DISTRIBUTION OF LARVAL BIVALVES IN THE COOS BAY ESTUARY, OREGON

by

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THESIS ABSTRACT

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Bivalves are considered ecosystem engineers and are important for ecosystem health within estuaries. The Olympia oyster *Ostrea lurida* was historically important along the Pacific Coast of the United States but currently has low population abundances along much of its historical distribution. However, despite restoration efforts, little recovery has been observed. Here, we provide a short review of the biology of the species and recent efforts of restorations. We then examine potential contributing factors to limited recovery in the Coos Bay estuary. We noticed distinct variations in larval supply along the bay and proposed hydrodynamics of the bay could be causing these variations. We then collected observational data on the hydrodynamics of the bay and the distribution of other larval bivalves. These data support the presence of a null zone within the estuary that may be driving the distribution of larval bivalve taxa.

This thesis includes unpublished co-authored material.

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CHAPTER I

GENERAL INTRODUCTION

Ecosystem engineer is a term used to refer to an organism that directly or indirectly modifies the availability of resources to other species by causing physical changes in the biotic or abiotic environment (Jones et al.1994). In both marine and freshwater ecosystems, bivalves are considered allogenic ecosystem engineers (Karatayev et al. 1997, Strayer et al. 1999, Sousa et al. 2009). Services provided by bivalves are numerous, and include filtration of the water column (Coen et al. 2007, Grizzle et al. 2008), influencing the phytoplankton community composition (MacIsaac 1996, Strayer et al. 1999), stabilization of shorelines (Meyer et al. 1997, Coen & Bolton-Warberg 2005), provision of essential shelter and habitat (Piazza et al. 2005, Borthagaray & Carranza 2007), benthic-pelagic coupling (Karatayev et al. 1997, Crooks & Khim 1999, Escapa et al. 2004), acting as gate-way organisms for secondary introduced species (Strayer et al. 1999, Guiterrez et al. 2003), and providing alternative thermal regimes in intertidal areas (Dame 1996, Padilla 2010).

The first bivalves appear in the fossil records during the Cambrian period (~620 Mya), before land creatures emerged. By the Mesozoic era, they had out-competed similar groups of sessile marine organisms, and were morphologically similar to those we have today (Dame 1996). Today, bivalves occur in every ocean (Padilla 2010), and are of special interest to ecologists and managers because of the suite of ecosystem services they provide. Overharvesting and the introduction of non-native invasive species are

causing dramatic changes to some bivalve populations, as well as disrupting ecosystem function (Strayer et al. 1999, Breitburg et al. 2000, Guiterrez et al. 2003).

One ecosystem service provided by bivalves frequently referenced within the literature is filtration of the water column (e.g., Cohen et al. 1984, Grosholz 2002, Coen et al. 2007, Grizzle et al. 2008). Many bivalves are filter feeders, and have the ability to filter large volumes of water when in dense beds or reefs, positively affecting water quality (Cohen et al. 1984, MacIsaac 1996, Coen et al. 2007). By Newell's (1988) estimates, before *Crassostrea virginica* became heavily fished in the mid-1800s, the oyster population in Chesapeake Bay would have had the capacity to filter the entire bay within 3.3 days. Due to overharvesting and a subsequent contraction of the population, a 1988 estimate increased to 325 days for the full volume of water in the Bay to be filtered by oysters. Studying in San Francisco Bay, Cohen et al. (1984) found that the Asiatic clam *Corbicula fluminea* , introduced into the bay in 1977, was actually responsible for a visual "sag" in phytoplankton biomass associated with the highest biomass of the clams during the summers of 1980 and 1981. Working in the Netherlands, Reeders et al. (1993) found cyanobacteria blooms in tanks without, but not with zebra mussels, and Bastviken et al. (1998) report that after introduction of zebra mussels to the Hudson River, cyanobacteria density decreased by a factor of 778.

Bivalves are effective filter feeders, but many also have the ability to partition polluted matter in the water column from particles such as phytoplankton and sediment (Reeders & Bij de Vaate 1992). These polluted particles (such as heavy metals, organic pollutants, and polycyclic aromatic hydrocarbons) are wrapped in mucus pellets without digestion, and deposited in the sediment as pseudofeces, effectively removing them from

the water column. As water quality issues continue to be of concern within water masses internationally, the impact of filtration on water columns by bivalves has been of interest as a possible solution to controlling phytoplankton blooms in eutrophic waters. Reeders & Bi Vaate (1992) measured production of pseudofaeces of mussels in the Netherlands, in hopes of developing a biofilter at the inlet of the water body. They found sediment surrounding the mussels was indeed more polluted than the surrounding water column, and that pollutants were up to ten times more concentrated in sediment after filtration by the bivalves than in the surrounding water column after 217 days. Interestingly, however, control of algal blooms and limitation of phytoplankton biomass in the water column is not always observed. Doeing et al. (1986) found that *Mercinaria mercinaria* did not control phytoplankton biomass in mesocosm experiments. They remind us that this service could be dependent on bivalve density, water residence time, and circulation.

Associated with filtration, bivalves also provide benthic-pelagic coupling (Huettell & Gust 1992, Crooks & Khim 1999, Escapa et al. 2004) or the ability to sequester carbon suspended in the water column and excrete it into the surrounding sediment in the form of fecal pellets (Coen et al. 2007, Dame 1996) . These pellets are rich in organic nutrients compared to the surrounding sediment (Reusink et al. 2005). Doeing et al. (1986), working in mesocosm experiments, found both net and gross sedimentation rates were twice as high in tanks with the clam *M. mercenaria* than in controls. Newell (1988) also estimated very high filtration rates. He estimated pre-1870s populations of *C. virginica* could have filtered 21-42% of the suspended carbon in Chesapeake Bay in 1982. Although this rate is no longer sustainable based on current low populations of *C. virginica*, it does illustrate the impact these oysters can have on their

ecosystem, by moderating water quality. This process is especially important in short time periods (days or weeks), when the nutrients become available for uptake by other invertebrates (MacIsaac 1996, Vaughn & Hakencamp 2001), but also in long-term processes, such as particle and nutrient incorporation, including CO_2 as $CaCO_3$, into their shells, which is not recycled and is essentially buried when they die (Karatayev et al. 1997).

Within reefs or beds produced by bivalves, there is also shelter and habitat for other species, vertebrates and invertebrates alike (Beekey et al. 2004, Piazza et al. 2005, Coen et al. 2007). Reefs and beds increase structural diversity in subtidal and intertidal areas, which supports increased abundances, species richness, and biomass of finfish and invertebrates (Ricciardi et al. 1997, Coen & Luckenbach 2000, Luckenbach et al. 2005, Byrnes et al. 2007, Robinson et al. 2007, Sylvester et al. 2007, Sousa et al. 2008). Sylvester et al. (2007) found the biomass of invertebrates such as oligochaetes, nematodes, copepods, and gastropods, among others, were 43-100% higher in areas with the mussel *Limnoperna fortunei* present, and invertebrate biomass was observed to have a positive relationship with mussel density. Silver Botts et al. (1996) observed invertebrates more commonly on live mussels than mussel shells, and more commonly on shells than areas of bare substrate where mussels were absent. Oyster reefs are also used extensively by commercially important invertebrate species, such as Dungeness crab (*Cancer magister*; Dumbauld et al. 1993).

Increased species diversity is not always correlated with bivalves, however, and dense aggregations of bivalves can reduce diversity as well, especially when the bivalve is an introduced species (Napela et al. 1998, Reush 1998, Crooks & Khim 1999, Lozano

et al. 2001). In surveys completed over a three-year span, reduced diversity of the taxa, Oligochaeta, Sphaeriidae, and *Diporiea,* were associated with density of mussel beds of the zebra mussel, with the greatest decreases seen in the years with the highest mussel densities (Lozano et al. 2001). Increased filtration rates by mussels may have reduced the algae available as food for these invertebrates. This suppression of available primary production for transfer up the food chain may have long-standing effects on the associated dependent food-webs.

Within intertidal regions, bivalves may also provide alternative thermal regimes (Dame 1996, MacIsaac 1996, Padilla 2010). Padilla (2010) observed that non-native *C. gigas* shells were mostly white in color while the surrounding rocks were black. In the low intertidal zone during summer, limpets (who are known to graze on seaweeds in this zone) were seen in higher abundance with oysters as well, as compared to black rocks. Oysters are able to modify the thermal regime by reflecting light with white shells (up to 25 times more light), whereas black rocks absorb the light. The physiology in the color of the oyster shell results in an average decrease in temperature on oyster shells of 3.3° C, with a daily maximum difference of 6 °C compared to the black rocks.

This set of services is one that other groups of organisms likely cannot provide (Newell 1988). When these ecosystem engineers are removed or invaded, there can be detrimental effects on ecosystem health, and economic productivity as these shellfish fisheries decline. Bivalves, whether introduced or native, such as mussels, oysters, and clams provide a suite of services to their ecosystem, and should be considered when making management decisions in environments susceptible to anthropogenic disturbances, invasions of new species, or restoration projects.

Bivalve populations are changing in many areas, however, due to direct anthropogenic disturbances such as overfishing, dredging, and introduction of non-native species. Along the Pacific Northwest, for instance, the native oyster, *Ostrea lurida,* is now estimated to have populations along much of its distribution below 1% of historical populations (Beck et al. 2011) due to historical overharvesting. *O. lurida* has become a primary restoration target for many shellfish managers, largely due to their potential for providing ecosystem services, and restoration efforts are being investigated California to Washington, including within the Coos Bay estuary, Oregon. However, in order for restoration efforts to be successful, it is imperative to identify potential primary drivers behind the limited recovery. For example, recovery could be supply limited, recruitment limited, or even habitat limited.

To understand important aspects of the biology, which could inform the direction of experiments and observations aimed at identifying current population limitations of *O. lurida* in the Coos Bay estuary, I undertook a review of the literature available on the species. Specifically, I focused on recent work done on the species not published in other, previous reviews, such as Couch & Hassler (1989) and Baker (1995). This review is presented in Chapter II. The research presented in this thesis focuses on larval supply, dispersal, and recruitment. Chapter III is co-authored by Rose Rimler who measured larval recruitment while I measured larval supply.

Observations recorded in Chapter III concerning the larval supply of *Ostrea lurida* along the Coos Bay estuary showed high larval abundances in upper regions of the bay, but low larval abundances in the lower regions. This pattern was persistent throughout both years, 2012 and 2013, and matches patterns of adult population

distribution (Groth & Rumrill 2009). We suspected that hydrodynamics within the bay could be controlling larval dispersal and subsequent larval delivery to the shore. Data provided in Chapter IV support this hypothesis. In order to understand the potential of hydrodynamic in controlling adult populations of other bivalves through larval delivery, the distribution of eight other larval bivalve taxa were investigated as well.

Data presented in this thesis indicate hydrodynamic conditions (specifically, the null zone, see Chapter IV) may strongly influence adult bivalve distributions in the Coos Bay estuary, by controlling larval supply. These data can be used by shellfish managers and area planners to evaluate the potential for larval dispersal of species of interest, such as *O. lurida*, and sites most likely to receive naturally high larval supply and recruitment needed to build self-sustaining oyster populations.

Furthermore, these data come at an opportune moment. The Oregon International Port of Coos Bay is considering large-scale modifications and expansions to the shipping channel located in the estuary. These changes, particularly dredging, could influence the hydrodynamics of the bay, which in turn could affect the distribution of larval bivalves, and thus the distribution of adult bivalves. These data will help area planners make informed decisions about changes to the estuary, based on goals for ecosystem health as a whole, and economic recovery of the region.

CHAPTER II

BIOLOGY OF *OSTREA LURIDA*

This chapter is meant to introduce the literature on the biology of *Ostrea lurida* with an emphasis on information that has arisen after Baker's review with annotated bibliography in 1995. The review will have an emphasis on recent work contributing to inform restoration efforts. Readers are encouraged to read both Couch & Hassler (1989) and Baker (1995) for more comprehensive reviews on some topics as cited in the text.

Ostrea lurida (the Olympia oyster) is the only native oyster occurring along the western coast of the United States, with a historical distribution from Baja California to Sitka, Alaska (Dall 1914, Coan et al. 2000). The current range of *O. lurida* is estimated to be up to 40% smaller than its historic range, with the northern limit now near Queen Charlotte Island, British Columbia and the southern limit near Bahia San Quintin, Baja California, Mexico (Gillespie 2009). Additionally, Beck et al. (2011) have classified the distribution and health of *O. lurida* beds along the majority of the Pacific Northwest as poor (90-99% lost) or functionally extinct (>99% lost), with the exception of the few healthy populations in British Columbia. *O. lurida* is mainly confined to estuaries and sheltered waters (Cook et al. 2000), and is found in both intertidal and in shallow subtidal euryhaline waters, although Hertlein (1959) reports their distribution from 0-71 m depth. For a comprehensive compilation of *O. lurida* populations, see Baker (1995).

Phylogeny

Members of the genus *Ostrea* (flat-shelled oysters) are considered more recently evolved from the oviparous *Crassostreinae* (cup-shelled oysters; Polson et al. 2009). Until recently, some considered *O. lurida* to be one species whose distribution extended from Alaska down into Central America, while others separated *O. lurida* from it's southern sister species, *O. conchaphila* (Polson et al. 2009), which is known to occur as far south as Panama (Polson et al. 2009). The characteristics of the shell shape of *O. lurida* lead, at one time, to the distinction of three different forms of the species: *f. rufoides, f. expansa,* and *f. laticaudata*, which may have been instrumental in splitting the species into two distinct species, *O. lurida* and *O. conchiphilla* (Arakawa 1990). In 1985, however, Harry (1985) merged *Ostrea lurida* and *Ostrea conchaphila* based on morphology, but recent genetic work indicates that the two species are indeed separate members of *Ostrea* (Polson et al. 2009). The approximate point of separation is Baja, California; *O. lurida* occurs north, while *O. conchiphila* occurs south. *O. lurida* gene region CO1 has also been successfully amplified, and *O. lurida*-specific primers and probes for qPCR have been produced (Wight et al. 2009).

Within *Ostrea lurida,* as it is now recognized, there appear to be many distinct isolated populations along the Pacific Northwest, and Stick (2011) found genetic distance and geographic distance to be related, in most cases. Stick (2011) discusses the need of restoration work to understand the genetic structure of the seed oysters that are introduced during restoration efforts, as the five metapopulations (Vancouver Island, Puget Sound, Willapa/Coos Bay, Yaquina Bay, and California) throughout the range are genetically different. However, Stick (2011) was unable to conclude if differences in the

current genetic structure of the populations was natural or anthropogenically-induced. Stick (2011) also suggests that, given the similar genetics, the Coos Bay oysters were brought in from Willapa Bay.

Reproductive Biology

Ostrea lurida is a sequential hermaphrodite, protandrous, viviparous, and larviparous (Coe 1931b). Some may argue that *O. lurida* is a simultaneous hermaphrodite, rather than a sequential hermaphrodite, because oysters are commonly found producing sperm and eggs simultaneously (Oates *personal communication*). However, they will only spawn the gametes of one sex at a time, which is characteristic of sequential hermaphroditism. There is also some anecdotal conjecture that this species (perhaps genus) isn't even protandrous; oogonia and spermatogonia appear to compete for the starting role in newly matured oysters, with some evidence that females occasionally develop first (Oates *personal communication*). See de Silva et al. (2009) for work done with a congener, *Ostrea edulis*.

Ostrea lurida can remain reproductive for the majority of the year, as long as temperatures are above those required for reproduction (Coe 1931b). The critical temperature for reproduction in southern California (near Scripps Institute of Oceanography) is near 16°C (Hopkins 1937), and is reported to be closer to 13°C in the more northern ranges of its distribution in British Columbia (Stafford 1913). However, preliminary data in the Coos Bay estuary, Oregon, indicate the critical temperature may be approximately 15°C (Garcia-Petiero *unpublished*, Oates *unpubublished*).

The first spawning within a year can occur as early as April, and the reproductive season may run through October or November (Coe 1931b). *O. lurida* may have either one or two spawning peaks in a summer (Hopkins 1937, Bonnot 1938, Carson 2010), and in some years there may be a relative failure of spawning. For example, in 2010, Garcia-Petiero (*unpublished*) observed larval densities up to 50 m^{-3} in plankton samples from the Coos Bay estuary, but no larvae were caught in similar tows in 2011. Larvae were again found in 2012, likely indicating a reproductive failure in 2011, rather than a large-scale mortality event of adult populations. Deck (2011), working in Tomales Bay, California, also found 60x more recruits at one site in 2008 than 2009, possibly due to a larval supply limitations.

Additionally, although the oysters may not be brooding, all stages of sexual reproduction can be found within a population year-round (Coe 1931b, Oates, *unpublished*), and many stages of male or female gamete development (see Reproductive Cycle, below) maybe found within a population at a single time (Coe 1931a, Hopkins 1936). Dinnel (2009) working in Fidaldgo Bay, Washington, followed the reproductive condition of oysters at the trestle restoration site in May, June and August 2006. In May, 1 in 10 oysters sampled contained eggs, while most other oysters sampled appeared to be developing ripe gonads. In June, 1 in 18 sampled oysters had larvae in the mantle cavity, and the other oysters were still in various stages of gamete development. In August however, no oysters (n=12) had larvae or eggs, and most appeared to have decreased gonad sizes compared to previous dates, suggesting that the reproductive season was at an end. These data suggest that the reproductive period may occur during a short (~ two to three month) window during summer.

Reproductive Cycle

An individual becomes reproductively mature within approximately one year after settlement, and gonads begin to appear within about eight weeks during periods of warm water (Coe 1932). During this period of preliminary gonad formation, there is no sexual differentiation (Coe 1931b). After 12-16 weeks, the gonads begin to differentiate, and both ovogonia and spermatagonia are present (Coe 1931b). Spermatagonia develop more quickly than ovogonia, resulting in a protandrous oyster (Coe 1931b). If water is above the critical point for spawning, spermatogenesis occurs, and spermatozoa are ripe at about five months of age (Coe 1931b). The sperm develop in aggregates or sperm balls, each with 250-2,000 sperm (Coe 1931b); each individual sperm in the sperm ball has its flagellum facing outward, and the adhesive holding the balls together dissolves once in contact with the seawater, at which time the sperm begin to swim independently (Coe 1932). These sperm balls are characteristic of the genus *Ostrea*. *Crassostrea* oysters do not develop this ultrastructure. It is thought that sperm ball formation prevents self-fertilization by sequestering spermatozoa from developing oocytes. Free spawning oysters that do not exhibit gamete retention of both sexes (such as *C. virginica*) do not aggregate their sperm (Coe 1931). It may also serve to deliver higher concentrations of sperm to nearby females who capture the spawned aggregates before they fully dissolve.

Within *O. lurida*, the peak of the male phase is characterized by sperm aggregation, followed by the release of the sperm ball. During this time, the female oogonia are also developing (Coe 1931b). After approximately six months, the oocytes are ripe, and fertilization may take place. The reproductive system lies within connective tissue below the epithelium, and can cover the entire body tissue (Coe 1932), and

fertilization occurs in the brachial chamber of the female stage (Coe 1931a, Hopkins 1936, 1937). Spermatozoa are pulled into the gills of the female-stage adults, enter the mantle cavity where they are exposed to the eggs, and larvae develop in the mantle cavity or on the labial palps and gills (Coe 1931a, Hopkins 1936, 1937). The brooded larvae are released through paired genital pores, located ventrally to the adductor muscle. While embryos are growing, spermatogenesis is occurring in what was previously a female, and reaches its peek once more after the embryos are released (Coe 1931b).

Once these three initial phases are complete (spermatogenesis, ovigenisis, spermatogenesis), the condition of the oyster seems to decline and the flesh becomes translucent (as opposed to white, when the oyster is considered in good condition). During this time, the oyster takes time to replenish its nutrient and energy stores. The duration of this interval depends on the condition of the individual (Coe 1931b). Upon recuperation, an individual may brood another round of eggs or sperm, and fertilization may take place again (Stafford 1913, Coe 1931b). This cycle may follow throughout the remainder of the oysters life, as long as temperatures remain above the critical temperature required for reproduction. When the temperature falls below the critical point, although growth and mass gain may continue, reproduction will halt, to be resumed only when temperatures rise above the threshold needed for reproduction (Coe 1931b). Throughout these cycles, both spermatozoa and ova may be present in the same individual at the same time, but one will be well developed, while the other will be developing (Coe 1931b). There does not appear to be a pre-determined number of sexual phases throughout the year, as the lengths of the cycles are dependent on environmental conditions and condition of the individual oyster (Coe 1932). But Coe (1930, 1932)

estimated that 1.5 generations each year are the normal output per individual oyster in southern California, the last half of the second generation being put on hold until the critical temperatures rise again after winter. This hypothesis supplements evidence suggesting two spawning peaks, which are often observed, with the first brood being carried over the winter, and the second brood being released after the individual oyster has gone through another male and female stage (Coe 1932).

Females brood an average of 250,000 to 300,000 larvae per brood (Hopkins 1937). According to Hopkins (1937), there are three stages of development while brooding. The first stage, composed of two days of development, is a zygote; Day 1 as a blastula, and Day 2 as a gastrula. During the second stage and the 3rd day, the zygote becomes a trochophore, and finally on Day 4, the brooded larva becomes a D-hinged larva, characterized by D-shaped shell. During an estimated 10-12 days, the larva maintains it shape, but grows in size, and is eventually released as a D-shaped veliger between 163.2-187 μm in diameter (Hopkins 1937, Zacherl et al. 2009, Coe 1931b). The initial shell (prodissoconch) is formed as the larva is brooded. Once the D-staged larva is released, there is a thickening of the shell, especially near the umbo (Zacherl et al. 2009) that contributes to the "umbo-stage" larvae developing a species-specific shape. These "umbo-stage" larvae then develop into pediveligers after further growth within the plankton, usually a few days to a few weeks. The larvae then become pediveligers. Pediveligers develop an eyespot (Zacherl 2005) and search for suitable settlement spots (mostly hard substrate). Once suitable substrate is found, the oyster will glue itself to the substrate (Galtsoff 1964). Pediveligers are estimated to be competent to settle at approximately 300 μm (Loosanoff 1966).

The planktonic larval duration of *O. lurida* is estimated to range from 7 days to 8 weeks (reviewed in Baker 1995). Imai et al. (1954) estimated it to be 11-16 days, while Hopkins (1937) estimated the larval duration to be at least 30 days. Baker (1995) and Carson (2010) estimate larvae may spend from 1-8 weeks in the water column before settling. Couch & Hassler (1989) estimate 2 weeks, Breese (1953) estimates 8 weeks and finally Wight et al. (2009) estimate 22 days (Table 1). These discrepancies, in addition to the paucity of information of maximum age, are areas that could benefit from future research.

Shell Morphology

Shells can be made of a variety of crystalline forms of calcium carbonate simultaneously: a mixture of calcite, aragonite, and vaterite, each of which is able to substitute different elements for Ca in the crystal structure (Campana 1999).
As a larval shell grows, elements with similar properties to Ca (such as Sr, Ba, Pb) can replace Ca in the calcium carbonate matrix (Campana 1999) depending on salinity, temperature, and element concentration (Zacherl et al. 2009). Higher concentrations of these elements relative to Ca are seen in the younger life stages. This mechanism of uptake of elements during the earlier life-stages enables researchers to identify the larva's native site through spectroscopy (Zacherl et al. 2009, Carson 2010). Zacherl et al. (2009) suggest changing growth rates and changes in the crystalline form of the shell as a mechanism for varying rates of uptake and hypothesize that the earlier shells are of aragonite, but the subsequent crystalline structures, approximately at the age of settlement, are calcite (Zacherl et al. 2009). It is possible that metamorphosis from a larva

to a juvenile causes this change in crystalline structure. Through spectroscopy, researchers have been able to determine source and sink populations in San Diego County (see Dispersal below; Carson 2010).

The adult shell of *O. lurida* is small, with both hinges being "finely serrated", the right valve being flat, while the left is more or less concave (Couch & Hassler 1989, Arakawa 1990). The shell lacks a periostracum, but the inner shell ranges from white to purple (Allen 1976), and the exterior of the shell may be striped purplish, brown or yellow (Hertlein 1959). See Baker (1995) for a more complete description of anatomy and characteristic shell morphologies.

Discrepancies exist in the descriptions of maximum shell size and shell growth. Hertlein (1959) reports a maximum shell length of approximately 7.5 cm, while Buhle & Ruesink (2009) report 6 cm, Arakawa (1990) 5-8 cm, and Peter-Contesse & Peabody (2005)10 cm. Growth rates also demonstrate variability, which may be related to a latitudinal gradient driven by temperature or food availability. Davis (1949) reports that larvae grown at temperatures above 10°C grew to be juveniles with sizes of 3.5-3.7 cm after approximately 70 days. Coe & Allen (1937), estimate a maximum size of 5 cm after 30 weeks while Chew reports a maximum size of 3.4-4.5 cm after 3 years (Fisheries Department, University of Washington, as cited in Couch & Hassler 1989) or in 3.5-5 years according to (Korringa 1976) at which point they appear to stop growing, although their shell may change shape (Peter-Contesse & Peabody 2005). Maximum age is unknown (Couch & Hassler 1989). However, as many of these growth rates and maximum sizes were mentioned in passing, and lacked a geographical location, a pattern of growth and maximum size in relation to a latitudinal gradient could not be established.

Physiological processes influenced by environmental parameters, such as the surrounding temperatures and salinity may affect not only the oyster's growth and maximum size, but also distributional limitations. For instance, populations may experience 100% mortality if present in the shallow subtidal or intertidal during cold weather, as they cannot survive freezing temperatures, even if not inundated or covered with ice (Davis 1955, Peter-Contesse & Peabody 2005). Additionally, Davis (1955) suggests that the oysters might not survive because low temperatures inhibit feeding. Davis (1955) also described oysters that died during cold weather still having adequate food reserves. When cultivated for commercial harvest, dykes were built to maintain a water level of 15-30 cm throughout the growing grounds, to reduce the risk of freezing (Hopkins 1936). Despite this sensitivity to freezing temperatures, the oysters have a fairly wide temperature tolerance range. For example, in San Francisco Bay, the monthly average temperatures recorded by Carson (2010) for intertidal *O. lurida* populations was between 18.5 °C and 27.3°C. However, high temperatures may also result in mortality; Trimble et al. (2009) observed very high losses of outplanted oysters, and suggested high temperatures in the summer could be responsible.

Although considered an estuarine species that presumably also requires a tolerance to a wide array of salinities, *O. lurida* does not appear to do well at extremely low salinity. Korringa (1976), estimates that oysters will do well at salinities above 25, although they can tolerate brief exposure to lower salinities; likewise, Peter-Contesse & Peabody (2005) report that these oysters cannot tolerate salinities lower than 23-24 ppt. Gibson (1974) found that oysters could survive salinities of 5 or lower for 2-3 weeks

before enduring 100% mortalities. Oysters kept at a salinity of 15 for five weeks experienced 83% survival (Gibson 1974).

Wasson (2010), working in Elkhorn Slough, CA found that sites with larger ranges in water quality parameters (including temperature, salinity, turbidity, dissolved oxygen, and fluorescence) lacked *O. lurida* populations, while sites with smaller ranges tended to have larger populations. Wasson (2010) also found that within a water quality nMDS plot (including temperature, salinity, turbidity, dissolved oxygen, and fluorescence) sites with high densities of oysters were very closely clustered, followed by areas with low densities loosely clustered, while sites with no oysters present were very scattered throughout the plot. This highlights the need for more information on the influence of water quality parameters in limiting the natural recovery or future restoration of *O. lurida* populations.

Harvesting

Little information is available on historic or baseline sizes of *O. lurida* populations. There are currently healthy populations in British Columbia (Nootka) with densities surpassing 1,100 individuals m^{-2}, but these densities may be uncharacteristically high as other sources site historical densities around 116 individuals m^{-2} (zu Ermgassen et al. 2012). However, historically, population sizes of *O. lurida* have been sufficient to support both tribal subsistence harvest and commercial harvesting, with individual oysters that obtained a shell length of approximately 5 cm (Steele 1957) being considered marketable. Large shell middens indicate how important the oysters were to the tribes (Steele 1957, Barrett 1963, Elsasser & Heizer 1966, Baker 1995, Baker et al. 1999, Groth

& Rumrill 2009). One particular midden found near San Francisco, California was at least 107 m in diameter and 13.7 m tall (Elsasser & Heizer 1966). It only contained O. *lurida* shells. Oyster fishers began realizing *O. lurida* was over-exploited as early as 1855, and new regulations for harvest were set; namely, no oysters could be harvested during the main reproductive season, July-August (Steele 1957) in Washington (although it was not yet a state). Washington eventually established oyster reserves in 1897, but initial populations were already devastated, and no significant increases in population growth were seen because of the harvest ban.

Not only were oysters harvested for sustenance of local tribes, but the American settlers also considered them a delicacy, a "premium oyster". In the 1850s, one plate of *O. lurida* on the half shell ran approximately $20, (about $400 today; Peter-Contesse & Peabody 2005), and *O. lurida* was said to be a favorite of Mark Twain (Beahrs 2012). Commercial takes of 7,043,409.7 liters $year^{-1}$ were reported in Washington State in the 1870s (Cook et al. 2000), but unsustainable extraction depleted the species early in the 1900s. Declines continued with the removal of adults, decreasing the reproductive outputs of populations, and removing the preferred substrate used for larval settlement (adult shells; Sayce 1976**,** Cook et al. 2000)**.** The fishing techniques used for oyster harvest (hand-picking, dredging, and "tongs") resulted in all size classes of oyster being removed, with those below the legal limit thrown back in the water, but unattached and left for dead (Coen & Luckenbach 2000). Between 1924-1926, approximately 50,000 bushels (1.5 million liters) of *O. lurida* were extracted for non-tribal consumption, but the catch decreased to 3,500 bushels (106,000 liters) by 1955 (Steele 1957). Coastal degradation and water quality problems followed in the 1930s-1950s, especially with

sulphur waste liquor produced by pulp mills (Gunter & McKee 1960), which further prevented their recovery (Cook et al. 2000). Between 1991-1996, only about 1,900 liters were commercially harvested (Cook et al. 2000). Once natural populations were depleted, farmers began cultivating them with dyke systems (see Steele 1957 for extensive details).

Association with Other Organisms

The movement of oysters for aquaculture is a notorious vector for introduced pest species, being the second highest cause of non-native marine species introductions after ballast waters (NRC 2004, Molnar 2008). Introduced parasites, protistans, diseases, and macrofauna including bivalves, crabs, and oyster drills have all been associated with *O. lurida* populations. However, likely due to the current low density of most *O. lurida* populations, these introductions have been little mentioned in recent literature. Despite this trend, however, it will be essential for managers to be able to identify and remedy infections and/or infestations of these introductions in order to promote future healthy populations.

A number of parasites have been found in *O. lurida*, most likely introduced with other bivalves brought in for aquaculture. A parasitic copepod, *Mytilicola orientalis*, affects both *C. virginica* and *O. lurida*. It appears to have been brought from Japan with oyster seed, and there is no treatment or prevention. Symptoms induced by this parasite range from undetectable (Bradley & Seibert 1978), to poor growth and condition, extreme damage in gut tissue, and in some cases, mortality (Sindermann 1974). This copepod then introduced a "red worm" that lives in the anus of the copepod, and animals found with this worm are usually in poor condition (Sinderman 1974, Peters 1993).

Flagellated protozoan parasites (*Hexamita* spp.) can be pathogens at low temperatures (Stein et al. 1959), and the parasitic flatworm *Pseudostylochus ostreaophagus* has also been introduced. Its presence is correlated to oysters in poor condition (Peters 1993). Additionally, a ectoparasitic gastropod, *Odostomia* spp., has been found on *Ostrea lurida*, but to date, has not been shown to cause negative effects on populations (Strong 1928).

Although not yet shown to cause widespread mortality in current populations, Bower et al. (1997) demonstrated that *O. lurida* is almost twice as susceptible to infection by a small protistan (*Microsytos mackini*) present in commercial beds of *C. gigas* in British Columbia, Canada compared to *C. gigas* (present in 96% of *O. lurida* vs. 48% of *C. gigas*; Bower et al. 1997). In the lab, *M. mackini* caused 89% of *O. lurida* (named *O. conchaphila* in the article, but would now be considered *O. lurida*, due to it's collection in British Columbia) to become moribund, but only 17% of *C. gigas* became moribund (Bower et al. 1997). Field-collected *O. lurida* were also found to be infected, suggesting *M. mackini* is already in the population, although it may not yet be problematic (Bower et al. 1997). Although not yet substantiated by empirical evidence, Bower et al. (1997) suggest that the introduction of *C. gigas* could have carried this protist "hitchhiker" (*M. mackini*), and that it could have played a role in the demise of *Ostrea lurida* in British Columbia during the 1940s.

Friedman et al. (2005) also found two diseases (a microcell and a hemic neoplasia) and an additional parasite (a haplosporidian-like plasmodium) in San Francisco Bay populations of *O. lurida*, in addition to finding *Mytilicola* sp., with no obvious effect on the infected individuals. However, no *M. mackini* was found, although the authors suggest the plasmodium could be related to *M. mackini.* Additionally, it

appears as though the presence of *M. mackini* has been confirmed in Washington in May 2002 (Friedman et al. 2005). The source of the hemic neoplasia, as well as it's impact on *O. lurida* remains unknown, (but see review on this disease in oysters by Elston et al. 1992). Mix & Sprague (1974) describe the first occurrence of the haplosporidian parasite in *O. lurida* in Yaquina Bay and Alsea Bay, Oregon in 1972 at low occurrences (5% at both sites through May, 1973). Atypical cells characteristic of infections with this parasite were seen in most organs and tissues, but no inflammation or degeneration was observed (Mix 1975). Despite the number of diseases and parasites known to affect *O. lurida*, little work has been done on the demographic consequences of large-scale infections. This information could prove to be crucial for managing future restoration efforts. Baker (1995) provides additional information on parasitic organisms that affect *O. lurida*.

Other introduced bivalves have also proven harmful to *O. lurida*, although indirectly. *C. virginica* was imported to supplement the commercial oyster industry when the *O. lurida* declines began in the early 1900s (Sayce 1976). Later, *C. gigas* was introduced (Sayce 1976), and the continued decline of *O. lurida* has been attributed, in part, to the aquaculture of the *C. gigas* (McKernan et al. 1949). Indirect effects, direct competition, or both could be contributing to this decline in the presence of *C. gigas.* For instance, when predatory oyster drills (see below) were absent, Buhle & Ruesink (2009) initially observed an increase in *O. lurida* survival when *C. gigas* was introduced (the authors suggest direct facilitation and shared predation risk). However, this trend was followed by a decline in *O. lurida* survival and mean relative growth rate as the density of *C. gigas* beds increased (the authors suggest a vague, "competition").

Another indirect effect possibly contributing to the decline of *O. lurida* within *C. gigas* beds includes *O. lurida* larval settlement onto *C. gigas* shells. *O. lurida* preferentially settle on shell and share many habitats with aquacultures of *C. gigas*, and *C. gigas* grows twice as quickly as *Ostrea lurid*a. Trimble et al. (2009) suggest that if spat of both oysters occur in the same place (within 5 cm of each other), *C. gigas* could be expected to outcompete or overgrow *O. lurida* within a single year. Furthermore, Trimble et al. (2009) suggest that due to a lack of hard substrate, naturally produced larvae of *O. lurida* are settling on C. g*igas* shells (located mainly above mean low low water), which are located higher in the intertidal than where *O. lurida* settle under natural conditions. This change in settlement height could impact mortality through thermal stress or desiccation, as well as removal of the *O. lurida* recruits during harvesting of *C. gigas*. In Coos Bay, Oregon, commercial *C. gigas* growers routinely find juvenile *O. lurida* on shells of *C. gigas* adults. The native oysters are removed and discarded (Groth *pers. comm*). For these reasons, there is some speculation C. *gigas* shells may actually be sinks for naturally-occurring *O. lurida* larvae.

O. lurida is negatively impacted by several native organisms. Native predators of the oyster include starfish, diving ducks (scaups and scoters; Galtsoff 1930, Cook et al. 2000), crabs (*Cancer productus*; Couch & Hassler 1989), bat rays (Matthiessen 1970) and native whelks. With the introductions of *C. virginica* and *C. gigas* also came a number of predatory gastropods. The Eastern drill (*Urosalpinx cinerea*) was introduced with *C. virginica* (Carlton 1979), while the Japanese drill (*Ocebrina inornata*) was introduced from Japan with *C. gigas* (Dall 1926). Because both drill species lack a planktonic larval stage, introduction is primarily through the transfer of infected oysters

by humans (Grason & Miner 2012). Both introduced drills have the potential to increase predation pressure on *O. lurida* populations.

Through feeding trials, Buhle & Ruesink (2009) determined that both *U. cinerea* and *O. inornata* preferred small *C. gigas* and *O. lurida* over large individuals, but preferred *C. gigas* over *O. lurida* when similar sizes were offered. In Willapa Bay, Oregon, Buhle & Ruesink (2009) found that 4.0% of mortality of *O. lurida* could be attributed to predation by oyster drills, and found up to 32% of *O. lurida* were drilled. Historically, *O. inornata*, has had an especially large impact on juvenile oysters, and due to the difficulty in eradication, some oyster growers eventually abandoned beds of *C. gigas* on the West Coast with persistent and abundant populations of the drill (Buhle & Ruesink 2009). *O. inornata* has also caused high mortality of *O. lurida* in Puget Sound (Chapman & Banner 1949)**,** and Carlton (1979 p 384) cites numerous works that suggest *O. inoranta* feeds preferentially not on *C. gigas*, but on *O. lurida, Mytilus edulis,* and *Tapes japonica* in Puget Sound, Washington.

In laboratory experiments, trophic cascades involving both native and non-native predators were examined for their influence on the recovery of *O. lurida* populations. Grason & Miner (2012) examined the feeding preferences of a native generalist crab (*Cancer productus*), which fed on both oysters and drills. Non-native drills (*O. inornata* and *U. cinerea*) served as intermediate predators, which fed only on oysters, *C. gigas* and *O. lurida*. The authors found *C. productus* does not exhibit a feeding preference between juveniles of *O. lurida* and *C. gigas*. When *C. productus* was offered a choice of two species of non-native oyster drill adults and juvenile *C. gigas*, *C. productus* consumed six times more juvenile oysters than either species of drill. These results indicate that

recovering *O. lurida* populations could be experiencing much stronger predation pressure than they did historically. The oyster populations will have to survive increased predation via two non-native drills, but also, this pressure is not likely to be eased by *C. productus* consumption of the drills. Despite *C. productus* being a generalist predator, it is not likely to be releasing *O. lurida* from increased predation pressure caused by the introduced oyster drills (Grason & Miner 2012) and is likely to be more of a competitor of drills than a predator on drills. The authors also suggest feeding rates on drills by *C. productus* in the field would likely be lower because of increased habitat heterogeneity and the ability of drills to escape. In addition, Kimbro et al. (2009) also determined that invasive crabs (*Carcinus maenas*) and whelks (*U. cinerea*) were disrupting trait- and density- mediated trophic cascades usually occupied by native crabs and whelks that resulted in increased mortality for *O. lurida*. The authors found patterns in oyster mortality in Tomales Bay, California to be related to invasive drill *U. cinerea* abundance, rather than abiotic conditions such as thermal stress or desiccation. These altered trophic cascades could have large impacts for restoration sites where drills and *C. productus* are both present, the predation pressure being too great to allow recovery.

Bioturbating thalassinidean shrimp also impact *O. lurida*. As sessile, benthic filter-feeders, sediment resuspension from resident fauna can be fatal. For example, *Neotrypaea californiensis* and *Upogebia pugettensis* cause sediment resuspension and sediment destabilization via bioturbation while making burrows up to 90 cm deep (Swinbanks & Luternauer 1987). The destabilized sediment may no longer support the oysters, at which point they begin to sink into the mud, preventing water flow needed for feeding and respiration. Furthermore, gills and ciliary tracts become clogged with

sediment, causing slower growth and higher mortality (Feldman et al. 2000). Shrimp populations are yet another variable managers should take into account when selecting restoration sites.

Large blooms of the diatom *Melosira borreri* pose another threat to *O. lurida*. During the 1950s when pollution by sulphur liquor from pulp mills was a problem, these diatoms "bloomed" all year long—the dead diatoms then accumulating up to 15 cm in dykes where Olympia oysters were grown, causing local extinction (Steele 1957). The sulphur waste liquor was determined as the cause of continuous *O. lurida* decline in the 1950s (Hopkins 1935, McKernan et al. 1949, Steele 1957), partially due to its facilitation of *M. borreri* growth. Despite the historic significance to *O. lurida*, however, no recent work was found to indicate if this diatom is still ecologically important.

As filter feeders, one would also suspect fouling organisms (many of which are also filter feeders) and conspecifics to affect growth and survival. Deck (2011) found competition effects on recruit growth in Tomales Bay. Competitors (typical fouling organisms such as bryozoans and tunicates) decreased average recruit size by up to about half. Interestingly, these competition effects appear only to influence early-stage recruits; there was no apparent affect of competition on juvenile (mean size 15 mm) or adult growth rate or survival. Competition effects may also be at play in San Francisco Bay, where recruit abundance also decreased in the presence of competitors (Deck 2011). To better understand the interactions between conspecifics and heterospecifics, Trimble (2009) out planted oysters on tiles in Fidalgo Bay, Washington, and followed growth and mortality of *O. lurida*. Indeed, fouling organisms (ascidians, hydroids, sponges) and conspecific competitors depressed the maximum *O. lurida* length by 2-35%, and

decreased survival from 15 to 7% (Trimble 2009). The author also discovered that removing fouling organisms (ex. barnacles, ascidians) from the tiles resulted in oysters that were twice as likely to survive as those with the fouling organisms left in place (Trimble 2009). Additionally, it was observed that the largest five oysters on each tile were those that were farthest separated from the nearest neighbor, further suggesting that intraspecific competition could affect growth, and subsequent success, including reproductive condition and fecundity (Trimble et al. 2009). Many consider *O. lurida* to be gregarious, and little work has been done specifically on intraspecific competition.

Other Threats to Recovering Populations

Staggering population declines to the point of functional extinction have been observed over the entire distribution of *O. lurida* (Kirby 2004, Beck et al. 2011). The dearth of hard substrate settling sites is often cited as an important factor that may hinder the recovery of *O. lurida* (Groth & Rumrill 2009, see Brumbaugh & Coen 2009 for a full review). Without sufficient hard substrate (rip-rap, shells, pilings etc.) settling larvae may be forced to settle on wood, mud, or debris, which could be washed away, buried in settling sediment, or resuspended and deposited in unsuitable environmental conditions. However, Polson & Zacherl (2009) hypothesize that substrate might not be a factor limiting the recovery of natural populations, but state that explicit studies are needed to confirm this hypothesis. Monitoring recruitment and survival on unenhanced (rip-rap, mud, debris) and enhanced (for example, with shell bags) areas would help illuminate the importance of hard substrate in promoting recovery.

Declining populations of *O. lurida* have also been attributed to land use changes (Clasen et al. 2010), sewage contamination (Galtsoff 1929) and long-term effects of sulphur liquor emissions from pulp mills in the early 1900s, which was shown to have negative affects on both reproduction and health (Hopkins et al. 1935, Odlaug 1949). Logging, mining, and high boat traffic could also be negatively impacting bay water quality and thus oyster habitat. Sedimentation caused by topsoil runoff in areas of logging and mining could cause clogging of gills and respiratory tracts in bays with low water movement and tidal flushing (Trimble et al. 2009). Bays are also being polluted by gasoline and motor oil, especially in areas of high boat traffic such as the Coos Bay estuary, where shipping, and commercial and recreational fishing are prevalent (Oregon International Port of Coos Bay). Clark et al. (1974) estimate about a 10% loss of outboard fuel for each boat on the waterways. Although Clark et al. (1974) suspect oysters can tolerate brief exposure to motor oil and gasoline by closing their shell, mortality results after 10 days at even dilute concentrations.

Larval Supply, Settlement, and Recruitment

In order to understand adult populations of sessile organisms such as *O. lurida*, the spawning, dispersal, larval supply, settlement/recruitment and adult survivorship all need to be addressed (Porri et al. 2006)**.** Beck et al. (2011) and zu Ermgassen et al. (2012) show current *O. lurida* populations are far below historic numbers. Despite bans on harvesting and widespread restorations efforts, the contributing factors to persistent, low population sizes remain unknown. One potential limitation could be larval supply—there simply aren't enough larvae arriving to replace past generations. This could be due to

either very low numbers of larvae being produced, or very low numbers being delivered. For example, in the Coos Bay estuary, *O. lurida* larval abundance is high in the mid- to upper-bay, but low in the lower bay (see Chapter III). It is likely, therefore, that local (within-bay) populations are reproductive, yet the larvae are not delivered to the lower portion of the bay. Whether this degree of larval supply in the mid- to upper- bay is sufficient to facilitate population growth is unknown, but demonstrates that small-scale variation in larval supply is present within a single bay. The amount of larval delivery should be carefully considered when selecting a restoration site.

Like many marine species, *O. lurida* seems to have populations which receive more larvae than they supply, and vice versa; populations which supply more larvae than they receive (source and sink populations). The dispersal that occurs between these populations is likely heavily influenced by hydrodynamic regimes and pelagic larval duration. Using shell elemental spectroscopy, within San Diego County, San Diego Bay was found to contribute 45.0% of recruits, followed by two North County lagoons (35.4%) and Mission Bay (19.6%)(Carson 2010). Carson (2010) also found that although Mission Bay supplied only 19.6% of the larvae in the area, it received 80% of larvae from San Diego Bay and the North County lagoons. The larval contribution of a population is extremely important from a management perspective. For example, when designing a marine reserve, it may be desirable to include both source and sink populations. Sink populations (as in Mission Bay) are receiving high larval input relative to their output, and could in the case of *O. lurida*, be a refuge for larvae to settle on increasingly healthy reefs, and subsequently help restore habitat health and function within the reserve. Additionally, if larvae are supplied to the sink population from a variety of local

populations, genetic diversity could increase, making the populations more genetically heterogeneous over time. Including source populations (for example, San Diego Bay and the North County lagoons) in marine reserves is also important to promote larval supply to nearby populations.

Despite the apparent larval connectivity at small geographic scales, as in Carson (2010), connectivity does not appear to extend between large geographical areas (for example, between California and Washington; Stick 2011). Although perhaps a rogue larva may disperse between the five regions presented in Stick (2011), the apparent genetic distinctions between oysters between these five regions suggest that large-scale population connectivity is slow enough for genetic differences to accumulate. These data may represent localized adaptations of each population, and should be considered before transferring oysters between regions.

Carson (2010) also found no clear pattern between the percentage of brooding adults at a site and the subsequent release of larvae from the site. Using elemental spectroscopy on recruit shells, Carson (2010) also found population connectivity between estuaries separated by 75 km in California, and suggested that California populations may be more connected than more northern populations in Oregon, Washington, and British Columbia, perhaps due to oceanographic characteristics of the region. In Coos Bay, Oregon, little larval supply and no settlement is seen past the bend located in the middle of the estuary, but high larval supply and settlement are seen in the upper portions of the bay (Chapter III). Furthermore, larvae are found at low concentrations offshore compared with concentrations within the bay (~3 m^3 vs. ~50 m^2; Petiero *unpublished*) which also suggests that large-scale, long-distance connectivity is rare near the Coos Bay estuary.

If larval supply is deemed sufficient, settlement and recruitment may be limiting population growth. Specific settlement cues used by *O. lurida* larvae remain unknown, although the presence of hard substrate, conspecifics, and biofilms are likely contributing cues, it is also possible that larvae evaluate the environment parameters (such as temperature and salinity) before settling. For example, within the Coos Bay estuary, larvae are supplied to two sites that, due to the sites proximity to the outflow of the Coos River, exhibit large daily tidal and seasonally ranges in temperature and salinity. Settlement and recruitment data collected approximately every two weeks at these two sites showed settlement was near zero despite sufficient larval supply (see Chapter III). Seaward of these two sites approximately 4 km, however, larval supply is slightly higher, but settlement is drastically higher, possibly due to the muted daily ranges in salinity. This suggests that either the larvae were not finding the two more riverward sites suitable for settlement, or they were not surviving the two-week sampling period between collections due to physiological stress from environmental parameters such as temperature, salinity, or desiccation, or alternatively, predation. Examining larval supply and settlement together will allow researchers and management to better understand the population dynamics; namely, whether the populations have limited recovery due to a lack of larvae and recruits, inadequate settlement surfaces, or post-settlement mortality.

Understanding more about larvae, settlers, and recruits is essential for successful restoration. Restoration efforts are being implemented throughout the entire range of *O. lurida*, at both small scales (individual landowners), and large scales (13% of Willapa Bay, Trimble et al. 2009). These efforts most commonly consist of artificially spreading hard substrate (such as adult shell), and releasing hatchery-reared "seed", i.e., late-stage

larval oysters capable of settling, with the hopes that these seed will settle, survive, reproduce, and contribute to future natural populations. However, very little work has addressed the factors contributing to successful settlement, survival, and growth on the early life-stages of *O. lurida* in the field. For example, Dinnel et al. (2011) seeded each of two sites within Fidalgo Bay with 10 bags of hatchery-reared *O. lurida* seed. Both sites subsequently had "not fared well for reasons presently unknown". Dinnel et al. (2011) also observed the mortality rate of seeded oysters at their restoration project. From 2002 through 2006, survival was consistently high, at about 90%, but dropped to 39% by 2009. Thus, although the conditions at this site were satisfactory for the early-stage oysters during 2002-2006, something went wrong by 2009, but the driver of reduced recruit survivorship currently remains unknown.

Not only is it important for future restoration efforts to compile information about larval survival, but also larval behavior and dispersal, factors, which will influence metapopulation connectivity. Dinnel et al. (2011) found *O. lurida* recruits within Fidalgo Bay in 2008-2011, where none were observed in previous years. The highest densities of recruits were found closest to their trestle restoration site, and the authors conclude that the larvae were from their nearby restoration site. The authors report, "Most seed appear to be staying on site and are not being carried very far by currents or waves". In the same study, nearby areas surveyed after restoration efforts were implemented revealed new populations close to the restoration site, with abundance decreasing along a gradient away from the trestle site. Do the larvae have some behavioral mechanisms that allow them to be retained relatively close to their natal populations? Should restoration managers be cautious about hoping restored populations will help seed distant

populations, namely from outside a particular estuary? Is this more support for Stick's work (2011) that long-range dispersal is a rare occurrence? Possibly, but again, this topic could benefit from future research.

Within the context of using oyster seed to initiate new adult populations, it is important to understand abiotic factors that could either render a site successful and promote self-sustaining populations, or predict relative failure. Where a competent larva settles is one of the most influential factors affecting its survival. Choosing an adequate settlement substrate can mitigate thermal stress, desiccation, food shortage, predation, and competition. Thermal stress is minimized when the surrounding water can act as a buffer from large shifts in temperature and can minimize the risk of desiccation. Thermal stress caused by extreme heat or cold can affect metabolic and reproductive performance, as well as growth and mortality within populations (Bertness et al. 1999, Leonard et al. 1999, Leonard 2000, Pineda et al. 2009). It appears most *O. lurida* larvae settle within the intertidal zone mid-way between high and low tide (Hopkins 1937). It also seems as though seed (settlers) become somewhat acclimated to the physical environment into which they settle; Steele (1957) reported that seed transported from one location to another after settlement would only grow if the second location had the same temperature, salinity and "mineral content" as the first location.

Choosing a suitable substrate on which to settle is one of the most important decisions a larva will make, and will drastically influence the physical stress (desiccation, temperature, salinity) to which it is exposed. However, even within a relatively small area, some habitats are more suitable than others. For example, according to (Hopkins 1935), 115x more spat were found on the under-side of horizontal surfaces compared to

the upper, and 3x more on the underside of horizontal surfaces compared with vertical surfaces. Hopkins hypothesizes that this is likely due to the swimming orientation of the larva, with the velum pointed upward (Hopkins 1935). Hopkins (1935) also demonstrated the oyster's preferential attachment is not a result of negative phototrophic behaviors, but suggests the larvae may be negatively geotactic; a possible evolutionary adaptation to reduce exposure to direct sunlight and thus decrease thermal stress to the future recruit. Working with settlement plates submerged for three months, however, Hopkins recognized that these recruitment data may reflect survivorship and not settling preference. However, even in a laboratory setting, we have observed almost all settlement occurring on the under-side of settlement plates. Settling on the underside of surfaces may be an adaptive trait, designed to protect the larva from exposure to the sun, and thus a higher risk of desiccation and larger daily temperature variation.

As *O. lurida* has a planktonic larval stage and is a benthic, filter feeding adult, the importance of settling in an area with sufficient water movement cannot be overstated. Once oysters become reproductive, water disperses sperm and delivers it to females; it provides a continuously renewed source of food and oxygen, and helps regulate the thermal and water quality parameters in which larvae and adults live. Larval dispersal and therefore delivery to other populations (perhaps less reproductive, or that have experienced a mortality event and are in need of reestablishment) also cannot occur without water movement (Bertness et al. 1991, Leonard et al. 1998). Conversely, very high flows can prevent larval attachment and settlement by whisking larvae away before they have an opportunity to attach solidly to the settlement surface (Pawlik & Butman 1993, Qian et al. 2000, Larsson & Jonsson 2006). There likely exists some balance

between high and low flow, which allows for successful larval attachment and sufficient oxygen and food delivery. Again, however, surveys have not been conducted to understand how flow regime affects settlement and growth.

Sedimentation may also be a significant concern, and may drive settlement preferences (Wasson 2010). Barrett (1963) suggested that *O. lurida* may have disappeared from Bolinas Lagoon and Morro Bay, California as a result of increased sedimentation rates at these sites caused by hydraulic mining. Likewise, the disappearance of the oyster from Coos Bay, Oregon may have been due to a tsunami or large fire followed by heavy rains, which resulted in heavy sedimentation that smothered *O. lurida* populations. *O. lurida* may also show a preference for settling on natural hard substrates such as rocks, shells and gravel in shallower mud, but not deep mud, where these substrates are absent or are likely to sink into the mud over time (Wasson 2010). Wasson (2010) found neither juvenile size nor density was significantly different between sites of high vs. low sedimentation, although mortality was significantly higher (p=0.03) in areas of high sedimentation (85% vs. 66%, respectively). Additionally, shell habitat was more preferred by recruits than bare sediment, which was preferred over eelgrass habitats (*Zostrea marina*) (Trimble et al. 2009). However, these recruitment patterns among substrate type could have been an effect of survival rather than settlement preference.

In addition to recruitment substrate, location in the intertidal also appears to be important to survival. Trimble et al. (2009) found over 50% mortality of juvenile oysters after exposure to air 2-10% of the time. *O. lurida* settlers are more than twice as likely to settle on cultch placed 0.3 m below MLLW than 0.3 m above (Trimble et al. 2009). In

addition, Wasson (2010) searched 32 sites (25 characterized as mudflats, where hard substrate constituted on average only 1.4% of the area, and 7 mudflats enhanced with anthropogenic hard substrate, with between 34-288 m^2 hard substrate) and found that oysters were only present at 5 of 7 sites where hard substrate was available. Hard substrate is also limited within the Coos Bay estuary. Here, Groth & Rumrill (2009) even observed subtidal settlement on old marine batteries, indicating there may be substrate limitations to recovering populations.

Settlement and survival of young settlers is spatially and temporally variable. Between 2002 and 2006, Trimble et al. (2009) followed survival of newly out-planted *O. lurida* juveniles in Willapa Bay, Washington. Although densities of juveniles were high when out-planted early in Summer 2002 (at least 100 per 11 cm^2), high mortality was seen throughout the rest of the year. Mortality decreased through the winter, but increased again in the spring (2003), with the authors suggesting intraspecific competition as a culprit (Trimble et al. 2009). Growth on settlement tiles was also measured, with newly settled oysters reaching 20 mm by the end of summer, and 30 mm by the end of their second summer. However, growth was slow in the winter, likely due to low temperatures (Trimble et al**.** 2009).

Hopkins (1937, working in La Jolla, California) suggested that the Olympia oyster typically has two settlement peaks 6-8 weeks apart. In Coos Bay in 2010, larval abundance peaks were observed 3-4 weeks apart (mid-August 2010, mid-September 2010; Petiero-Garcia, *unpublished*) while in 2010, Sawyer (2011) observed only one settlement peak (mid-October), with two lesser peaks (mid-September, mid-November). In 2012 in Coos Bay, one settlement peak was observed in late July and settlement

steadily declined through September (Chapter III). In 2013 in Coos Bay, one settlement peak occurred late June through early July (Chapter III). Spawning may be variable between years, and between, and even within geographic location.

One area of particular interest to restoration efforts is that of recruitment, or the survival of early-stages into the adult populations. One element of recruitment that appears to be especially important to *O. lurida* is the availability of hard substrate on which to settle, and the lack of hard substrate is often cited as one of the limiting factors to *O. lurida* population recovery (Brumbaugh & Coen 2009, Groth & Rumrill 2009). If larvae lack hard substrate on which to settle, they may cope through one of two choices: 1) settle in a sub-optimal area (for instance, on soft substrate, where they are likely to encounter heavy sedimentation and mortality) or 2) continue their pelagic larval stage, which may result in mortality due to predation or larval wastage.

Managers are looking for information that can help establish environmental parameters that would encourage successful recruitment. Deck (2011) found recruitment in Tomales Bay along an estuarine gradient to be strongly influenced by residence time. Recruitment was positively correlated with residence time of the bay, both intertidally and subtidally (Kimbro 2008, Deck 2011). Deck (2011) also found high recruitment mid-bay in Tomales Bay, as was observed in Coos Bay (Chapter III), and decreasing recruitment towards the head and mouth in both estuaries. We hypothesize this pattern may be driven by larval flushing on the mouth side of the bay, and physiological limitations at the head of the bay (see Chapters 3 and 4).

After recruitment, growth, especially to a reproductive age, becomes important. Deck (2011) found growth rates up to 81% higher subtidally than intertidally in 2008, but

not different in 2009. Growth of individuals subtidally was found to be more stable and higher throughout the estuary than for individuals intertidally**.** Because there were no clear differences between oyster growth along the estuarine gradient subtidally, Deck (2011) suggested that intertidal oysters are limited by feeding time and food concentration, as they would be expected to be more exposed to riverine than marine phytoplankton concentrations. Trimble et al. (2009), however, found tidal elevation (three treatments: 1) settlement plates always submerged, 2) 0.3 m below or 3) 0.3 m above MLLW, in WA) to have no effect on growth, but tidal height had a large influence on survival. Oysters 0.3 m above MLLW had <5% survival, while oysters on tiles that were continuously submerged had survival of 20%.

Working in Elkhorn Slough, CA, Wasson (2010) found adult and juvenile *O. lurida* to be totally absent from 13/13 areas with minimal (maximum 1-15 cm) tidal exchanges, and suggested that these areas could be more heavily influenced by pollution, hypoxia, and low salinities than areas with more tidal mixing. She also found up to 90% juvenile survival in muted tidal ranges (defined as a maximum range between 15-100 cm) but an average of only 65% survival at sites with full tidal exchanges. Wasson (2010) attributes the higher survival at sites with muted tidal ranges to decreased sedimentation, and states that these areas might be successful restoration sites, as long as tidal flushing is substantial enough to prevent water quality problems. Additionally, she found oysters present at high or low abundances in 5/7 sites in areas with high tidal changes (maximal tidal range 250 cm; Wasson 2010).

As previously stated, restoration efforts for *O. lurida* are currently underway throughout the species' distribution. With these efforts, data are being collected regarding

methods and progress and status of the restoration efforts, but little is understood of the mechanisms driving the subsequent progress. For example, in 2002, the Skagit County Marine Resources Committee began restoration efforts in South Fidalgo Bay (Dinnel et al. 2009). Fidalgo Bay was considered lacking the hard substrate necessary to allow natural, successful recruitment of the Olympia oyster. *C. gigas* shell was used under a railroad bridge to provide this hard substrate. Although shell bags were placed out in June 2003, the first recruitment at very low numbers was not detected until June 2005. However, no recruits were found again in 2006, which suggest that spawning/successful recruitment did not occur in 2005 (Dinnel et al. 2011). Low numbers of recruits were found in Spring 2007, which suggests 2006 was a mildly successful reproductive year. Further, no subsequent recruitment was seen using the same methods in 2008 and 2009, suggesting 2007 and 2008 were also bad reproductive years. "Substantial" recruitment (2.7 juveniles/cultch shell) was seen in 2010, however. The authors state that no recruits were found on shell bags in locations other than south Fidalgo Bay, (Cape Sante Head, Guemes Channel, or east March's Point). These patterns further support the idea that there may be relative reproductive failure every few years. Despite frequent poor recruitment, initially low densities of oysters recorded in 2003 in Fidalgo Bay, 45 m^{-2}, were up to 130 m^{-2} by June 2011 (Dinnel et al. 2011). Recruitment between 1.6% - 23.5% of the population was observed between 2008 and 2011. The Samish Tribe tried another restoration site at Weaverling Spit, in Fidalgo Bay in 2003. However, by 2006, no live oysters were found. It is hypothesized by (Dinnel et al. 2009) that restoration efforts failed at this site because it did not have standing water at extreme low tides.

Ocean Acidification

A very nice study was done by Hettinger et al. (2012) on the effects of ocean acidification on larval and juvenile growth. Larvae were reared in treatments of 700 (control), 800, or 1100 ppm CO^2, which correspond to pH of 8.0, 7.9, and 7.8, respectively, and are well within the ranges of current conditions in Tomales Bay (between 200 and up to 1500 ppm CO^2 during severe conditions). The mean summer condition of 700 ppm CO^2 was chosen as a control, while 800 and 1100 ppm CO^2 were chosen to simulate future mean conditions based on available projections. Hettinger et al. (2012) found that after nine days, larvae reared in a pH of 7.8 had 15% slower shell growth, relative to larvae reared in control conditions (pH 8.0). Furthermore, larvae reared in the pH 7.8 treatment had 7% smaller shells area at settlement relative to control larvae. Lastly, seven days after settlement, juveniles reared in pH 7.8 had 41% slower shell growth compared to control juveniles. Depending on the conditions to which they were exposed as larvae, this study concluded that persistent carry-over effects influence juvenile shell growth rates. In a restoration context, therefore, this study suggests that site selection for restoration efforts should consider pH.

With a lack of information about the relative locations of historical populations within estuaries, coupled with the slow recovery of natural populations, it remains unknown under what conditions *O. lurida* are most successful during the different life history stages. It has been suggested that the earliest life stages are most sensitive to physiological tolerances (Bayne et al. 1976), but there is currently no information on the physiological tolerances of *O. lurida* larvae to temperature and salinity, and how variations in these parameters might influence growth, settlement, or mortality. Although

it is relatively straight-forward to observe adult mortality and growth, understanding the physiological tolerances of the early life stages (larvae, settlers) of this oyster in the field is limited by the small size and the planktonic habitat. Understanding these tolerances may provide information to managers, who can evaluate potential restoration sites, based on their ability to promote high larval growth, settlement, and survival.

Conclusions

As with many bivalves, the contribution of *O. lurida* to ecosystem health is likely significant. They provide habitat and help prevent shoreline erosion, are important in food webs, and promote biodiversity. They provide environmental heterogeneity and thus refuge for many invertebrates and larval fish (Burrell 1986, Baker 1995, Posey et al. 1998, Breitburg et al. 2000, Coen and Luckenbach 2000, Lenihan et al. 2001). However, little historic information is available on the faunal communities supported by healthy reefs, and even less is known about reef depth, density of reefs, and where they occur naturally in both subtidal and intertidal environments. *Crassostrea virginica* (eastern coast of the United States) has been used more frequently in experimental manipulations seeking to understand their importance in ecosystem functioning. Coen & Luckenbach (2000) provide a useful review in Section 4, Ecology of Oyster Reefs. It is likely that on the West Coast, *O. lurida* may have provided these same ecosystem services.

Some of the most important services *O. lurida* delivers are due to their filter feeding. They sequester toxins such as pestides, PCBs, heavy metals, and even coliform bacteria from agricultural waste while filter feeding (Alzieu 1998, Aune et al. 1998, Scott et al. 1998, Nice et al. 2000, Dumbauld et al. 2001). What's more, they can provide long-

term storage for pollutants through incorporation into their shell or into pseudofeces, which become buried in the substrate. As filter feeders, they also facilitate nutrient cycling between the pelagic and benthic environments (Newell 2004), and improve water quality. The hypothetical benefits provided by these oysters are clear, but with very few current populations still having historic abundances, little empirical information exists on how communities residing within, or depending on the habitat heterogeneity oyster beds have changed.

In conclusion, a brief summary of advice for restoration efforts; first and patterns observed and recorded in the field pertaining to any aspect of *O. lurida* biology or ecology, be published and made available to parties interested in *O. lurida* restoration efforts. For example, Dinnel et al. (2009, 2011) have provided valuable data on their initiated restoration projects in Fidalgo Bay, WA and subsequent recruitment patterns observed over years. Yet the authors had no explanation for why some years exhibited successful recruitment, while other years did not. Furthermore, they observed what was apparent limited larval dispersal, which became apparent by increasing range of recruitment from the initial restoration site. These data are field-collected, and provide valuable data about patterns observed in the native environment of *O. lurida*. Furthermore, the authors admit what they do not know what is driving successful or unsuccessful recruitment between years. These field-collected data provide no shortage to interested parties of areas of the biology and ecology which could use more focused attention.

On a more conventional note, location within the estuary appears to be a very important factor having the potential to influence the success of restoration efforts. First,

areas need to have residence times facilitating *O. lurida* larval retention within their bay. Secondly, restoration locations should occur mid-bay (not too far seaward or riverward). This is where high larval supply has been seen (Coos Bay estuary; Garcia-Petiero *unpublished*, Chapter III), as well as recruitment (Kimbro 2008, Deck 2011, Chapter III). Furthermore, these mid-bay sites appear to have longer retention times than sites located close to the mouth of the bay, but yet not the large ranges in environmental parameters observed at the head of the bay. At the head of the bay, ranges in environmental parameters are generally high due to the proximity to the river, and Wasson (2010) has shown adult populations to be absent at these types of sites. Third, hard substrata should be available in the low intertidal, or high subtidal to protect oysters from desiccation, but also freezing temperatures in the northern part of their range. Fourth, ensure sufficient tidal flushing to allow for food resources and oxygen delivery. Lastly, ensure summer temperatures at restoration sites reach critical reproductive temperatures; this will enable populations to become self-sustaining, if successful. If restoration efforts were initiated at sites where the minimum temperature never rose above the minimum threshold, the site would be completely dependent on management-supplied spat.

This review was undertaken to provide a base of knowledge to initiate an informative and project valuable to *O. lurida* restoration efforts. During the literature search and subsequent review, no primary literature was found that attempted to directly measure larval supply *and* recruitment along an estuarine gradient. Larval supply had been inferred, and recruitment measured, but they had not been measured simultaneously and directly. In Chapter III, we measure larval supply and recruitment simultaneously along the Coos Bay estuary in 2012 and 2013.

CHAPTER III

LARVAL SUPPLY AND RECRUITMENT OF *OSTREA LURIDA* IN THE COOS BAY ESTUARY, OREGON

Rose Rimler and I develop the experimental set-up of the project in this chapter. I collected larval abundance data while Rose collected recruitment data. I wrote the majority of this chapter, but Rose contributed much to the production of both the Introduction and the Settlement Plate Design and Analysis portion of the Methods.

Introduction

Here, we examine the relationships between environmental parameters (temperature and salinity) and larval supply and recruitment of the Olympia oyster, *Ostrea lurida* in a Pacific Northwest estuary. *O lurida*, the only native oyster on the west coast of the United States, is currently a target organism for restoration; populations are estimated to be at only 1-10% of their historic numbers along the Pacific Northwest (Beck et al. 2009). This species has been severely negatively impacted by historical commercial exploitation and habitat degradation.

Shell deposits, indicative of historical harvesting, in the Coos Bay estuary, Oregon, provide evidence for large populations of the oyster that likely supported tribal subsistence fisheries. By the time European recruits arrived (mid-1800s), however, no oysters were found in the estuary (Dall 1897). It has been suggested that the introduction of Japanese oysters (*Crassostrea gigas*) from Willapa Bay to Coos Bay for mericulture

purposes reestablished *O. lurida* populations by transporting from Willapa Bay juvenile *O. lurida* "hitchhikers" attached to *C. gigas* shells. However, 60 years later, recovery has been minimal.

Marine invertebrate populations can vary greatly over both space and time. For example, Beck et al. (2011) have classified current *O. lurida* populations along the West Coast of the United States ranging from "functionally extinct" (more than 99% lost) to "good" (less than 50% lost), and zu Ermgassen et al. (2012) have estimated that less than 1% of historic populations are remaining at some locations in both California and Washington. *O. lurida* populations were historically harvested both tribally and commercially, but despite current restrictions on harvesting, recovery has been weak in most populations. The mechanisms driving these persistently low populations and the limited recovery of *O. lurida* are poorly understood.

One possibility is recruitment-limitation; an insufficient number of larvae are being delivered or settling to replace previous generations. If this is the case, it is important to understand whether populations are open or closed. Open populations are characterized by strong larval input from distant populations, while closed populations receive the majority of larvae from local populations. Stick (2011) identified five genetically distinct regions in which *O. lurida* populations now exist, suggesting that most *O. lurida* populations are relatively closed. *O. lurida* populations in Coos Bay, where portions of this study were conducted, were genetically grouped with Willapa Bay populations, but this has been hypothesized to be due to the transfer of adult individuals in the earlier part of the century, rather than larval connectivity. Therefore, it is likely that due to the 1) estuarine nature of these oyster populations, and 2) reproductive season

coinciding with increased residence times of the estuaries, that populations may be relatively closed, with little long-range dispersal. If this assumption is correct, population recovery will depend on larvae both being supplied and settling within local populations.

Alternatively, *Ostrea lurida* populations may be recruitment-regulated, or driven by biotic or abiotic factors. Examples of biotic regulations may include predation and density-dependent interactions, while examples of abiotic factors include physiological constraints such as desiccation, and critical temperature thresholds that control feeding, reproduction or recruitment.

The lifecycle of *O. lurida* consists of three stages; 1) planktonic larvae, 2) benthic settlers, and 3) benthic adults (see Chapter II for more details). Reproduction in *O. lurida* is thought initiate only after a critical minimum daily temperature is reached (Garcia-Peteiro *unpublished,* Oates *unpublished*). In the Coos Bay estuary, this temperature is thought to be 15°C and it is assumed that below this critical temperature, adults are incapable of reproducing. However, after reproduction is initiated, brood larvae are spawned. After the pelagic larval stage, a successful larva settles and undergoes metamorphosis to become a juvenile settler, and eventually a benthic adult. Settlement is often a complex process, and can also be dictated by a wide variety of variables, including the physiological condition of the larva (Tremblay et al. 2007), small-scale hydrodynamics (Millineaux & Butman 1991, Millineaux & Garland 1993), larval competency, gregariousness, predation, substrate availability, and abiotic environmental stressors. At settlement, the pelagic larva goes through metamorphosis to become a benthic juvenile within a short period. Recruitment examines the longer-term survivorship of the settlers, and is generally discussed in terms of the number of

individuals that survive after a prescribed period per unit area (Pineda et al. 2009). Settlement and recruitment are thus considered two different measurements. By some estimates, less than 1% of spawned marine invertebrate larvae are recruited to the adult population (Pineda et al. 2009). However, to have sustainable populations, much less than 1% successful recruitment is required; each adult only needs to contribute one successful offspring over their lifetime in order for the population to be stable. However, the processes affecting each successive life-stage are not always well understood.

Planktonic larvae, settlers, and adults may be subject to population pressures independently (Yoshioka 1982, Caley et al. 1996, Eckman 1996, Palmer et al. 1996, Tremblay et al. 2007, Beck et al. 2009, zu Ermgassen et al. 2012). Studies aiming to understand the factors influencing the abundance of adult stages of a multi-phasic species must investigate each life-stage independently in order to understand the relationship between them, and their effects on population size (Gaines & Bertness 1993). Groth & Rumrill (2009) examined local adult population abundances and distribution of *O. lurida* in the Coos Bay estuary, Oregon, although this study did not investigate factors that could be driving local abundances. Here we will only be considering larval supply and recruitment, and discussing the potential causes of these abundance patterns.

Traditionally, studies simultaneously examining the abundance of pelagic larvae and settlers or recruits, have used a combination of spatiotemporally disjointed methods. First, pelagic larvae are collected using plankton tows or pumps. Both methods are generally performed from a boat, where a boat can be handled safely, generally in deeper waters than the intertidal. If researchers are interested in the larval supply and recruitment of intertidal species, however (for example *O. lurida*), it is prudent to observe larval

supply in the same habitat where competent larvae settle; namely the intertidal. Secondly, both plankton tows and plankton pumps constitute instantaneous sampling, generally over a period of minutes. Settlement plates, however, may be deployed for days to months. The larval abundance from instantaneous methods is then extrapolated to match deployment duration of the plates. However, the distribution of larvae has been shown to be patchy (Jones & Epifanio 1995, McQuaid & Phillips 2000, Eggleston et al. 2006), and extrapolated larval abundances often predict much different abundances than those obtained from integrated sampling.

A more appropriate alternative to understanding the relationships between larval supply and recruitment or recruitment is the use of time-integrated approaches for both measurements (Seed 1976, Suchanek 1985, Yund et al. 1991, Setran 1992, Whitlatch & Osman 1998, Underwood & Keough 2001, Todd 2003, Porri et al. 2006). For example, passive larval tube traps (a time-integrated approach to larval sampling, Yund et al. 1991, Gaines & Bertness 1993) have been shown to correlate more strongly than plankton pumps with settlement rates (Gaines & Bertness 1993, Dudas et al. 2009). These integrated methods allow researchers to obtain a more accurate picture of the factors influencing adult populations because they are obtained in the same habitat, and over the same period. Additionally, integrated methods allow larval supply to be measured in the same habitat as measurements of recruitment (Jeffery & Underwood 2000, Todd et al. 2006, Tremblay et al. 2007).

In Coos Bay, we have information on modern *O. lurida* populations. Polson & Zacherl (2009) found the Coos Bay estuary to have one of the five largest populations of adult Olympia oysters on the West Coast. Baker (1995) estimated populations to be up to

201 m^{-2}, and Groth & Rumrill (2009) found 61.3 large adults m^{-2} (> 20 mm). Multiple size classes have also been observed in the Coos Bay estuary, indicating reproductive events that have resulted in recruitment over the last few years (Polson & Zacherl 2009). Surveys conducted intertidally in 2006 in the Coos Bay estuary (Groth & Rumrill 2009) found numerous adult populations in the estuary, including at relatively polyhaline sites such as Haynes Inlet and Downtown Coos Bay, in addition to mesohaline sites like Coalbank Slough. However, surveys have not found populations of adult *O. lurida* at more marine sites, such as Empire, or sites located near the input of the Coos River, such as Catching Slough (Figure 1).

In this study, we used integrated sampling techniques to quantify the relative larval supply and recruitment of *O. lurida* throughout the Coos Bay estuary during the reproductive period in 2012 and 2013. Specifically, we asked: 1) does the relationship between supply and recruitment vary with location and over time? 2) do water quality parameters such as temperature and salinity predict larval abundance or recruitment? and 3) are larvae supplied to areas outside of their adult range, and, if so, will larvae settle in areas outside of their adult range when given appropriate substrate? This study is the first study that we are aware of to examine the relationships between larval supply and recruitment of *Ostrea lurida* in the field.

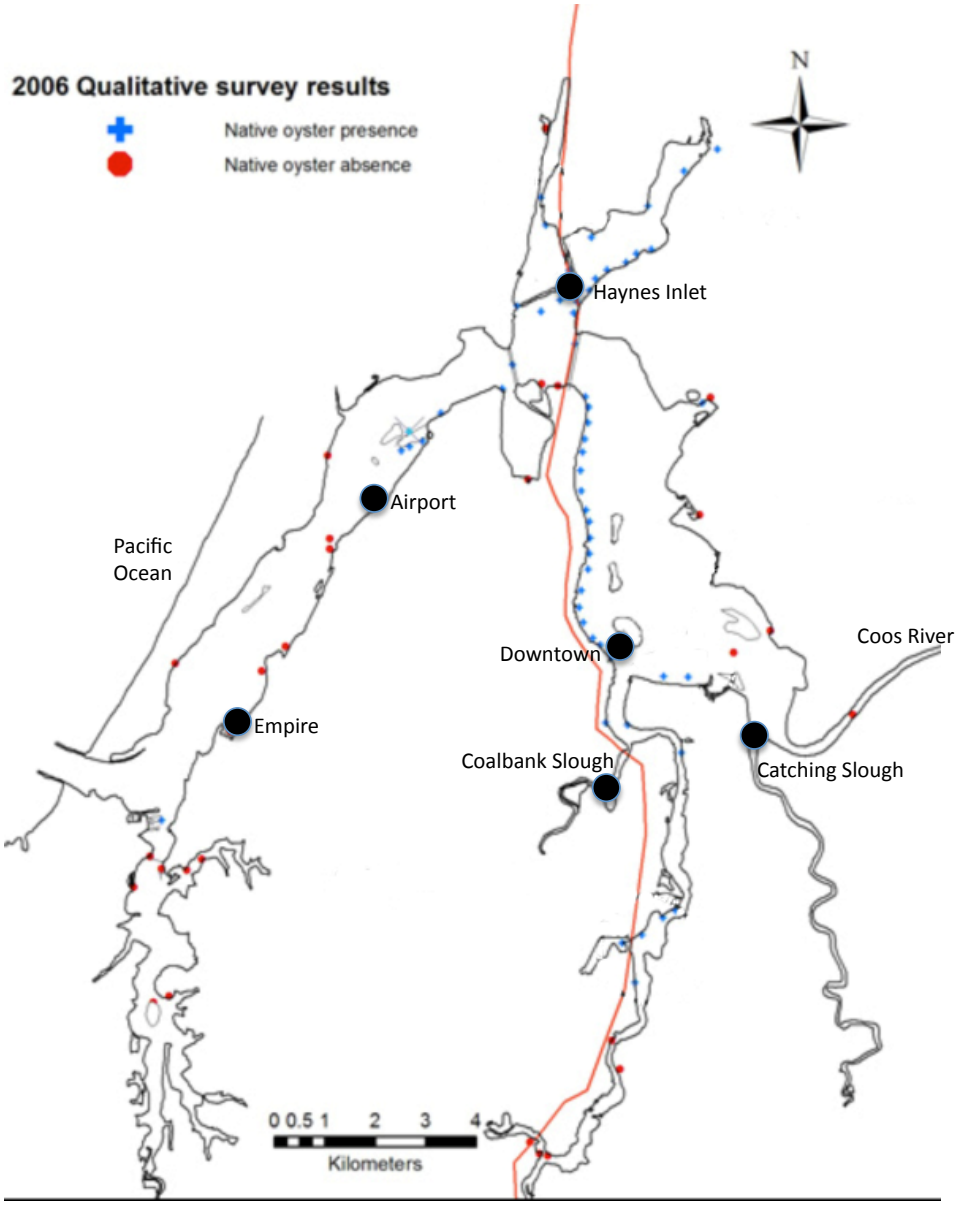


Figure 1. Sampling sites (indicated by black dots) in the Coos Bay estuary (adapted from Groth & Rumrill 2009). Small red dots along the estuary indicate sites where adult populations have not been found. Blue crosses along the estuary indicate sites where adult populations have been found.

Methods

Site Selection

The Coos Bay estuary (43.3667°N, -124.2167°W) is a large, drowned river estuary located on the southern coast of Oregon, USA. Sampling was conducted at five sites along the marine-estuarine gradient in 2012, and six sites in 2013 (Figure 1). Sample sites were, in order from the most marine to most riverine; Empire (43.35912°N, -124.31152°W), Airport (2013 only: 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). Three sites (Haynes Inlet, Downtown Coos Bay, and Coalbank Slough) were locations with known adult oyster populations (Groth & Rumrill 2009), and three sites were outside the known range of adults, two relatively marine (Empire, Airport) and one relatively fresh (Catching Slough). In 2013, the Airport site was added to increase the spatial resolution in the gap between Empire and Haynes Inlet.

Complications with variability in passive larval trap efficiency may arise with differing current speed. In addition, the relationship between larval supply and settlement may be complicated by fast current speeds. In a simple world, faster current speeds would bring more larvae to a site purely by the volume of water passing through the site and over larval traps and plates. However, high current speeds may actually prevent larvae from settling on settlement plates (Pawlik & Butman 1993, Qian et al. 2000, Larsson & Jonsson 2006), and may decrease trap efficiency (Butman et al. 1996, Butman 1996). In

order to ensure equal trap efficiency, sites with similar current speeds were selected, using a model of current speeds in the Coos Bay estuary, which was ground-truthed with ADCP data (Jordan Cove report citation).

Trap Design and Larval Abundance Analysis

Larval traps have been used successfully in a variety of habitats (Yund et al. 1991, Gaines & Bertness 1993, Todd et al. 2006). Larval traps were modified from their most basic form (Yund et al. 1991) in order to ensure efficiency with the high-velocity tidal flows observed in the Coos Bay estuary. Each trap was composed of a funnel (7.62 cm x 5.08 cm PVC reducer and funnel), a cylinder (70 cm x 5.8 cm), and a base (Figure 2). The base of the trap consisted of five separate parts: a 5.08 cm PVC coupler, a 5.08 cm x 1.9 cm PVC reducer, 1.9 cm male and female PVC screws, and a 1.9 cm diameter PVC stake. The stakes were pounded into the substrate until the base reducer was flush with the substrate. The traps were designed such that a male and female PVC screw component allowed the trap to be separated into two parts. If the substrate was difficult to sink the trap stake into, the old trap could be disconnected from the stake and the new trap attached without having to pull up the stake.

The traps were filled with a 10% solution of buffered formalin and filtered seawater. The solution was dyed with Rose Bengal, allowing visual confirmation of trap fluid retention during retrieval, as well as dying the organisms, ultimately simplifying the separation of the organisms from sediment during analysis.

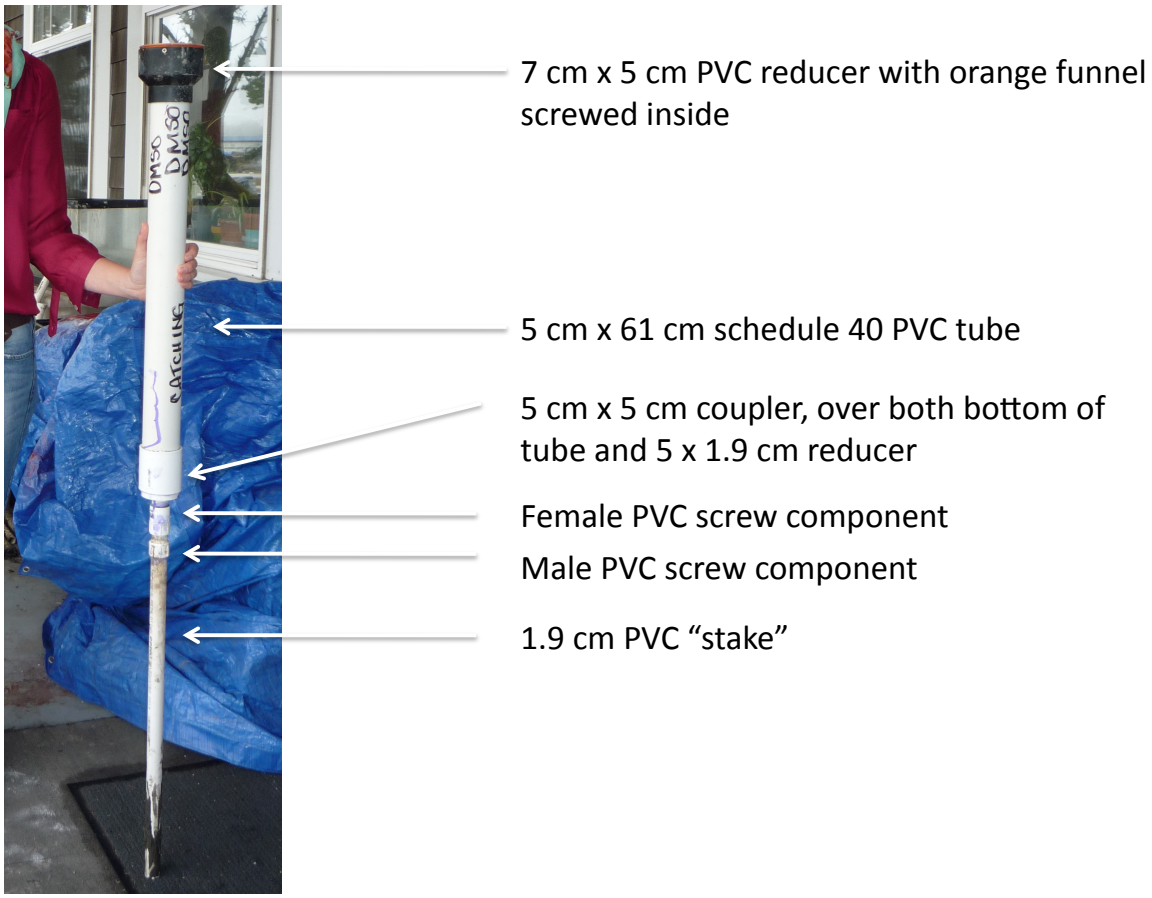


Figure 2. Trap design. Traps consisted of three regions. A funnel and PVC reducer were screwed together and constituted the top of the tap, in order to prevent resuspension of collected materials at high current velocities seen in the Coos Bay estuary. The second region was the tube itself, where a stained, buffered formalin solution was used. The third region consisted of a PVC coupler, male and female screw components, and a PVC "stake". The coupler allowed the tube to be connected to a "stake" of smaller diameter, increasing our ability to pound it into the intertidal. The male and female screw components facilitated trap exchange at sites where it was difficult to pound the stakes in; once the stakes were in, the trap could be unscrewed, and the next trap reattached without having to pull up the stake and pound it in again. The stakes were pounded far enough into the substrate that the male PVC screw component was the first to stick out of the substrate.

At each site, we sampled in the low intertidal, approximately 30.5 cm below Mean Low Low Water to ensure traps and plates were submerged as much as possible (see below) while still being accessible at the neap low tides of each month. Emersion times were quantified and compared among sites using water level data (Onset HOBO U20-001-02-Ti) from loggers that were placed at the same depth as top of the traps and settlement plates.

In 2012, sampling began on July 19th and traps and settlement plates were exchanged approximately every two weeks during low tides until November 29th. Exact dates of each deployment are available in Appendix A. Evidence at the time suggested these dates would encompass and exceed the initiation and termination in spawning and settlement of *O. lurida* larvae in Coos Bay (Garcia-Peteiro *unpublished*, Sawyer *unpublished*). However, we suspect we missed the initiation of spawning in 2012. For this reason, in 2013, sampling began mid-May and concluded mid-August, when logistical constraints demanded the termination of sampling. Traps and plates were exchanged simultaneously during both years to ensure temporal continuity in data.

At each sampling interval, traps were retrieved from the field and replaced with a second set of traps. The retrieved traps were returned to the lab for processing. The trap fluid was poured through a 145 m sieve, and the traps were rinsed well to ensure all plankton and sediment was collected from the bottom of the trap. The plankton in the sieve was then rinsed, and preserved in 5% formalin-buffered seawater. Larvae were examined on an inverted microscope, and were not subsampled.

Larvae were divided into two size classes: 1) D-stage: young larvae, which lacked the distinctively shaped umbo that would allow for definite identification based on

available resources at the time, and 2) umbo-stage larvae, which were identified using regional guides (Loosanoff et al. 1966, Shanks 1991, and Baker *pers. comm*). Furthermore, we considered it prudent to separate the larvae into these two categories to determine if there was any pattern of larval size between sites. It is also important to separate the bivalve larvae by life-stage (larvae vs. competent pediveligers) as they may have different priorities (i.e. dispersal or retention vs. settlement; Finelli & Wethey 2003). In 2013, the ability to correctly visually identify both D-stage and umbo-stage larvae was established through molecular identification using the 18S gene region (see Chapter IV for methods).

With this study, larval trapping rates were considered to be relative to the absolute abundance within the water column, and observing differences of these relative abundances between sites was the aim of this portion of the study.

Settlement Plate Design and Analysis

Settlement plates were 15.24 cm^2 unglazed white ceramic tiles. The plates were bolted to PVC "T" shaped holders, one plate per arm of the T, each arm being 61 cm in length, modeled after plates deployed in Seale & Zacherl (2009). Human disturbance, however, was not an issue for plates, and no plastic mesh was placed around them (as in Seale & Zacherl 2009). The vertical portion of the T's were reinforced with rebar, and placed at each field site adjacent to the traps. The T's and rebar were driven into the substrate so the plates would be approximately level with the tops of the traps, within 30 cm.

Like the traps, the plates were replaced with a second set of plates upon retrieval and brought back to the lab to be analyzed. Each plate was sub-sampled with the aid of an area grid; 96.8 cm^2 were counted or 41.7% of the total area of the plate. The squares to be counted were generated for each plate using a random number generator. Only intact oyster recruits were counted. Oyster identification relied on umbo shape (Loosanoff et al. 1966, Shanks 1991, Baker *pers. comm*.) After analysis, plates were carefully scrubbed and washed with freshwater before being allowed to generate a biofilm for at least 12 hours in the flow-through seawater system before re-deployment at the next low tide.

Traps were slightly positively buoyant, and needed to be well-pounded into the substrate to prevent them from popping up during deployment. Settlement plates were negatively buoyant, however, and could simply be slipped over the rebar stake and remain in place. Due to the difficulty in pounding in trap stakes at some sites, it was necessary to ensure the bottom of the traps could be reached to exchange them, even at neap tides. This resulted in the traps being placed slightly higher than settlement plates. However, even during extreme low spring tides, both traps and plates were exposed for minimal periods of time (~<60 min), based on observations when working in the field and water-level logger data (data not shown). Traps and plates were placed parallel to the direction of the main current flow, with the hopes of minimizing any trap fluid that escaped from negatively impacting the settlement plates (Figure 3).

Physical Data

HOBO loggers (Onset Computer Corp.) recorded temperature and conductivity (U24-002) every ten minutes and water level (U20-001-01-Ti) every fifteen minutes. A

temperature and conductivity logger was deployed at each site, but as we were in possession of only three water level loggers, these were moved among the sites over the course of the study, allowing us to estimate water level at all six sites. As with the water-level loggers, temperature and salinity loggers were deployed at approximately the same depth as trap tops and settlement plates. Data were downloaded throughout the sampling period, and periods when loggers were exposed to air at low tides were identified by large, quick drops and subsequent increases in salinity, and were excluded from analyses. Conductivity data were transformed using the HOBOware Software into Salinity.

Information available at project initiation indicated the HOBO U24-002 loggers would be well suited for our needs; their cost reasonable, and sensitivity appropriate for our uses. However, they have since been taken off the market due to accuracy errors in conductivity. Unfortunately, the magnitude of error is dependent on the range of salinity observed, and no regressions can be calculated. Evidence suggests our error may be very large. Therefore, salinity data should be considered very conservatively. To date, there are no indications temperature data are affected by this logger malfunction.

Logger data are discussed as “means per deployment”, and the term refers to the mean seen throughout one deployment of plates and traps. Logger data were matched deployments and retrievals of plates and traps using NOAA tide charts. Each parameter discussed (mean, range, minimum, maximum of temperature and salinity) was calculated for each day, and then averaged again over the specific deployment period of traps and plates.

Figure 3. Field set-up. Traps and plates were deployed and exchanged concurrently. Traps and plates were set slightly staggered relative to one another, but parallel to the main current flow. By keeping traps and plates slightly separate, we hoped to minimize the impact of any resuspended trap fluid on biofilms or settlers on plates. Particularly when traps become exposed and are submerged again, a period of slight fluid loss occurs, visible by the Rose Bengal dye in the trap fluid. This typically lasts ~5 seconds after resubmersion (*pers. obs*.) and clearly is not a significant volume after two weeks. All traps, unless disturbed (for instance, found fallen or at sharp angles) had brightly stained fluid visible from the top of the trap when returned to the lab, indicating minimal fluid loss. Buffered formalin likely has an unpleasant effect on *O. lurida* settlers, although their sensitivity to chemicals at this life-stage is unknown.

Results

Physical Data

2012

2012 temperature and salinity observation for each site are plotted in Figure 4, and are available in Appendix A. Temperature and salinity data were recorded from July 19th 2012 through October 14th 2012 at Empire. Although sampling with traps and plates continued through November 15th, temperature and salinity data between October 15th and November 15th were not recorded. Between July 19th and October 14th, however, mean daily temperatures during each trap and plate deployment period at Empire were low, and remained between 11.9 and 12.8°C, with mean daily ranges between 3.5 and 4.4°C. The mean maximum temperature for each deployment was also low relative to other sites, between 13.8 and 15.0°C, while the mean daily minimum was between 10.2 and 10.6°C.

Salinity at Empire remained very stable and high relative to other sites. Throughout the recorded period, mean daily salinities for each deployment were between 25.3 and 26.6, with ranges between 1.5 and 2.1. The mean minimum daily salinity per deployment was between 24.2 and 26.1, and mean maximum daily salinity for each period was between 26.3 and 27.5.

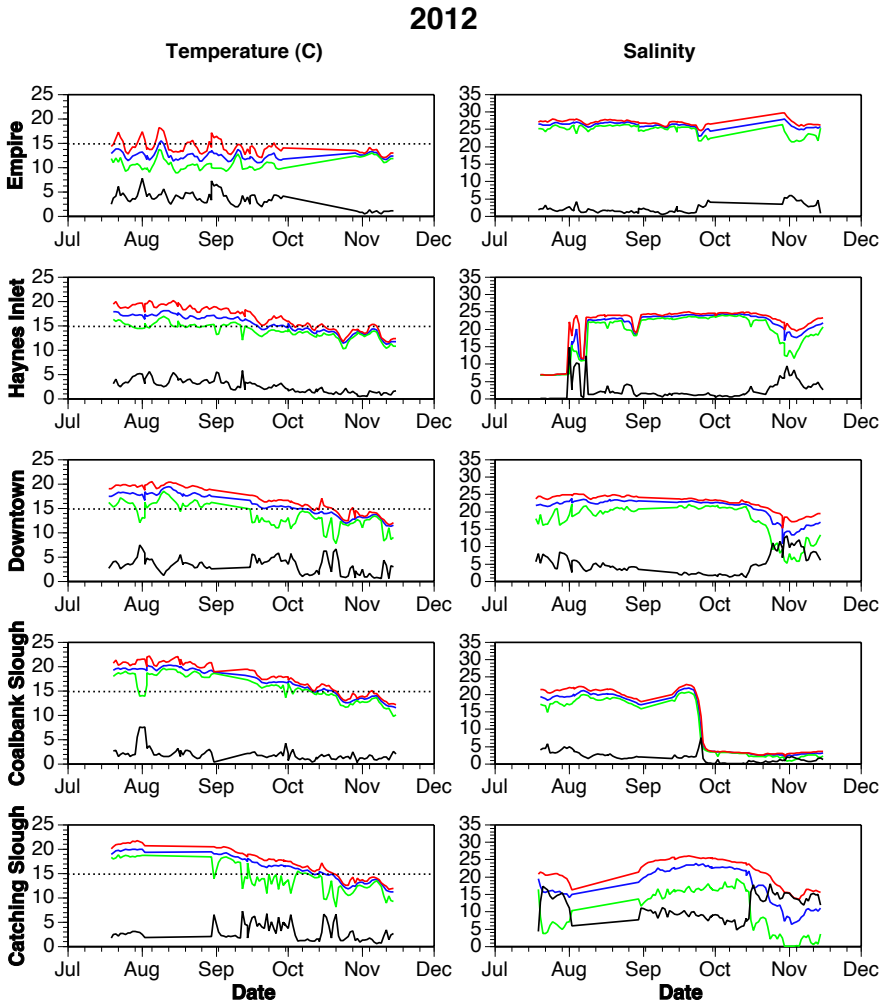


Figure 4. Temperature and salinity during 2012. Temperature graphs for each site are on the left, salinity are on the right. Y-axis indicates site and parameter value (temperature, °C, and salinity), and x-axis indicates date. Key: Black lines, daily range; green lines, daily minimum: blue, daily mean; red, daily maximum; dotted black line, 15°C. 15°C in the Coos Bay estuary is thought to be a critical reproductive temperature for *O. lurida*, meaning that below this critical temperature spawning may not occur.

At Haynes Inlet, mean daily temperature between deployments trended downward, while those at Empire did not. Daily means between 17.3°C (July 20th through August 2nd), gradually decreased to 12.9°C (September 30th to November 15th).

The mean daily range in temperature per deployment was small, between 1.1 and 3.9°C. Mean daily minimum temperature was between 12.4 and 15.6°C, while mean daily maximum temperature was between 14.3 and 19.1°C.

The salinity patterns at Haynes Inlet have not yet fully been resolved, and their accuracy remains unknown. During the first deployment period from July 20th through August 2nd the mean salinity was very low, at 7.9. This was likely due to logger error. During all successive deployments, however, daily salinity means remained between 19.4 and 24.3, with ranges between 0.8 and 5.1. Minimum daily salinity per deployment was between 7.5 and 23.8, and maximum daily salinity per deployment was between 8.9 and 24.6.

Downtown displayed temperature patterns similar to those of Haynes Inlet. Mean daily temperature per deployment was between 12.8 and 18.5°C, with mean daily range per deployment between 1.7 and 4.5°C. The minimum daily temperature per deployment was between 11.1 and 16.5°C, and the maximum was between 13.3 and 19.9°C.

Salinity at Downtown, too, was relatively stable throughout much of 2012. The mean daily salinity per deployment was between 15.0 and 23.2, but the mean daily salinity per deployment remained above 22 between July 18th and October 2nd 2012, after which point it decreased to 15.0 by November 14th. Mean daily salinity ranges per deployment were slightly higher than those seen at Empire and Haynes Inlet, a low of 1.8 but peaking to 9.3 from October 29th to November 14th. Mean minimum daily salinity per deployment was between 8.9 (October 29th to November 14th) and 21.5. Mean maximum daily salinity per deployment was between 18.2 and 24.6. Temperature and salinity data are not available for Downtown between August 30th and September 15th.

Coalbank Slough displayed temperature patterns similar to those of both Downtown and Haynes Inlet. Mean daily temperature per deployment was between 20.0°C, gradually decreasing to 13°C with mean daily ranges per deployment between 1.2 and 3.5°C. Mean minimum temperatures per deployment were between 12.2 and 19.0°C, and mean maximum temperatures per deployment were between 21.2 and 13.5°C.

Salinity at Coalbank Slough is more variable between deployment periods than seen at Downtown. Mean daily salinity per deployment was from 20.3 (August 3rd through 17th), gradually decreasing to 2.8 by the last sampling period (October 30th through November 15th). Interestingly, mean daily ranges in salinity remained low (0.3 to 4.2) despite the large decrease in mean daily salinity. Minimum daily salinity per deployment was between 1.9 and 19.0, while maximum daily salinity per deployment was between 2.8 and 20.3. Coalbank Slough exhibited the lowest mean daily salinity of all sites monitored (<2), which was sustained between October 1st and the end of sampling, on November 15th. This, however, could have been logger error. Temperature and salinity data are not available for Coalbank Slough between August 31st and September 14th, 2012.

Catching Slough also had temperatures similar to those of Coalbank, Downtown, and Haynes Inlet in 2012. Mean daily temperatures per deployment were between 19.7 and 12.7°C, with mean daily ranges per deployment between 1.6 and 4.4°C. Mean minimum daily temperature per deployment was between 11.7 and 18.5°C, with mean maximum daily temperatures between 13.3 and 21.1°C.

Salinity at Catching Slough in 2012, however, was highly variable both within and between deployment periods. Mean daily salinity per deployment was between 23.2 (September 14th to 30th) and 9.0 (October 29th through November 14th), while the mean daily salinity range within a deployment period was between 14.1 (October 14th through October 29th, and October 29th through November 14th) and 7.4 (September 30th through October 14th). Catching Slough exhibited the largest mean daily range of salinity of all sites monitored. Mean minimum daily salinity was between 1.3 and 17.3, while mean maximum daily salinity was between 15.3 and 25.6.

2013

2013 temperature and salinity data are plotted in Figure 5 and are also listed in Appendix B. As in 2012, Empire appeared to be strongly influenced by proximity to the ocean, and had low, but variable temperatures throughout the sampling season (between mid-May and mid-August), relative to other sites in 2013. Mean daily temperatures per deployment were between 12.3 and 15.9°C, with mean daily ranges per deployment between 2.9 and 5.0°C. Mean minimum daily temperatures per deployment were between 10.1 and 13.5°C, and mean maximum daily temperatures were between 14.2 and 18.0°C, higher than those observed in 2012.

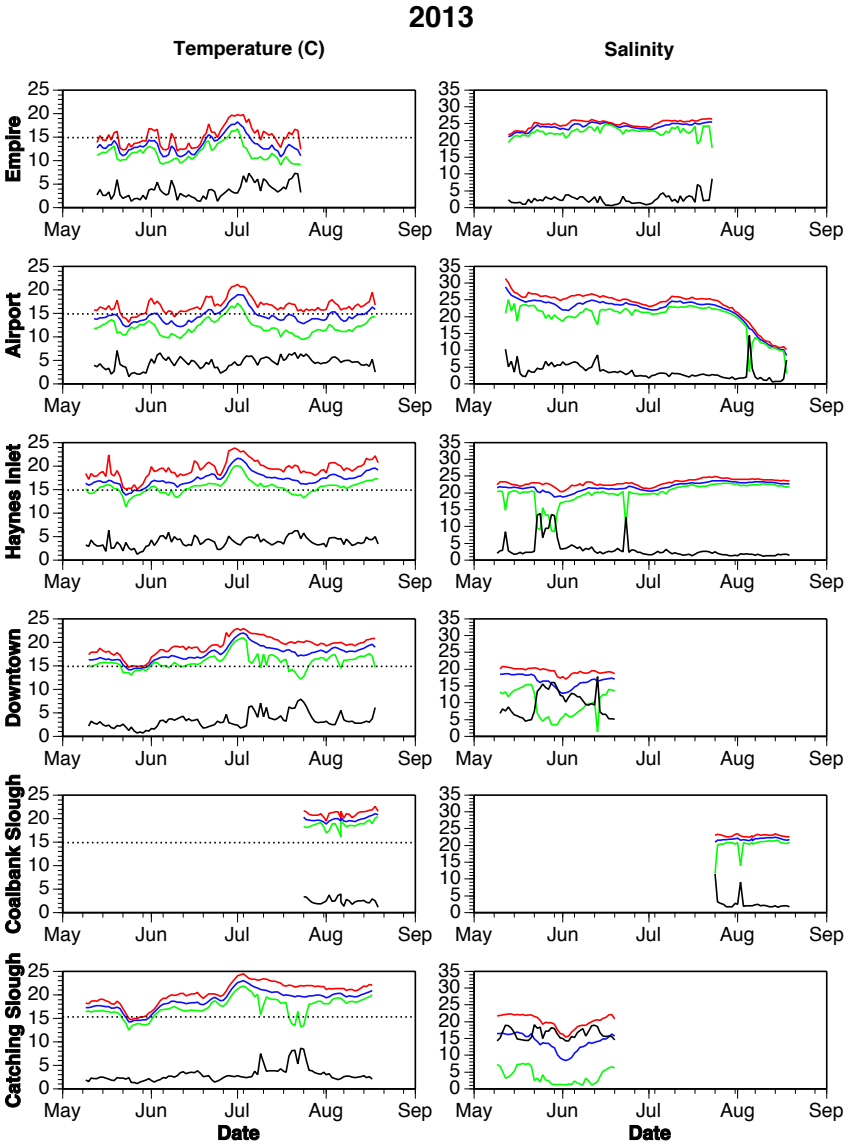


Figure 5. Temperature and salinity in 2013. Temperature graphs for each site are on the left, salinity graphs for each site are on the right. Y-axis indicates site and parameter value (temperature, °C, and salinity), and x-axis indicates date. Key: Black lines, daily range; green lines, daily minimum: blue, daily mean; red, daily maximum; dotted black line, 15°C temperature thought to control spawning of *O. lurida* in the Coos Bay.

Also, as in 2012, salinity at Empire was very stable, with relatively high salinity compared to other sites in 2013. Mean daily salinity per deployment was between 22.6 and 25.0, with small mean daily ranges between 1.8 and 3.5. Mean minimum salinity per

deployment was between 21.6 and 23.5, and mean maximum daily salinity per deployment was between 23.3 and 26.0. No temperature and salinity data were available between July 23rd and August 19th, 2013.

The site added in 2013, Airport, displayed temperature and salinity profiles similar to those of Empire. Mean daily temperatures per deployment were between 13.6 and 16.9°C, with mean daily ranges per deployment between 3.7 and 5.4°C. Mean minimum daily temperatures remained between 11.0 and 14.8°C, and mean maximum daily temperatures remained between 15.6 and 19.0°C—slightly higher than maximums seen at Empire.

Airport also appeared to be strongly influenced by oceanic water for much of the sampling season, as is seen at Empire. Mean daily salinity per deployment remained between 21.2 and 25.6 from May 12th through August 6th, but decreased to 12.0 by August 18th, 2013. Mean daily ranges in salinity per deployment were between 1.9 and 5.7. Mean minimum daily salinity per deployment was between 10.8 and 22.9, but remained between 19.6 and 22.9 between May 12th and August 6th, and only dropped to it's minimum of 10.8 between August 7th and August 18th. Mean maximum daily salinity was between 12.7 and 27.5, but again, remained above 22.4 until the last sampling period, between August 7th and August 18th.

As in 2012, Haynes Inlet temperatures were slightly higher than those observed at Empire, and those at Airport in 2013. Mean daily temperatures per deployment remained between 15.9 and 19.5°C for the duration of sampling. Mean daily ranges per deployment similar to those of Airport and Empire, between 3 and 5°C. Mean minimum daily temperature per deployment was between 15.1 and 17.7°C, and mean maximum daily

temperature was between 17.9 and 21.7°C—both the daily minimum and maximum were greater than those recorded and Empire and Airport.

As in 2012, salinity at Haynes Inlet was slightly lower than salinity at Empire, and in 2013, Airport. Mean daily salinity per deployment was between 19.7and 23.4, with ranges between 1.5 and 6.4. Mean minimum daily salinity per deployment was between 18.6 and 22.4, and mean maximum salinity per deployment was from 21.9 to 24.3.

In 2013, Downtown had mean temperatures similar to those of Haynes Inlet—between 15.6 and 19.8°C, but was more consistently in the upper portion of this range, whereas Haynes was more consistently in the lower portion of that range. Mean daily ranges per deployment were also higher at Downtown than those at Haynes inlet—between 0.1 and 13.3°C at Downtown. Mean minimum temperatures per deployment were between 14.5 and 17.9°C, and mean maximum temperatures per deployment were between 16.5 and 21.5°C, similar to those of Haynes Inlet in 2013.

Unlike Empire, Airport, and Haynes Inlet, however, the range in salinity throughout sampling at Downtown was high. Beginning approximately June 20th, it appears as the logger suffered complete failure in its ability to measure salinity, recording only very low salinity. Other data in the bay during the recordings indicate the logger was malfunctioning (O'Neill, *pers. comm*). Salinity data after June 20th have been excluded from analysis. Mean daily salinity per deployment before June 20th was between 14.8 and 18.3, with mean daily ranges per deployment between 6.9 and 13.2. Mean minimum daily salinity was between 5.6 and 19.4, while mean maximum salinity per deployment was between 18.8 and 20.3. All four measurements of salinity—mean, range, minimum and

maximum—showed more variation than those measurements recorded at Haynes Inlet, Airport, and Empire.

Logger malfunction prevented recording at Coalbank Slough for the majority of sampling in 2013. Data recorded spanned only between July 23rd and August 18th, 2013, during two deployments. Between these dates, however, mean daily temperature per deployment was 19.7 and 20.0°C, with a mean daily range of temperature per deployment of 2.2 and 2.6°C. Mean minimum daily temperature was 18.3 and 19.0°C, and mean maximum daily temperature was 20.9 and 21.3°C.

At Coalbank Slough, mean daily salinity per deployment remained above 21.7, with a mean daily range between 2.0 and 3.3. Mean minimum salinity per deployment was 19.6 and 21.1, and mean maximum salinity per deployment was 22.8 and 23.0.

Catching Slough also had higher mean daily temperatures per deployment than those at Empire, Airport and Haynes Inlet, between 16.1 and 21.1°C—slightly warmer than those of Downtown and Coalbank Slough as well. Mean daily temperature ranges remained between 1.9 and 5.0°C. Mean minimum daily temperatures per deployment were between 15.1 and 19.8°C, and mean maximum daily temperatures per deployment were between 17.0 and 22.6°C.

Like Downtown, Catching Slough also exhibited a large range in salinities between deployments in 2013 and logger failure in recording salinity mid-June, again with other data supporting the assumed logger failure (O'Neill, *pers. comm.*). Excluding clearly inaccurate data beginning June 20th, mean daily salinity per deployment was between 11.2 and 15.9, and mean daily ranges were between 16.2 and 16.4. Mean daily

minimum salinity was between 1.8 and 5.4, and mean maximum salinity was between 18.0 and 21.9.

Larval Abundance

D-stage Larvae 2012

D-stage, umbo-stage, and settler abundances for both 2012 and 2013 are graphed in Figure 6, and are available in Appendix C. Sampling took place between mid-July and mid-November 2012. D-stage larvae were present from the first deployment mid-July through early August and were observed through early October. After early-October, D-stage larvae were no longer observed. D-stage larvae were most abundant at Downtown, followed by Coalbank Slough, and Haynes Inlet in 2012. Very few were observed at Catching Slough and Empire. All sites exhibited peak D-stage abundances during the first deployment period from mid-July through early August, with the exception of Empire (Downtown, 142 ± 28.4; Coalbank Slough, 78±35.3; Haynes Inlet, 59.3±10.5; Catching Slough, 8 larvae per trap). All sites (with the exception of Empire) exhibited sharp declines in D-stage larval abundance beginning between early and mid-August, and abundances at all sites continued to decline until larvae were no longer observed after early-October. Empire had very low D-stage larval abundance throughout sampling, with a maximum of 1.5±1.1 D-stage larvae per trap between mid- and late August. Logistical difficulties prevented larval sampling Catching Slough during the majority of August.

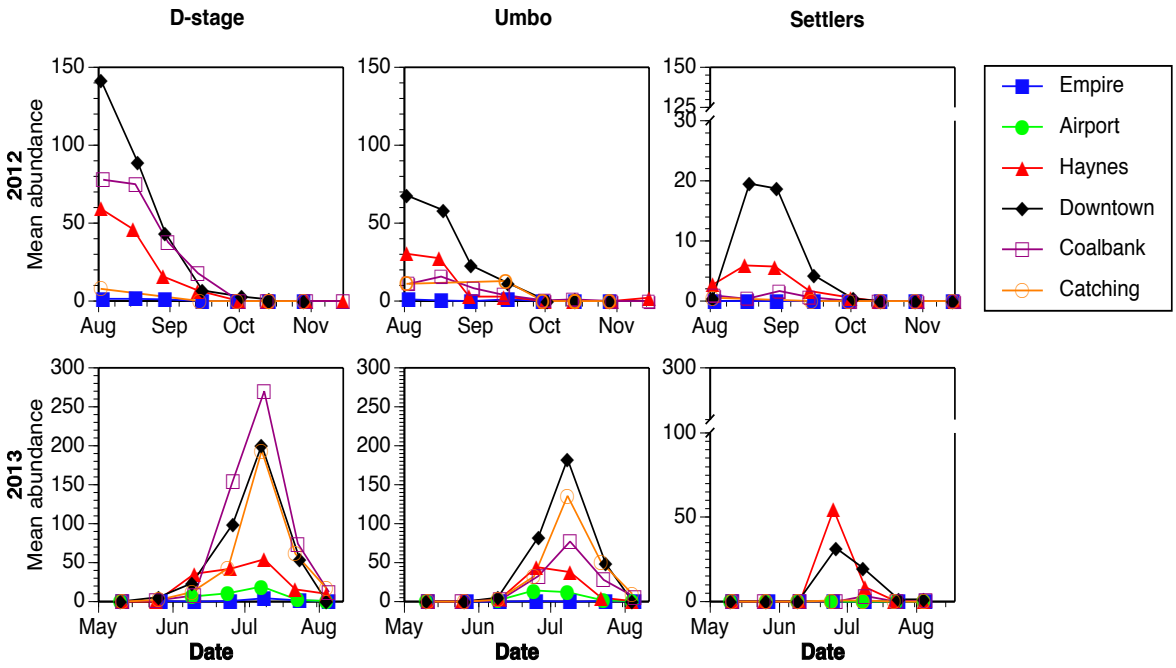


Figure 6. D-stage, umbo-stage, and settler abundance in 2012 and 2013, by stage. D-stage larval abundance in presented in the left column, umbo-stage larval abundance in the center column, and settler abundance in the right column. 2012 data are presented in the top row of figures, and 2013 in the bottom.

D-stage Larvae 2013

Sampling took place between mid-May and mid-August, 2013. Peak larval abundance was seen at each site during mid-July with a gradual increase and gradual decrease of abundance before and after. Larvae were not present before mid-May at any site, and very few larvae were seen in mid-August (maximum, Catching Slough, 17.3±8.3 larvae per trap) at the end of the study. D-stage larvae were most abundant at Coalbank Slough, Downtown, and Catching Slough in 2013, followed by Haynes Inlet, Airport, and finally, Empire. Peak abundances during mid-July were as follows: Coalbank 269.7±116.4; Downtown 201±15.3; Catching 193.3±22.4; Airport 19±6.8; and Empire

4±2 D-stage larvae per trap. Peak abundance of D-stage larvae also occurred at Haynes Inlet during mid-July (54.3±44.1 larvae per trap), however, we expect these numbers were low due to sampling error (see Discussion, below).

Umbo-stage Larvae 2012

Umbo-stage larvae were present from the first deployment interval, mid-July 2012 through early August 2012. Larvae were present in the water column until mid-October, when both Coalbank Slough and Downtown had one umbo-stage larva between all replicate traps. Most sites displayed peak abundances during the first deployment period in mid-July 2012. In general, the highest larval abundances were seen at Downtown, followed by the Haynes Inlet, and Coalbank Slough. Catching Slough and Empire both had very low larval abundance. Larval abundance peaked from mid-July through early August at Downtown (67.7±7.7 larvae per trap) and Haynes Inlet (30.3±6.2 larvae per trap), but larval abundance was similar at these sites during early- to mid-August (58.3±18.7, and 27.3±6.8 larvae per trap, respectively). Peak abundance at Coalbank Slough was during early to mid-August (15.7±4.6 larvae per trap). Larval abundance at Catching Slough peaked during early to mid-September (13±3.7 larvae per trap). Logistical difficulties prevented larval sampling Catching Slough during the majority of August, however. Empire consistently had low supply, with a maximum of one umbo-stage larva per trap. There was a steady decline in larval supply during the sampling season, with no second peaks.

Umbo-stage Larvae 2013

In 2013, umbo-stage larvae were not observed before mid-June, and were then only observed at low abundances from mid-to late June. One abundance peak occurred during mid-July, and was followed by a rapid decrease in larval abundance at all sites within the following two weeks. This decline continued through mid-August when sampling was terminated. At that time, maximum larval abundance was at Catching Slough, where 9.7±1.7 umbo-stage larvae per trap were observed. During the peak, abundance was highest at Downtown (183±28.9 larvae per trap), followed by Catching Slough (135.3±17.5 larvae per trap), Coalbank Slough (77±27.5 larvae per trap), Haynes Inlet (44±49 larvae per trap), and Airport (12.3±1.3 larvae per trap). No larvae were seen at Empire during mid-July, but the highest abundances occurred during late June to early July, and late July through early August, when 0.7±0.7 larvae per trap were seen.

Recruitment

2012

Recruits were observed from our first deployment period, mid-July through early August, through the fifth collection, mid- to late September, and were not observed thereafter, although we continued to sample until November 15th. Recruitment was highest at Downtown, followed by Haynes Inlet, Coalbank Slough, Catching Slough, and Empire. Recruitment peaked during mid- and late August at Downtown Coos Bay and Haynes Inlet. Recruitment during these two successive deployments was much higher at Downtown Coos Bay than at Haynes Inlet (Downtown; 19.5±6 and 18.7±7.1: Haynes

Inlet; 5.9±1.2 and 5.7±2.1 recruits 100 cm^{-2}). At Coalbank Slough, recruitment was consistently low with a maximum of 1.7±1.8 during mid-to late August. Catching Slough recruitment data are missing from early to mid-August but are available for every other date. However, recruitment was only observed at very low numbers with a maximum of 0.5±0.4 recruits 100 cm^{-2} during the first deployment, mid-July through early August. At Empire, no recruitment was observed throughout the experiment.

2013

Recruits were not observed before mid-June in 2013, but were present from mid-June through mid-August. Recruitment was highest at Haynes Inlet, followed by Downtown, Coalbank Slough, Catching Slough, and Airport and Empire. At Haynes Inlet and Downtown, we observed one recruitment peak in 2013, which occurred in the deployment interval spanning late June through early July. Peak recruitment during this interval at Haynes Inlet was 54.5±19.3 recruits 100 cm^{-2}, and Downtown 31.5±9 recruits 100 cm^{-2}. Coalbank Slough had its second highest recruitment during this deployment period, although abundance was low (1.3±0.5 recruits 100 cm^{-2}). Peak recruitment at Coalbank was observed during the next deployment, spanning mid-July (3.2±1.6 recruits 100 cm^{-2}). *O. lurida* recruits were present in Catching Slough samples on only two deployments, late June through early July, and mid-July. No recruits were observed at any site prior to mid-June, and recruitment gradually tapered off after peaks. No recruitment was seen at either Airport or Empire during 2013.

Critical Temperatures

In 2012, minimum daily temperatures above 15°C were observed at Haynes Inlet, Downtown, Catching Slough, and Coalbank Slough from the first deployment in mid-July. Larvae and recruits were also present from the first deployment. Minimum daily temperatures remained above 15°C at Haynes Inlet through late August. Larvae were present through late August, and recruits were observed through mid-September, when mean daily temperature was 13.9°C. At Downtown, minimum daily temperature remained above 15°C through late August, or perhaps mid-September, but data are missing for this deployment. Umbo-stage larvae were present through mid-September, while D-staged larvae were observed until early October, although at very low abundances (3±2 D-stage larvae per trap). Recruits at Downtown were observed through mid-October. At Coalbank Slough, minimum daily temperatures of 15°C were observed through mid-October, the latest of any site. However, larvae were observed only through early-October, and recruits through mid-September. At Catching Slough, minimum daily temperatures, larvae, and recruits were all observed through mid-September. At Empire, minimum daily temperature never reached 15°C.

In 2013, minimum daily temperature at Haynes Inlet rose above 15°C beginning early June and were sustained through the end of sampling in mid-August. Larvae were also present from mid-June, and recruits were observed beginning late-June. Both larval supply and recruitment were also observed through the end of sampling. At Downtown, minimum daily temperatures reached 15°C in mid-May, but dipped below 15°C from late May to early June, and then rose again. D-stage larval supply was observed from late

May to early June and could have been a product of early spawners during mid-May. Although D-stage larvae were observed during this time, no umbo-stage larvae or recruits were observed. D-stage larvae, umbo-stage larvae were present beginning mid-June, and were present throughout sampling, and recruits were present beginning late June. At Coalbank Slough minimum daily temperatures are not available for mid- May through mid-July, but were above 15° C mid-July through the end of sampling in mid-August, when both larvae are recruits were observed. At Catching Slough, minimum daily temperatures above 15°C were observed beginning mid-May, and continued through the end of sampling in mid-August. D-stage larvae were observed from mid-May through the end of sampling, and umbo-stage larvae from early June. Recruits were observed only from late June through late July, and at very low abundances. In 2013, neither Empire nor Airport had minimum daily temperatures exceeding 15°C.

Discussion

Plankton Traps

The use of modified traps has been discouraged in the literature (see Hargrave & Burns 1979, Butman 1986, Butman et al. 1986). In our case, however, we felt that they were both necessary and acceptable (but see Yund et al. 1991 for further discussion). Here, we modified the traps by adding funnels, which increased the diameter of the mouth of the trap while keeping the traps relatively short, and therefore appropriate for use in the low intertidal. Also, while most of the objections to modified traps center around sampling bias, we were sampling the relative abundance of a single taxa at different sites, and not attempting to describe the planktonic community including a wide

variety of taxa. Furthermore, our study sites experienced similarly low current velocities relative to other parts of the bay (Jordan Cove Report) and therefore if sampling were biased, it would presumably be biased in the same way at all sites.

However, we believe Haynes Inlet trap samples during 2013 may not be representative of abundances relative to other sites. During 2013, trap samples were consistently disturbed, and were found knocked over or sitting at sharp angles, no longer perpendicular to the substrate. However, these disturbances likely resulted in an increase in resuspension of collected materials or a loss in trap efficiency, rather than increased trap efficiency. For this reason, these data can still shed light on 1) the presence or absence of *O. lurida* larvae and 2) a baseline which can be used as a *minimum* likely larval supply.

Physical Data

Figures 4 and 5 can be used to easily compare temperature and salinity between sites and years. Both Empire and Airport seem to be largely characterized by cool, marine water with relatively low temperatures and high, stable salinity, with no apparent downward trend throughout the year as the rainy season begins. The temperature does appear to have distinct oscillations, which were well correlated with upwelling indices (see Chapter IV). Haynes Inlet is similar to Empire and Airport, although a bit warmer with slightly lower salinity. Haynes Inlet also appears to have much more muted temperature oscillations that those seen at Empire and Airport. Downtown appears to have slightly higher temperatures on average than Empire, Airport, and Haynes Inlet, and does not display the periodic change in temperature observed at Empire, Airport, and to a

lesser degree, Haynes Inlet. Downtown may either have salinities that are comparable to those seen at the three lower sites during the dry season, or may be strongly influenced by freshwater outflow (as seen in October and November 2012). Coalbank Slough is generally warmer than Downtown, and appears to also be more influenced by freshwater outflow, resulting in slightly lower salinity. Catching Slough is also warm, but experiences large variation in salinity over both long (five month) and short (one day) intervals. The large span between mean minimum and mean maximum daily salinity per deployment at Catching Slough may indicate large daily variation in salinity, likely tidally driven, rather than seasonal variation driven by precipitation. However, we cannot discount the possibility of large recording error.

In 2013, salinity at Airport dropped quickly between early and mid-August. The Coos Bay estuary is influenced not only by the Coos River inflow, but also by approximately 20 additional freshwater creeks, one located directly above the banks above the Airport site. Indeed, looking at rain records for Coos County in early August, we see a 13-day period where rain was recorded each day, from July 31st to August 12th, 2013. Although throughout much of the season Airport temperature and salinity parameters appeared to be dominated largely by the site's close proximity to the ocean, salinity dropped quickly during this rainy period, indicating the creek above the site may strongly influence salinity throughout the rainy season. An alternative is logger error.

Larval Supply and Recruitment Summary

D-stage larvae were most abundant at Downtown in 2012, followed by Coalbank Slough and Haynes Inlet, with very low larval abundance at both Catching Slough and

Empire. Umbo-stage larval abundances followed the same general pattern, with highest abundance at Downtown, followed by Haynes inlet, Coalbank Slough, Catching Slough, and finally, Empire. This pattern was similar in 2013, although Coalbank Slough had the highest D-stage larval abundance, followed by Downtown, Catching Slough, and Haynes Inlet, although, again, Haynes Inlet abundances are likely much higher. Both Airport and Empire had very low abundances of both D-stage and umbo-stage larvae in 2013. In summary, larvae were most abundant at the sites in the upper bay (Downtown, Coalbank Slough and Catching Slough), as well as Haynes Inlet, but were consistently low at sites closer to the ocean (Empire, Airport).

Following high larval abundance, recruitment was much higher at Downtown than at any other site in 2012, with Haynes Inlet having the second highest recruitment abundance. In 2013, the highest abundance occurred at Haynes Inlet, followed by Downtown. Catching Slough and Coalbank Slough exhibited low recruitment throughout both years, and Empire and Airport did not display any recruitment in either year. During both 2012 and 2013, we observed only one recruitment peak, but, given the early recruitment peak seen in 2013, it is possible that another peak occurred early in 2012 before sampling was initiated.

During 2013, Downtown and Catching Slough trap data are more similar than either is to Coalbank Slough. Both Downtown and Catching Slough received approximately equal supply of D-stage and umbo-stage larvae in 2013, while Coalbank Slough received more D-stage larvae than either Downtown or Catching Slough, yet fewer umbo-stage larvae were present. This provides support that exchange of water between Coalbank Slough and the estuary channel is relatively weak. If water were

readily exchanged, we would expect larval abundance to follow more closely to that of Downtown and Catching Slough. In 2012, we do not have enough data from Catching Slough to compare larval abundance there with Downtown, and Coalbank Slough.

O. lurida recruitment was followed at a site between our Downtown and Coalbank sites in 2010 (Sawyer 2011), and the peaks in recruitment were quite different between years. Sawyer (2011) documented a recruitment peak in early to mid-October 2010, while we observed a recruitment peak in mid- to late August 2012, and late June to early July in 2013. Although data are not presented here, recruitment in 2013 was followed through November 20th, and no further recruitment was observed. Literature suggests that *O. lurida* may have two peaks in recruitment (see Chapter II), but our observation of a single recruitment peak does not appear to be limited to the Coos Bay estuary; Seale & Zacherl (2009) also found only one recruitment peak in San Francisco Bay.

Larval Supply, Recruitment, and Environmental Factors

Abiotic conditions, including temperature and salinity, influence the distribution of adult oyster populations (Shumway 1996). Wasson (2010) demonstrated that *O. lurida* is likely also influenced by these physical parameters. One would assume that locations with smaller daily ranges in both temperature and salinity would be less physiologically stressful for both larvae and adults. Indeed, Wasson (2010) working in Elkhorn Slough, California, found sites with high ranges in water quality parameters including temperature, salinity, turbidity, dissolved oxygen, and fluorescence lacked *O. lurida* populations, while sites with smaller ranges in these parameters tended to have larger

populations. However, we suspect salinity is more likely to drive our recruitment patterns than temperature. Although metamorphosis from larva to settler has been positively correlated with temperature in two closely related bivalves, *Crassostrea gigas* (Rico-Villa et al. 2009) and *Saccostrea glomerata* (Dove & O'Connor 2007), wide temperature tolerances in bivalve larvae have also been observed in *D. polymorhpha* (Sprung 1993), *M. edulis* (Almada-Villela et al. 1982), *M. leucophaeata* (Verween et al. 2007), and a congener of *O. lurida*, *O. edulis* (Newell et al. 1977).

Within the Coos Bay estuary, stable salinities are present in the lower estuary, where the estuary is dominated by marine waters and is less influenced by river outflow. However, despite both temperature and salinity at these sites (Empire, Airport) being well within the physiological range of the oyster, no adult populations are known to exist between the jetties at the mouth of the bay and the Airport along the main channel of the estuary (Figure 1, Groth & Rumrill 2009). Adult populations of *O. lurida* have been found between the Airport and outflow of the Coos River, as well as in Haynes Inlet (Groth & Rumrill 2009). In the upper estuary (Downtown, Coalbank Slough, Catching Slough), however, near the outflow of the Coos River, intertidal regions experience large tidally-driven daily salinity ranges, as well as long periods of exposure to relatively fresh water during the rainy season. For instance, between October 29th and November 14th, 2012 at Catching Slough, mean daily salinity was 9.0, while the mean daily range was 14.1. These large daily variations were also present at Catching Slough in 2013 and to a lesser degree at Downtown during 2012 and 2013. The error of loggers is clearly an issue with this dataset, however, although the absolute values of salinity are desirable, reasonable assumptions can be made without them. Specifically, it is logical to assume

that due to the proximity to the river, Catching Slough, Downtown, and perhaps Coalbank Slough are likely strongly influenced by freshwater outflow on both daily and seasonal scales. Daily, at falling tides, freshwater outflow penetrates down into the estuary, and returns upstream during rising tides. During the rainy season, the volume, distance, and influence of the riverine plume likely increases relative to the dry season. It is also reasonably safe to assume that for these reasons, Catching Slough, followed by Downtown and Coalbank Slough, experience larger ranges in salinity on both daily and seasonal scales, than sites farther from the river, such as Airport and Empire.

This potentially long-term exposure to low salinity during the rainy season is likely detrimental to the oyster. However, larvae likely have some sense of their chemical surroundings, and may preferentially settle where conditions are most suitable. Our data suggest larvae do not settle where variation in salinity is likely high (such as Catching Slough; Figure 7). At Catching Slough during 2013, recruitment was not observed to be greater than 0.5±0.7 (late June through early July) and 0.5±0.4 (mid-July). In fact, these were the only deployment periods where any recruitment occurred, despite high larval abundances during the larval peak in mid-July (135.3±17.5 umbo-stage larvae per trap). This pattern of low recruitment at sites with high variability in physical parameters follows Wasson's (2010) data on adult populations in Elkhorn Slough. Additionally, sites with high variability also consistently display low salinities and Sawyer (2011), in one of the only laboratory experiments with early life-stages of *O. lurida*, found significantly lower settlement of *O. lurida* at a salinity of 15 compared to treatments of 25, 29, and 33, and in general, saw a trend of decreasing settlement with decreasing salinity.

In 2013, peak larval abundance and recruitment do not occur concurrently, or successively. Rather, peak recruitment occurs approximately two weeks before peak larval abundance. At Downtown in 2013, peak recruitment occurred mid-June to early July (31.5±9 recruits per 100 cm^2). Larval abundance was increasing at this time, from lows, presumably due to the recent onset of spawning, and was recorded at 83±15.6 umbo-stage larvae per trap. However, peak larval abundance occurred two weeks after peak recruitment, in mid-July (183±28.9 umbo-stage larvae per trap). Recruitment during this interval in mid-July was recorded as 20±4.5 recruits per 100 cm^2. Thus, approximately twice as many larvae were present during peak larval abundance than during the recruitment peak. Recruitment during peak larval abundance was approximately 33% lower than the two previous weeks during the recruitment peak. Furthermore, recruitment continued to decline after peak larval abundance, indicating that long pelagic larval duration of *O. lurida* is not likely the cause of the mismatch between peak larval supply and peak recruitment. The cause of this mismatch between peak larval supply and peak recruitment remains unknown.

Direct effects to abiotic conditions, such as increased mortality from long-term exposure to low salinity, are extreme consequences of physiological limitations under suboptimal environmental conditions. However, suboptimal conditions may also affect species distributions less directly. For example, temperature and food availability influence growth, settlement, and mortality of oyster larvae and juveniles (Devakie & Ali 2000, Rico-Villa et al. 2009), and when larvae grow slowly, they often settle later. Kennedy (1996) estimated an 89% reduction in *Crassostrea virginica* recruits when pelagic larval duration (PLD) was increased from 20 to 25 days. Longer PLDs expose

larvae to predators for a longer period, as well as put planktonic larvae at risk of being carried away by currents from suitable habitat on which to settle.

Water temperature can also strongly influence the reproductive status of marine invertebrates (Keck et al. 1975, Kassner & Malour 1982), and larval abundance is strongly influenced by the fecundity and reproductive output of adult populations. A critical minimum temperature has been shown to correlate well with the onset of spawning in *O. lurida* (Hopkins 1937, Oates *unpublished*). This critical temperature in the Coos Bay estuary is estimated to be approximately 15°C (Garcia-Peteiro *unpublished,* Oates, *unpublished*), and was reached in the estuary in both 2012 and 2013 (see Figures 3 and 4). This critical temperature was observed at Haynes Inlet, Downtown, Coalbank Slough and Catching Slough in 2012 and 2013, but not at Empire in 2012 or 2013 and not at Airport in 2013. Larval supply generally followed the timeline set by a 15°C critical temperature, with a two-week lag. This minimum temperature may greatly affect population structure and dynamics by controlling reproductive output, particularly affecting species that tend to exhibit low dispersal and are unlikely to receive a large larval input from other populations. *Ostrea lurida* is suspected of having limited larval dispersal. For instance, Dinnel et al. (2011) seeded one site with oyster spat in Fidalgo Bay, Washington, and in subsequent years found natural recruits within a maximum of 4.8 km of the restoration site. As no adult populations were present in the area before restoration work began, the authors hypothesize that these recruits were naturally produced descendants of the applied spat. Furthermore, Stick (2011) determined genetic divergences between *O. lurida* populations could be observed within small geographic areas, such as Puget Sound, demonstrating that larval exchange between some sites is low

enough that genetic differences can build up over time within a single bay. However, this has not always been shown to be the case. Stick (2011) also found five regions within the oyster's distribution, which were genetically distinct (see Chapter II), and Carson (2010) found larval connectivity of up to 75 km (see Chapter II). These data suggest that within enclosed bays, larval retention may be high; within open bays where tidal exchange is greater, the possibility for large-scale larval connectivity increases.

Our data support findings of small-scale dispersal within the Coos Bay estuary; although high larval abundance was seen at Downtown, Coalbank Slough, Catching Slough, and Haynes Inlet, very low supply was available to Airport and Empire. However, there are clearly additional drivers to recruitment patterns, other than larval supply or critical temperature. Both Coalbank and Catching Slough received relatively high larval supply, and sufficient temperatures to support reproduction, but both experienced very little recruitment in both 2012 and 2013.

Patterns of recruitment presented here correspond nicely with known distributions of intertidal adult *O. lurida* recorded by Groth & Rumrill (2009; Figure 1), although we suspect the drivers of recruitment are different in the upper and lower bay. Low larval supply and no recruitment was seen at either Airport or Empire, and no adult populations are currently known at these locations. It appears that low larval supply is driving recruitment at these sites. We observed both high larval supply and recruitment at Haynes Inlet and Downtown, where adults occur (Groth & Rumrill 2009). However, few recruits were observed at Coalbank Slough and Catching Slough, *despite* high larval supply. Adults are not known to exist at Catching Slough, and a few populations are known to exist at Coalbank Slough, although the known populations are located closer to the main

channel of the estuary. Furthermore, the adult populations in Coalbank Slough were experimental restoration sites and not naturally occurring. Data suggest environmental parameters such as low salinity or large variability in salinity, may be driving recruitment in the upper estuary, at Coalbank Slough and Catching Slough, but much more work needs to be done on this subject.

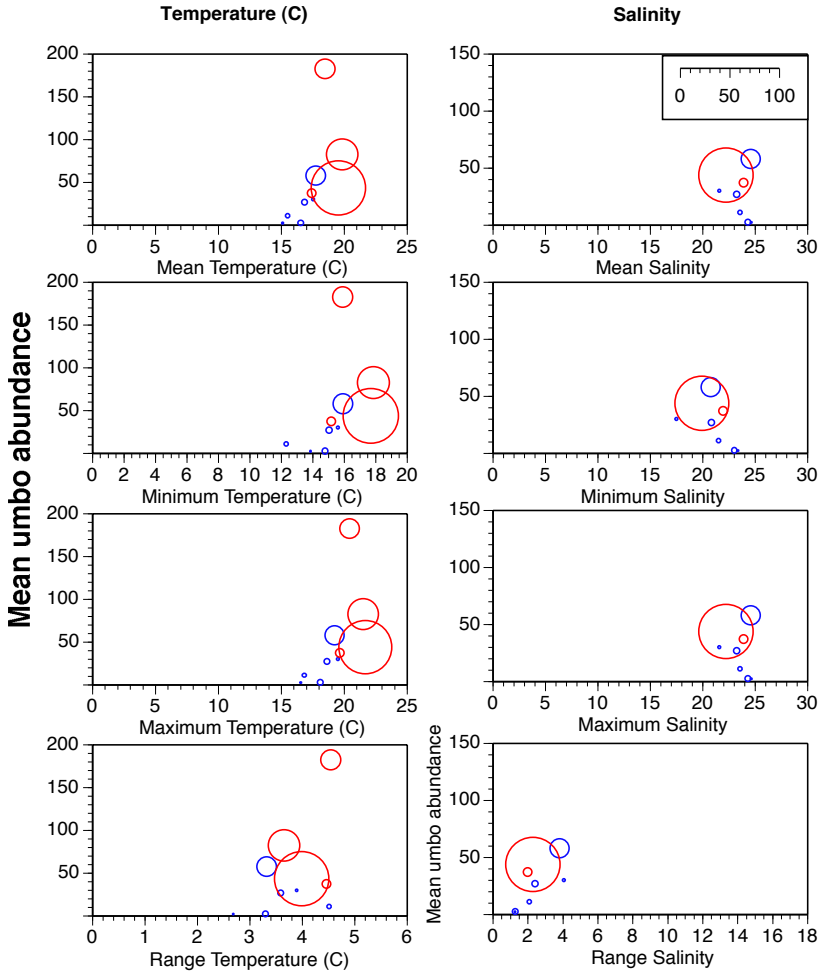


Figure 7. Bubble plot of mean umbo-stage larval abundance per trap (Y-axis), physical parameters (mean, range, minimum and maximum of temperature or salinity) and the number of settlers found during each condition (bubbles). Red bubbles indicate 2013 data, blue bubbles indicate 2012 data.

It appears as though recruitment limitations, rather than larval supply or settlement substrate limitations may be the limiting factor preventing *O. lurida* populations recovery in the upper Coos Bay estuary. Particularly at Downtown in 2013, peak larval supply was not matched with peak recruitment, and the cause of low recruitment relative to larval supply despite the addition of hard substrate, remains unknown. At Coalbank and Catching Slough in both 2012 and 2013, very low recruitment was observed despite high larval supply, and despite the presence of settlement plates, which supplied hard substrate. The cause of low recruitment at each of these sites remains unknown.

Conclusions

Restoration

Although the direct over-exploitation of *O. lurida* has been the primary driver of population decline, natural recovery has presumably been hampered by removal of the oyster larvae's preferred settlement substrate; oyster shell (Brumbaugh & Coen 2009). This removal has not only prevented recruits from replacing the harvested populations, but the locations of natural shell would indicate to shellfish managers the precise historical location of naturally occurring adult populations within the estuaries. Restoration efforts concerning *O. lurida* commonly consist of replacing the harvested shell with that of heterospecifics, such as the Japanese oyster, *Crassostrea gigas*, which is commercially cultivated on the West Coast. Once the shells are placed, hatchery-reared *O. lurida* "seed" (spat) are released to settle on this shell. However, if these seed are

either unsuccessful in becoming established in large numbers, or are tidally flushed resulting in larval wastage, restoration efforts will need to be more intensely managed until adult populations are dense enough to augment natural populations and become self-sustaining.

Piecing together knowledge of the species preferred habitat, potentially limited dispersal, and critical spawning temperatures, then, we can say that first, adults are estuarine dependent (see Chapter II), and are often present in higher abundances mid-bay than outer bay (Groth & Rumrill 2009, Wasson 2010). Secondly, recruits follow this pattern, with lower abundances in outer bays than inner bays (Deck 2011, Kimbro 2008, this manuscript). Lastly, larval supply also follows this pattern (Seale & Zacherl 2009, this manuscript). Therefore, it is possible that *O. lurida* has evolved some mechanism to remain in the upper bay, and prevent flushing to the open ocean. Garcia-Peteiro (*unpublished*) found *O. lurida* to exhibit vertical migration behavior that would promote retention within the bay, although only during periods of weak current speeds. Additionally, all sizes of larvae are present in the bay (Garcia-Peteiro *unpublished*, Pritchard *unpublished*), suggesting larvae are retained for their entire PDL rather than being exported and reentering the bay to settle. Furthermore, adults spawn during the dry season, when rainfall is low, and residence times in the upper bay are likely high, also promoting retention of larvae.

It appears that limitations in larval supply could be driving the adult population distribution in the lower estuary, as low abundances at all life stages (larvae, recruits and adults) are documented at these sites (Groth & Rumrill 2009, this chapter). One potential mechanism by which larval supply, and thus subsequent life stages, maybe limited to the

lower estuary is through hydrodynamic barriers to dispersal. We hypothesize the null point in the Coos Bay estuary acts as an effective barrier to downstream transport of *Ostrea lurida* larvae (see Chapter IV).

CHAPTER IV

DISTRIBUTION OF LARVAL BIVALVES IN THE COOS BAY ESTUARY, OREGON

Introduction

In Chapter III, we demonstrated that few *Ostrea lurida* larvae are supplied to the lower reaches of the estuary. In 2012 and 2013, larval and recruit abundances of *O. lurida* were followed at five, and six sites, respectively, in the Coos Bay estuary. The distribution of larvae and recruits was similar to that of known adult populations (Groth & Rumrill 2009). Specifically, we observed that larvae are only supplied in very low abundances at sites below the McCullough Bridge (Figure 1), but can be present in high numbers at sites above the Bridge during the same time period. Logically, recruitment follows this pattern, as does adult abundance (Groth & Rumrill 2009). However, the driving forces behind these patterns remain unknown.

Ostrea lurida has been shown to make vertical migrations when currents are weak. This has been hypothesized to promote larval retention within the estuary (Garcia-Peteiro, *unpublished*). During strong currents common in the estuary, however, *O. lurida* was equally distributed throughout the water column. Furthermore, in general, larvae are considered to be weak swimmers relative to typical horizontal current speeds (Chia et al. 1984). Larvae may be capable of moving vertically through horizontal currents, but are incapable of controlling their horizontal position directly through swimming against the

current, for example. If larvae do not possess these active migration behaviors, it would imply they are simply at the mercy of currents, both vertical and horizontal.

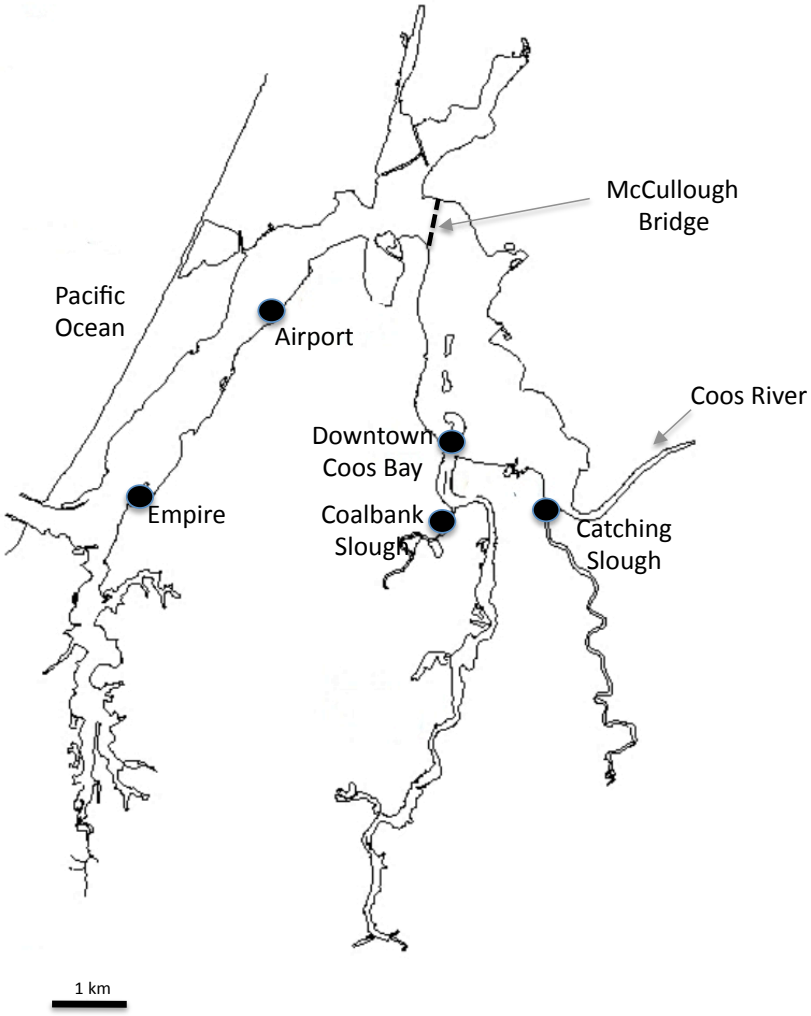


Figure 1. Map of the Coos Bay estuary. Trap sampling sites are indicated by black dots, and relevant landmarks (Coos River, McCullough Bridge, Pacific Ocean) have been labeled.

If larvae are often at the mercy of the currents, then, what is preventing them from being routinely flushed out of the bay during falling tides? Do larval bivalves other than *O. lurida* also have a presence in one part of the estuary, but absence in another? Or are they ubiquitously distributed throughout the estuary? Do some taxa have a restricted distribution within the bay while others have a uniform distribution? If taxa were consistently observed in only one section of the bay, but not another, what could be driving this distribution?

The hydrodynamics of the bay may be driving the distribution. Estuaries in particular may be environments that exhibit both areas of high retention and high tidal flushing. Estuarine waters are characterized by a range of processes that include tidal mixing, freshwater outflow, and marine inflow. The relative strength of each of these components changes throughout an estuary, with tidal mixing and marine inflow dominating near the mouth of the estuary, and freshwater input dominating near the head of the estuary resulting in salinity and sometimes temperature, gradients along the estuary.

If larvae are at the mercy of hydrodynamic features, then currents may determine larval advection, dispersal and where the larvae are delivered. If larvae are not delivered to a particular location, then they cannot establish themselves. If they are delivered, however, they may settle and become reproductive adults. Retention of larvae in estuaries can drive recruitment patterns (Graham & Largier 1997, Sponaugle et al. 2002), with retention areas having higher recruitment, while areas frequently tidally flushed will likely result in lower recruitment. Larvae present in tidally flushed areas are more likely to be carried out of the bay, and, in the case of estuarine-dependent species such as *O.*

lurida, away from suitable settlement substrate as they become diluted in the coastal ocean.

Oceanographic processes can also penetrate the bay, affecting the hydrodynamics, but also driving physical parameters. For example, the Pacific Northwest coastal waters are affected by upwelling between April and September. Driven by interactions between northerly winds and Eckman transport, warm surface waters are pushed away from the coast, and are replaced by cool, high-salinity, and often nutrient rich water from below. One consequence of upwelling is the presence of cold seawater in the estuary (Roegner & Shanks 2001), and daily upwelling indices can be correlated to daily temperatures. If the correlation is strong, it indicates that that parcel of water is influenced by upwelling, and thus connected to the open ocean on fairly short timescales.

In addition to oceanographic processes such as upwelling, changes in precipitation and residence times can cause gradients in physical parameters along the estuary. In estuaries in the Pacific Northwest, hydrodynamic influences such as tidal mixing, marine inflow, and freshwater outflow may be particularly strong in determining species distributions. The climate in the Pacific Northwest is characterized by a rainy season (November-April) and a dry season (May-September). During the rainy season, river outflow strongly affects waters at the head of the estuary, creating density gradients that dampen vertical mixing with ocean waters. During the dry season, however, river outflow is low and evaporation may be high (Largier et al. 1997). When these high salinity conditions are present throughout inner bays, density stratification between inner- and outer-estuary waters is minimal, and the water becomes well mixed. Mixing then, becomes dominantly tidally driven, resulting in tidal exchanges and short residence times

between the mouth of the bay and the open ocean, but low tidal exchange (as low as 10s m^2s^{-1}) and long residence times at the head of the estuary (Largier et al. 1997).

Residence times in the Coos Bay estuary have not been published, but the characteristics and patterns observed in California estuaries, due to the similar climate, (Largier et al. 1997) are likely also observed in the Coos Bay estuary. Furthermore, these seasonal patterns are especially likely in topographically simple estuaries, such as the Coos Bay estuary (Largier et al. 1997). We assume that during the rainy season, due to the increased inflow of freshwater from the Coos River, the water in the Coos Bay estuary has reduced residence times, but during the dry season, residence times are longer. During falling tides in summer, water from the head of the bay likely does not reach the mouth of the bay by the end of the ebb tide. When the tide changes and begins to rise, this water mass is pushed back towards the head of the estuary, and makes no further seaward progress. If this change of direction occurs around the same location, it is referred to as a *null zone*. Specifically, a zone of oscillation within the estuary, driven by the interaction of freshwater river input and ocean tides which allows a body of water to be retained within the estuary during multiple tidal exchanges (Miller 1983). Essentially, the water mass above this zone sloshes back and forth within the estuary during each tide, but does not exit the mouth of the bay before the tide changes. Water riverward of this zone should have longer residence times than water seaward. Water riverward of this zone should also have a longer residence time during low freshwater input (summer) than during high freshwater input (winter). It is also likely that the location of this zone changes with tidal amplitude.

One can follow water masses with drogues (Davis 1985, Kimbro et al. 2009; Figure 2). Previous data (Garcia-Petier *unpublished*) collected with drogues in 2010 suggests that in summer, the null zone is located near the bend of the Coos Bay estuary, near the McCullough Bridge (Figure 1). Within the Coos Bay estuary, river kilometers 19-24 have the highest rate of sediment accumulation (Kate Groth, *pers. comm.*), and this position is consistent with our estimated null zone, as waters seaward will be flushed during falling tides, transporting sediments trapped in that water out to sea. Thus, the outer portion of the bay would be characterized by daily tidal flushing and mixing, and short retention times. Conversely, the upper portions of the bay, above the null zone, would be characterized by longer retention times.

Data to date suggest this type of hydrodynamic barrier to larval supply may be at play in determining *O. lurida* (which spawns in the dry season) population distributions elsewhere. Deck (2011) working in Tomales Bay, California, suggested that larvae might be retained near the head of the estuary. In Tomales Bay, the recruitment of *O. lurida* has been shown to increase with residence time (Kimbro 2008) and with increasing distance from the mouth of the bay (Deck 2011). High *O. lurida* recruitment mid-bay, and decreasing recruitment towards the mouth of the bay has also been observed in the Coos Bay estuary (see Chapter III). Anecdotal evidence further supports the hypothesis that there are areas that promote high retention of *O. lurida* larvae within estuaries. Couch & Hassler (1989) reported that historically, *O. lurida* oyster shells were "placed in locations favored for [*Ostrea lurida*] spat collection", indicating it was known that areas within estuaries exist where more larvae were present, or where preferential settlement occurs. We propose that this pattern of high abundance of *O. lurida* in the upper bay may be

driven by the null zone, resulting in high larval retention within the upper bay. Conversely, low larval supply, followed by larval flushing, dilution and transport to the open ocean may characterize locations seaward of the null zone. If the null zone is effective in determining the distribution of *O. lurida* larvae, we hypothesize it will also influence the distribution of other larval bivalves in the bay.

Following the null zone, in conjunction with associated larval abundances riverward and seaward of the zone, will help us understand the hydrodynamics of the estuary. In particular, it will inform us about the location in the estuary where *Ostrea lurida* larvae are likely to be flushed out into the open ocean during falling tides. In this study, we used drogues, oblique plankton tows, and larval traps to determine if the null zone is an effective barrier to larval bivalve dispersal in the Coos Bay estuary.

Drogues were used to follow water from the head of the bay to the null zone during falling tides. Oblique plankton tows were used to determine estimates of the effectiveness of the null zone on a short time scale (after one falling tide), while trap data were used to determine its influence throughout the majority of the dry season, between May 9 and August 19, 2013.

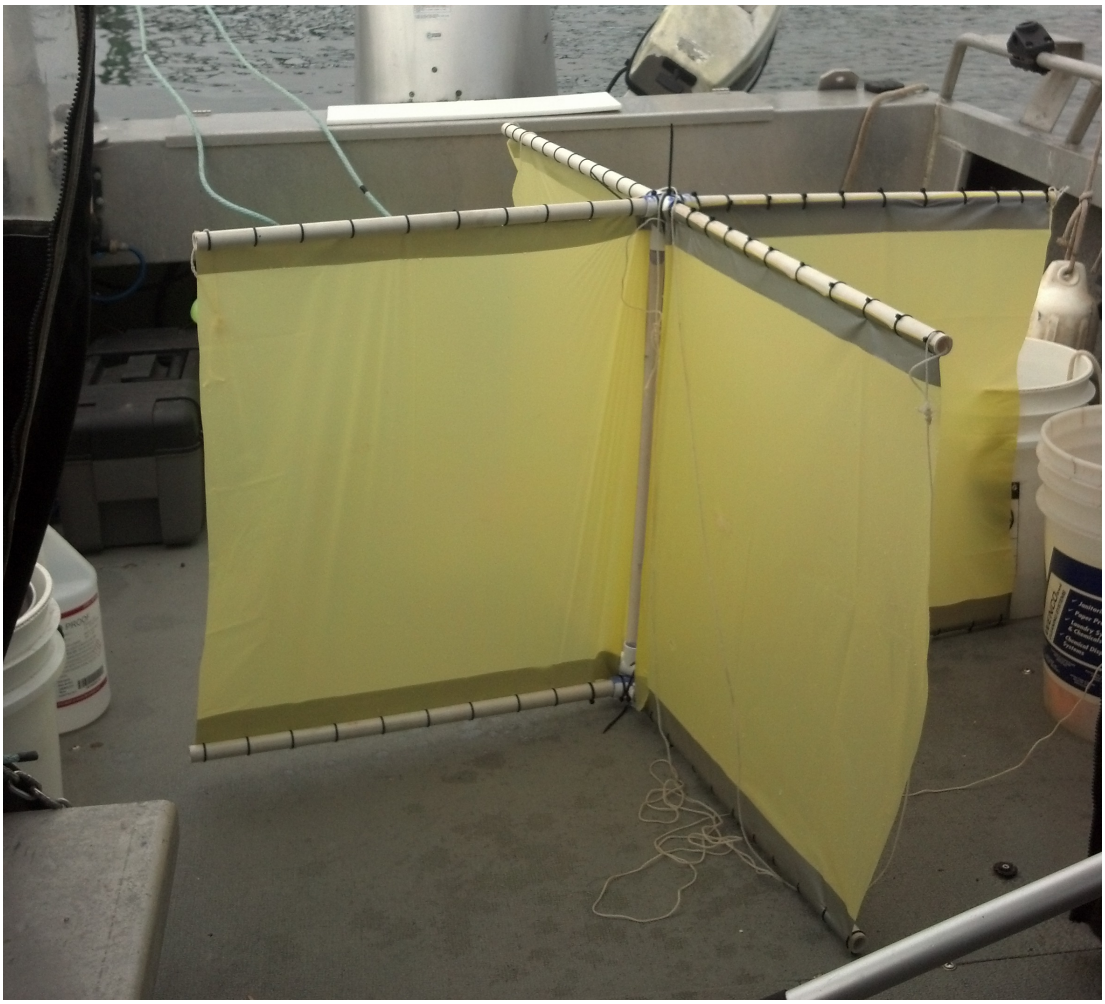


Figure 2. Drogue. Drogues were designed after Davis (1985), and were constructed of ½" PVC pipe. Each arm was 61 cm, as was the central rib. Top and bottom arms were connected with plastic sheeting, and secured to each arm using cable ties. Floats were secured to the tip of each top arm, so the drogue would ride at approximately 5 m depth. A Garmin eTrex20 GPS was attached to the center of the drogue, and recoded the track during deployment.

Methods

Molecular Identification of Larval Taxa

In order to create a key to larval bivalves that could be used to identify individuals in trap and tow samples, we sequenced the 18S gene region of over 90 larval bivalves. Specimens for molecular work were collected on July 31st, 2013 in the Coos Bay estuary, near Downtown Coos Bay. Larvae were collected using oblique plankton tows (see below), and preserved in 95% ethanol. Individuals were examined using an inverted microscope, at which time they were removed using a pipette, and placed in individual 1.5 mL tubes with >99% ethanol. Each larva was photographed at 4x, 10x, and 20x before being processed for sequencing. Each larva was sequenced using the 18S gene region, with forward and reverse primers (Larsen et al. 2005; Table 1). Larvae were centrifuged briefly in ethanol, pipetted into another tube with Ambion, and crushed. DNA was extracted using InstaGene Matrix (Biorad) following the manufacturer's instruction. PCR amplification was carried out using the Qiagen PCR Master mix system. Master mix reactions included 11.4 µl dH20Ambion, 4.0 µl 5X Green Buffer, 0.4 µl dNTP mix 10mM, 0.2 µl Go Taq polymerase, and 1.0 µl of each 18SR and 18SF primers (Table 1), as well as 2.0 µl of DNA template, for a final volume of 20 µll. Amplification was initiated with a 95°C denaturation for 2 minutes, followed by 35 cycles (95°C, 40s; 55°C, 40s; 72°C, 60s), and finished with a 72°C final extension for 2 minutes. Amplification was visualized by loading 2 µll of PCR product onto 1% Agarose gel in 0.5X TBE buffer, premixed with 0.1 µlg/ml of ethidium bromide. PCR products were purified using SV Wizard Gel and PCR clean-up kit (Promega), following the manufacturer's instructions. Samples contained approximately 150 ng of DNA, at approximately 10ng/µl, and were

sequenced by Sequetech. Sequences were trimmed and aligned using Codon Code Aligner, and closest species match to returned sequences were obtained using the BLAST tool in GenBank.

Table 1. Primers used (from Larsen et al. 2005) for amplification of 18S gene region. These primers return a band approximately 367 base pairs.

Primer	Sequence
18SF	5'-TTAGTTGGTGGAGCGATTT-3'
18SR	5'-TAGCGACGGGCGGTGTG-3'

The Influence of the Null Zone on Physical Interactions within the Bay

Daily upwelling indices were obtained for the region (pfeg.noaa.gov). Daily temperatures were recorded at each trap collection site in 2013 and 2013 with the use of a logger (Onset HOBO U20-001-02-Ti, see Chapter II for methods). Mean daily temperatures at each site were cross-correlated to upwelling indices using STATISTICA.

Drogues and Oblique Plankton Tows

Drogue and oblique plankton tow sampling were conducted on three days in 2013 (July 31st, August 1st, August 15th) during daylight ebb tides. Due to logistical constraints, night sampling was not possible. Dates were selected to (1) occur during the dry season, (2) have weather facilitating successful work (i.e. little wind and fog), and (3) have an ebb tide beginning early enough in the day to allow the drogues to be followed for the entire duration of the ebb tide, followed by plankton tows. Drogues (Figure 2) were similar to Davis' (1985) CODE surface drifters. Each of the four arms was 61 cm long, as was the central rib. Each upper arm was connected to its corresponding partner using

plastic sheeting, and secured to each ½" PVC arm using cable ties. The drogues were deployed to ride at a depth of 5 m, to approximate an intermediate distance between surface-water flow and flow at depth (the Coos Bay estuary is between 10-15 m deep in the main channel). Each drogue was attached to a Garmin eTrex20 GPS, which was set to record the track at five-minute intervals.

Drogues were released at slack tide, just before ebb tide at Downtown Coos Bay (Figure 1) where larval abundance is the highest in the bay (Garcia-Petiero *unpublished*, Chapter III). Drogues were followed in a boat, and once they made no further seaward progress and began returning riverward (which generally happened approximately 60-30 minutes before the predicted low tides in Downtown, Coos Bay, using NOAA tide charts for Coos Bay), they were hauled in, and plankton sampling began.

Oblique plankton tows (50 cm diameter net, 153 m mesh) were taken at the end of the drogue's track, when the drogue made no further seaward progress, approximately at slack low tide, we considered this to be the null zone for that day. Drogues followed the main channel of the estuary closely, and this allowed tows to be taken immediately after the drogue was retrieved. Tows were taken in the null zone, and approximately 1 and/or 3 km riverward of the null zone, and 1 and/or 3 km seaward from the null zone. On July 31st, tows were taken in the null zone and approximately ±1 km (n=1) on either side of the null zone. On August 1st, tows were taken in the null zone and ±1, ±3 km (n=1) of the null zone. On August 15th, tows were taken in the null zone, and ±3 km (n=3) of the null zone. The net was deployed at approximately 10 m depth, using standard wire out-angle methods, and retrieved at approximately two m min^{-1}, allowing the majority of the water column to be sampled within the five minute tow. A flow meter

was used to determine the volume of water filtered through the net. Net clogging was not observed during any of the tows.

Plankton samples were preserved in 95% ethanol in the field. For processing, samples were subsampled (Shanks et al. 2002) until a total of 200 larval bivalves were counted. Samples were examined with an inverted compound microscope at 4x. A key to larval identification was created using the molecular identifications. Number of individual bivalves was calculated as number/m^3.

Trap Data

Traps (see Chapter III) used to collect *Ostrea lurida* larvae at five sites in the Coos Bay estuary (Empire, Airport, Downtown, Coalbank Slough, Catching Slough) during Summer 2013 were also used to observe other species of bivalve larvae for this dataset. Many taxa of larvae exhibited strong peaks in abundance, with very low abundances at all sites for the remaining deployments. This indicated that the reproductive season, and spawning in particular may not yet have taken place. The trap deployments where low abundances were observed at all sites were excluded from these results.

Statistical Analyses

We hypothesized that mean daily temperatures at sites seaward of the hypothesized null zone would be strongly affected by coastal upwelling, and temperatures at sites riverward of the null zone would be less affected. The effect of coastal upwelling at each site was examined using cross-correlations in STATISTICA, with mean daily temperature as a function of upwelling. In 2012, Downtown and

Coalbank Slough had data gaps of two to four weeks. Data before and after missing data were analyzed separately. Time series were de-trended before analysis, if necessary. For the cross-correlations, the upwelling index time series was held stationary and the temperature time series were lagged. We assumed three conditions needed to be met in order for correlations to be relevant: 1) the correlations were significant at or below alpha=0.05, 2) as upwelling should drive lower temperatures in the bay, only negative lags were considered (- days), and 3) correlations (r-value) needed to be negative (i.e. as upwelling index increased, temperatures decreased).

Oblique plankton tow data were scaled by dividing the density of each larval group by the highest abundance of that group observed during a particular day. For instance, on July 31st, the highest abundance of *Ostrea lurida* was observed riverward of the null zone (150 individuals m^{-3}), and densities of *O. lurida* observed within the null zone (60 individuals m^{-3}) and seaward (130 individuals m^{-3}) were divided by 150. The density of each larval group was different between sampling days, and by scaling densities this way, we were able to use multiple days within analyses. Specifically, we used 2nd order polynomial correlations in DeltaGraph (v5) to relate the scaled abundances to the distance from the null zone (negative values indicating distance seaward, positive value indicating distance riverward, n=18). Pearson's correlation coefficients were then generated for each larval group to indicate patterns of significant interactions between larval supply, and distance (riverward or seaward) to the null zone.

Trap sites were divided into two groups; those seaward of the null zone (Empire, Airport), and those riverward of the null zone (Downtown, Coalbank Slough, Catching Slough). The mean larval abundance of each larval group in trap replicates (n=3) was

used in analyses. Due to non-normal and heterogeneous data, nonparametric Wilcoxon rank-sum test, followed by Welch's F test were used to compare species abundances on either side of the null zone for trap data using JMP.

Results

Drogues

Drogues were released at slack high tide near Downtown Coos Bay on July 31st, August 1st, and August 15th (Figure 3). High tides were 0.58, 0.61, and 0.67 m above 0 tide level on these dates, respectively. Drogues generally stayed within the shipping channel (observed by depth-finder on the boat). Oceanward transport of the drogues ceased approximately 30-60 minutes before predicted low tide at which time they began to move back up the estuary. The drogues did not pass the McCullough Bridge on any day.

Oceanographic Data and the Position of the Null Zone

Significant cross-correlations between the upwelling index and mean daily temperature at all sites in both 2012 and 2013 are presented in Table 2. Daily upwelling indices for 42°N, -125°W and mean daily temperatures at all five sites are plotted in Figure 4. Upwelling occurred throughout the sampling periods in both 2012 (mid-July through mid-November) and 2013 (mid-May through mid-August). In 2012, the influence of upwelling on temperature at Empire occurred at -2 to -5 d lag (max r=-0.601, n=72); upwelling explained at most about 36% of the daily variation in temperature. No data were recorded at Airport in 2012. At the Downtown site, directly riverward of the apparent null zone, upwelling signals did not occur until -6d lag and the correlation was

much weaker (r=-0.2854, n=60) with upwelling explaining only 8% of the daily variation in temperature. At both Coalbank and Catching Slough in 2012, no correlations met the three listed requirements.

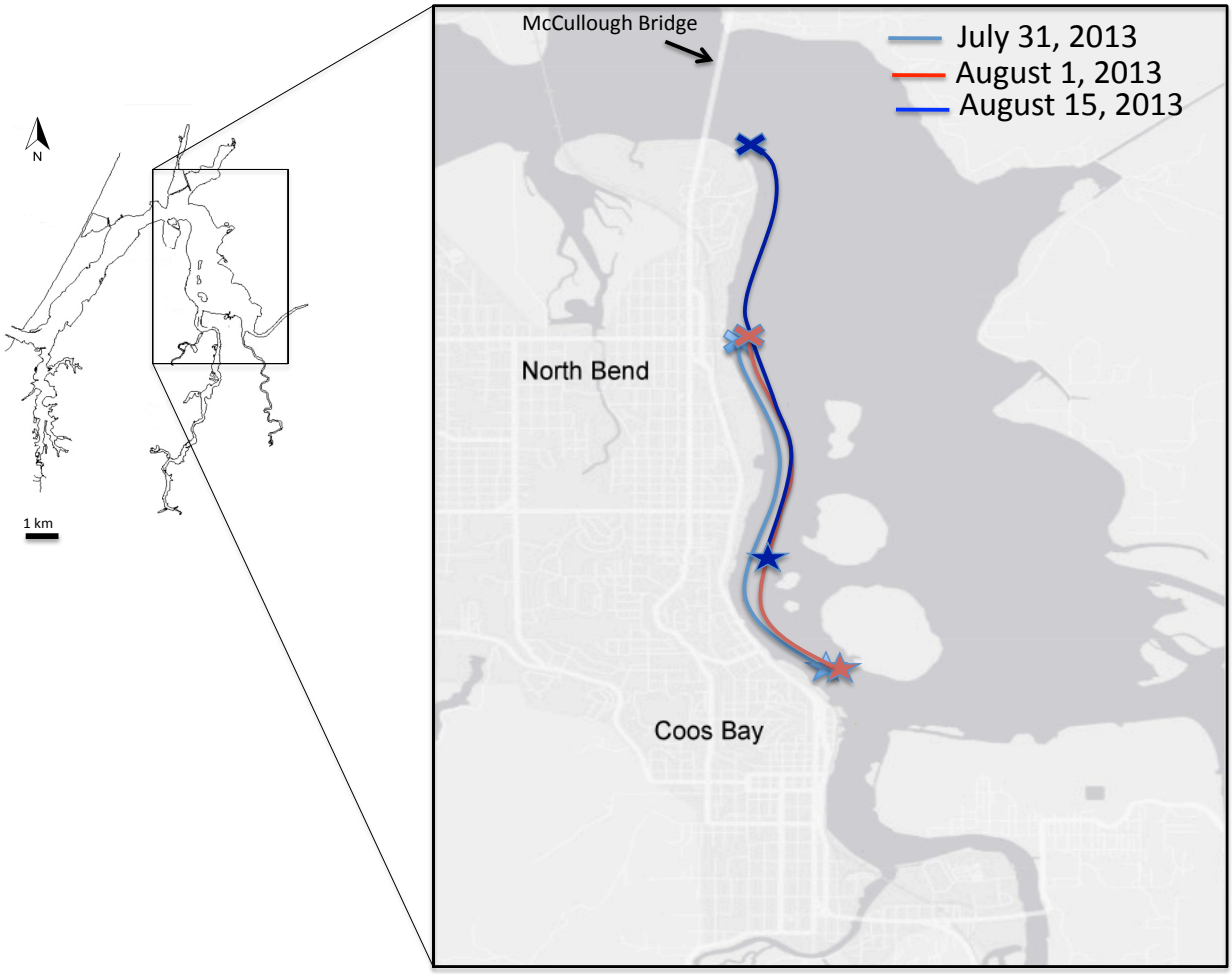


Figure 3. Drogue tracks. Drogues were released on July 31, August 1, and August 15 2013. The start of each track is indicated by the star, and the end of the track is indicated by the X. The Xs indicate the approximate location of the null zone.

In 2013, upwelling was stronger than in 2012. At Empire, the influence of upwelling on temperature at Empire occurred between -1d and -7d lag (max -4d, r=-0.708, n=70) and the correlation explains about 49% of the variability in temperature. At the Airport site, the influence of upwelling on temperature occurred between -2d and -8d lag (max -4d, r=-0.546, n=98) and the upwelling index explained almost 30% of the variability in temperature. At the Downtown site, the influence of upwelling on temperature occurred between -6d and -10 d lag (max -10d, r=-0.33, n=100), but the upwelling index explained only about 11% of the variability. At the Catching Slough site, the largest correlation was observed at -3 days and the correlation was positive with a small r (r=0.2079, n=101). The time series at Coalbank Slough was too short for analysis in 2013.

Table 2. Auto cross-correlations of mean daily temperatures and upwelling indices at sites where trap data were collected in 2012 and 2013. Lags (negative values) indicate a lag of mean daily temperature to upwelling index.

2012												
Empire			Airport			Downtown			Coalbank Slough			Catching Slough		
Lag	r	n	Lag	r	n	Lag	r	n	Lag	r	n	Lag	r	n
-5	-0.389	72				-6	-0.2854	60	-2	-0.319	42	-2	0.2758	76
-4	-0.601	72							-1	0.3859	42	-1	0.256	76
-3	-0.543	72	No data			-6	-0.2854	60						
-2	-0.319	72				-2	0.2805	60	-1	0.293	26			
						-1	0.0307	60						
2013														
Empire			Airport			Downtown			Coalbank Slough			Catching Slough		
Lag	r	n	Lag	r	n	Lag	r	n	Lag	r	n	Lag	r	n
-7	-0.602	70	-8	-0.432	98	-10	-0.33	100				-3	0.2079	101
-6	-0.628	70	-7	-0.461	98	-9	-0.302	100				-2	0.29982	101
-5	-0.674	70	-6	-0.502	98	-8	-0.265	100				-1	0.3612	101
-4	-0.708	70	-5	-0.545	98	-7	-0.236	100	Few Data					
-3	-0.653	70	-4	-0.546	98	-6	-0.21	100						
-2	-0.526	70	-3	-0.454	98									
-1	-0.299	70	-2	-0.299	98									

Drogue data indicate the location of the null zone is near or above the McCullough Bridge, located between Airport and Downtown Coos Bay. Correlations between upwelling indices and mean daily temperatures also change between Airport and Downtown; mean daily temperatures at Downtown have longer lags to upwelling indices, and the signal (r) is weaker. Drogue data, and correlations between upwelling indices and temperature suggest the location of a null zone between Airport and Downtown. There appears to be slow mixing between Airport and Downtown, and water riverward of the null zone seems to be retained above the null zone during falling tides.

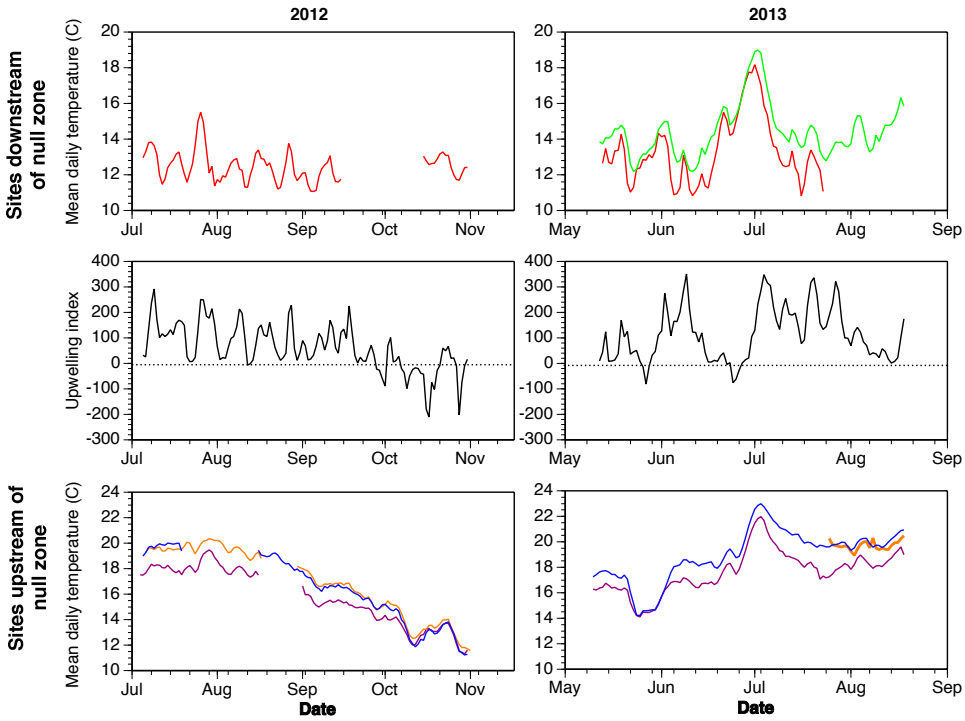


Figure 4. Mean daily temperature and upwelling index. The top row of figures shows the mean daily temperature (°C) at sites seaward of the null zone. Daily upwelling indices are presented in the middle row of figures for 2012 and 2013. The dotted horizontal line indicates a value of 0; positive values indicate upwelling. The bottom row of figures shows the mean daily temperatures (°C) at sites riverward of the null zone. Key: Red-Empire; Green-Airport; Purple-Downtown; Orange- Coalbank Slough: Blue-Catching Slough

Biological Data

Molecular Identification of Larval Taxa

Photographs of individuals identified with molecular barcoding (Figure 5) were used as keys to quantify the number of individuals of these taxa in trap and tow samples. Six taxa were identified using the 18S gene region, and were considered sufficiently morphologically distinct that they could be enumerated: 1) *Ensis* sp., 2) *Mytilus* sp., 3) *Mya arenaria*, 4) *Ostrea edulis*, 5) *Teredo navalis* and 6) *Cyrenoida floridana*. The 18S gene region in bivalves appears to be sensitive enough to identify individuals to the genus level, but was not able to provide species-level identifications for *Ensis* sp., or *Mytilus* sp. Additionally, although multiple sample sequences were identified as *Ostrea edulis,* a European congener of *O. lurida,* we believe that this is the closest match to *Ostrea lurida* available using the 18S gene region. We will therefore refer to this taxa as *Ostrea lurida*, which we believe is the correct identification. *Ensis* sp., *Mytilus* sp., *M. arenaria*, *O. lurida* and *T. navalis* are known to be represented in the Coos Bay estuary or outer shelf.

Barcoding identified one taxa as *Cyrenoida floridana*, a native of Florida and Georgia waters, which is not known to have any populations in the Pacific Northwest. Further, it is unlikely to be invasive in the area due to the stark contrasts in environmental parameters between its native range and the Pacific Northwest. Additionally, 18S data from our samples were only 96% similar to those of *C. floridana*, indicating our samples are unlikely to be *C. floridana*. However, the samples did represent a morphologically distinct group. For the purpose of putting a name to a larva, larvae displaying the morphology of the samples whose 18S sequences returned *C. floridana* are referred to as

Species 1; we are not suggesting *C. floridana* is the correct identification—it is simply the closest match using the 18S gene region.

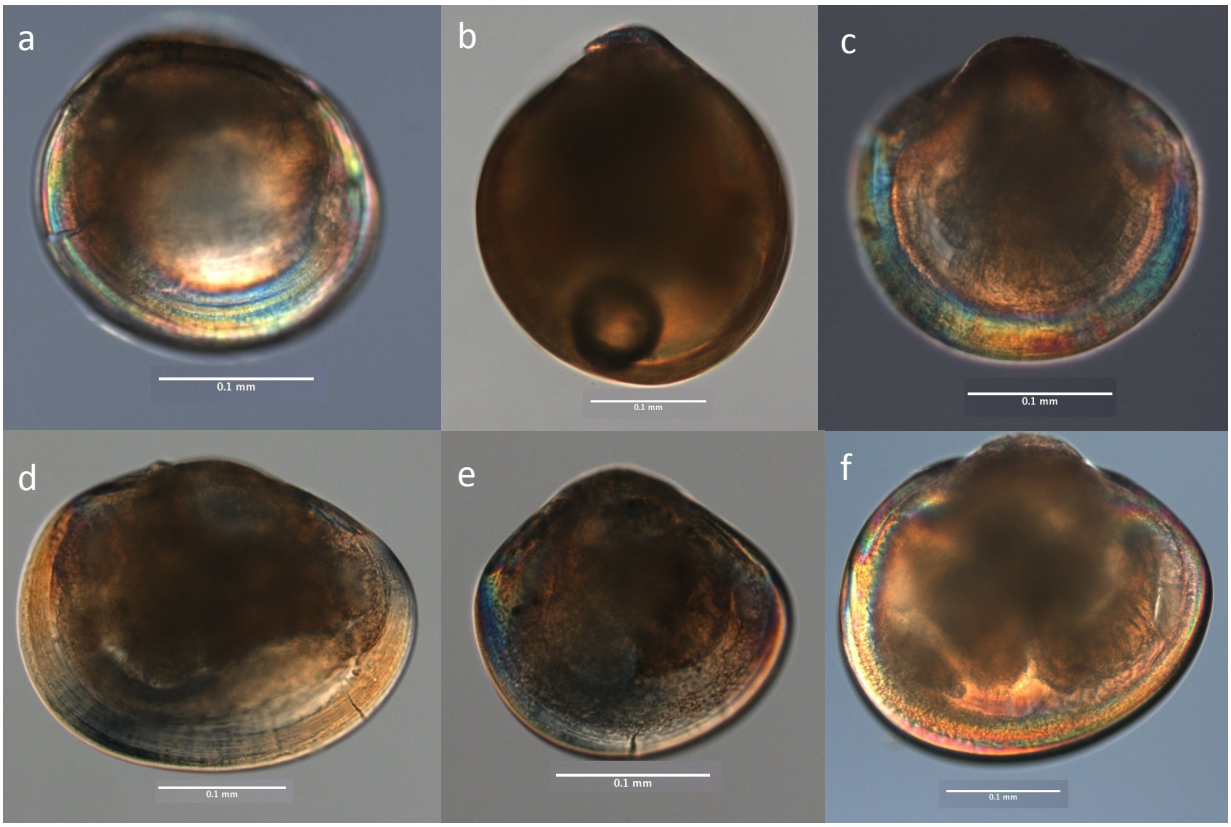


Figure 5. Larval bivalves identified through sequencing of 18S gene region: a) *Ostrea lurida* b) *Teredo navalis* c) Species 1 d) *Ensis* sp. e) *Mya arenaria* f) *Mytilus* sp.

One additional taxon was identified based on morphology alone, referred to as Species 4 (Figure 6), was sufficiently morphologically distinct to warrant the formation of a distinct taxon of its own. However, Species 4 was not identified molecularly due to very low abundances during oblique plankton tow sampling. Higher abundances were

observed at other times during the year in trap samples, but the samples were preserved in formalin preventing molecular identification of the larvae. Lastly, it was necessary to form a group of morphologically unidentifiable and rare larvae. Garland & Zimmer (2002) state that there is a general trend that rather than leaving a larva unidentified, it is usually given a name based on the species surrounding the area and forced into an identifiable group. Additionally, morphological identification can be dependent on the researcher. Larvae, which did not appear to strongly group morphologically with any group used for analysis, were put into the classification as "Other", rather than forcing them into an identified category.

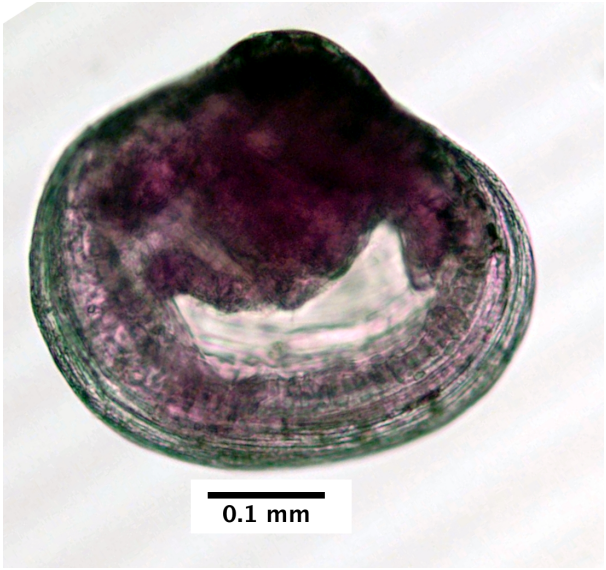


Figure 6. Species 4, a larval bivalve taxon based on morphology alone. The pink color is due to Rose Bengal dye.

Larval Distributions around the Null Zone

To determine the abundance of bivalve larvae relative to the null zone, plankton tows were taken at the point where drogues ceased moving seaward during the falling tide, and we considered this the riverward side of the null zone for that particular day. Plankton tows were then taken where the drogue stopped its seaward movement and riverward and seaward of this location by 1 and/or 3 km. Larval taxon Species 4 was too rare in the plankton tow samples for analysis. The abundance of six of seven larval taxa was significantly correlated with distance to the null zone. Five of the taxa were more abundant seaward of the null zone than riverward: *Ensis* sp. (p=<.0001, r=0.851, n=18), *Mytilus* sp. (p=<.0001, r=0.810, n=18), Species 1 (p=<.001, r=0.712, n=18), *Mya arenaria* (p= <.0001, r=0.841, n=18), and Other (p=<.001, r=.813, n=18). *Ostrea lurida*, the remaining taxon, was significantly more abundant riverward of the null zone than seaward (p=<.0001, r=0.779, n=17). *Teredo navalis* was the single taxon which was not significantly more abundant seaward or riverward of the null zone (p=0.1176, r=0.382, n=18), but it tended to be more abundant riverward of the null zone than seaward.

Trap Data

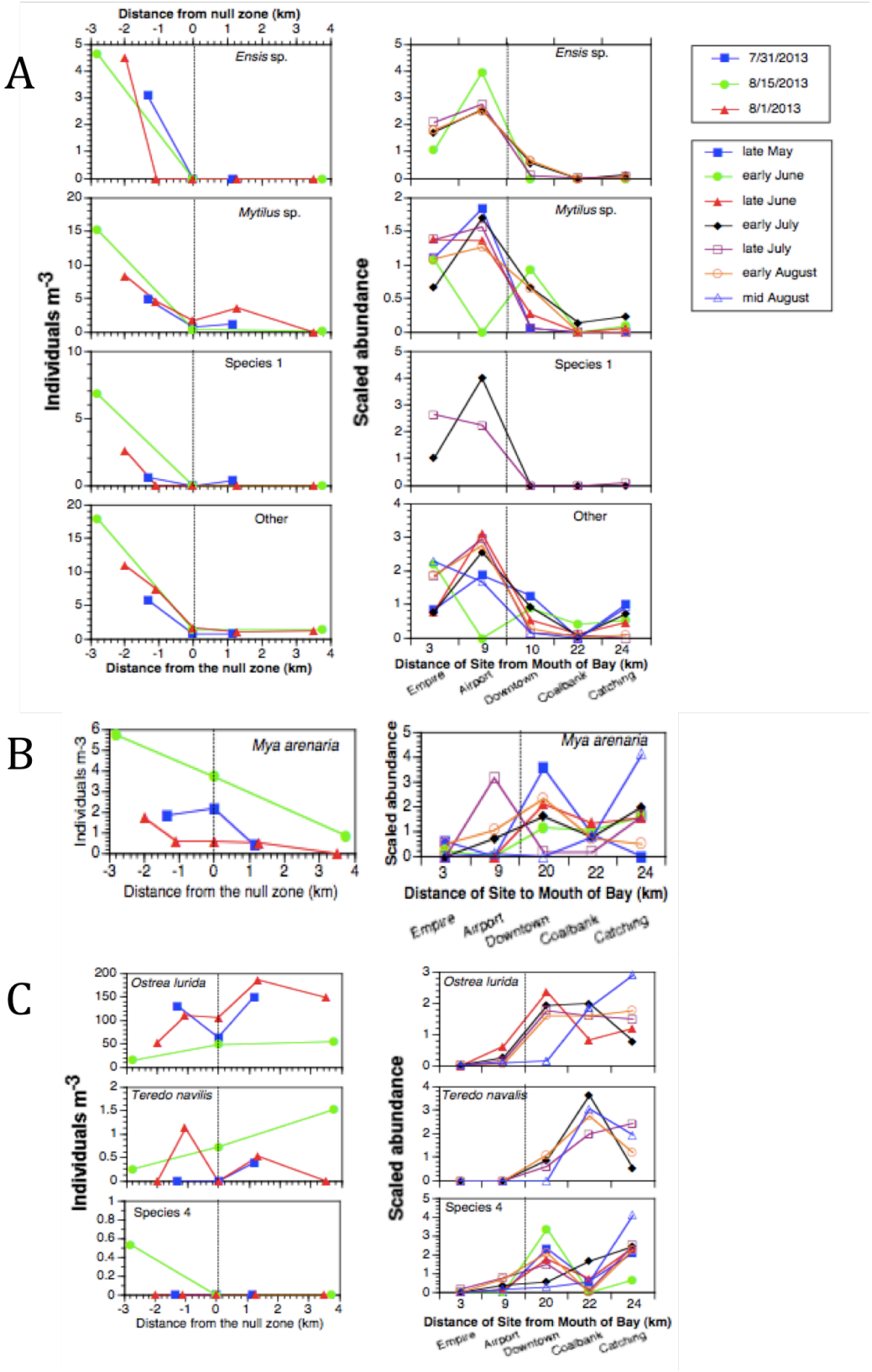
Trap data were used to collect samples during two-week deployments between mid-May and mid-August. Between the two-week deployments, large variations in abundance were observed in most larval taxa. These variations consisted of both low abundances observed at all sites (possibly indicating spawning had not yet taken place), and low abundances at some sites, but high abundances at others (indicating limitations in larval supply). Trap deployments during which all sites had low abundances of a specific taxon were not used in the analysis, as they did not provide informative data on the

influence of the null zone on larval distribution. This restriction of the data used for analyses did not drastically change the outcome of analyses, however. If a larval taxon was significantly (p=0.05) more abundant riverward or seaward of the null zone when data from all trap deployments were used (i.e., data not restricted to dates with adequate abundances), the larval taxon was also significantly more abundant riverward or seaward of the null zone when using the restricted data set (i.e., with high abundances only), however, the magnitude of significance increased when using the restricted data set. The one exception, Species 1, was not significantly more abundant seaward or riverward of the null zone using all trap data (non-restricted data), however, Species 1 became significantly more abundant seaward of the null zone using the restricted data set.

Larval abundances in the traps for all taxa between mid-May and mid-August 2013 are represented in Figure 7. Four taxa, including *Mytilus* sp., *Ensis* sp., Species 1, and Other, were more abundant at sites seaward of the null zone (Empire, Airport) than riverward (Downtown, Coalbank Slough, Catching), particularly during peak abundances. Based on Welch's F-test, these four taxa were statistically more abundant seaward of the null zone than riverward, i.e., *Mytilus* sp. ($F(1,15.787)=71.4303$, p=<.0001), *Ensis* sp. ($F(1,7.1981)=9.3257$, p=0.0179), Species 1 ($F(1,3.0049)=5.1983$, p=0.048), and Other ($F(1,12.84)=11.566$, p=0.0051). *T. navalis, O. lurida*, and Species 4 were all significantly more abundant at riverward sites than seaward sites; *T. navalis* ($F(1,20.066)=13.2952$, p=0.0016), *O. lurida* ($F(1,14.442)=11.9393$, p=0.0037), Species 4 ($F(1,23.77)=22.5944$, p=<.0001). *Mya arenaria* seemed to have a more uniform distribution throughout the estuary, and was not significantly more abundant riverward or seaward of the null zone ($F(1,26.724)=2.87$, p=0.102) using trap data.

Of the eight taxa, five were significantly more abundant riverward or seaward of the null zone (using trap data), or with distance from the null zone (using plankton tow data). Four, i.e., *Mytilus* sp., *Ensis* sp., Species 1, and Other, were significantly more abundant seaward of the null zone than riverward. One, *Ostrea lurida,* was significantly more abundant riverward of the null zone than seaward. *Teredo navalis* tended to have higher abundances riverward of the null zone using tow data, but this was not significant. *Teredo navalis* was significantly more abundant riverward of the null zone than seaward, however, using trap data. *Mya arenaria* was significantly more abundant seaward of the null zone than riverward using tow data, but not trap data. Species 4 could not be analyzed for tow data. However, Species 4 was significantly more abundant riverward than seaward using trap data.

Figure 7 (next page). Figures on the left are distributions of each larval bivalve group based on oblique plankton tow data, and are represented as individuals m^{-3}. Figures on the right are distributions based on trap data-only dates with high abundances have been included here, and are represented as scaled abundances at each site. Scaled abundances were created by dividing the mean (n=3) of each larval bivalve group recorded at a site by the average of that group observed among all sites for one trap deployment. So, for example, if a group is recorded as having a scaled abundance of 5, it indicates that group had an abundance 5 times the average seen at all sites for the same deployment. Dotted vertical lines indicate the approximate location of the null zone; data points to the left of this line were collected downstream, data points to the right were collected upstream. Figure 7A: The distribution of larval bivalve groups with higher abundances riverward of the null zone than downstream. Figure 7B: The distributions of larval bivalve groups with higher abundances seaward of the null zone than upstream of the null zone. Figure 7C: The distributions of *M. arenaria*, did not have any tendency to be more abundant upstream than downstream.


A
Distance from null zone (km)
Ensis sp.
Mytilus sp.
Species 1
Other
Individuals m-3
Distance from the null zone (km)
Scaled abundance
Distance of Site from Mouth of Bay (km)
Empire
Airport
Downtown
Coalbank
Catching
7/31/2013
8/15/2013
8/1/2013
late May
early June
late June
early July
late July
early August
mid August
B
Mya arenaria
Individuals m-3
Distance from the null zone (km)
Scaled abundance
Distance of Site to Mouth of Bay (km)
C
Ostrea lurida
Teredo navalis
Species 4
Individuals m-3
Distance from the null zone (km)
Scaled abundance
Distance of Site from Mouth of Bay (km)

Discussion

Drogues released at Downtown, where *O. lurida* larval populations have been found at their highest abundance (Garcia-Petiero *unpublished*, Chapter III) did not pass the McCullough Bridge on any day, suggesting that a null zone is located within the estuary; water riverward of this location should have longer residence times and be less influenced by ocean water. This pattern of high retention in the upper estuary was also observed by Garcia-Petiero using drogues (*unpublished*), and these data will be combined in a future manuscript. The cross-correlations between the upwelling index and daily temperature time series at the sample sites provide further support for the presence of a null zone around the McCullough Bridge. Mean daily temperatures at sites seaward of the null zone were strongly influenced by coastal upwelling. In 2013, Empire (~3 km from the mouth of the bay) and Airport (~9 km from the mouth of the bay) temperatures both had strong maximum correlations with upwelling indices at -4d lag. Downtown (~20 km from the mouth), however, did not have it's maximum correlation until -10d lag, and the correlation was much weaker than that observed at Airport and Empire. The temperature time series at Catching Slough was not correlated with the upwelling index. Thus, water coming from the open ocean was transported to the Empire and Airport sites within a couple of days, but did not influence the water at the Downtown site until several days later and then only weakly. Upwelling had no obvious influence at the Catching Slough site. The strong cross-correlations between the upwelling index and water temperature seaward of the null zone suggest waters seaward of the null zone should have short residence times and water should be frequently exchanged with the open ocean. Temperature at sites above the null zone were little influenced by the upwelling index

suggesting that water in the estuary riverward of the null zone should have longer residence times. The drogue data and time series analysis of the relationship between the upwelling index and water temperature at the study sites all strongly suggest the presence of a null zone around the McCullough Bridge.

The null zone seems to have a large impact on larval bivalve distribution. Based on trap data, four (*Ensis* sp., *Mytilus* sp., Other, Species 1), of eight taxa had significantly higher abundances seaward of the null zone than riverward. Three taxa had significantly higher abundances riverward of the null zone than seaward (*O. lurida*, *T. navalis*, Species 4). The distribution of *Mya arenaria* larvae did not have a clear relationship with the null zone, as *M. arenaria* was significantly more abundant seaward of the null zone using plankton tow data but not significantly more abundant seaward using trap data, possibly indicating adult populations throughout the estuary. Using plankton tows, all but one group analyzed were significantly more abundant riverward or seaward of the null zone, *T. navalis* was the exception.

Plankton tows around the location of the null zone, as defined by drogue data, were conducted in late July, early August, and mid-August. Species that appeared to have higher abundances seaward of the null zone included *Ensis* sp., *Mytilus* sp., Other, and Species 1. At the time these plankton samples were collected, these four taxa were also abundant in the trap samples from Empire and Airport. However, each taxa's abundance dropped off significantly between the Airport and Downtown sample sites.

Ostrea lurida, Species 4, and *Teredo navalis* were significantly more abundant at stations above of the null zone, i.e., at Downtown, Coalbank Slough, and Catching Slough using trap data. In plankton tow samples collected around the null zone, *O. lurida*

larvae were also more abundant on the riverward side of the null zone but the abundance of *T. navalis* did not vary significantly. Species 4 was significantly more abundant in the trap samples from above the null zone. However, while they were consistently present in the trap samples, they were always present at very low abundances. These low abundances are reflected in tow samples from around the null zone, where they were present in only one tow (August 15th, 3 km seaward); their rarity in the plankton tows prevented statistical analyses.

Lastly, *Mya arenaria* was not significantly more abundant seaward or riverward of the null zone using trap data, but was significantly more abundant seaward using tow data. When looking at the trap data, however, the non-significant was likely driven by a larval peak occurring at Airport, but not Empire, in mid-June where 18 individuals per trap were counted. However, this could also represent that *Mya arenaria* adults may be present both seaward and riverward of the null zone. In general, it seems as though *M. arenaria* is considered an inner bay species. Carlton (1992) describes the species as "now one of the most common upper bay clams from Washington to San Francisco" Morris et al. (1980) also describe the distribution as the "upper reaches of bays, including brackish areas". *M. arenaria* also appears to tolerate a wide variety of salinities. Mattiessen (1957) found *Mya arenaria* could tolerate salinities between fully saline water, down to 1‰ for up to 24 hours. He also found *M. arenaria* living at salinities between 0-11.8 for slightly over two months. Furthermore, *M. arenaria* was living in environments with a range of salinities with means between 3.5 and 14, indicating they can tolerate long-term exposure to low salinities (Mattiessen 1960).

Other taxa exhibited the same tendency to have larval distributions where their adults are located. For instance, *Ensis myrae* (the only member of the genus known to occur in this region) is considered an offshore species in the Pacific Northwest (Light 2007a) and *Mytilus* sp. adults are found more commonly in the intertidal along the open coast than within the bay. However, Braby & Somero (2005) established that in regions of the Coos Bay estuary close to the mouth of the bay, *M. trossulus* dominated mussel populations. *M. trossulus* abundances have been negatively correlated throughout California and Oregon estuaries with increasing salinity, but positively correlated with temperature and salinity range. This indicates that although this species has generally been described as an organism with an affinity for cool, euryhaline waters, it does have the ability to survive within the polyhaline waters within an estuary.

Ostrea lurida, whose larvae were found riverward of the null zone, is considered an estuarine-dependent species, and is infrequently found on the open coast (Light 2007b). *T. navalis* is also common in the upper reaches of estuaries. Although it can tolerate salinities between 5 and 35, it has been described as thriving at mid-range salinities down to 9 (Tuene et al. 2002). Furthermore, its larvae can survive in salinities as low as 6 (Hoagland 1986), conditions well within the ranges seen in the upper bay during the apparent reproductive season. Trap data indicate *T. navalis* to be present throughout the estuary riverward of the null zone, but it is possible the range of its adult distribution extends farther seaward than where plankton tow sampling took place, yet not extending as far seaward as Airport.

Interestingly, Júlio & Guerreiro (1966) found similar results of relative position in the Mira estuary, Portugal, when examining multiple larval bivalve taxa including *Ensis*,

Mytilus, and *Ostrea*. *Ensis* and *Mytilus* taxa both displayed marine affinities, while *Ostrea edulis* was found in the inner bay. Furthermore, the authors wrote, "salinity showed to be the major barrier to larval dispersion". However, salinity changes are not likely to be barriers to dispersal. The barrier, potentially the null zone, however, could be *identified* through changes in salinity. For example, inner-bay water riverward of the null zone would most likely be brackish, while oceanic water seaward would be more saline. The location of the null zone and its apparent affect on larval distributions clearly has implications for the distribution of adult populations. For example, both *Ensis* and *Mytilus* appear to be more prevalent seaward (at Empire and Airport) of the null zone than landward. With low larval supply riverward, then, we would expect that adult populations are more scarce or possibly nonexistent riverward. Likewise, with higher larval supply seaward, it would follow that adult populations are likely to be more abundant, or larger, with likely annual larval supply to supplement, or replace previous generations.

Despite the strong evidence presented here for the presence of a null zone in driving larval bivalve distributions, we cannot discount the possibility that vertical migrations of the larvae are also affecting larval distributions. However, it is unlikely that all seven of eight taxa which were significantly more abundant either seaward or riverward of the null zone have vertical migration behaviors that would result in these patterns, by changing drastically around our estimated null zone. Furthermore, it has been documented that *Mytilus* sp. does not exhibit vertical migration behaviors ((McQuaid & Phillips 2000), and it's distribution therefore is likely controlled hydrodynamically.

Conclusion

Drogue data suggest a null zone exists between Airport and Downtown. Temperature patterns observed at Empire, Airport, and Downtown, also suggest that the null zone during the dry season is located between the Airport and Downtown sampling sites. Specifically, strong correlations between the daily upwelling index and mean daily temperature were observed at Empire and Airport, but strong upwelling signals did not persist through the estuary to Downtown, Coalbank Slough or Catching Slough, indicating that both Empire and Airport are strongly influenced by proximity to coastal upwelling while the Downtown,Coalbank Slough and Catching Slough site were not. These data support minimal mixing of water between Airport and Downtown, where we hypothesize the null zone exists in the dry season. Larvae of six bivalve taxa analyzed were significant more abundant either seaward or riverward of the null zone (five more abundant seaward, one more abundant riverward). Trap data indicate the larvae of four of eight bivalve taxa were more abundant at sites seaward of the null zone, and three taxa more abundant riverward of the null zone. The data suggest that the the low mixing around the null zone may be sufficient to maintain separate larval bivalve communities seaward and riverward of the null zone.

Implications

The position of the null zone is not static; it should be heavily influenced by the ratio of ocean water intrusion to freshwater outflow. For example, assuming a constant river outflow, we would expect the location of the null zone to move riverward during a

spring flood tide, relative to that of a neap flood tide (Miller 1983). Likewise, assuming a constant tidal amplitude, we would expect the position to move seaward during winter months, relative to summer months due to increased river outflow (Miller 1983). With this in mind, it seems plausible that stable adult populations of bivalves are located in the correct general area, according to their ecology. *O. lurida*, an estuarine-dependent species, is not known to occur on the open coast, and is buffered from larval flushing by establishing populations in the upper bay. During their reproductive season, residence times are likely to be high within their habitat, retaining the larvae within the bay, and promoting successful settlement near adult populations and suitable substrate. *M. arenaria*'s distribution may also be attributed to lower salinity regions providing refuge from the clam's major predators, such as the green crab (*Carcinides maenas*), that cannot withstand such low salinities for long periods of time (Matthiessen 1960).

The Coos Bay estuary has been, and continues to be, modified through a variety of mechanisms (Coos Bay Estuary Plan 1975, USACE), although lately predominantly through dredging. Other sources of modification include erosion, increased sedimentation due to poor land practices surrounding the estuary, and filling (Coos Bay Estuary Plan 1975). By 1975, it was estimated that approximately 3,500 acres had been removed from the estuary by filling (Coos Bay Estuary Plan 1975).

Beginning in the late 19th century or early 20th, the US Army Corp of Engineers (USACE) began altering the Coos Bay estuary to facilitate large ship used for transporting lumber. In 1928 and 1929, the two jetties at the entrance of the estuary were built. An initial federal shipping channel was dredged and maintained at 13.7 m deep, and 213 m wide (USACE). In 1996, the channel was deepened in the first 1.6 river

kilometers to 14.3 m deep, and extended to river kilometer 24, at a depth of 11.3 m. Also in 1996, the width of the shipping channel near the bend at McCullough Bridge was increased by 30.5 m in order to facilitate navigation around the bend (USACE). Shipping channel depth was deepened again in 1997, by 1 m (USACE). Further channel expansion is currently being sought by Oregon International Port of Coos Bay, and includes deepening the shipping channel maintained by USACE from the current depth of 11.3 m down to 15.5 m, and widening the shipping channel from 91 to 137 m. The jetties, too, might be modified to allow larger ships' entrance (Oregon International Port of Coos Bay). Each of these changes made to the estuary likely affect the hydrodynamics of the bay and have likely altered the position of the null zone.

The proposed future channel modifications would increase the volume of oceanic intrusion, perhaps shifting the null zone riverward and closer to the river. If the null zone is an effective barrier to larval dispersal, as this research suggests, estuarine dependent larvae, such as *O. lurida,* would likely be confined above the shifted null zone. It is plausible that the distribution of species that occur riverward of the current null zone (*O. lurida*, *T. navalis*, Species 4) would likely shift riverward with the new null zone, and any current populations below the new null zone would gradually be lost due to larval flushing to the open ocean. However, *O. lurida* recruitment is low in areas with high, short-term variability in temperature and salinity such as Coalbank Slough and Catching Slough (Chapter III). Thus, appropriate changes in settlement to maintain or promote population growth are not likely to happen. Likewise, species occurring below the current null zone could potentially shift their distributions up to the current null zone, replacing the current estuarine-dependent species, including *O. lurida*.

CHAPTER V

GENERAL DISCUSSION

The distribution of known adult populations of *Ostrea lurida* in the Coos Bay estuary closely followed recruitment patterns observed in 2012 and 2013. No recruitment was observed at sites in the lower bay, where there are no adult populations (e.g., Empire in 2012 and 2013, Empire and Airport in 2013). A few adult populations do exist slightly above Airport. If the critical temperature for reproduction of 15°C in the Coos Bay estuary hold true and controls reproduction (as indicated by Garcia-Petiero *unpublished*, Oates *unpublished*) then populations near Airport likely contribute very little, if at all, as minimum daily temperatures above 15°C were not observed at Airport.

In the upper bay, however, minimum daily temperatures equal to or above 15°C were reached at Haynes Inlet, Downtown, Coalbank Slough and Catching Slough. Recruitment was high at both Haynes Inlet and Downtown in both 2012 and 2013, where adult populations exist. At Catching Slough and Coalbank Slough, however, recruitment was very low in both sampling years. Furthermore, adults have not been observed in Catching Slough, and have only been observed near the main channel in Coalbank Slough.

Despite recruitment patterns being similar to the distribution of adult populations, there was a mismatch between larval supply and recruitment; high larval supply did not always result in high recruitment, indicating *O. lurida* recovery in the Coos Bay estuary may not be limited by larval supply. At Empire and Airport, very low larval supply was

observed and no recruitment was observed. High larval supply and recruitment was observed at Downtown and Haynes Inlet. At Coalbank and Catching Slough, however, high larval supply was observed, yet recruitment was low. Substrate limitation has often been cited as a reason for low natural recruitment (Brumbaugh & Coen 2009, Groth & Rumrill 2009). Yet despite the addition of settlement plates (providing hard substrata on which to settle), recruitment remained low at Coalbank and Catching Slough. These data suggest environmental cues may be influencing settlement. We collected only temperature and salinity data, and the salinity data appears to be in error. However, at Coalband and Catching Slough, where larval supply was high but settlement was low, are characterized by large daily and annual variations in salinity. Wasson (2010) also observed an absence of *O. lurida* adult populations at sites where there were large variations in salinity (in addition to large ranges in other parameters). Other water parameters such as dissolved oxygen, chlorphyll *a*, or turbitity could also be contributing to the distribution of adults, but more work needs to be done on this subject.

The onset of reproduction appears to be variable between years, possibly because annual variation in the date on which the critical temperature for spawning is reached. When data collection began in 2012, minimum daily temperatures of 15°C had already been reached and larvae were already present. In 2013, minimum daily temperatures reached 15°C, after which the temperature dropped below 15°C, then rose again after which larvae were observed. In 2012, peak larval abundance was observed in late-July through early August 2012, but in 2013 early through mid-July 2013. However, peak larval abundance in 2012 was likely missed, and we saw only the tail-end of the reproductive season.

Throughout both 2012 and 2013, *Ostrea lurida* larvae were present in the upper bay, but not in the lower. Drogue data indicated the presence of a null zone located slightly above the McCullough Bridge; *O. lurida* larvae were likely retained in the upper bay resulting in low larval supply to the lower bay. Other groups of larval bivalves, too, appeared to have high abundances to either side of the null zone. Nine of ten groups examined followed this pattern. These data indicate little mixing between water downstream of the null zone and upstream. Further support for minimal mixing comes from physical data; temperature data at Empire and Airport indicate the influence of coastal upwelling, yet the signal of upwelling at Downtown is much weaker than at Airport, and lags behind that observed at Airport by approximately six days. However, the signal of upwelling in mean daily temperatures at Catching Slough is close to that Downtown, indicating mixing between these two sites is more substantial than the mixing between Downtown and Airport. With the location of the null zone estimated to be between Airport and Downtown, this makes sense.

The data presented here indicate a general area in the bay, the null zone, which separates two water masses in the bay; the characteristics of the lower water mass is strongly influenced by coastal waters while the upper water mass has properties more influenced by river input. Associated with these differences water masses are different larval bivalve communities. In the case of *O. lurida,* the distribution of larvae affects recruitment and possibly adult population distributions. Future changes made to the bay should consider the modification's influence on the position of the null zone (whether it will shift it upstream or downstream), and how this might affect ecosystem health and restoration work in the bay.

APPENDIX A

DEPLOYMENT DATES FOR TRAPS AND PLATES AT EACH SITE IN 2012 AND 2013

Time Interval 1 2012			
	Initial Deployment	Exchange Date	Total Days Deployed
Empire	7/19/12	8/3/12	15
Haynes Inlet	7/20/12	8/2/12	13
Downtown	7/18/12	8/2/12	15
Coalbank Slough	7/20/12	8/3/12	14
Catching Slough	7/19/12	8/2/12	14
Time Interval 2 2012			
	Initial Deployment	Exchange Date	Total Days Deployed
Empire	8/3/2012	8/17/12	14
Haynes Inlet	8/2/12	8/16/12	14
Downtown	8/2/12	8/18/12	16
Coalbank Slough	8/3/12	8/17/12	14
Catching Slough			
Time Interval 3 2012			
	Initial Deployment	Exchange Date	Total Days Deployed
Empire	8/17/12	8/30/12	13
Haynes Inlet	8/16/12	8/29/12	13
Downtown	8/18/12	8/30/12	12
Coalbank Slough	8/17/12	8/31/12	14
Catching Slough			
Time Interval 4 2012			
	Initial Deployment	Exchange Date	Total Days Deployed
Empire	8/30/12	9/15/12	16
Haynes Inlet	8/29/12	9/13/12	15
Downtown	8/30/12	9/15/12	16
Coalbank Slough	8/31/12	9/13/12	13
Catching Slough	8/30/12	9/14/12	15
Time Interval 5 2012			
	Initial Deployment	Exchange Date	Total Days Deployed
Empire	9/15/12	9/30/12	15
Haynes Inlet	9/13/12	10/1/12	18
Downtown	9/15/12	10/2/12	17
Coalbank Slough	9/13/12	10/1/12	18
Catching Slough	9/14/12	9/30/12	16
Time Interval 6 2012			
	Initial Deployment	Exchange Date	Total Days Deployed
Empire	9/30/12	10/14/12	14
Haynes Inlet	10/1/12	10/13/12	12
Downtown	10/2/12	10/14/12	12
Coalbank Slough	10/1/12	10/13/12	12
Catching Slough	9/30/12	10/14/12	14

Time Interval 7 2012			
	Initial Deployment	Exchange Date	Total Days Deployed
Empire	10/14/12	10/29/12	15
Haynes Inlet	10/13/12	10/30/12	17
Downtown	10/14/12	10/29/12	15
Coalbank Slough	10/13/12	10/30/12	17
Catching Slough	10/14/12	10/29/12	15
Time Interval 8 2012			
	Initial Deployment	Exchange Date	Total Days Deployed
Empire	10/29/12	11/14/12	16
Haynes Inlet	10/30/12	11/15/12	16
Downtown	10/29/12	11/14/12	16
Coalbank Slough	10/30/12	11/15/12	16
Catching Slough	10/29/12	11/14/12	16
Time Interval 1 2013			
	Initial Deployment	Exchange Date	Total Days Deployed
Empire	5/13/13	5/25/13	12
Airport	5/12/13	5/24/13	12
Haynes Inlet	5/9/13	5/25/13	16
Downtown	5/10/13	5/24/13	14
Coalbank Slough	5/10/13	5/25/13	15
Catching Slough	5/9/13	5/25/13	16
Time Interval 2 2013			
	Initial Deployment	Exchange Date	Total Days Deployed
Empire	5/25/13	6/10/13	16
Airport	5/24/13	6/9/13	16
Haynes Inlet	5/25/13	6/8/13	14
Downtown	5/24/13	6/9/13	16
Coalbank Slough	5/25/13	6/8/13	14
Catching Slough	5/25/13	6/9/13	15
Time Interval 3 2013			
	Initial Deployment	Exchange Date	Total Days Deployed
Empire	6/10/13	6/24/13	14
Airport	6/9/13	6/23/13	14
Haynes Inlet	6/8/13	6/24/13	16
Downtown	6/9/13	6/23/13	14
Coalbank Slough	6/8/13	6/24/13	16
Catching Slough	6/9/13	6/23/13	14
Time Interval 4 2013			
	Initial Deployment	Exchange Date	Total Days Deployed
Empire	6/24/13	7/9/13	15
Airport	6/23/13	7/8/13	15
Haynes Inlet	6/24/13	7/9/13	15
Downtown	6/23/13	7/10/13	17
Coalbank Slough	6/24/13	7/10/13	16
Catching Slough	6/23/13	7/8/13	15

Time Interval 5 2013			
	Initial Deployment	Exchange Date	Total Days Deployed
Empire	7/9/13	7/23/13	14
Airport	7/8/13	7/22/13	14
Haynes Inlet	7/9/13	7/23/13	14
Downtown	7/10/13	7/22/13	12
Coalbank Slough	7/10/13	7/23/13	13
Catching Slough	7/8/13	7/22/13	14
Time Interval 6 2013			
	Initial Deployment	Exchange Date	Total Days Deployed
Empire	7/23/13	8/7/13	15
Airport	7/22/13	8/6/13	15
Haynes Inlet	7/23/13	8/5/13	13
Downtown	7/22/13	8/7/13	16
Coalbank Slough	7/23/13	8/6/13	14
Catching Slough	7/22/13	8/5/13	14
Time Interval 7 2013			
	Initial Deployment	Final Collection	Total Days Deployed
Empire	8/7/13	8/19/13	12
Airport	8/6/13	8/18/13	12
Haynes Inlet	8/5/13	8/19/13	14
Downtown	8/7/13	8/18/13	11
Coalbank Slough	8/6/13	8/19/13	13
Catching Slough	8/5/13	8/18/13	13

APPENDIX B

ENVIRONMENTAL PARAMETERS FOR EACH DEPLOYMENT PERIOD

Appendix B. Environmental parameters for each deployment period. Values were calculated by averaging daily minimum, maximum, and ranges values for temperature and salinity over dates corresponding to deployments of traps and plates. Mean temperature and salinity values were calculated by creating daily means, and averaging these means over the corresponding deployment period of traps and plates.

Site	Time Interval	Mean Minimum Temp	Mean Mean Temp	Mean Max Temp	Mean Range Temp	Mean Minimum Salinity	Mean Mean Salinity	Mean Maximum Salinity	Mean Range Salinity	Year
Catching	1	18.5	19.7	21.1	2.6	6.9	15.9	20.2	13.3	2012
Catching	4	16.6	18.7	19.8	3.2	14.5	21.2	24.4	9.9	2012
Catching	5	13.7	16.9	18.1	4.4	16.5	23.2	25.6	9.1	2012
Catching	6	14.1	15.8	16.6	2.5	17.3	22.5	24.7	7.4	2012
Catching	7	11.4	13.7	14.5	3.1	6.6	15.7	20.6	14.1	2012
Catching	8	11.7	12.7	13.3	1.6	1.3	9.0	15.3	14.1	2012
Coalbank	1	17.3	19.5	20.8	3.5	17.1	19.3	21.3	4.2	2012
Coalbank	2	19.0	20.0	21.2	2.2	19.0	20.3	21.6	2.6	2012
Coalbank	3	18.4	19.3	20.4	2.1	17.9	18.9	19.9	2.0	2012
Coalbank	4	No Data	No Data	No Data	No Data	No Data	No Data	No Data	No Data	2012
Coalbank	5	16.2	17.2	18.2	2.0	13.7	14.7	15.7	2.0	2012
Coalbank	6	15.2	15.8	16.4	1.2	3.2	3.4	3.4	0.3	2012
Coalbank	7	13.3	14.1	14.7	1.4	2.3	2.7	2.9	0.7	2012
Coalbank	8	12.2	13.0	13.5	1.4	1.9	2.8	3.2	1.4	2012
Downtown	1	15.4	17.9	19.6	4.2	18.2	22.4	24.4	6.2	2012
Downtown	2	16.5	18.5	19.9	3.4	20.0	23.0	24.6	4.6	2012
Downtown	3	15.9	17.7	19.3	3.3	20.8	23.2	24.6	3.8	2012
Downtown	4	No Data	No Data	No Data	No Data	No Data	No Data	No Data	No Data	2012
Downtown	5	12.3	15.5	16.8	4.5	21.5	22.8	23.6	2.1	2012
Downtown	6	13.2	14.7	15.5	2.3	21.2	22.3	22.9	1.8	2012
Downtown	7	11.1	13.3	14.4	3.3	14.8	19.3	21.2	6.3	2012
Downtown	8	11.6	12.8	13.3	1.7	8.9	15.0	18.2	9.3	2012
Empire	1	10.6	12.8	15.0	4.4	25.4	26.6	27.5	2.1	2012
Empire	2	10.8	12.8	14.8	4.0	25.5	26.5	27.3	1.8	2012
Empire	3	10.3	12.3	14.2	3.9	26.1	26.8	27.5	1.3	2012
Empire	4	10.3	12.4	14.4	4.1	25.2	26.0	26.7	1.5	2012
Empire	5	10.2	11.9	13.8	3.5	24.2	25.3	26.3	2.1	2012
Empire	6	No Data	No Data	No Data	No Data	No Data	No Data	No Data	No Data	2012
Empire	7	No Data	No Data	No Data	No Data	No Data	No Data	No Data	No Data	2012

Haynes Inlet	1	15.2	17.3	19.1	3.9	7.5	7.9	8.9	1.3	2012
Haynes Inlet	2	15.6	17.5	19.5	3.9	17.5	19.4	21.6	4.1	2012
Haynes Inlet	3	15.0	16.9	18.6	3.6	20.8	22.1	23.3	2.4	2012
Haynes Inlet	4	14.8	16.6	18.1	3.3	23.0	23.7	24.3	1.3	2012
Haynes Inlet	5	13.9	15.1	16.6	2.7	23.4	24.0	24.6	1.3	2012
Haynes Inlet	6	13.5	14.2	15.1	1.6	23.8	24.3	24.7	0.8	2012
Haynes Inlet	7	12.6	13.2	14.0	1.4	20.7	22.7	23.7	3.1	2012
Haynes Inlet	8	12.4	12.9	13.4	1.1	16.2	19.5	21.3	5.1	2012
Airport	2	11.7	13.6	15.6	3.9	20.2	23.4	25.9	5.7	2013
Airport	1	12.0	13.9	15.8	3.7	22.7	25.6	27.5	4.8	2013
Airport	3	11.8	13.8	16.3	4.5	21.4	24.1	25.8	4.4	2013
Airport	4	14.8	16.9	19.0	4.2	21.3	22.9	24.1	2.7	2013
Airport	5	11.3	14.2	16.7	5.4	22.9	24.1	25.5	2.6	2013
Airport	6	11.0	13.9	16.2	5.2	19.6	21.2	22.4	2.8	2013
Airport	7	12.3	14.6	16.7	4.4	10.8	12.0	12.7	1.9	2013
Catching	1	15.9	17.0	18.0	2.1	5.4	15.9	21.9	16.4	2013
Catching	2	15.1	16.1	17.0	1.9	1.8	11.2	18.0	16.2	2013
Catching	3	17.0	18.4	20.0	3.1	4.2	14.5	20.6	16.4	2013
Catching	4	No Data	No Data	No Data	No Data	No Data	No Data	No Data	No Data	2013
Catching	5	No Data	No Data	No Data	No Data	No Data	No Data	No Data	No Data	2013
Catching	6	No Data	No Data	No Data	No Data	No Data	No Data	No Data	No Data	2013
Catching	7	No Data	No Data	No Data	No Data	No Data	No Data	No Data	No Data	2013
Coalbank	1	No Data	No Data	No Data	No Data	No Data	No Data	No Data	No Data	2013
Coalbank	2	No Data	No Data	No Data	No Data	No Data	No Data	No Data	No Data	2013
Coalbank	3	No Data	No Data	No Data	No Data	No Data	No Data	No Data	No Data	2013
Coalbank	4	No Data	No Data	No Data	No Data	No Data	No Data	No Data	No Data	2013
Coalbank	5	No Data	No Data	No Data	No Data	No Data	No Data	No Data	No Data	2013
Coalbank	6	18.3	19.7	20.9	2.6	19.6	21.7	22.8	3.3	2013
Coalbank	7	19.0	20.0	21.3	2.2	21.1	22.1	23.0	2.0	2013

Downtown	1	15.2	16.2	17.5	2.4	13.3	18.3	20.3	7.0	2013
Downtown	2	14.5	15.6	16.5	2.0	5.6	14.8	18.8	13.2	2013
Downtown	3	15.7	16.9	18.8	3.1	19	16.8	19	3.1	2013
Downtown	4	No Data	No Data	No Data	No Data	No Data	No Data	No Data	No Data	2013
Downtown	5	No Data	No Data	No Data	No Data	No Data	No Data	No Data	No Data	2013
Downtown	6	No Data	No Data	No Data	No Data	No Data	No Data	No Data	No Data	2013
Downtown	7	No Data	No Data	No Data	No Data	No Data	No Data	No Data	No Data	2013
Empire	1	11.3	12.7	14.2	2.9	21.6	22.6	23.3	1.8	2013
Empire	2	11.2	12.7	14.3	3.1	22.4	24.1	25.2	2.8	2013
Empire	3	11.7	12.9	14.2	2.4	23.5	24.8	25.3	1.8	2013
Empire	4	13.5	15.9	18.0	4.5	22.7	23.9	24.8	2.1	2013
Empire	5	10.1	12.3	15.1	5.0	22.5	25.0	26.0	3.5	2013
Empire	6	No Data	No Data	No Data	No Data	No Data	No Data	No Data	No Data	2013
Empire	7	No Data	No Data	No Data	No Data	No Data	No Data	No Data	No Data	2013
Haynes	1	14.7	16.1	17.9	3.2	18.6	21.4	22.7	4.1	2013
Haynes	2	14.4	15.9	17.8	3.4	15.5	19.7	21.9	6.4	2013
Haynes	3	15.3	17.0	19.3	4.0	19.3	21.3	22.6	3.4	2013
Haynes	4	17.7	19.5	21.7	4.0	19.9	21.2	22.2	2.3	2013
Haynes	5	15.2	17.4	19.7	4.5	21.9	22.8	23.9	2.0	2013
Haynes	6	15.1	17.1	19.3	4.2	22.6	23.4	24.3	1.7	2013
Haynes	7	16.4	18.3	20.3	3.9	22.4	23.0	23.8	1.5	2013

APPENDIX C

LARVAL AND RECRUIT ABUNDANCES

Appendix C. D-stage, umbo-stage and settler abundances (± confidence intervals) for each deployment period in 2012 and 2013.

Site	Deployment	Deployment date	Means D-stage larvae per trap ± Confidence Interval	Means umbo-stage larvae per trap ± Confidence Interval	Mean settlers per 100 cm^2 ± Confidence Interval
Catching	1	July 19-August 2	8 (n=1)	0	0.5±0.4
Catching	4	August 30-September 14	8±2.3	13±3.7	0.1±0.3
Catching	5	September 14-September 30	0	0	0
Catching	6	September 30-October 14	0	0	0
Catching	7	October 14-October 29	0	0	0
Catching	8	October 29-November 14	0	0	0
Coalbank	1	July 20-August 3	78±35.3	11±4.1	0.9±0.8
Coalbank	2	August 3-August 17	75.7±17.4	15.7±4.6	0.4±0.4
Coalbank	3	August 17-August 31	38±13.1	8.3±4.6	1.7±1.8
Coalbank	4	August 31-September 13	18.5±8.7	4±2.9	0.6±0.8
Coalbank	5	Septemer 13-October 1	0	0.5±1	0
Coalbank	6	October 1-October 13	0	0	0
Coalbank	7	October 13-October 30	0	0	0
Coalbank	8	October 30-November 15	0	0	0
Downtown	1	July 18-August 2	142±28.4	67.7±7.7	0.4±0.5
Downtown	2	August 2-August 18	89±39.8	58.3±18.7	19.5±6
Downtown	3	August 18-August 30	43.7±12.2	23±5.2	18.7±7.1
Downtown	4	August 30-September 15	6.8±3.3	11.5±2.9	4.3±1.9
Downtown	5	September 15-October 2	3±2	0	0.4±0.4

Downtown	6	October 2-October 14	0	0	0
Downtown	7	October 14-October 29	0	0	0
Downtown	8	October 29-November 14	0	0	0
Empire	1	July 19-August 3	0	0	0
Empire	2	August 3-August 17	1.3±1.7	0.3±0.7	0
Empire	3	August 17-August 30	1.5±1.1	0	0
Empire	4	August 30-September 15	1±2	1±2	0
Empire	5	September 15-September 30	0	0	0
Empire	6	September 30-October 14	0	0	0
Empire	7	October 14-October 29	0	0	0
Haynes Inlet	1	July 20-August 2	59.3±10.5	30.3±6.2	2.7±0.9
Haynes Inlet	2	August 2-August 16	46±9.9	27.3±6.8	5.9±1.2
Haynes Inlet	3	August 16-August 29	15.8±11.4	3±2	5.7±2.1
Haynes Inlet	4	August 29-September 13	6.7±7.9	2.7±2.8	1.7±0.9
Haynes Inlet	5	September 13-October 1	0	0	0.5±0.4
Haynes Inlet	6	October 1-October 13	0	0	0
Haynes Inlet	7	October 13-October 30	0	0	0
Haynes Inlet	8	October 30-November 15	0	0	0
Airport	1	May 12-May 24	0	0	0
Airport	2	May 24-June 9	0	0	0
Airport	3	June 9-June 23	6.3±0.7	1.3±0.7	0
Airport	4	June 23-July 8	10.3±7.9	14±3.4	0
Airport	5	July 8-July 22	19±6.8	12.3±1.3	0
Airport	6	July 22-August 6	2.3±2.8	1.3±1.7	0
Airport	7	August 6-August 18	0.3±0.7	0.3±0.7	0

Catching	1	May 9-May 25	0	0	0
Catching	2	May 25-June 9	2±2	0	0
Catching	3	June 9-June 23	12.3±7.5	2.3±2.6	0
Catching	4	June 23-July 8	43±24.5	32.3±25.7	0.5±0.7
Catching	5	July 8-July 22	193.3±22.4	135.3±17.5	0.5±0.4
Catching	6	July 22-August 5	61.7±20	50.3±10.1	0
Catching	7	August 5-August 18	17.3±8.3	9.7±1.7	0
Coalbank	1	May 10-May 25	0	0	0
Coalbank	2	May 25-June 8	1.5±2.9	0	0
Coalbank	3	June 8-June 24	8±3.9	0	0.1±0.3
Coalbank	4	June 24-July 10	154.3±17.6	33±10.8	1.3±0.5
Coalbank	5	July 10-July 23	269.7±116.4	77±27.5	3.2±1.6
Coalbank	6	July 23-August 6	74±16	28±7.8	0
Coalbank	7	August 6-August 19	12±4.5	5.3±0.7	0.8±0.3
Downtown	1	May 10-May 24	0	0	0
Downtown	2	May 24-May 9	6±2	0	0
Downtown	3	May 9-May 23	23.7±11.4	5±3	0
Downtown	4	May 23-July 10	99±5.9	83±15.6	31.5±9
Downtown	5	July 10-July 22	201±15.3	183±28.9	20±4.5
Downtown	6	July 22-August 7	53.7±16.5	48.7±11	1.2±1
Downtown	7	August 7-August 18	0.7±1.3	0.7±1.3	1.3±0.7
Empire	1	May 13-May 25	0.3±0.7	0	0
Empire	2	May 25-June 10	0	0	0
Empire	3	June 10-June 24	0	0	0
Empire	4	June 24-July 9	0.3±0.7	0.7±0.7	0

Empire	5	July 9-July 23	4±2	0	0
Empire	6	July 23-August 7	1.3±1.3	0.7±0.7	0
Empire	7	August 7-August 19	0.3±0.7	0	0
Haynes	1	May 9-May 25	0	0	0
Haynes	2	May 25-June 8	0	0	0
Haynes	3	June 8-June 24	35.3±12.1	3.3±1.7	0
Haynes	4	June 24-July 9	42±43.1	44±49	54.5±19.3
Haynes	5	July 9-July 23	54.3±44.1	37.7±35	8.7±2.4
Haynes	6	July 23-August 5	16±3.9	4.7±1.7	0.1±0.3
Haynes	7	August 5-August 19	9.7±4.7	0.7±0.7	0.1±0.3

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