baker et al., 2000, see Chapter I). There is considerable interest in encouraging the growth of this population in order to improve the health and biodiversity of the Coos estuary. Additionally, this species is of cultural and economic value (see Chapter I).

Restoration efforts are likely to involve the laying down of shell or rock to act as settlement material (cultch), but choosing locations to place cultch is often the result of guesswork. Recent work suggests that the population of this estuary may be subject to different kinds of bottlenecks at different locations (see Chapter II). This chapter assesses the suitability of some of these locations for potential oyster restoration in terms of post-settler performance by monitoring growth and survival of two different size classes of oyster at two to four locations throughout the Coos estuary over a six-month period.

MATERIALS AND METHODS

Four sites were selected in Coos Bay, Oregon according to the known range of the adult population of *O. lurida*, which is mainly restricted to the mesohaline portion of the upper estuary (Figure 1). Haynes Inlet (43.44070°N, 124.22086°W); Downtown Coos Bay (43.37852°N, 124.21559°W); and Coalbank Slough (43.35590°N, 124.2091°W) were all within the range of the adult oyster and had adult oysters present. Catching Slough (43.36366°N, 124.17705°W), in the upper, fresher part of the estuary near the mouth of the Coos River was outside the range of adults. These four field sites were among the six sites where we also assessed larval supply and settlement of this species (see Chapter II).

Oysters used in this study were taken from spat-collecting shell bags that had been placed under a railroad bridge in Coalbank Slough in the summer of 2010 (S.

Rumrill, *pers. comm.)*. In December 2012, shell bags were removed from Coalbank Slough and sorted. Two size classes of oysters were selected and used: "medium" (17.5-27.5 mm shell height) and "small" (2-7 mm shell height). Height (distance from umbo to the ventral margin of the shell), length (the longest distance on the anterior-posterior axis of the shell, perpendicular to height), and surface area of each oyster was recorded at each sampling interval, but only analyses of length will be reported in order to compare results from this study with other studies that recorded oyster length. The average height of the medium size class was 22.13±0.50 mm (95% CI) and the average length was 21.90±0.85 mm (95% CI). The average height of the small size class was 4.77±0.40 mm (95% CI) and the average length was 4.66±0.45 mm (95% CI).

Once oysters were sorted by size class, individuals were haphazardly selected and bonded with Z-spar epoxy to the smooth underside of unglazed ceramic tiles. Some of the medium and all of the small oysters were attached to shells of other living or dead oysters. In the case of those attached to shells, the shell was epoxied to the tile, and in the case of larger oysters not attached to another shell, the individual itself was epoxied to the tile. Seven to eight medium-size individuals were attached to each of four plates, for a total of 30 at Catching Slough, 30 at Coalbank Slough, 29 at Downtown Coos Bay, and 29 at Haynes Inlet. Fewer small-size individuals were available, so only five individuals were attached to each of four plates, which were outplanted at Haynes Inlet and Coalbank Slough only. Several small individuals on the Haynes Inlet plates were crushed during the epoxy process, so there were only 17 of these individuals at Haynes Inlet as opposed to 20 at Coalbank Slough. Each tile was numbered and each individual identified numerically by marking, with permanent marker, an area of the tile next to the animal.

The tiles were bolted to PVC “T” shaped holders (Seale and Zacherl, 2009), which each held two plates (Figure 2). Each T was 61 cm high, and each arm 30 cm long. The vertical part of the T was reinforced with rebar, which was pounded into the substrate. The T’s were deployed at approximately 35 cm below MLLW, between 0.5 and 1 m apart.

Plates with oysters were placed in the field and sampled four times at four to ten week intervals to follow growth and survival over six months. Oysters were measured with calipers and photographs were taken. In the case of medium-size individuals, the entire plate was photographed; for small-size individuals, a picture was taken of each individual oyster. Plates with attached oysters were placed in the field on January 10, 11, and 12, 2013. Because settlement in Coos Bay occurs in the summer and fall (see Chapter II) the winter is an appropriate time of year to assess post-settlement mortality. Sampling continued every four to six weeks (February 8-10, March 29-30, and April 27-28) until April, after which plates remained in the field but were not assessed again until the study concluded on July 9-10.

On sampling days, oysters were measured and photographed in the field. Mortality was also recorded. An oyster was marked as “dead” if the shell was present but empty, present and gaping, or if only the lower valve was present. It was recorded as “missing” if the oyster itself or the oyster and the shell to which it was bonded were absent from the epoxy, or if the epoxy and the oyster or epoxy and shell were gone. Average oyster size over time was analyzed using size data from all oysters alive at each sampling date; seasonal oyster growth was analyzed using size data only from oysters

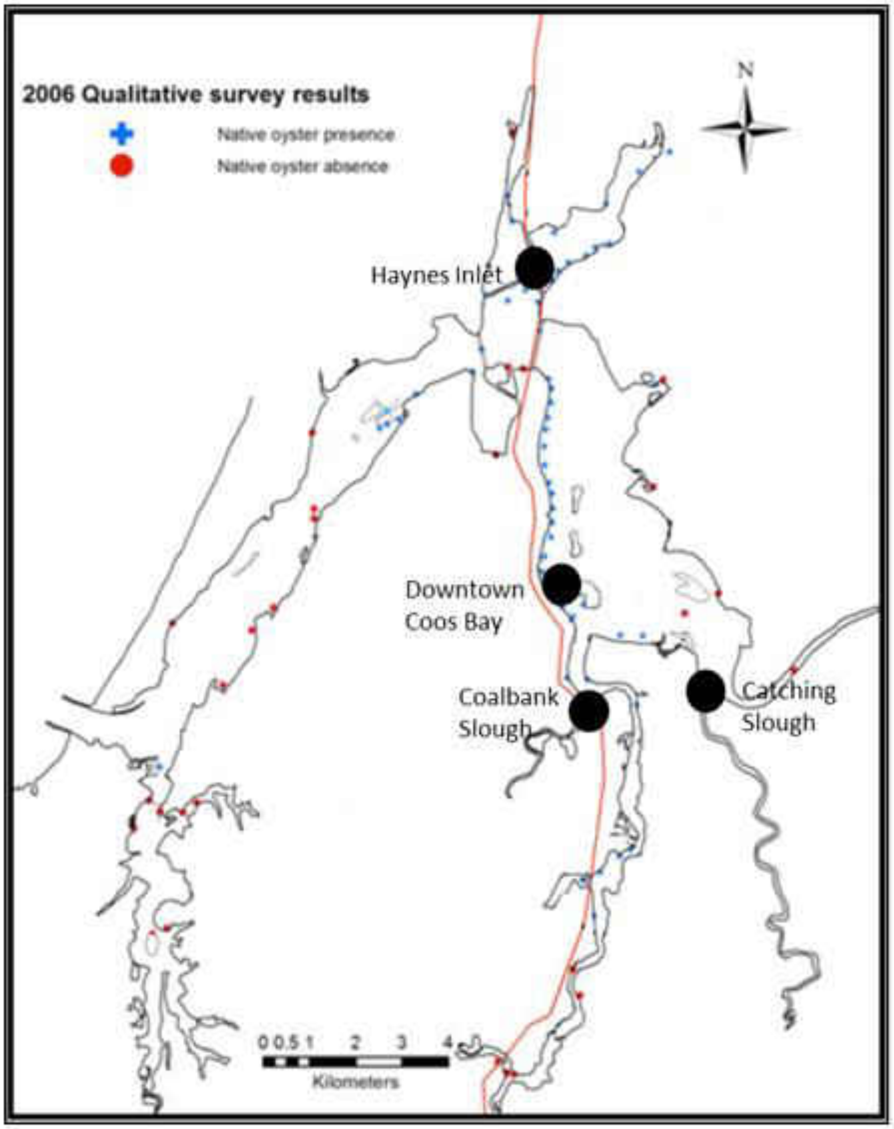

Figure 1. Distribution of adults of *Ostrea lurida* in Coos Bay (adapted from Groth and Rumrill, 2009). Blue dots indicate oyster presence and red dots oyster absence (dots are based on surveys in 2006 as reported in Groth and Rumrill 2009). Black circles indicate sampling sites for the present study. Red line represents US Highway 101.

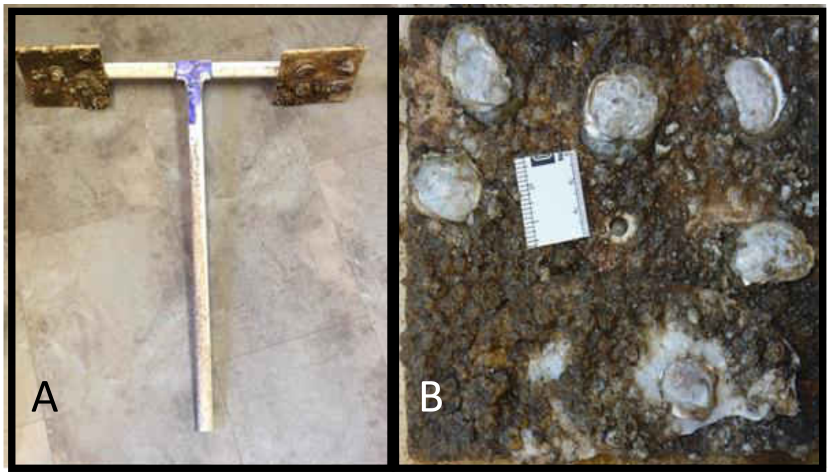

Figure 2. A) PVC "T" with two plates attached.
B) Close-up of plate with oysters attached

alive in July. Growth rates were calculated by finding the difference in length of each individual oyster still alive between the beginning and end of the season in question, or of the total experiment, and dividing that difference by the number of days in that period.

Physical data

HOBO (Onset Computer Corp.) temperature and conductivity loggers (U24-002) recorded temperature and conductivity every ten minutes at each site. Loggers were deployed in a PVC housing drilled with holes to allow water to flow in and out and attached to rebar which was then pounded into the substrate. Loggers were positioned in the housing so that they were approximately even with the plates supported on T's. The average temperature of all ten-minute data points for each week of deployment was calculated and is presented below. All temperature data points are included in this analysis, even during periods when the logger and plates were likely exposed to air. Although these loggers measured salinity, those data are not reported because the loggers were found by the manufacturer to erroneously report salinity when deployed in places like estuaries where salinity fluctuates; these loggers have subsequently been recalled.

HOBO (Onset Computer Corp.) water level data loggers (U20-001-01-Ti) were also employed at each site, although not simultaneously. One logger remained at Haynes Inlet continuously, and the other two were moved from site to site. Loggers recorded pressure every ten minutes. To estimate aerial exposure (emersion) and submersion in water (immersion) times from these data, any data point greater than 102 kPa was considered "immersed" and any data point below 102 kPa was considered "emersed." For each site other than Coalbank Slough, where the logger appears to have malfunctioned, the total time of logger emersion was divided by the total time the loggers recorded in order to get an estimate of proportion of time loggers (and plates) were emersed. At Coalbank Slough, a rough approximation of emersion time was made by comparing estimated tidal height of our equipment with tide heights reported in the program JTides (v 5.2) and counting anything less than our tide height as "emersed" and anything greater as immersed. Emersion values subtracted from 1 are reported as estimates of the time the loggers were immersed.

RESULTS

Temperature

The average weekly temperature at all sites during the winter was similar, with Haynes Inlet tending to be slightly warmer (Figure 3). In the summer, Haynes Inlet and Downtown Coos Bay were of very similar temperature, and Catching Slough was warmer. Data are unavailable for Coalbank Slough after April.

Water level

Proportion of time equipment was emersed, or exposed to air, was similar at Haynes Inlet and Catching Slough (0.017 and 0.015, respectively), slightly larger at Downtown Coos Bay (0.034) and smaller at Coalbank Slough (0.003) (see Table 2, Chapter II).

Survival

On average, less than half of the medium size class oysters on each plate survived to July at Haynes Inlet and Catching Slough, and more than half survived at Coalbank Slough and Downtown Coos Bay (Figure 4A); survival was significantly different among sites ($F=3.491$, $p=0.05$) but Holm-Sidak multiple pairwise comparisons were not powerful enough to identify the source of the difference at $p<0.05$ ($p=0.094$). Average survival was higher at Coalbank Slough than at any other site.

None of the small oysters survived to July. Within the small size class, a large die-off occurred at Coalbank Slough after the February sample date (Figure 4B).

There was no clear relationship between size and mortality within each size class (Figures 5 and 6) except that within the medium size class, the very largest oysters survived every month. Site was not a statistically significant factor in average length at death within the medium size class ($F=0.747$, $p=0.533$) or within the small size class ($F=2.957$, $p=0.097$). Therefore, the lengths at death of oysters pooled from all sites are presented below. “Missing” oysters are treated as a category separate from dead or living.

There was no clear pattern as to the incidence of “missing” oysters either (Figures 5 and 6). Missing individuals could have been removed by predators, or could have fallen

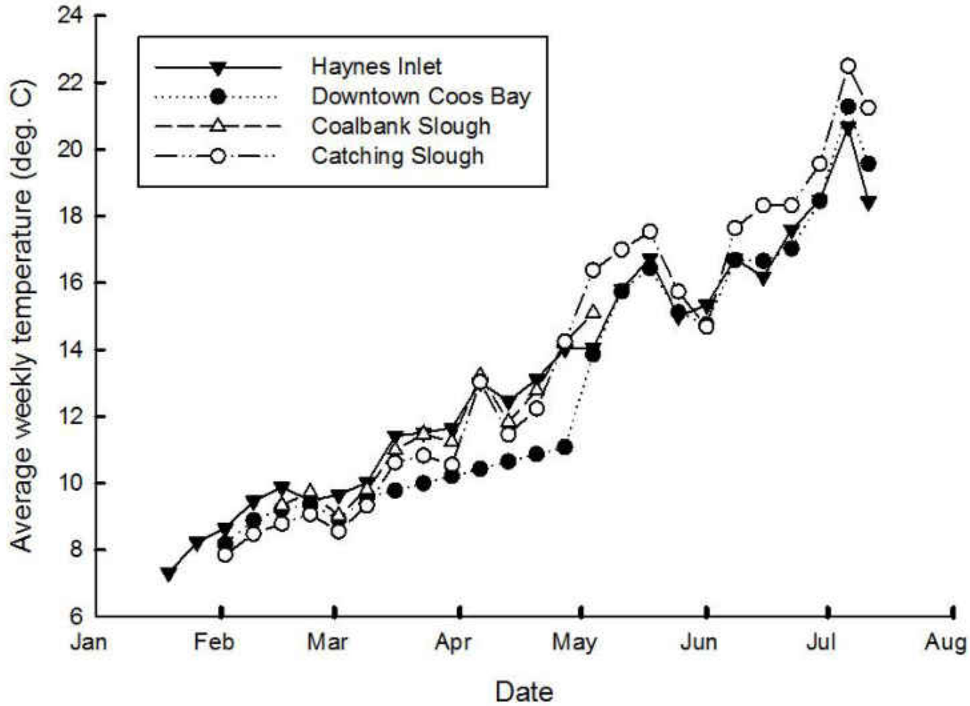

Figure 3. Average weekly temperature, calculated data loggers recorded every ten minutes. Temperature when equipment was likely exposed is included.

from the plate as a result of a failure of the epoxy. No effort was made to locate the missing oysters or the shells to which the oysters were attached, because the individuals would likely have been washed away or buried. The highest incidence of missing oysters occurred at the last measurement date among the small size class at Haynes Inlet.

Growth

By the end of observations in July, medium oysters at Haynes Inlet were larger than oysters at any other site (Figure 7, Table 2). Among the medium oysters, site was a significant factor in oyster growth rate (F=18.339, p<0.001). *O. lurida* at Haynes Inlet grew significantly faster than at any other site (p<0.001 at Catching, p=0.003 at Coalbank, and p=0.005 at Downtown Coos Bay, one-way ANOVA, Tukey pairwise Slough (p=0.05, one-way ANOVA, Tukey pairwise comparison). Within the small size

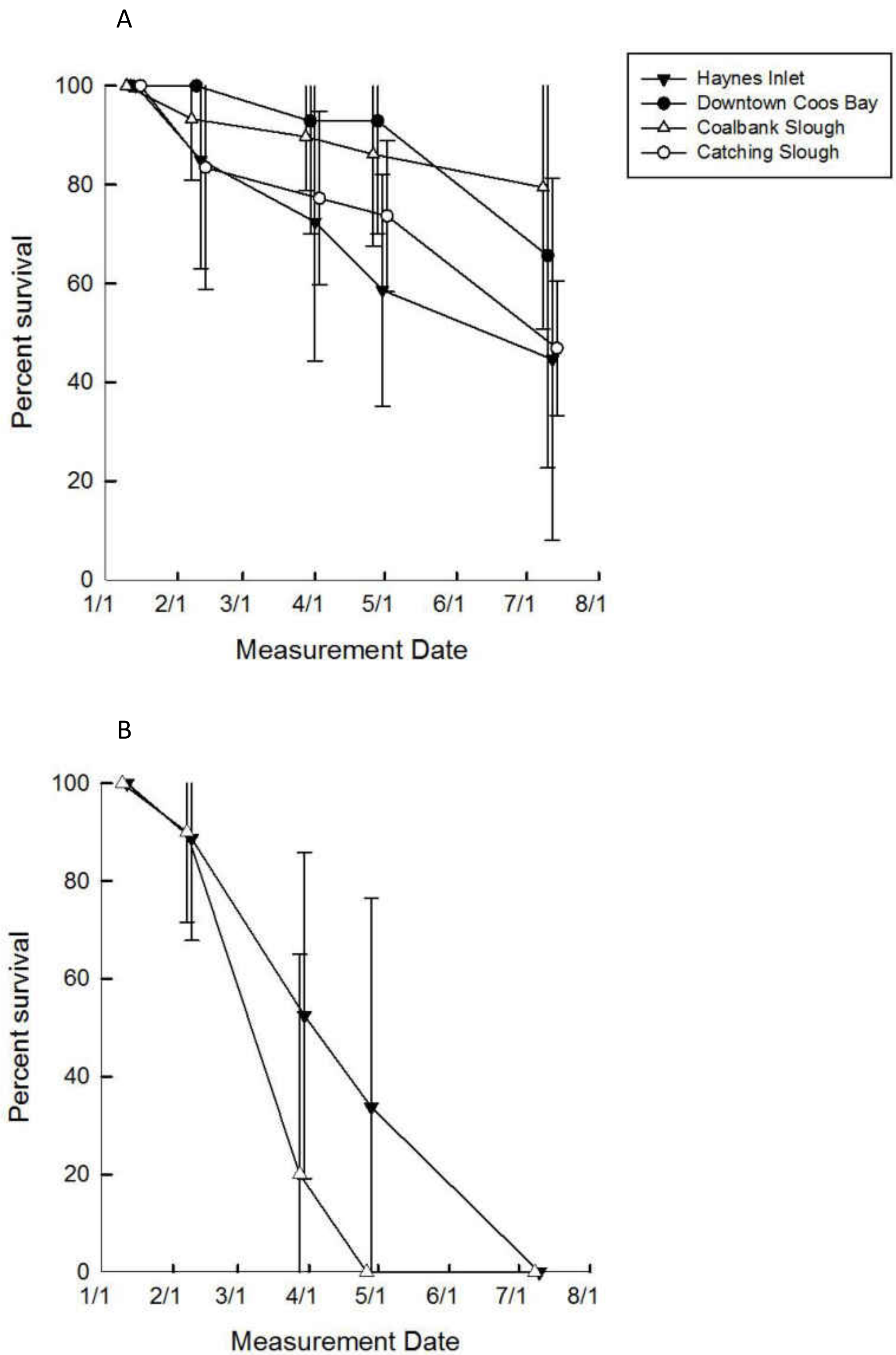

Figure 4. Percent survival per plate of initial group of oysters A) among the medium size class and B) among the small size class. Error bars indicate 95% confidence interval.

comparisons) and those at Downtown grew significantly faster than those at Catching class, comparing growth between Coalbank Slough and Haynes Inlet from January to March (the last date for which growth data is available for both sites) indicated that site was not a significant factor in growth rate (F=0.399, p=0.572).

DISCUSSION

Growth rate, estimated age, and survival of oysters

Growth rates observed in this study (Table 1) are low when compared with growth rates of *O. lurida* observed elsewhere (Deck, 2011; Dinnel et al., 2009; Grosholz et al., 2008; Trimble et al., 2009). It should be noted that some of these estimates come from studies that followed oyster growth over the summer only, when oysters typically grow faster (Sellers 1984). In San Francisco Bay, CA, *O. lurida* grew between 0.03 mm/day and 0.10 mm/day, depending on location within the estuary, when followed for an entire year (Grosholz et al., 2008). In Tomales Bay, CA, a cohort of *O. lurida* in the intertidal (which at the initiation of the study measured, on average, 15 mm length) grew between 0.09 and 0.16 mm/day one summer, and between 0.042 and 0.074 mm/day the next. Again, growth varied with location in the estuary (Deck, 2011).

Another study in Tomales Bay found growth to vary between 0.03 mm/day and 0.3 mm/day (Kimbro et al., 2009) in the summer, depending on location. In Fidalgo Bay, WA, *O. lurida* at initial length 24.8 mm grew 0.05 mm/day between May and November and 0.02 mm/day thereafter (Dinnel et al., 2009). In Willapa Bay, WA, *O. lurida* at initial

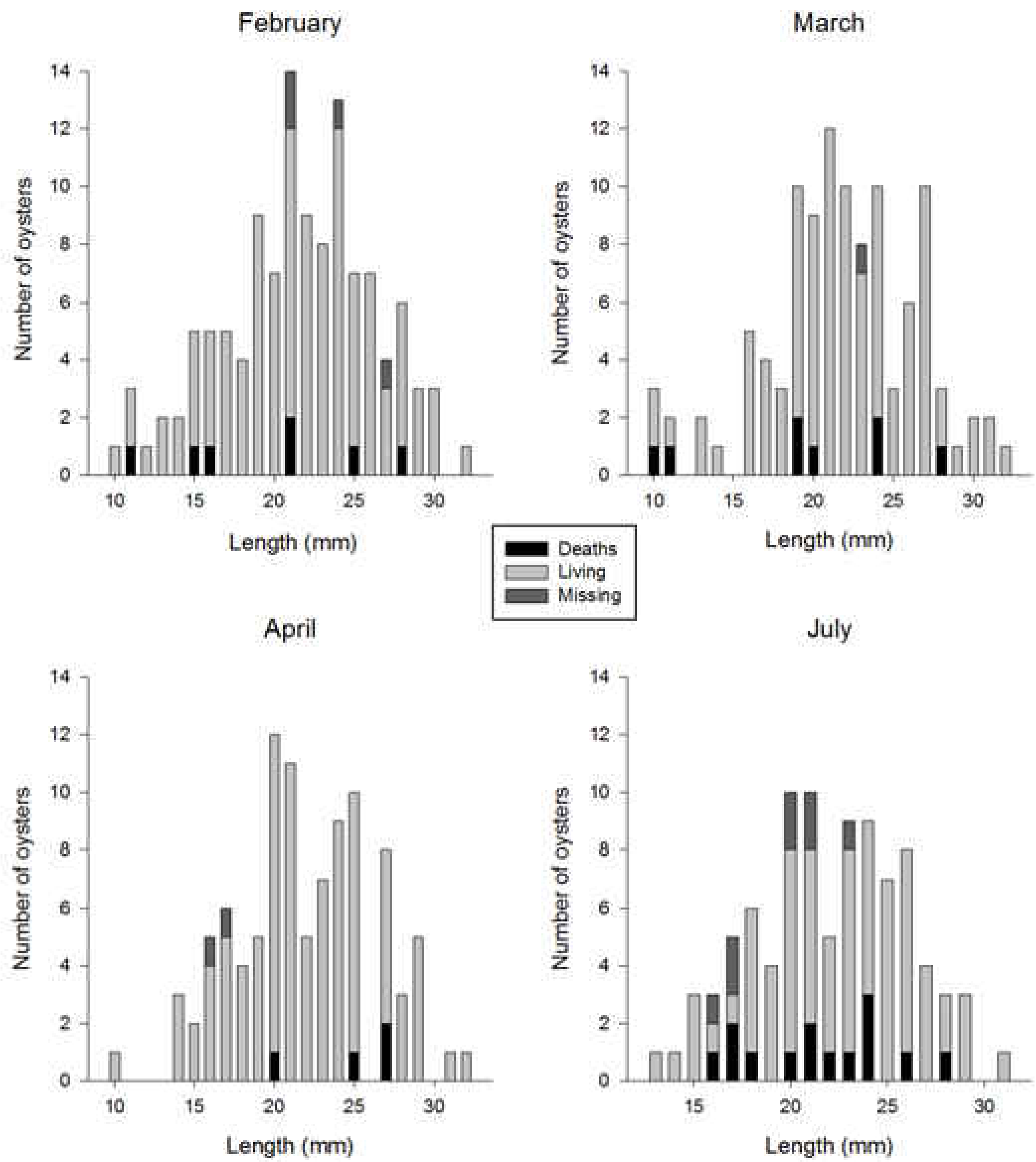

Figure 5. Percentage alive, dead, and missing of each size every month, medium size class oysters only. Sizes are lengths at previous sampling date.

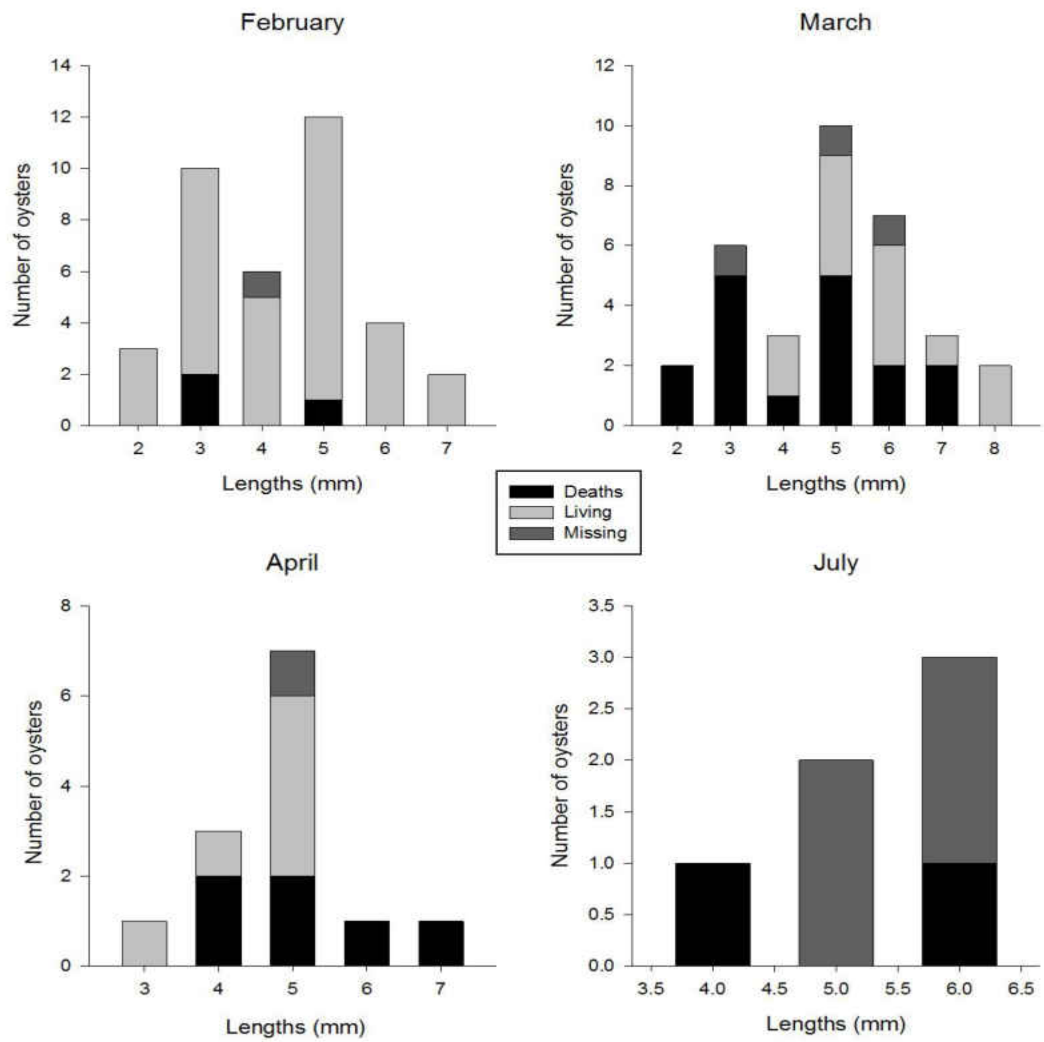

Figure 6. Percentage alive, dead, and missing of each size every month, small size class oysters only. Sizes are lengths at previous sampling date.

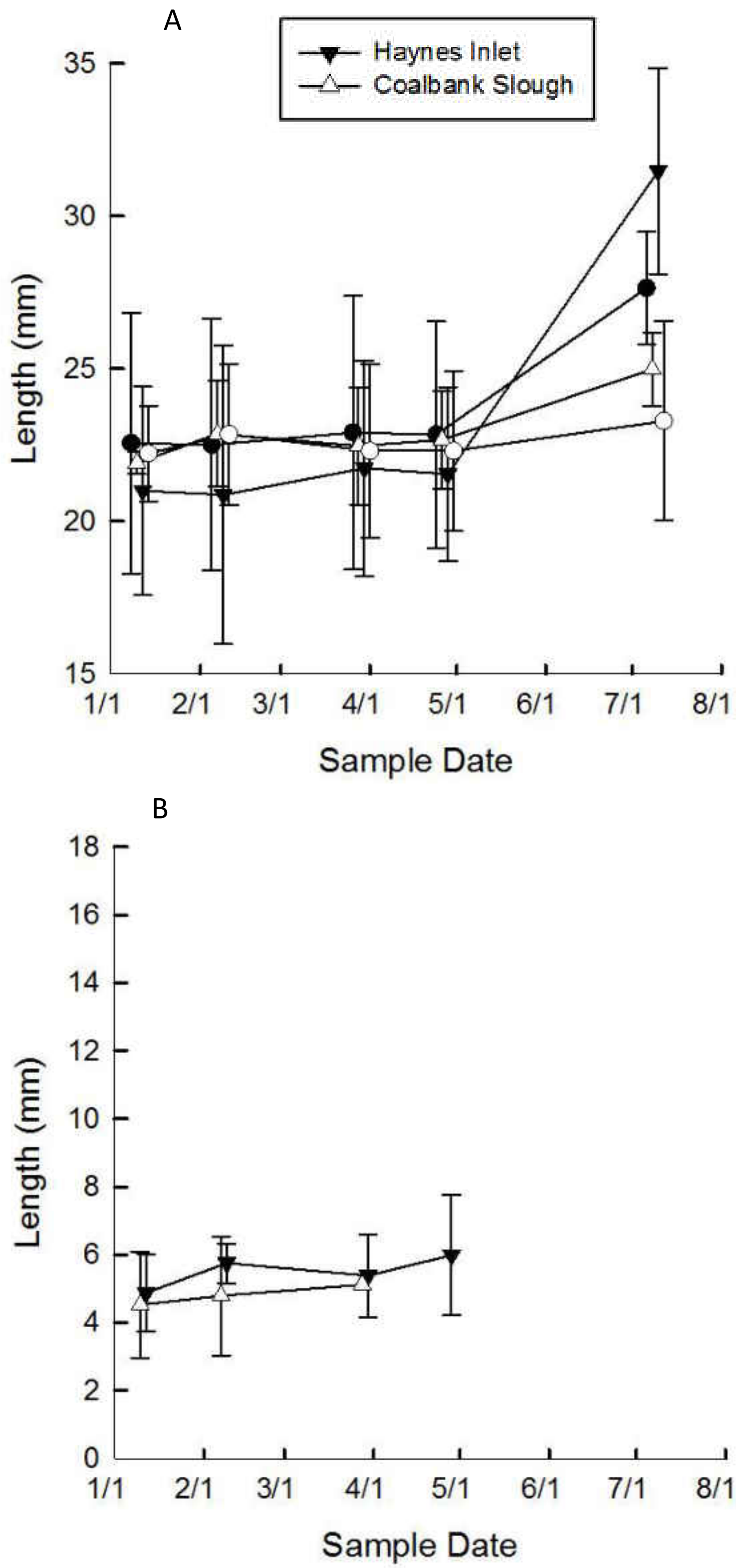

Figure 7. Size of *O. lurida* (average per plate) over time among A) medium oysters and B) small oysters

Table 1. Growth of *O. lurida* in Coos Bay

Site	Size	Total growth (mm ± 95% CI)	Average growth rate, Jan-July (mm ± 95% CI/ day)	Average growth rate, January-April (mm ± 95% CI/ day)	Average growth rate, April-July (mm ± 95% CI/ day)
Haynes Inlet	Medium	9.52 ± 4.09	0.05 ± 0.02	0.003 ± 0.03	0.14 ± 0.03
Downtown Coos Bay	Medium	3.57 ± 4.27	0.02 ± 0.02	-0.008 ± 0.018	0.06 ± 0.04
Coalbank Slough	Medium	3.26 ± 1.09	0.02 ± 0.01	0.01 ± 0.02	0.03 ± 0.03
Catching Slough	Medium	-0.49 ± 1.30	-0.003 ± 0.007	0.01 ± 0.009	0.004 ± 0.02
Haynes Inlet	Small	0.56 ± 0.35	NA	0.005 ± 0.003	N/A
Coalbank Slough	Small	0.0333 ± 7.6217	NA	0.0004 ± 0.1003 (Jan- March)	N/A

length 2 mm grew roughly 0.37 mm/day in late summer and early fall, 0.01 mm/day in the winter, and about 0.08 mm/ day in the spring and early summer (Trimble et al., 2009).To summarize, the range of growth rates of *O. lurida* is 0.01 mm/ day to 0.37 mm/ a day; or, roughly, 0.2 mm /month to 10 mm/month. The lowest positive growth rate we observed in Coos Bay, during the winter, was 0.09 mm/month among medium size oysters and 0.012 mm/month among small size oysters, and the fastest rate, during the spring and early summer, was 4.2 mm/month among medium size oysters. *O. edulis* reaches a shell length of 60 mm in 2-5 years, for an average growth rate of 1-1.67 mm/month (Richardson et al., 1993), although faster growth has been reported (Carlucci et al., 2010). *C. virginica* grows, on average, 1.67 mm/month (Sellers), during the first nine months after setting and *C. gigas* grows 3.33- 4.17 mm/ month during the first year after setting (Pauley et al., 1988) but these studies do not distinguish seasonal growth rates.

The variation in growth rates observed in *O. lurida* is likely due to seasonality, but may also be due to differential growth rate of oysters of different ages. Our study is unique among those cited above in that we followed two size classes of oysters simultaneously, so that the effect of season could be differentiated from the effect of oyster size. Unfortunately, all the small oysters died before the July sampling date, so we can only compare the winter growth rates of these two size classes. Growth rates of medium and small oysters in the winter were not significantly different ($F=0.581$, $p=0.455$) although the test may not have been powerful enough to detect a difference (power of the performed test with $\alpha=0.05$ is 0.048, much less than the desired power of 0.8). Given the attenuation of growth with age seen in other bivalve species, one would expect the growth rate of very young oysters to grow faster than older oysters (Gaspar et al., 1999; Hall Jr. et al., 1974; Jones et al., 1978; Roegner and Mann, 1995; Tanabe, 1988). It should be noted, however, that a San Francisco Bay survey found that growth rate did not vary with size of *O. lurida* (Grosholz et al., 2008).

It seems likely that growth among the small oysters would have accelerated in the summer months. Estimating oyster age using the winter and summer growth rates supports this hypothesis. The oysters used in this study originally settled and grew in Coalbank Slough. Settlement at that site in 2012 occurred from early August through mid-September, so the young-of-the-year here would have been four or five months old. Using the summer growth rate observed in medium oysters at Coalbank Slough (0.03 mm/day), the average small oyster (length 4.66 mm) would have been just over four months old at the time of collection in December 2012. However, using the winter growth rate of 0.01 mm/day, the same oyster would have been just over 15 months old. It is unlikely that an individual of *O. lurida* would reach only 4.66 mm in over a year: in one year, young-of-the-year *O. lurida* in Washington grew to 30 mm (Dinnel et al., 2009).

Using the overall average growth rate observed in the medium size oysters at Coalbank Slough of 0.02 mm/day, the average oyster in the medium size class (length 21.9 mm) would have been 3 years old in December of 2012. However, no oyster used in this study could have been more than 2.5 years old, as the spat-collecting shell bags were first deployed in the summer of 2010. Therefore, growth at this site may vary between years, or these oysters may slow down growth, at least in terms of shell accumulation, as they age. Future studies should compare small, medium, and very large oysters simultaneously to find the effect of age on growth rate.

Size class did affect survival, although only when comparing medium and small oysters. Survival was clearly higher among oysters in the medium size class than among those in the small size class, which is consistent with previous findings (Grosholz et al., 2008) (Figure 4). However, we did not find evidence for size-dependent mortality within these size classes.

Growth and survival variation among sites

We observed significantly different survival and growth of *O. lurida* on a relatively small spatial scale, which has been the case for researchers working in other estuaries (Deck 2011; Grosholz et al., 2008; Kimbro et al., 2009; Trimble et al., 2009). These researchers have offered a variety of explanations as to why oysters in one part of the estuary fare better or worse than those in another part of the same estuary, including chlorophyll concentration, temperature, aerial exposure, presence of the invasive oyster drill *Urosalpinx cinerea*, predation, and competition for space.

Concentration and delivery of nutrients can affect oyster growth (Kimbro *et al.,* 2009). Chlorophyll-*a* data from Coos Bay in 2012 show that concentration of nutrients can vary within this estuary: chl-*a* was higher at Coalbank Slough than at Haynes Inlet in the spring but lower in the fall (Oates 2013). Current speeds, too, may have differed at our study sites, which can affect oyster filtration rates; faster current has been associated with higher filtration rate and better growth (Walne, 1972). Currents at our Haynes Inlet study site are faster than at any other site, which may be a factor in the higher growth seen at Haynes Inlet (Coast & Harbor Engineering technical report, 2010).

Temperature was very similar at all sites during the summer, when oysters grew most, so the significant growth advantage observed at Haynes Inlet is likely due to another factor.

While the invasive oyster drill *U. cinerea* has not been reported in Coos Bay (McLean, 2007, Groth, S. *pers. comm.*) there are certainly other potential predators in this estuary, including crabs, sea stars, and carnivorous snails (Baker et al., 2000; Harper, 1991; Koeppel 2011; Pineda, 1994). Oysters occupying the fresher portions of the upper estuary may have an advantage in terms of decreased predation pressure, since many of these species are intolerant of brackish conditions and occupy the lower portion of the bay (Gunter, 1955; Shanks and Butler, 2013). During periods of high precipitation, which typically occur during the fall and winter on the Oregon coast, salinity in Coos Bay decreases dramatically; in fact, a transect in January of 2013 found salinity to be as low as 5 near the mouth of Coalbank Slough (O'Neill, M. *unpublished*). In *Crassostrea virginica*, growth rate slowed at lower salinity but mortality was not significantly different between young and old oysters at low salinity (Loosanoff 1952).

According to pressure data collected by water level loggers, oysters were likely exposed to air for very similar amounts of time at each site; the greatest amount of aerial exposure occurred at Downtown Coos Bay, where oysters were exposed to air 2% more often at any other site. Longer immersion time led to faster growth in *O. lurida* in Tomales Bay (Deck, 2011) as well as in *C. virginica* in Virginia (Bartol et al., 1999; Roegner and Mann, 1995), and in *C. gigas* in Australia (Sumner, 1981), and anecdotal evidence of commercial oyster growers suggests that oysters fare better in man-made dikes than in the intertidal (Matthiessen, 1970). A difference in immersion times might also explain a difference in survival, as aerial exposure is a known cause of oyster mortality (Roegner and Mann, 1995; Trimble et al., 2009). Whether or not a 2% increase in aerial exposure time is enough to affect growth rate or survival is unclear. Oysters at this site grew and survived relatively well, but perhaps they would have grown and survived even better if submerged more often. According to our estimate, oysters at Coalbank Slough were exposed to air the least; perhaps this explains the relatively high survival among medium size oysters at this site, although growth here was poor. The effect of immersion time on growth is not always consistent, however: *O. lurida* in Washington grew slower when immersed longer, which the authors suggest was due to increased competition from fouling organisms (Trimble et al., 2009), and *Crassostrea rhizophorae* in Jamaica grew equally well subtidally and intertidally (Littlewood, 1988).

Deck (2011) found that competition from other members of the fouling community reduced growth of *O. lurida* in Tomales Bay. While the fouling community on these plates was not quantified, we noticed differences among sites in the communities present. Both Haynes Inlet and Downtown Coos Bay plates were dominated by barnacles and, in the summer, hydroids; Coalbank Slough plates also collected barnacles, but generally had fewer hydroids and for a shorter period of time; Catching Slough plates tended to be relatively bare.

A variety of factors may explain the growth and survivorship of *O. lurida* we observed in Coos Bay. As in other estuaries, temperature, salinity, immersion time, predation, and current speed are all possible contributors. While survival was highest within medium size oysters at Coalbank Slough, survival within small oysters was poor, and growth in both size classes was mediocre; therefore, we do not recommend Coalbank Slough as a restoration site. Survival at Haynes Inlet was fairly low, but oysters grew well here. Haynes Inlet may be a suitable restoration site for *O. lurida*. Oysters at Downtown Coos Bay grew and survived fairly well despite experiencing slightly longer aerial exposure times, which suggests that Downtown Coos Bay is also a suitable restoration site. Lastly, Catching Slough oysters did not survive or grow particularly well, making it an unsuitable site for restoration.

CHAPTER IV

GENERAL CONCLUSION

The main goal of this thesis was to assess the suitability of different locations within the Coos estuary as potential restoration sites for the Olympia oyster, *O. lurida*. Although this is a fairly specific goal, our results can help inform restoration efforts in other estuaries; they also contribute to the fields of reproductive biology of *O. lurida* and marine invertebrate population dynamics.

Recommendations for restoration of *O. lurida* in Coos Bay

On average, medium size oysters were most likely to survive the winter at Coalbank Slough than at any other site. High survival within medium oysters at Coalbank Slough was unexpected because several other measures of oyster health and reproductive success indicate that this is not an area where oysters thrive: small oysters did not survive the winter here, growth was relatively low (Chapter III), settlement was low (Chapter II), and adult oysters in 2012 had a lower condition index here than those at Haynes Inlet (Oates 2013.) However, this was the source of the oysters used in the growth and survival study (Chapter III). Also, these oysters were exposed to air less often than at any other site, which is a confounding factor that could explain increased survival within the medium size class here. Still, adult oysters are present in Coalbank Slough, so perhaps higher survival (of oysters that survive their first winter) accounts for their presence here more than any other factor. Coalbank Slough is not recommended as a restoration site in Coos Bay, although adults of *O. lurida* are abundant nearby, under the Isthmus Slough Bridge. Researchers intent on restoring the oyster population in this area might choose to focus on the location under the Isthmus Slough Bridge and not on the location under the Coalbank Slough Bridge.

Oysters survived relatively well and grew relatively fast at Downtown Coos Bay, where the adult population of *O. lurida* was more dense that at any other site surveyed in both 1996-1997 and 2006 (Baker et al., 2000; Groth and Rumrill, 2009). Slightly increased aerial exposure time at this site may be a confounding factor, although if anything increased exposure time would likely decrease survival and growth rate. Additionally, larvae at this site were abundant and settlement was high. The density of adults at this site could be attributed to relatively high survival and growth as well as high larval supply and settlement, but could also be attributed to more available substrate for settlement. Downtown Coos Bay is recommended as a restoration site.

Oysters at Catching Slough grew slowly and survived moderately well. Catching Slough is outside the range of the adult oyster and close to the mouth of the Coos River, so it was not expected to be an area where oysters thrive. Larval supply to this site was relatively high, but settlement was very low. Because our measurement of settlement excluded any settlers that died within a two-week period, "low settlement" could include both lack of settlement and high early post-settlement mortality. We have no information about survival of young oysters at this site because we did not deploy small oysters here. Therefore, the barrier to success of *O. lurida* at this site is likely low settlement success, high post-settlement mortality, or a combination of the two. Regardless, Catching Slough is not recommended as a restoration site.

Medium size oysters outplanted at Haynes Inlet were less likely to survive than at any other site and small size oysters did not survive the winter here; however, growth at this site was significantly faster than at any other site. Oysters were less dense here than at Downtown Coos Bay (Baker et al., 2000; Groth and Rumrill, 2009); this is likely due to a combination of moderately high larval supply and settlement, mediocre survival, and possibly, fast growth. Haynes Inlet is recommended as a restoration site.

Comparison with other estuaries

O. lurida is not well-studied compared with other marine invertebrates of the Pacific Northwest and with other, more commercial, oyster species. Our results are in agreement with observations of settlement timing in other estuaries, but we saw somewhat higher peak settlement densities. We also observed settlement variability on both spatial and temporal scales and a reproductive failure year, as has been the case in other estuaries.

Comparison with other assessments of population bottlenecks

We found that larval supply restricted the population to the adult range and settlement restricted the population further to areas where adult density is high. Growth appeared to accentuate this pattern, although the effect of survival was less clear. Therefore, within the range of the adult oyster, settlement was the bottleneck that restricted the population to certain sites. A similar finding was reported in barnacles in the Atlantic (Jenkins, 2005). We also found that precipitation could disrupt the relationship between larval supply and settlement, so larval supply should not be used as a proxy for settlement, as cautioned by other researchers (Pineda 2000, Yoshioka 1986).

General recommendations for restoration of *O. lurida* and future studies

In Chapter II, we found that larval supply restricts *O. lurida* to the upper part of the Coos estuary, while settlement success controls the population within that range. Therefore, it is reasonable to hypothesize that in general, areas of high adult density are more likely to be successful restoration sites than areas lacking adults or with low adult density. Efforts to seed oysters or add cultch to an area where no or few adult oysters are present should be preceded by careful assessment of existing larval supply and settlement, as well as an understanding of the hydrodynamics of the region that might influence larval retention. While the relation of temperature and salinity to settlement success (or to growth and survival, see below) is unclear, water temperature at a potential restoration site should exceed the local spawning threshold with some frequency so that spawning can occur.

In Chapter III, we confirmed the results of other researchers in terms of the seasonality of oyster growth and the higher mortality of very young oysters. We also found that oysters grew faster in the summer at the sites where adult density was the highest, accentuating the pattern dictated by larval supply and settlement. Again, these results indicate that restoration efforts are more likely to succeed at sites where adult density is higher. Furthermore, we recommend that those interested in comparing oyster growth rates should follow oysters in the summer, as growth in the winter was negligible; or if oysters are followed over a year, growth data should be collected at least once a season to accurately assess oyster growth patterns. We also recommend that because mortality of very young oysters was high, those interested in following such a cohort should use a large sample size.

APPENDIX A

COLLECTION DATES AND COUNTS OF LARVAE AND RECRUITS

Site	Year	Date collected	Mean D-stage larvae per trap (±95% CI)	Mean D-stage larvae per trap/prop of time submerged (±95% CI)	Mean umbo-stage larvae per trap (±95% CI)	Mean umbo-stage larvae per trap/ prop of time submerged (±95% CI)	Mean recruits per 100 cm² (±95% CI)	Mean recruits per 100 cm² / prop of time submerged (±95% CI)
Empire	2012	8/3	0	0	0	0	0	0.0
Empire	2012	8/18	1.3±1.7	1.3±1.7	0.3±0.7	0.3±0.7	0	0.0
Empire	2012	8/30	1.5±1.1	1.5±1.1	0	0.0±0.0	0	0.0
Empire	2012	9/15	1±2	1.0±2	1±2	1±2	0	0.0
Empire	2012	9/29	0	0	0	0	0	0.0
Empire	2012	10/14	0	0	0	0	0	0.0
Empire	2012	10/29	0	0	0	0	0	0.0
Haynes Inlet	2012	8/2	59.3±10.5	60.3±10.7	30.3±6.2	30.8±6.3	2.71±0.85	2.8±0.9
Haynes Inlet	2012	8/16	46±9.9	46.8±10.1	27.3±6.8	27.8±6.9	5.95±1.20	6.1±1.2
Haynes Inlet	2012	8/29	15.8±11.4	16.1±11.6	3±2	3.1±2	5.69±2.10	5.8±2.1
Haynes Inlet	2012	9/13	6.7±7.9	6.8±8.0	2.7±2.8	2.7±2.8	1.68±0.93	1.7±0.9
Haynes Inlet	2012	9/30	0	0	0	0	0.52±0.38	0.5±0.4

Haynes Inlet	2012	10/13	0	0	0	0	0	0.0
Haynes Inlet	2012	10/30	0	0	0	0	0	0.0
Haynes Inlet	2012	11/15	0	0	0	0	0	0.0
Downtown Coos Bay	2012	8/2	142±28.4	147±29.4	67.7±7.7	70.1±8	0.39±0.53	0.4±0.5
Downtown Coos Bay	2012	8/19	89±39.8	92.1±41.2	58.3±18.7	60.4±19.4	19.52±6.00	20.2±6.2
Downtown Coos Bay	2012	8/30	43.7±12.2	45.2±12.6	23±5.2	23±5.4	18.74±7.07	19.4±7.3
Downtown Coos Bay	2012	9/15	6.8±3.3	7.0±3.4	11.5±2.9	11.9±3	4.27±1.85	4.4±1.9
Downtown Coos Bay	2012	10/1	3±2	3.1±2.1	0	0	0.39±0.37	0.4±0.4
Downtown Coos Bay	2012	10/14	0	0	0	0	0	0.0
Downtown Coos Bay	2012	10/29	0	0	0	0	0	0.0
Downtown Coos Bay	2012	11/14	0	0	0	0	0	0.0
Coalbank Slough	2012	8/3	78±35.3	78.2±35.4	11±4.1	11±4.1	0.9±0.81	0.9±0.8
Coalbank Slough	2012	8/18	75.7±17.4	75.9±17.5	15.7±4.6	15.7±4.6	0.39±0.37	0.4±0.4
Coalbank Slough	2012	8/30	38±13.1	38.1±13.1	8.3±4.6	8.3±4.6	1.68±1.75	1.7±1.8
Coalbank Slough	2012	9/13	18.5±8.7	18.6±8.7	4±2.9	4±2.9	0.65±0.76	0.7±0.8

Coalbank Slough	2012	9/30	0	0	0.5±1	0.5±1	0	0
Coalbank Slough	2012	10/13	0	0	0	0	0	0
Coalbank Slough	2012	10/30	0	0	0	0	0	0
Coalbank Slough	2012	11/14	0	0	0	0	0	0
Catching Slough	2012	8/2	8 (n=1)	8.1±0	0	0	0.52±0.38	0.5±0.4
Catching Slough	2012	8/30	N/A	NA	N/A	NA	0.13±0.25	0.1±0.3
Catching Slough	2012	9/14	8±2.3	8.1±2.3	13±3.7	13.2±3.8	0	0.0
Catching Slough	2012	9/29	0	0	0	0	0	0.0
Catching Slough	2012	10/14	0	0	0	0	0	0.0
Catching Slough	2012	10/29	0	0	0	0	0	0.0
Catching Slough	2012	11/14	0	0	0	0	0	0.0
Empire	2013	6/10	0	0	0	0	0	0.0
Empire	2013	6/24	0	0	0	0	0	0.0
Empire	2013	7/9	0.3±0.7	0.3±0.7	0.7±0.7	0.7±0.7	0	0.0
Empire	2013	7/23	4±2	4.0±2	0	0	0	0.0
Empire	2013	8/7	1.3±1.3	1.3±1.3	0.7.±0.7	0.7±0.7	0	0.0
Empire	2013	8/19	0.3±0.7	0.30±0.7	0	0	0	0.0
Empire	2013	10/8	N/A	N/A	N/A	NA	0	0.0
Empire	2013	10/21	N/A	N/A	N/A	NA	0	0.0

Empire	2013	11/5	N/A	N/A	N/A	NA	0	0.0
Empire	2013	11/19	N/A	N/A	N/A	NA	0	0.0
Airport	2013	6/9	0	0	0	0	0	0.0
Airport	2013	6/23	6.3±0.7	6.4±0.7	1.3±0.7	1.3±0.7	0	0.0
Airport	2013	7/8	10.3±7.9	10.5±8	14±3.4	14.2±3.5	0	0.0
Airport	2013	7/22	19±6.8	19.3±6.9	12.3±1.3	12.5±1.3	0	0.0
Airport	2013	8/6	2.3±2.8	2.3±2.8	1.3±1.7	1.3±1.7	0	0.0
Airport	2013	8/18	0.3±0.7	0.30±0.7	0.3±0.7	0.3±0.7	0	0.0
Airport	2013	9/4	N/A	N/A	N/A	NA	0	0.0
Airport	2013	9/17	N/A	N/A	N/A	NA	0	0.0
Airport	2013	10/7	N/A	N/A	N/A	NA	0	0.0
Airport	2013	11/18	N/A	N/A	N/A	NA	0	0.0
Haynes Inlet	2013	6/8	0	0	0	0	0	0.0
Haynes Inlet	2013	6/24	35.3±12.1	35.9±12.3	3.3±1.7	3.4±1.7	0	0.0
Haynes Inlet	2013	7/9	42±43.1	42.7±43.8	44±49	44.8±49.8	54.54±19.28	55.5±19.6
Haynes Inlet	2013	7/23	54.3±44.1	55.2±44.9	37.7±35	38.4±35.6	8.66±2.39	8.8±2.4
Haynes Inlet	2013	8/5	16±3.9	16.3±4.0	4.7±1.7	4.8±1.7	0.52±0.54	0.5±0.5
Haynes Inlet	2013	8/19	9.7±4.7	9.9±4.8	0.7±0.7	0.7±0.7	0.13±0.25	0.1±0.3
Haynes Inlet	2013	9/5	N/A	N/A	N/A	NA	0.13±0.37	0.1±0.4
Haynes Inlet	2013	9/18	N/A	N/A	N/A	NA	0	0.0
Haynes Inlet	2013	10/8	N/A	N/A	N/A	NA	0	0.0
Haynes Inlet	2013	10/21	N/A	N/A	N/A	NA	0	0.0

Haynes Inlet	2013	11/5	N/A	N/A	N/A	NA	0	0.0
Haynes Inlet	2013	11/19	N/A	N/A	N/A	NA	0	0.0
Downtown Coos Bay	2013	6/9	6±2	6.2±2.1	0	0	0	0.0
Downtown Coos Bay	2013	6/24	23.7±11.4	24.5±11.8	5±3	5.2±3.1	0	0.0
Downtown Coos Bay	2013	7/10	99±5.9	102.5±6.1	83±15.6	85.9±16.1	31.54±8.9	32.7±9.2
Downtown Coos Bay	2013	7/22	201±15.3	208.1±15.8	183±28.9	189.4±29.9	20.03±4.48	20.7±4.6
Downtown Coos Bay	2013	8/7	53.7±16.5	55.6±17.1	48.7±11	50.4±11.4	1.16±0.97	1.2±1.0
Downtown Coos Bay	2013	8/18	0.7±1.3	0.7±1.3	0.7±1.3	0.7±1.3	1.29±0.74	1.3±0.8
Downtown Coos Bay	2013	9/4	N/A	N/A	N/A	NA	0.9±1.04	0.9±1.1
Downtown Coos Bay	2013	9/17	N/A	N/A	N/A	NA	0.26±0.51	0.3±0.5
Downtown Coos Bay	2013	10/7	N/A	N/A	N/A	NA	0	0.0±0.0
Downtown Coos Bay	2013	10/20	N/A	N/A	N/A	NA	0	0.0±0.0
Downtown Coos Bay	2013	11/4	N/A	N/A	N/A	NA	0	0.0±0.0
Downtown Coos Bay	2013	11/18	N/A	N/A	N/A	NA	0	0.0±0.0
Coalbank Slough	2013	6/8	1.5±2.9	1.5±2.9	0	0	0	0.0

Coalbank Slough	2013	6/24	8±3.9	8±3.9	0	0	0.37±0.25	0.4±0.3
Coalbank Slough	2013	7/10	154.3±17.6	154.8±17.7	33±10.8	33.1±10.8	0.73±0.51	0.7±0.5
Coalbank Slough	2013	7/23	269.7±116.4	270.5±116.8	77±27.5	77.2±27.6	2.37±1.64	2.4±1.6
Coalbank Slough	2013	8/6	74±16	74.2±16	28±7.8	28.1±7.8	0.37±0.25	0.4±0.3
Coalbank Slough	2013	8/19	12±4.5	12±4.5	5.3±0.7	5.3±0.7	0.48±0.33	0.5±0.3
Coalbank Slough	2013	9/5	N/A	N/A	N/A	NA	0	0.0
Coalbank Slough	2013	9/18	N/A	N/A	N/A	NA	0.77±0.53	0.8±0.5
Coalbank Slough	2013	10/8	N/A	N/A	N/A	NA	0	0.0
Coalbank Slough	2013	10/21	N/A	N/A	N/A	NA	0	0.0
Coalbank Slough	2013	11/5	N/A	N/A	N/A	NA	0	0.0
Coalbank Slough	2013	11/18	N/A	N/A	N/A	NA	0	0.0
Catching Slough	2013	6/9	2±2	2.0±2	0	0	0	0.0±0.0
Catching Slough	2013	6/23	12.3±7.5	12.5±7.6	2.3±2.6	2.3±2.6	0	0.0±0.0
Catching Slough	2013	7/8	43±24.5	43.7±24.9	32.2±25.7	32.7±26.1	0.65±0.66	0.7±0.7
Catching Slough	2013	7/22	193.3±22.4	196.2±22.7	135.3±17.5	137.4±17.8	0.52±0.38	0.5±0.4

Catching Slough	2013	8/5	61.7±20	62.6±20.3	50.3±10.1	51.1±10.3	0	0.0±0.0
Catching Slough	2013	8/18	17.3±8.3	17.6±8.4	9.7±1.7	9.8±1.7	0	0.0±0.0
Catching Slough	2013	9/4	N/A	N/A	N/A	NA	0	0.0±0.0
Catching Slough	2013	9/18	N/A	N/A	N/A	NA	0	0.0±0.0
Catching Slough	2013	10/7	N/A	N/A	N/A	NA	0	0.0±0.0
Catching Slough	2013	10/20	N/A	N/A	N/A	NA	0	0.0±0.0
Catching Slough	2013	11/4	N/A	N/A	N/A	NA	0	0.0±0.0
Catching Slough	2013	11/18	N/A	N/A	N/A	NA	0	0.0±0.0

APPENDIX B

ENVIRONMENTAL PARAMETERS

			Minimum Temperature (°C)	Mean Temperature (°C)	Max temperature (°C)	Mean Daily Range Temperature (°C)	Minimum Salinity (°C)	Mean Salinity (°C)	Max Salinity (°C)	Mean Daily Range Salinity (°C)
2012	Haynes Inlet	7/20/2002	14.47	17.30	19.95	4.07	21.98	23.39	24.98	1.44
2012	Haynes Inlet	8/3/2016	14.59	17.53	20.25	3.95	22.01	23.12	24.20	4.30
2012	Haynes Inlet	8/17/2029	13.41	16.82	19.83	3.71	17.88	21.16	24.35	2.49
2012	Haynes Inlet	8/30/2013	9.25	12.40	17.23	4.17	16.75	17.31	18.29	1.31
2012	Haynes Inlet	9/14/1930	7.74	14.86	17.96	5.32	22.92	24.00	25.03	1.29
2012	Haynes Inlet	10/1/2013	8.41	14.13	16.04	2.67	23.51	24.31	24.94	0.90
2012	Haynes Inlet	10/14/1930	8.83	13.15	16.82	2.76	10.23	22.56	24.92	3.83
2012	Haynes Inlet	10/31/2015	7.28	12.77	15.27	1.78	10.16	19.54	23.35	5.42
2013	Haynes Inlet	5/25/2008	8.38	15.90	19.87	4.03	8.50	19.70	23.02	6.46
2013	Haynes Inlet	6/9/2024	12.03	16.99	21.09	4.62	19.24	21.36	23.35	2.80
2013	Haynes Inlet	6/25/2009	15.65	19.62	23.85	4.23	19.54	21.20	23.23	2.29
2013	Haynes Inlet	7/10/2023	13.10	17.28	20.15	4.66	21.48	22.92	24.96	2.04

2013	Haynes Inlet	7/24/2005	13.23	17.15	20.75	4.13	22.17	23.36	24.98	1.69
2013	Haynes Inlet	8/6/2019	15.16	18.28	22.46	4.13	21.77	23.04	24.20	1.53
2013	Haynes Inlet	8/20/2005	14.66	19.11	22.57	3.40	16.81	19.38	24.35	1.20
2013	Haynes Inlet	9/6/2018	14.29	19.48	23.88	3.34	16.75	17.24	17.76	0.55
2013	Haynes Inlet	9/19/2008	No data	No data	No data	No data	No data	No data	No data	No data
2013	Haynes Inlet	10/9/2021	No data	No data	No data	No data	No data	No data	No data	No data
2013	Haynes Inlet	10/22/2005	8.28	11.89	13.17	1.56	No data	No data	No data	No data
2013	Haynes Inlet	11/6/2019	7.48	11.74	13.65	1.37	No data	No data	No data	No data
2013	Airport	5/24/2009	7.63	13.52	18.25	4.49	18.66	23.39	26.53	5.65
2013	Airport	6/10/2023	9.69	13.89	18.67	5.14	17.64	24.12	26.75	4.40
2013	Airport	6/24/2008	12.04	16.94	21.09	4.61	20.36	22.83	25.95	2.75
2013	Airport	7/9/2022	9.56	14.02	17.41	5.60	22.47	24.12	26.12	2.72
2013	Airport	7/23/2006	9.49	13.88	17.92	5.25	15.02	20.69	25.08	2.00
2013	Airport	8/7/2018	11.09	14.78	19.59	4.63	3.05	11.70	15.90	1.72
2013	Airport	8/19/2004	10.72	15.93	21.31	4.15	2.08	9.64	12.24	2.99
2013	Airport	9/5/2017	12.58	16.93	22.95	4.65	7.56	9.22	11.79	1.51
2013	Airport	9/18/2007	No data	No data	No data	No data	No data	No data	No data	No data
2013	Airport	11/4/2018	No data	No data	No data	No data	No data	No data	No data	No data
2012	Downtown Coos Bay	7/18-8/2	12.12	17.93	19.89	4.23	16.13	22.33	24.98	6.54
2012	Downtown Coos Bay	8/3-8/18	12.97	18.39	20.52	3.44	18.85	22.96	25.26	4.54

2012	Downtown Coos Bay	8/19-8/30	15.21	17.76	19.69	3.23	20.17	23.24	24.89	3.80
2012	Downtown Coos Bay	8/31-9/15	No data	No data	No data	No data	No data	No data	No data	No data
2012	Downtown Coos Bay	9/16-10/1	11.00	15.44	17.70	4.56	20.82	22.81	23.95	2.10
2012	Downtown Coos Bay	10/2-10/14	10.85	14.70	16.52	2.41	20.65	22.30	23.49	1.78
2012	Downtown Coos Bay	10/15-10/29	7.84	13.25	17.04	3.42	8.11	19.19	22.70	6.72
2012	Downtown Coos Bay	10/30-11/14	8.31	12.77	14.36	1.69	5.28	15.18	19.51	9.44
2013	Downtown Coos Bay	5/24-6/9	8.77	15.56	19.17	3.02	0.54	14.89	20.10	13.53
2013	Downtown Coos Bay	6/10-6/24	10.74	16.98	19.56	4.24	0.77	14.98	19.56	10.91
2013	Downtown Coos Bay	6/25-7/10	14.57	20.04	22.87	3.82	1.00	4.73	9.50	2.92
2013	Downtown Coos Bay	7/11-7/22	12.41	18.34	21.29	4.94	No data	No data	No data	No data
2013	Downtown Coos Bay	7/23-8/7	12.21	18.03	20.35	4.22	No data	No data	No data	No data
2013	Downtown Coos Bay	8/8-8/18	14.69	18.67	21.05	3.39	No data	No data	No data	No data
2013	Downtown Coos Bay	8/18-9/4	12.76	19.32	21.71	3.71	No data	No data	No data	No data
2013	Downtown Coos Bay	9/5-9/17	17.08	20.12	21.99	2.70	No data	No data	No data	No data
2013	Downtown Coos Bay	9/18-10/7	12.01	17.75	20.52	6.48	No data	No data	No data	No data
2013	Downtown Coos Bay	10/8-10/20	6.78	13.83	15.09	5.30	No data	No data	No data	No data

2013	Downtown Coos Bay	10/21-11/4	7.68	12.29	13.94	2.03	No data	No data	No data	No data
2013	Downtown Coos Bay	11/5-11/18	5.76	11.66	12.59	2.44	No data	No data	No data	No data
2012	Coalbank Slough	7/20-8/3	13.91	19.54	21.95	3.65	16.46	19.25	22.00	4.09
2012	Coalbank Slough	8/4-8/18	18.25	19.96	0.00	2.23	18.37	20.32	22.35	2.58
2012	Coalbank Slough	8/19-8/30	17.78	19.24	21.03	2.16	16.29	18.79	21.43	1.83
2012	Coalbank Slough	8/31-9/13	15.27	18.36	19.42	3.17	15.87	18.37	19.94	1.82
2012	Coalbank Slough	9/14-9/30	8.17	16.67	19.47	6.69	3.52	15.07	22.86	2.13
2012	Coalbank Slough	10/1-10/13	9.34	15.69	17.92	2.98	3.03	3.36	3.68	0.18
2012	Coalbank Slough	10/14-10/30	7.78	13.91	17.54	3.62	1.72	2.68	3.23	0.66
2012	Coalbank Slough	10/31-11/14	7.61	12.98	15.11	2.18	0.86	2.78	3.62	1.73
2013	Coalbank Slough	5/25-6/8	No data	No data	No data	No data	No data	No data	No data	No data
2013	Coalbank Slough	6/9-6/24	No data	No data	No data	No data	No data	No data	No data	No data
2013	Coalbank Slough	6/25-7/10	No data	No data	No data	No data	No data	No data	No data	No data
2013	Coalbank Slough	7/11-7/23	No data	No data	No data	No data	No data	No data	No data	No data
2013	Coalbank Slough	7/24-8/6	12.20	19.39	12.20	5.17	19.89	21.71	23.40	2.34
2013	Coalbank Slough	8/7-8/19	14.10	19.81	14.10	5.00	20.37	22.05	23.45	2.02
2013	Coalbank	8/20-9/5	11.40	20.46	23.35	4.61	19.74	22.40	23.70	1.71

	Slough									
2013	Coalbank Slough	9/6-9/18	13.25	20.66	22.88	5.37	21.30	22.26	23.45	1.39
2013	Coalbank Slough	9/19-10/8	No data	No data	No data	No data	No data	No data	No data	No data
2013	Coalbank Slough	10/9-10/21	No data	No data	No data	No data	No data	No data	No data	No data
2013	Coalbank Slough	10/22-11/5	8.28	12.61	15.76	2.51	No data	No data	No data	No data
2013	Coalbank Slough	11/6-11/18	5.86	19.85	19.85	4.17	No data	No data	No data	No data
2012	Catching Slough	7/19-8/2	15.21	19.80	21.72	3.38	3.71	15.31	21.43	15.30
2012	Catching Slough	8/3-8/30	No data	No data	No data	No data	No data	No data	No data	No data
2012	Catching Slough	8/31-9/14	11.86	18.63	20.48	3.30	11.65	21.29	25.66	No data
2012	Catching Slough	9/15-9/29	10.91	16.82	17.66	4.63	15.65	23.25	26.06	No data
2012	Catching Slough	9/30-10/14	10.92	15.71	17.56	2.30	15.82	22.52	25.47	No data
2012	Catching Slough	10/15-10/29	8.07	13.67	17.18	3.27	2.13	15.75	23.77	No data
2012	Catching Slough	10/30-11/14	8.92	12.74	14.23	1.57	0.15	8.97	16.52	No data
2013	Catching Slough	5/25-6/9	9.21	16.16	20.10	2.72	1.03	10.57	19.34	16.74
2013	Catching Slough	6/10-6/23	11.97	18.38	20.50	20.55	1.02	13.29	22.17	15.25
2013	Catching Slough	6/24-7/8	15.92	21.22	24.44	2.79	1.12	5.73	9.89	4.38
2013	Catching Slough	7/9-7/22	13.41	20.33	23.46	5.34	0.78	1.71	2.25	0.81

2013	Catching Slough	7/9-7/22	13.41	20.33	23.46	5.34	0.78	1.71	2.25	0.81
2013	Catching Slough	7/23-8/5	13.27	19.79	22.00	4.10	0.64	1.14	1.39	0.42
2013	Catching Slough	8/6-8/18	17.94	20.13	22.35	2.64	No data	No data	No data	No data
2013	Catching Slough	8/19-9/4	14.95	20.79	22.75	3.32	No data	No data	No data	No data
2013	Catching Slough	9/5-9/18	18.88	21.08	22.90	1.87	No data	No data	No data	No data
2013	Catching Slough	9/19-10/7	No data	No data	No data	No data	No data	No data	No data	No data
2013	Catching Slough	10/8-10/20	No data	No data	No data	No data	No data	No data	No data	No data
2013	Catching Slough	10/21-11/4	7.88	12.64	14.23	1.15	No data	No data	No data	No data
2013	Catching Slough	11/5-11/18	9.57	11.66	12.30	1.08	No data	No data	No data	No data
2012	Empire	7/19-8/3	9.25	12.81	17.40	4.46	23.57	26.57	27.92	2.24
2012	Empire	8/4-8/18	8.96	12.79	18.17	4.00	23.78	26.57	23.78	1.74
2012	Empire	8/19-8/30	9.38	12.41	17.23	4.23	24.54	26.77	27.72	1.43
2012	Empire	8/31-9/15	9.25	12.30	16.42	3.96	24.23	26.04	27.26	1.48
2012	Empire	9/16-9/29	9.52	11.88	15.11	3.50	21.67	25.24	27.08	2.13
2012	Empire	9/30-10/14	No Data	No Data	No Data	No Data	No Data	No Data	No Data	No Data
2012	Empire	10/15-10/29	No Data	No Data	No Data	No Data	No Data	No Data	No Data	No Data
2013	Empire	5/25-6/10	7.44	12.65	16.81	3.42	20.71	24.12	26.02	2.87
2013	Empire	6/11-6/24	9.48	12.89	17.85	2.52	21.80	24.77	26.28	1.81
2013	Empire	6/25-7/9	10.46	15.87	19.83	4.52	21.51	23.89	25.94	2.12
2013	Empire	7/10-7/23	9.09	12.40	16.62	4.99	18.90	25.03	26.52	3.24
2013	Empire	7/24-8/7	8.66	12.14	16.36	4.70	24.69	25.90	26.76	1.34

2013	Empire	8/8-8/19	9.78	13.55	19.29	4.32	24.23	25.71	26.73	1.16
2013	Empire	9/24-10/8	13.26	14.78	16.92	1.64	19.97	25.24	26.67	2.67
2013	Empire	10/9-10/21	No Data	No Data	No Data	No Data	No Data	No Data	No Data	No Data
2013	Empire	10/22-11/5	No Data	No Data	No Data	No Data	No Data	No Data	No Data	No Data
2013	Empire	11/6-11/19	No Data	No Data	No Data	No Data	No Data	No Data	No Data	No Data

Appendix B. "Minimum" and "maximum" temperature and salinity is the smallest and largest value, respectively, recorded for these parameters during each two-week time interval; "mean" is the mean value reported within each two-week time interval; and "mean daily range" is the mean of the daily range of values observed within each two-week time interval. "No data" indicates missing or unusable data. Salinity statistics exclude outlier data, which may represent logger failure or exposure; all recorded temperature data points were included in these analyses unless logger malfunction is suspected

REFERENCES CITED

Baker, P., Richmond, N., and Terwilliger, N. (2000). Reestablishment of a native oyster, O*strea conchaphila*, following a natural local extinction. In Marine Bioinvasions: Proceedings of the First National Conference MA MIT Sea Grant Program, J. Pedersen, ed. pp. 221–231.

Barrett, E.M. (1963). The California Oyster Industry. The Resources Agency of California Department of Fish and Game

Bartol, I.K., Mann, R., and Luckenbach, M. (1999). Growth and mortality of oysters (Crassostrea virginica) on constructed intertidal reefs: effects of tidal height and substrate level. J. Exp. Mar. Biol. Ecol. *237*, 157–184.

Bohn, K., Richardson, C.A., and Jenkins, S.R. (2013). The importance of larval supply, larval habitat selection and post-settlement mortality in determining intertidal adult abundance of the invasive gastropod *Crepidula fornicata*. J. Exp. Mar. Biol. Ecol. *440*, 132–140.

Brink, L.A. (2001). Mollusca: Bivalvia. in An Identification Guide to the Larval Marine Invertebrates of the Pacific Northwest, A.L. Shanks, ed. (Corvallis, OR: Oregon State University Press),.

Brumbaugh, R.D., and Coen, L.D. (2009). Contemporary approaches for small-scale oyster reef restoration to address substrate versus recruitment limitation: a review and comments relevant for the Olympia oyster, *Ostrea lurida* Carpenter 1864. J. Shellfish Res. *28*, 147–161.

Carlucci, R., Sassanelli, G., Matarrese, A., Giove, A., and D'Onghia, G. (2010). Experimental data on growth, mortality and reproduction of *Ostrea edulis* (L., 1758) in a semi-enclosed basin of the Mediterranean Sea. Aquaculture *306*, 167–176.

Carson, H.S. (2010). Population connectivity of the Olympia oyster in Southern California. Limnol. Oceanogr. *55*, 134–148.

Coe, W.R. (1932). Season of attachment and rate of growth of sedentary marine organisms at the pier of the Scripps Institution of Oceanography, La Jolla, California. Scripps Inst. Oceanogr.

Connell, J.H. (1985). The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. J. Exp. Mar. Biol. Ecol. *93*, 11–45.

Coon, S.L., Bonar, D.B., and Weiner, R.M. (1985). Induction of settlement and metamorphosis of the Pacific oyster, *Crassostrea gigas* (Thunberg), BY L-Dopa and Catecholamines. J. Exp. Mar. Biol. Ecol. *94*, 211–221.

Davis, H.C. (1955). Mortality of Olympia Oysters at Low Temperatures. Biol. Bull. *109*, 404–406.

Deck, A.K. (2011). Effects of interspecific competition and coastal oceanography on population dynamics of the Olympia oyster, *Ostrea lurida*, along estuarine gradients. University of California, Davis.

Dinnel, P.A., Peabody, B., and Peter-Contesse, T. (2009). Rebuilding Olympia oysters, *Ostrea lurida* Carpenter 1864, in Fidalgo Bay, Washington. J. Shellfish Res. *28*, 79–85.

Dudas, S.E., Rilov, G., Tyburczy, J., and Menge, B.A. (2009). Linking larval abundance, onshore supply and settlement using instantaneous versus integrated methods. Mar. Ecol.-Prog. Ser. *387*, 81–95.

Ermgassen, P.S.E.Z., Gray, M.W., Langdon, C.J., Spalding, M.D., and Brumbaugh, R.D. (2013). Quantifying the historic contribution of Olympia oysters to filtration in Pacific Coast (USA) estuaries and the implications for restoration objectives. Aquat. Ecol. *47*, 149–161.

Gaines, S.D., and Bertness, M. (1993). The dynamics of juvenile dispersal: why field ecologists must integrate. Ecology *74*, 2430–2435.

Gaines, S., Brown, S., and Roughgarden, J. (1985). Spatial Variation in Larval Concentrations as a Cause of Spatial Variation in Settlement for the Barnacle, *Balanus glandula.* Oecologia *67*, 267–272.

Garibaldi, A., and Turner, N. (2003). Cultural keystone species: Implications for ecological conservation and restoration. Conserv. Ecol. 11955449 *8*.

Gaspar, M.B., Ferreira, R., and Monteiro, C.C. (1999). Growth and reproductive cycle of *Donax trunculus* L., (Mollusca: Bivalvia) off Faro, southern Portugal. Fish. Res. *41*, 309–316.

Gibson, G.G. (1974). Oyster mortality study summary report 1966-1972. Fish Commision of Oregon Management and Research Division, U.S. Department of Commerce National Marine Fisheries Service

Gillespie, G. (2009). Status of the Olympia oyster, *Ostrea lurida* Carpenter 1864, in British Columbia, Canada. J. Shellfish Res. *28*, 59–68.

Gosselin, Louis A., and Qian, Pei-Yuan (1996). Early post-settlement mortality of an intertidal barnacle: a critical period for survival. Mar. Ecol. Prog. Ser. *135*, 69–75.

Gosselin, Louis A., and Qian, Pei-Yuan (1997). Juvenile mortality in benthic marine invertebrates. Mar. Ecol. Prog. Ser. *146*, 265–282.

Griffiths, A.M., and Gosselin, L.A. (2008). Ontogenetic shift in susceptibility to predators in juvenile northern abalone, *Haliotis kamtschatkana* J. Exp. Mar. Biol. Ecol. *360*, 85–93.

Grosholz, E.D., Moore, J., Zabin, C., Attoe, S., and Obernolte, R. (2008). Planning for Native Oyster Restoration in San Francisco Bay Final Report to California Coastal Conservancy Agreement # 05-134.

Groth, S., and Rumrill, S. (2009). History of Olympia oysters (*Ostrea lurida* Carpenter 1864) in Oregon estuaries, and a description of recovering populations in Coos Bay. J. Shellfish Res. *28*, 51–58.

Gunter, G. (1955). Mortality of oysters and abundance of certain associates as related to salinity. Ecology *36*, 601–605.

Hall Jr., C.A., Dollase, W.A., and Corbató, C.E. (1974). Shell growth in *Tivela stultorum* (Mawe, 1823) and *Callista chione* (Linnaeus, 1758) (Bivalvia): annual periodicity, latitudinal differences, and diminution with age. Palaeogeogr. Palaeoclimatol. Palaeoecol. *15*, 33–61.

Harper, E. (1991). The role of predation in the evolution of cementation in bivalves. Paleontology *34*, 455–460.

Harris, H.E. (2004). Distribution and limiting factors of *Ostrea conchaphila* in San Francisco Bay. San Francisco State University.

Harry, H.W. (1985). Synopsis of the supraspecific classification of living oysters (Bivalvia: Gryphaediae and Ostreidae). The Veliger *28*, 121–158.

Hopkins, A.E. (1937). Experimental observations on spawning, larval development, and setting in the Olympia oyster *Ostrea lurida*. Bull. Bur. Fish. *XLVIII*, 439–503.

Howard, T.G., and Goldberg, D.E. (2001). Competitive Response Hierarchies for Germination, Growth, and Survival and Their Influence on Abundance. Ecology *82*, 979–990.

Jenkins, S. (2005). Larval habitat selection, not larval supply, determines settlement patterns and adult distribution in two chthamalid barnacles J. Anim. Ecol. *74*, 893–904.

Jones, D.S., Thompson, I., and Ambrose, W. (1978). Age and growth rate determinations for the Atlantic surf clam *Spisula solidissima* (Bivalvia: Mactracea), based on internal growth lines in shell cross-sections. Mar. Biol. *47*, 63–70.

Jonsson, P.R., Berntsson, K.M., and Larsson, A.I. (2004). Linking larval supply to recruitment: flow-mediated control of initial adhesion of barnacle larvae. Ecology *85*, 2850–2859.

Kimbro, David L., Largier, John, and Grosholz, Edwin D. (2009). Coastal oceanographic processes influence the growth and size of a key estuarine species, the Olympia oyster. Limnol. Oceanogr. *54*, 1425–1437.

Koeppel, J.A. (2011). High predation may hinder native oyster (*Ostrea lurida* Carpenter), 1864) restoration in North Humboldt Bay, California. Humboldt State University.

Largier, J.L., Hollibaugh, J.T., and Smith, S.V. (1997). Seasonally Hypersaline Estuaries in Mediterranean-climate Regions. Estuar. Coast. Shelf Sci. *45*, 789–797.

Larsson, A.I., and Jonsson, P.R. (2006). Barnacle larvae actively select flow environments supporting post-settlement growth and survival. Ecology *87*, 1960–1966.

Littlewood, D.T.J. (1988). Subtidal versus intertidal cultivation of *Crassostrea rhizophorae*. Aquaculture *72*, 59–71.

Loosanoff, V.L., Davis, H.C., and Chanley, P.E. (1966). Dimensions and shapes of larvae of some marine bivalve mollusks. Malacologia *4*, 351.

Matthiessen, G.C. (1970). A review of oyster culture and the oyster industry in North America.

McLean, J.H. (2007). Mollusca: Gastropoda. In Intertidal Invertebrates from Central California to Oregon, J.T. Carlton, ed.

Meyer, G.R., Lowe, G.J., Kim, E., Abbott, C.L., Johnson, S.C., and Gilmore, S.R. (2010). Health Status of Olympia oysters (*Ostrea lurida*) in British Columbia, Canada. J. Shellfish Res. *29*, 181–185.

Michener, W.K., and Kenny, P.D. (1991). Spatial and temporal patterns of *Crassostrea virginica* (Gmelin) recruitment: relationship to scale and substratum. J. Exp. Mar. Biol. Ecol. *154*, 97–121.

Minchinton, T.E., and Scheibling, R.E. (1991). The Influence of Larval Supply and Settlement on the Population Structure of Barnacles. Ecology *72*, 1867–1879.

Ó Foighil, D., and Taylor, D.J. (2000). Evolution of Parental Care and Ovulation Behavior in Oysters. Mol. Phylogenet. Evol. *15*, 301–313.

Oates, M. (2013). Observations of Gonad Structure and Gametogenic Timing in a Recovering Population of *Ostrea lurida* (Carpenter 1864). University of Oregon.

Pauley, G.B., Van Der Raay, B., and Troutt, D. (1988). Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (Pacific northwest). Pacific oyster. US Fish Wildl. Serv. Biol. Rep. *82*.

Peter-Contesse, T., and Peabody, B. (2005). Reestablishing Olympia oyster populations in Puget Sound, Washington (Puget Sound Restoration Fund).

Pineda, J. (1994). Spatial and temporal patterns in barnacle settlement rate along a southern California rocky shore. Mar. Ecol. Prog. Ser. *107*, 125–138.

Pineda, J. (2000). Linking larval settlement to larval transport: assumptions, potentials, and pitfalls. Oceanogr. East. Pac. *1*, 84–105.

Pineda, J., Porri, F., Starczak, V., and Blythe, J. (2010). Causes of decoupling between larval supply and settlement and consequences for understanding recruitment and population connectivity. J. Exp. Mar. Biol. Ecol. *392*, 9–21.

Polson, M.P., Hewson, W.E., Eernisse, D.J., Baker, P.K., and Zacherl, D.C. (2009). You say conchaphila, I say lurida: molecular evidence for restricting the Olympia oyster (*Ostrea lurida* Carpenter 1864) to temperate western North America. J. Shellfish Res. *28*, 11–21.

Pritchard, C.E. Distribution of Larval Bivalves in the Coos Bay Estuary, Oregon.

Raimondi, Peter T. (1990). Patterns, mechanisms, consequences of variability in settlement and recruitment of an intertidal barnacle. Ecol. Monogr. *60*, 283–309.

Richardson, C.A., Collis, S.A., Ekaratne, K., Dare, P., and Key, D. (1993). The age determination and growth rate of the European flat oyster, *Ostrea edulis*, in British waters determined from acetate peels of umbo growth lines. ICES J. Mar. Sci. *50*, 493–500.

Roegner, G.C., and Mann, R. (1995). Early recruitment and growth of the American oyster *Crassostrea virginica* (Bivalvia: Ostreidae) with respect to tidal zonation and season. Mar. Ecol. Prog. Ser. *117*, 91–101.

Satumanatpan, S., and Keough, M.J. (2001). Roles of larval supply and behavior in determining settlement of barnacles in a temperate mangrove forest. J. Exp. Mar. Biol. Ecol. *260*, 133–153.

Sawyer, K.M. (2011). Settlement preference and the timing of settlement of the Olympia oyster, *Ostrea lurida*, in Coos Bay, OR. University of Oregon.

Seale, E.M., and Zacherl, D.C. (2009). Seasonal settlement of Olympia oyster larvae, *Ostrea lurida* Carpenter 1864 and its relationship to seawater temperature in two southern california estuaries. J. Shellfish Res. *28*, 113–120.

Sellers, M.A., and Stanley, Jon G. (1984). Species Profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic): American oyster

Shanks, A., and Butler, B. (2013). Oregon Estuarine Invertebrates (Second Edition).

Shinen, J.L., and Navarrete, S.A. (2010). Coexistence and intertidal zonation of chthamalid barnacles along central Chile: Interference competition or a lottery for space? J. Exp. Mar. Biol. Ecol. *392*, 176–187.

Stick, D.A. (2011). Identification of optimal broodstock for Pacific Northwest oysters. Oregon State University.

Strathmann, M.F. (1987). Phylum Mollusca, Class Bivalvia. In Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast: Data and Methods for the Study of Eggs, Embryos, and Larvae, (University of Washington Press), p. 329.

Sumner, C. (1981). Growth of Pacific oysters, *Crassostrea gigas* Thunberg, cultivated in Tasmania. II. Subtidal culture. Mar. Freshw. Res. *32*, 411–416.

Tanabe, K. (1988). Age and growth rate determinations of an intertidal bivalve, *Phacosoma japonicum*, using internal shell increments. Lethaia *21*, 231–241.

Todd, C.D. (2003). Assessment of a trap for measuring larval supply of intertidal barnacles on wave-swept, semi-exposed shores. J. Exp. Mar. Biol. Ecol. *290*, 247–269.

Trimble, A.C., Ruesink, J.L., and Dumbauld, B.R. (2009). Factors preventing the recovery of a historically overexploited shellfish species, *Ostrea lurida* Carpenter 1864. J. Shellfish Res. *28*, 97–106.

Walne, P.R. (1972). The Influence of Current Speed, Body Size and Water Temperature On the Filtration Rate of Five Species of Bivalves. J. Mar. Biol. Assoc. U. K. *52*, 345–374.

Wasson, Kerstin (2010). Informing Olympia oyster restoration: Evaluation of factors that limit populations in a California estuary. Wetlands *30*, 449–459.

White, J., Ruesink, J.L., and Trimble, A.C. (2009). The nearly forgotten oyster: *Ostrea lurida* Carpenter 1864 (Olympia oyster) history and management in Washington state. J. Shellfish Res. *28*, 43–49.

Yoshioka, P.M. (1982). Role of Planktonic and Benthic Factors in the Population Dynamics of the Bryozoan *Membranipora membranacea*. Ecology *63*, 457–468.

Yoshioka, P.M. (1986). Chaos and recruitment in the bryozoan, *Membranipora membranacea*. Bull. Mar. Sci. *39*, 408–417.

Yund, P.O., Gaines, S.D., and Bertness, M.D. (1991). Cylindrical tube traps for larval sampling. Limnol. Oceanogr. *36*, 1167–1177.

(2010). Technical Report- DRAFT Volume 1- Jordan Cove Energy Project and Pacific Connector Gas Pipeline: COastal Engineering Modeling and Analysis.