The Olympia Oyster *Ostrea lurida*: Recent Advances in Natural History, Ecology, and Restoration

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Published By: National Shellfisheries Association
DOI: [http://dx.doi.org/10.2983/035.034.0207](http://dx.doi.org/10.2983/035.034.0207)
THE OLYMPIA OYSTER OSTREA LURIDA: RECENT ADVANCES IN NATURAL HISTORY, ECOLOGY, AND RESTORATION

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ABSTRACT This article reviews recent literature on the biology of Ostrea lurida, emphasizing information that has arisen subsequent to Baker’s review in 1995. The review highlights recent work that contributes to improvements in restoration efforts. Included are sections on phylogeny, reproductive biology, shell morphology, harvesting, associations with other organisms, threats to recovering populations, ocean acidification, and larval supply, settlement and recruitment.

KEY WORDS: Olympia oyster, Ostrea lurida, native oyster, oyster reef restoration

The Olympia oyster Ostrea lurida (Carpenter, 1864), is the only native oyster occurring along the western coast of the United States with a historical distribution from Baja California to Sitka, AK (Dall 1914, Coen et al. 2000). The current range of O. lurida is estimated to be up to 40% smaller than its historic range, with the southern limit now near Bahia San Quintin, Baja California, Mexico and the northern limit near Queen Charlotte Island, British Columbia (Gillespie 2009). Additionally, the health of O. lurida populations along the majority of the Pacific Northwest have been classified as either poor (90%–99% lost) or functionally extinct (>99% lost), with the exception of healthy populations in British Columbia (Beck et al. 2011). Mainly confined to estuaries and sheltered waters, O. lurida (Cook et al. 2000) is found both intertidally and in shallow, subtidal, euryhaline waters. It has been reported as deep as 71 m (Hertlein 1959), and appears to be more tolerant of shallow, subtidal, euryhaline waters. It has been reported as deep as 71 m (Hertlein 1959), and appears to be more tolerant of full strength seawater than of freshwater (Gibson 1974). For a comprehensive compilation of O. lurida populations, see Baker (1995).

As with other bivalves capable of producing dense aggregations, healthy populations of Ostrea lurida could likely contribute considerably to the health of the ecosystem in which they live. They form reefs that provide habitat and help prevent shoreline erosion, are important in food webs, and promote biodiversity. They also 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 & Luckenbach 2000, Lenihan et al. 2001). Little historic information, however, is available on the faunal communities supported by healthy O. lurida reefs, and even less is known about reef depth, density of reefs, and where they occurred naturally in both subtidal and intertidal environments. In experimental manipulations, Crassostrea virginica has been used more frequently to understand their importance in ecosystem functioning. Coen and Luckenbach (2000) provide a comprehensive review in Section 4, Ecology of Oyster Reefs. It is likely that on the West Coast, O. lurida may have historically provided these same ecosystem services.

One of the most important services bivalves provide is filter feeding. They sequester toxins such as pesticides, polychlorinated biphenyls (PCBs), heavy metals, and even coliform bacteria from agricultural waste during filter feeding (Alzieu 1998, Aune et al. 1998, Scott et al. 1998, Nice et al. 2000, Dumbauld et al. 2001). They can provide long-term storage of pollutants by their incorporation into shell or pseudofeces, which become buried in the substrate. As filter feeders, they also facilitate nutrient cycling between the pelagic and benthic environments and improve water quality (Newell 2004). Very few current populations still occur at historic abundances, and little empirical information exists on how communities dependent on oyster beds have changed. However, the hypothetical benefits provided by these oysters are clear. If ecosystem health in Pacific Northwest estuaries are a goal, restoration of healthy Ostrea lurida populations may be one tool to help achieve this goal.

PHYLOGENY

Until recently, some considered Ostrea lurida to be one species whose distribution extended from Alaska to Central America, whereas others separated O. lurida from its southern sister species, Ostrea conchaphila, which occurs as far south as Panama (Polson et al. 2009). The characteristics of the shell shape of O. lurida led, 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. conchaphila (Arakawa 1990). In 1985, however, O. lurida and O. conchaphila were merged based on morphology (Harry 1985), 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, CA; O. lurida occurs north, whereas O. conchaphila occurs south.

Within Ostrea lurida, as it is now recognized, there appear to be isolated populations along the Pacific Northwest. Five genetically distinct metapopulations (Vancouver Island, Puget Sound, Willapa/Coos Bay, Yaquina Bay, and California) were recently identified, and genetic and geographic distances were related in most cases (Stick 2011). However, it was unclear if the divergence in the current genetic structure of the populations...
was naturally or anthropogenically induced, with the exception of the Willapa Bay and Coos Bay population. \(O. \textit{lurida}\) is suspected to have been moved manually from Willapa Bay to Coos Bay.) As adaptations to local conditions may have contributed to this genetic divergence, it may be important to understand how the genetic structure of seed oysters transferred from one location to another during restoration efforts influences their success in restoration efforts (Stick 2011).

Characterizing the genetic structure of local oyster populations is possible due to the sequencing of microsatellite regions. Whereas the \textit{Ostrea lurida} genome in its entirety has not been sequenced, the CO1 gene region has been successfully amplified, and \textit{O. lurida}-specific primers and probes for qPCR have been produced (Wight et al. 2009).

**REPRODUCTIVE BIOLOGY**

As reported by Coe (1931b), \textit{Ostrea lurida} is a protandrous, sequential hermaphrodite, viviparous, and larviparous. Gametes from both sexes are commonly found simultaneously in the gonad follicles (Coe 1931b, Oates 2013). However, oysters of this genus are only known to spawn the gametes of one sex at a time, which is characteristic of sequential hermaphroditism. There is also some conjecture that this species (and perhaps genus) occasionally deviates from the protandrous life history; oogonia and spermatogonia appear to compete for the starting role in newly matured oysters, with some evidence that females occasionally develop first (Coe 1931b, Coe 1932). See Orton (1927, 1933) and Orton and Amirthalingam (1931) for reproductive studies conducted with a congener, \textit{Ostrea edulis}.

For the majority of the year, \textit{Ostrea lurida} can remain reproductive if temperatures persist above those required for reproduction (Coe 1931b). The critical threshold for reproduction in southern California \(32^\circ\ 52.0^\prime\ N\ 117^\circ\ 15.4^\prime W\) is about 16°C (Hopkins 1937), whereas it is reported to be closer to 13°C in the more northern range of the distribution of \textit{O. lurida} in British Columbia (Stafford 1913). Preliminary data in the Coos Bay estuary, OR, indicate the critical temperature may be somewhere between those two values, at approximately 14.5–16°C (Garcia-Peteiro unpublished, Oates 2013).

Spawning may begin as early as April, and the reproductive season may continue through October or November (Coe 1931b). In a summer, \textit{Ostrea lurida} may have either one or two spawning peaks (Hopkins 1937, Bonnot 1938, Carson 2010), although years with an apparent reproductive failure have been observed several times. For example, in 2010, larval densities up to 50 m\(^{-3}\) were observed in plankton samples from the Coos Bay estuary, but larvae were absent in 2011 (Garcia-Peteiro unpublished). Larvae were again found in 2012 (Pritchard et al. in preparation), likely indicating a reproductive failure in 2011, rather than a large-scale mortality event of adult populations. In Tomales Bay, CA, 60\(\times\) more recruits were found at one site in 2008 than 2009, also likely due to larval supply limitations (Deck 2011).

Although oysters may not be actively spawning or brooding, all stages of sexual reproduction can be found within a single population year-round (Coe 1931b, Oates 2013), and many stages of male or female gamete development (see Reproductive Cycle, below) may be found within a population at a single time (Coe 1931a, Hopkins 1936, Oates 2013). For instance, in May 2006 at a restoration site in Fidalgo Bay, WA, 1 in 10 oysters sampled contained eggs, whereas most other oysters sampled appeared to be developing ripe gonads (Dinnel et al. 2009). In June, 1 in 18 sampled oysters had larvae in the mantle cavity, and other oysters were 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, suggesting the termination of the reproductive season. These data suggest the reproductive period may occur during a short \((2–3\ mo)\) window during summer in some locations.

**REPRODUCTIVE CYCLE**

The gonad follicles lie within connective tissue below the epithelium, and can cover the entire body tissue (Coe 1932). Within approximately 1 y after settlement, \textit{Ostrea lurida} becomes reproductively mature and gonads begin to appear within about 8 wk during periods of warm water (Coe 1932). During this period of preliminary gonad formation, there is little sexual differentiation (Coe 1931b). After 12–16 wk, the gonads begin to differentiate, and both oogonia and spermatogonia are present. The spermatagonia develop more quickly than oogonia, resulting in a protandrous oyster (Coe 1931b). If water temperatures are sufficient, spermatogenesis occurs, and spermatozoa may be ripe at about 5 mo of age (Coe 1931b). Sperm develop in aggregates or sperm balls, each with 250–2,000 sperm (Coe 1931b); the flagellum of each individual sperm in the sperm ball faces outward, and the adhesive holding the sperm heads together dissolves once in contact with the seawater, allowing sperm to begin swimming independently (Coe 1932). The sperm balls are characteristic of the genus \textit{Ostrea}, as \textit{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 \textit{Crassostrea virginica}) do not aggregate their sperm (Coe 1931a). It may also serve to deliver higher concentrations of sperm to nearby females who capture the spawned aggregates before they fully disaggregate. If and how current sparse \textit{O. lurida} populations may be limited by diffuse sperm delivery remains a topic for future research.

The peak of the male phase of \textit{O. lurida} is characterized by aggregations of spermatozoa, followed by the release of sperm balls. Within the same individual, alongside male gametes, female oogonia also develop (Coe 1931b). After approximately 6 mo, the oocytes are ripe, and fertilization may take place when mature oocytes are discharged from the gonad and transported internally to the incumbent chamber of the female oyster. Spermatozoa are pulled into the gills of the female-stage adults, and enter the mantle cavity where they fertilize the eggs. 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. Whereas embryos are growing within a brooding oyster, spermato genesis continues in the gonad amongst remnant oocytes, and reaches its peak again after the embryos are released (Coe 1931b).

Oysters that undergo three successive spawning events in one season (spermatogenesis, ovigenesis, and spermato genesis) may exhibit decreased meat condition where their flesh becomes translucent (as opposed to white, when oyster growers and consumers consider the oyster to be in good condition). During
this decline in condition, the oyster takes time to replenish nutrient and energy stores. Upon recuperation, an individual may resume its reproductive cycle, ready to produce another round of eggs or sperm (Stafford 1913, Coe 1931b). This cycle may continue throughout the remainder of the oyster’s life, given that water temperatures remain sufficiently high. When temperatures fall below the critical temperature, growth and mass gain may continue, but reproduction will halt, and resume only when temperatures rise again (Coe 1931b). A predetermined number of sexual phases throughout the year are not apparent, as the length of each cycle is dependent on both oyster and environmental conditions (Coe 1932). Approximately 1.5 generations each year are the normal output per individual oyster in southern California, with development of the second generation of male- or female-phase development held in stasis throughout low temperatures in winter (Coe 1932). This estimate supplements evidence of two spawning peaks during the reproductive season which are often observed, where larvae appear rapidly after water temperatures rise, and the second larval peak appears later in the season, after the individual oyster has gone through another male and female stage (Coe 1932).

Females carry an average of 250,000–300,000 larvae per brood (Hopkins 1937). Unlike free-spawning oysters, the larvae of Ostrea lurida complete much of their development in the brood chamber of the egg-bearing oyster. Although larval growth likely depends to some degree on environmental factors, according to Hopkins (1937) working in California, the larva spends 2 days as a zygote, Day 1 as a blastula, and Day 2 as a gastrula. On Day 3, the zygote becomes a trophophore, and on Day 4, the trophophore becomes a D-stage larva, so named because of the shape of the prodissoconch, or initial shell. During a subsequent 10–12 days, the larva maintains its shape, but grows in size, and is released as a D-stage veliger between 163 and 187 μm in diameter (Coe 1931b, Hopkins 1937, Zacherl et al. 2009). After its release, the veliger shell begins to thicken, especially near the umbo—resulting in a characteristic shape for the older larva of this species (Zacherl et al. 2009). These “umbo-stage” larvae propel themselves with a ciliated velum, and after a period ranging from a few days to a few weeks, they develop an eyespot and are considered pediveligers (Zacherl 2005). Pediveligers are estimated to be competent to settle at approximately 300 μm (Loosanoff et al. 1966). Once suitable substrate is found, the oyster will cement itself to the substrate and undergo metamorphosis to the juvenile stage (Galtsoff 1964).

The planktonic larval duration of Ostrea lurida is estimated to range from 7 days to 8 wk (reviewed in Baker 1995). Imai et al. (1954) estimated it to be 11–16 days, whereas Hopkins (1937) estimated the larval duration to be at least 30 days. Baker (1995) and Carson (2010) estimate larvae may spend from 1 to 8 wk in the water column before settling. Couch and Hassler (1989) estimate 2 wk, Breese (1953) estimates 8 wk and finally Wight et al. (2009) estimate 22 days (summarized in Table 1). These discrepancies are areas that could benefit from future research, especially when considering that larvae may be estuarine dependent, and likely need to be retained within an estuary for their entire larval duration to successfully settle (Pritchard et al. in preparation).

Settlement generally occurs in the summer and fall in Washington and Oregon. In Puget Sound, WA, settlers were observed between June and October and settlement peaked multiple times each summer (Hopkins 1937). The settlement period in Coos Bay, OR, has been observed from July to December, with a peak in settlement occurring in July, August, or October, depending on the year (Sawyer 2011, Rimler 2014). In Tomales Bay, CA, settlement occurred between August and November and peaked in September of 2008 and in August of 2009 (Deck 2011). In La Jolla, CA, an anomalous open coast population of Ostrea lurida settled from April to November (Coe 1932). In the Upper Newport Bay in Southern California, settlement occurred from May to November and peaked in June; in Aqua Hedionda Lagoon, a slightly more southern estuary, settlement occurred from June to February, again with a peak in June (Seale & Zacherl 2009). Natural recruitment was observed from December to February in 2006 and 2007 in San Francisco Bay (Grosholz et al. 2008).

### TABLE 1.

<table>
<thead>
<tr>
<th>Source</th>
<th>Maximum size (mm)</th>
<th>Growth duration (days)</th>
<th>Season</th>
<th>Location</th>
<th>Growth rate (mm/day)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Davis (1949)</td>
<td>35</td>
<td>70</td>
<td></td>
<td>San Francisco Bay, CA</td>
<td>0.5</td>
</tr>
<tr>
<td></td>
<td>37</td>
<td></td>
<td></td>
<td></td>
<td>0.53</td>
</tr>
<tr>
<td>Coe and Allen (1937)</td>
<td>50</td>
<td>210</td>
<td></td>
<td>Tomales Bay, CA</td>
<td>0.24</td>
</tr>
<tr>
<td>Korringa (1976)</td>
<td>35</td>
<td>1,277</td>
<td></td>
<td>Coos Bay, OR</td>
<td>0.03</td>
</tr>
<tr>
<td>Grosholz et al. (2008)</td>
<td></td>
<td></td>
<td>Summer 1</td>
<td>Tomales Bay, CA</td>
<td>0.03–0.10</td>
</tr>
<tr>
<td>Deck (2011)</td>
<td></td>
<td></td>
<td>Summer 2</td>
<td>Coos Bay, OR</td>
<td>0.04–0.07</td>
</tr>
<tr>
<td>Kimbro et al. (2009a)</td>
<td></td>
<td></td>
<td>Summer</td>
<td>Tomales Bay, CA</td>
<td>0.03–0.3</td>
</tr>
<tr>
<td>Rimler (2014)</td>
<td></td>
<td></td>
<td>Summer</td>
<td>Coos Bay, OR</td>
<td>0.14</td>
</tr>
<tr>
<td>Trimble et al. (2009)</td>
<td></td>
<td></td>
<td>Late summer/early fall</td>
<td>Willapa Bay, WA</td>
<td>0.37</td>
</tr>
<tr>
<td>Trimble et al. (2009)</td>
<td></td>
<td></td>
<td>Winter</td>
<td>Willapa Bay, WA</td>
<td>0.01</td>
</tr>
<tr>
<td>Trimble et al. (2009)</td>
<td></td>
<td></td>
<td>Spring, early summer</td>
<td>Willapa Bay, WA</td>
<td>0.08</td>
</tr>
</tbody>
</table>

Maximum size and growth duration and were converted into growth rate (mm/day) when reported as days, months or years (Davis 1949, Coe & Allen 1937, Korringa 1976). Remaining values were reported as mm/day (Grosholz et al. 2008, Kimbro et al. 2009a, Trimble et al. 2009, Deck 2011, Rimler 2014). Empty cells indicate data were not reported.
SHELL MORPHOLOGY

Shells of *Ostrea lurida* are 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 a variety of elements for Ca in the shell’s 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 younger life stages. Shell elemental uptake during earlier life-stages is a potential tool for researchers wishing to identify a larva’s natal site through elemental spectroscopy (Zacherl et al. 2009, Carson 2010). Changing growth rates and changes in the crystalline form of the shell are mechanisms for varying rates of elemental uptake, and earlier shells may be composed of aragonite (Zacherl et al. 2009). The subsequent crystalline structures, approximately at the age of settlement, are calcite (Zacherl et al. 2009). Through spectroscopy of shell material, researchers have determined source and sink populations in San Diego County (Carson 2010).

The adult shell of *Ostrea lurida* is small relative to members of *Crassostrea*, and both hinges are serrated. The right valve is flat, whereas the left is approximately concave (Couch & Hassler 1989, Arakawa 1990). The shell lacks a periostracum, but the inner shell ranges from white to purple (Allen 1977), and the exterior of the shell may be striped purplish, brown, or yellow (Hertlein 1959). By the presence of chomata, small bumps on the inside of the hinge (a characteristic of the *Ostrea* genus), *O. lurida* can also be distinguished from small *Crassostrea gigas* although chomata in older specimens may be obscured by a build up of nacre (Light 2007, Carlton, Williams College, 2013, personal communication). See Baker (1995) for a more complete description of anatomy and characteristic shell morphologies.

Descriptions of maximum shell size and shell growth of *Ostrea lurida* vary. Hertlein (1959) reports a maximum shell length of approximately 7.5 cm, whereas Buhle and Ruesink (2009) report 6 cm, Arakawa (1990) 5–8 cm, and Peter-Contesse and Peabody (2005) report a maximum shell length of 10 cm. Growth rates are variable (Table 1), and may be related to a latitudinal gradient driven by temperature or food availability, although enough data to conclusively support this hypothesis are lacking. The range of growth rates of *O. lurida* taken in the field is 0.01–0.53 mm per day (Trimble et al. 2009, Dinnel et al. 2009, Rimler 2014).

Environmental parameters such as temperature and salinity may not only affect this oyster’s growth and maximum size, but also distributional limitations. For instance, populations may experience 100% mortality in the intertidal or shallow subtidal during cold weather, as they cannot survive freezing temperatures, even if not inundated or covered with ice (Davis 1955, Peter-Contesse & Peabody 2005). This mortality may not be due to feeding inhibition, as dead oysters often have adequate food reserves (Davis 1955). When cultivated for commercial harvest in the late 1800s and early 1900s, dykes were built to maintain a water level of 15–30 cm across the growing grounds to reduce the risk of freezing (Hopkins 1936). Despite this sensitivity to freezing temperatures, *Ostrea lurida* maintains a wide temperature tolerance. For example, in San Francisco Bay, the monthly average temperatures for intertidal *O. lurida* populations were between 18.5 and 27.3°C (Carson 2010). High temperatures, however, may also result in mortality. For example, Trimble et al. (2009) observed very high losses of outplanted oysters, and suggested high temperatures in the summer could have been responsible.

Although considered an estuarine species that presumably also requires a tolerance to a wide array of salinities, *Ostrea lurida* does not appear to do well at extremely low salinities. Oysters may do well at salinities above 25, although they can tolerate brief exposure to lower salinities (Korringa 1976, Peter-Contesse & Peabody 2005). For instance, *O. lurida* kept at a salinity of 15 for 5 wk experienced 83% survival, and oysters survived salinities of 5 or lower for 2–3 wk before suffering 100% mortality (Gibson 1974).

HARVESTING

Little information is available on historic (baseline) sizes of populations of *Ostrea lurida* throughout its entire range. There are currently healthy populations on Nootka Island, British Columbia, with densities surpassing 1100 individuals m$^{-2}$ (Beck et al. 2009), but these densities may be uncharacteristically high. Others report historical densities around 116 individuals m$^{-2}$ (zu Ernsgassen et al. 2012). Regardless, historically, populations of *O. lurida* were sufficient to support both tribal subsistence and commercial harvesting. Large shell middens indicate the importance of the oysters to tribes (Steele 1957, Barrett 1963, Elsasser & Heizer 1966, Baker 1995, Groth & Rumrill 2009). For instance, one particular midden found near San Francisco, CA, was at least 107 m in diameter and 13.7 m tall and contained only *O. lurida* shells (Elsasser & Heizer 1966).

Settlers of the American West also considered this oyster a delicacy. In the 1850s, one plate of *Ostrea lurida* on the half shell cost approximately $20 (about $400 in 2005 currency: Peter-Contesse & Peabody 2005), and *O. lurida* was said to be a favorite of Mark Twain (Beahrs 2012). Commercial takes were once high—over 7 million liters year$^{-1}$ were reported in Washington in the 1870s (Cook et al. 2000), but unsustainable extraction depleted the species early in the 1900s throughout its range. Declines continued with the removal of adults, decreasing the reproductive output of populations and removing the preferred substrate (adult shells) used for larval settlement (Sayce 1976, Cook et al. 2000). Commercial oyster harvesters realized *O. lurida* was being overexploited as early as 1855, and new regulations for harvest were set; namely, no oysters could be harvested during the main reproductive season, July–August, in the Washington area (Steele 1957). Washington eventually established oyster reserves in 1897, but populations were already devastated, and no significant increases in population growth were observed despite the harvest ban. One potential reason for limited recovery may have been the fishing techniques used for oyster harvest, which included hand-picking, dredging, and “tongs.” The methodologies resulted in all size classes of oysters being removed. Those below the legal limit were thrown back into the water but left unattached, likely to be buried in the sediment (Coen & Luckenbach 2000). Between 1924 and 1926, approximately 1.5 million liters of *O. lurida* were extracted for nontribal consumption in Washington, but the catch decreased to approximately 106,000 L by
Another indirect effect possibly contributing to the decline of *Ostrea lurida* within *Crassostrea gigas* beds includes *O. lurida* larval settlement onto *C. gigas* shells. *O. lurida* is likely to settle on shell, and often settles among the aquacultures of *C. gigas* that, however, grows twice as quickly as *O. lurida*. 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 (Trimble et al. 2009). Furthermore, owing to a lack of hard substrate, naturally produced *O. lurida* larvae are settling on *C. gigas* shells (located mainly above mean low low water [MLLW]), which are located higher in the intertidal than where *O. lurida* settle under natural conditions (Trimble et al. 2009). 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, OR, commercial *C. gigas* growers routinely find juvenile *O. lurida* on shells of *C. gigas* adults, and visual inspections of
C. gigas shells indicate ~5% incidence of O. lurida settlement on C. gigas shells (Rumrill, personal observation). The native oysters are removed and discarded from C. gigas before sale (Groth, OR Department of Fish and Wildlife 2013, personal communication). For these reasons, there is speculation that C. gigas shells are sinks for naturally occurring O. lurida larvae, but more work needs to be done in the future.

With the introductions of Crassostrea virginica and Crassostrea gigas also came a number of predatory gastropods. The Eastern drill (Urosalpinx cinerea) was introduced with C. virginica (Carlton 1979), whereas the Japanese drill (Ocebrinia inornata) was introduced from Japan with C. gigas (Dall 1926). Both drill species lack a planktonic larval stage, and introduction is primarily through the anthropogenic transfer of infected oysters (Grason & Miner 2012). Both species of introduced drills have the potential to increase predation pressure on Ostrea lurida populations.

Through evidence based on feeding trials, it appears that both Urosalpinx cinerea and Ocebrinia inornata prefer Crassostrea gigas over Ostrea lurida when similarly sized individuals are offered, but prefer small individuals over large individuals of either species (Buhle & Ruesink 2009). As adult C. gigas are larger than adult O. lurida, predation pressure on O. lurida is likely greater in locations with both species present. In Willapa Bay, WA, 4.0% of mortality of O. lurida could be due to predation by oyster drills, and up to 32% of O. lurida were drilled (Buhle & Ruesink 2009).

Historically, Ocebrinia inornata has had an especially large impact on juvenile oysters. Because of difficulties in eradication once a population became infected, some oyster growers abandoned beds of Crassostrea gigas on the West Coast with persistent and abundant populations of the drill (Buhle & Ruesink 2009). In addition, O. inornata has caused high mortality of Ostrea lurida in Puget Sound (Chapman & Banner 1949), and numerous other works suggest O. inornata feeds preferentially not on C. gigas, but on O. lurida. Mytilus edulis, and Tapes japonica in Puget Sound, WA (reviewed in Carlton 1979). Among these, Ostrea lurida is also preyed upon by several native organisms, including sea stars, diving ducks (scapads and scoters; Galtsoff 1930, Cook et al. 2000), crabs (Cancer productus; Couch & Hassler 1989), bat rays (Matthiessen 1970), and native whelks.

In laboratory experiments, trophic cascades involving both native and nonnative predators have been examined for their influence on the recovery of Ostrea lurida populations. For instance, Grason and Miner (2012) examined the feeding preferences of a native generalist crab (Cancer productus) on both oysters (O. lurida and Crassostrea gigas) and nonnative drills (Ocebrinia inornata and Urosalpinx cinerea) that may serve as intermediate predators, feeding only on oysters. Results from feeding trials suggested that C. productus does not exhibit a feeding preference between juveniles of O. lurida and C. gigas. When, however, offered a choice of two species of nonnative oyster drill adults and juvenile C. gigas, C. productus consumed six times more juvenile oysters than either species of drill. As O. lurida and C. gigas were consumed equally, these results indicate recovering O. lurida populations could be experiencing much stronger predation pressure, via invasive drills, than they did historically. Despite the classification of C. productus as a generalist predator, it is likely not releasing O. lurida from increased predation pressure from the introduced oyster drills; it is likely a competitor of drills, rather than a predator of drills (Grason & Miner 2012). Importantly, feeding rates on drills by C. productus in the field may be lower than those observed in the laboratory because increased habitat heterogeneity would facilitate the escape of drills (Grason & Miner 2012).

Invasive crabs (Carcinus maenas) and drills (Urosalpinx cinerea) have also been deemed culprits in disrupting trait- and density-mediated trophic cascades usually occupied by native crabs and whelks, resulting in increased mortality of Ostrea lurida. Patterns of oyster mortality in Tomales Bay, CA, have been positively related to U. cinerea abundance, rather than abiotic conditions such as thermal stress or desiccation (Kimbro et al. 2009b). These altered food webs and trophic cascades could have large impacts on restoration sites where drills and Cancer productus are both present, the predation pressure possibly being too great to allow recovery.

A number of species may also indirectly compromise Ostrea lurida populations. As O. lurida is a sessile, benthic filter-feeder, sediment resuspension from resident fauna, such as bioturbating thalassaindean shrimp, can be fatal. For example, Neotrypaea californiensis and Upogebia pugettensis destabilize and resuspend sediment when making burrows (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 can become clogged with sediment, causing slower growth and higher mortality (Feldman et al. 2000). Thus, shrimp populations are yet another variable managers should be taken into account when selecting restoration sites.

Large blooms of the diatom Melosira borraei may pose another threat to Ostrea lurida. During the 1950s, sulfur liquor pollution from pulp mills was problematic, notably in Puget Sound, where these diatoms “bloomed” all year long—the dead diatoms accumulated up to 15 cm in dykes where O. lurida was grown, causing local extinction (Steele 1957). The sulfur waste liquor caused a continuous decline of O. lurida in the 1950s (Hopkins 1935, McKernan et al. 1949, Steele 1957), partially owing to its facilitation of M. borraei growth. Despite the historic impact on O. lurida, no recent work was found for this review 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. Indeed, the presence of competitors (typical fouling organisms such as bryozoans and tunicates) can decrease average Ostrea lurida recruit size by up to ~50% (Deck 2011). Interestingly, these competition effects appear only to influence early-stage recruits; there was no apparent effect of competition on juvenile (mean size 15 mm) or adult growth rate or survival (Deck 2011). Competition effects may also be at play in San Francisco Bay, where recruit abundance decreased in the presence of competitors (Deck 2011). In out-planted oysters on tiles in Fidalgo Bay, WA, fouling organisms (ascidians, hydroids, sponges) and conspecific competitors depressed the maximum length of O. lurida by 2%–35%, and decreased survival from 15%–7% (Trimble et al. 2009). Furthermore, removing fouling organisms (e.g., barnacles, ascidians) from tiles resulted in oysters twice as likely to survive as those with fouling organisms left in place (Trimble et al. 2009). In addition, the largest five oysters on each tile were those...
farthest separated from the nearest neighbor, further suggesting intraspecific competition could affect growth and subsequent success, including reproductive condition and fecundity (Trimble et al. 2009). Whereas settlement of *O. lurida* may be gregarious—encouraged by the presence of other larvae or other settled conspecifics—little work (see Bayne 1969) has been done to identify or understand this behavior, or to understand its connection to intraspecific competition.

**LARVAL SUPPLY, SETTLEMENT, AND RECRUITMENT**

To understand population dynamics of multiphasic organisms such as *Ostrea lurida*, all stages of its lifecycle need to be investigated, including larval supply, settlement/recruitment and adult survivorship (Porri et al. 2008). Current adult *O. lurida* populations are far below historic numbers (Beck et al. 2011, zu Ermgassen et al. 2012). Despite bans on harvesting and widespread restoration efforts, some population sizes remain perplexingly low. One potential limitation could be larval supply—either because few larvae are being produced, or because few larvae are surviving and settling successfully. In the latter scenario, the retention of larvae within estuaries should be considered, as it can greatly influence recruitment patterns (Graham & Largier 1997, Sponaugle et al. 2002).

In the Coos Bay estuary, OR, larval abundance and recruitment of *Ostrea lurida* is high in the mid to upper-bay, but low in the more marine reaches of the bay (Garcia-Peteiro unpublished, Pritchard et al. in preparation). During the dry season in the Coos Bay estuary, the water mass in the upper bay is characterized by long residence times, but in the lower bay, short residence times prevail. Thus, it is feasible that larvae produced in the upper bay are retained within the bay for their pelagic larval duration, and may settle successfully, whereas larvae transported to, or produced in the lower bay are swept out of the bay before settlement, resulting in larval wastage. Likewise, in Tomales Bay, CA, recruitment along an estuarine gradient was strongly influenced by the water residence time within the estuary, and recruitment to intertidal and subtidal habitats was positively correlated with residence time (Kimbro 2008, Deck 2011). These patterns demonstrate that small-scale variation in larval supply can be important within a single bay. In the future, expanding channels and bays through dredging may decrease the portion of the bays with long residence times, increasing the likelihood of larval wastage of already established *O. lurida* populations (Pritchard et al. in preparation).

Most evidence to date suggests larval dispersal distances in *Ostrea lurida* may be low. For example, at a restoration site in Fidalgo Bay, WA, the highest densities of recruits were found closest to the restoration site, with abundance decreasing with distance away from the site, suggesting that larvae were from the nearby site (Dinnel et al. 2011). In Coos Bay, OR, larvae are found at low concentrations offshore compared with concentrations within the bay (∼3 m⁻³ versus ∼50 m⁻³, respectively) (Garcia-Peteiro unpublished) which suggests that large-scale, long-distance connectivity is rare near the Coos Bay estuary. The five genetically distinct regions presented by Stick (2011) also support this hypothesis. Although it is possible that rogue larvae may disperse among the five regions, the apparent genetic distinctions of oysters among these five regions suggest that population connectivity is low enough for genetic differences to accumulate.

Like many marine species, *Ostrea lurida* seems to have source and sink populations. Using shell elemental spectroscopy in San Diego County, CA, for instance, San Diego Bay was found to contribute 45.0% of recruits to surrounding bays, followed by two North County lagoons (35.4%) and Mission Bay (19.6%) (Carson 2010). Although Mission Bay supplied about 20% of the larvae in the area, it received approximately 80% of larvae from San Diego Bay and the North County lagoons. At larger scales, population connectivity between estuaries separated by 75 km in California has been observed, and California populations may be more strongly or frequently connected than northern populations in Oregon, Washington, and British Columbia (Carson 2010). Dispersal that occurs between these populations is likely heavily influenced by hydrodynamic regimes and pelagic larval duration.

The larval contribution of a population is 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, CA) receive high larval input relative to their output, and could accumulate a healthy oyster bed relatively quickly, subsequently helping to restore habitat health and function. In addition, if larvae are supplied to the sink population from a variety of local source populations, genetic diversity increases, making the populations more genetically heterogeneous and perhaps robust over time. Including source populations (e.g., San Diego Bay and the North County lagoons) in marine reserves is also important to promote larval supply to nearby populations.

Do *Ostrea lurida* larvae have behavioral mechanisms allowing them to be retained close to their natal population, resulting in short dispersal distances? Should restoration managers be cautious about expecting restored populations to seed distant populations (e.g., outside a particular estuary)? Is there more support for Stick’s work (2011) that long-range dispersal is a rare occurrence? These questions could benefit from future research.

Restoration efforts are currently being implemented throughout the entire range of *Ostrea lurida*, at both small scales (individual landowners; Rumrill personal observation), 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. Very little work has, however, addressed factors contributing to successful settlement, survival, and growth by the early life-history stages of *O. lurida* in the field, which could obviously help improve the success of future similar projects. For example, in 2002, the Skagit County Marine Resources Committee began restoration efforts in South Fidalgo Bay (Dinnel et al. 2009). Fidalgo Bay was thought to lack the hard substrate necessary to allow natural, successful recruitment of *O. lurida*. Shell of *Crassostrea gigas* was used under a railroad bridge to provide this hard substrate. Shell bags were placed out in June 2003, and from 2002 to 2006, survival was consistently high, about 90%, but dropped to 39% by 2009. Thus, although the conditions at this site were satisfactory for the early-stage oysters between 2002 and 2006, some unknown factor led to higher mortality between 2006 and 2009 (Dinnel et al. 2011). In terms of recruitment,
young of the year were not detected until June 2005, and then only in very low numbers. No young of the year were found in 2006, suggesting that spawning and/or successful recruitment did not occur in 2005. Moderate numbers of recruits were found in 2007, suggesting 2006 was a mildly successful reproductive year. No recruits were found again until 2010, when moderate recruitment (2.7 juveniles/cultch shell) was again observed (Dinnel et al. 2011). No recruits, however, were found on shell bags in locations other than south Fidalgo Bay (Cape Sante Head, Guemes Channel, or east March’s Point). These patterns of irregular successful recruitment further support the idea that populations of O. lurida may be subject to reproductive and/or recruitment failure in some years. An alternative explanation is that the oysters were not surviving the winter. Despite frequent poor recruitment, initially low densities of oysters recorded in 2003 in Fidalgo Bay (45 ind. m$^{-2}$), were up to 130 m$^{-2}$ by June 2011 (Dinnel et al. 2011). The Samish Tribe tried another restoration site at Weaverling Spit, Fidalgo Bay in 2003. By 2006, however, no live oysters were found. It was suggested that restoration efforts failed at this site because it did not have standing water at extreme low tides (Dinnel et al. 2009). In Coos Bay, OR, 100% mortality occurred among very small (2–7 mm) oysters over the winter, and mortality was roughly 50% among the larger group (17.5–27.5 mm) (Rimler 2014). In addition to size, location within the estuary and time of year also contributed to variations in mortality rates. Future research should focus on the mechanisms (larval supply, settlement, and recruitment) limiting temporal consistency in population recovery.

It is essential to understand the abiotic factors that could either render a site successful and thus promote self-sustaining populations, or lead to failure. Newly settled oysters and adults are vulnerable to thermal stress, desiccation, food shortage, predation, and competition. Thermal stress caused by extreme heat or cold affects metabolic and reproductive performance, growth, and mortality within invertebrate populations (Bertness et al. 1999, Leonard et al. 1999, Leonard 2000, Pineda et al. 2009). Thermal stress is minimized when the surrounding water acts as a buffer from large shifts in temperature and minimizes risk of desiccation. Seed (settlers) also appear to become somewhat acclimated to the physical environment into which they settle. For instance, seed transported from one location to another after settlement may only grow if the second location had the same temperature, salinity and “mineral content” as the first location (Steele 1957).

Specific settlement cues used by larvae of Ostrea lurida, which could strongly contribute to variations in recruitment, remain unknown, although the presence of hard substrate, conspecifics, and biofilms all may contribute. Another possibility is that larvae are sensitive to environmental parameters such as temperature and salinity, which could strongly influence their survival. For example, within the Coos Bay estuary, larvae are supplied to two sites (Catching and Coalbank Sloughs) that, due to their proximity to the outflow of the Coos River, are subject to large fluctuations in temperature and salinity on both daily (tidal) and seasonal scales. Recruitment data collected approximately every 2 wk at these sites revealed recruitment was near zero despite sufficient larval supply (Pritchard et al. in preparation). Seaward of these two sites approximately 4 km, the larval supply, however, is slightly higher (in Downtown Coos Bay), but recruitment is dramatically higher, possibly because of the muted daily ranges in salinity. Perhaps either the larvae were not finding the two more riverward sites suitable for settlement, or they were not surviving the 2 wk period between collections due to stress from environmental parameters such as temperature, salinity, or desiccation, or alternatively, predation. Examining larval supply and settlement or recruitment simultaneously allows researchers and managers to better understand population dynamics; namely, whether populations have limited recovery due to a lack of larvae, inadequate settlement surfaces, or postsettlement mortality.

As Ostrea lurida exhibits both a planktonic larval stage and a benthic, filter-feeding adult stage, the importance of settling in an area with sufficient water movement cannot be overstated. Water provides a continuously renewed source of food and oxygen, helps regulate thermal and water quality parameters in which larvae and adults live, and once reproductive, water disperses sperm and delivers it to females. Larval dispersal to other populations 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 (Connell 1985, 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.

Because of their dependence on water flow, tidal height of a settlement location may also play a role in the growth and survival of Ostrea lurida. For instance, growth rates up to 81% higher have been documented subtidally than intertidally (Deck 2011). Because there were no clear differences between oyster growth along the estuarine gradient subtidally, perhaps intertidal oysters are limited by feeding time and food concentration, as they would likely be more exposed to riverine input than to phytoplankton-rich seawater (Deck 2011, Kimbro et al. 2009a). In other field studies, tidal elevation had no effect on growth, but did have a large influence on survival (Trimble et al. 2009). Oysters 0.3 m above MLLW had <5% survival, whereas oysters on tiles that were continuously submerged had survival of 20%. Settlers of O. lurida were more than twice as likely to settle on cultch placed 0.3 m below MLLW than 0.3 m above, and juvenile oysters experienced over 50% mortality after air exposure (2%–10% of the time) (Trimble et al. 2009).

In Elkhorn Slough, CA, adults and juveniles of Ostrea lurida were absent all at 13 sites with minimal (maximum 1–15 cm) tidal exchanges (Wasson 2010). These areas could be more heavily influenced by pollution, hypoxia, and low salinities than areas with more tidal mixing. Juvenile survival, however, was up to 90% in areas with muted tidal ranges (defined as a maximum range between 15 and 100 cm) but an average of only 65% survival at sites with full tidal ranges (250 cm). Higher survival at sites with muted tidal ranges may be due to decreased sedimentation, and suggests that these areas might be successful restoration sites, provided that tidal flushing is substantial enough to prevent water quality problems (Wasson 2010). Few studies, however, have been conducted to understand how flow regime directly affects settlement, growth, and survival in O. lurida.

Flow may also directly influence sedimentation rates, and may be a significant component that drives settlement preferences (Wasson 2010). Increased sedimentation rates caused by
hydraulic mining may have caused *Ostrea lurida* to disappear from Bolinas Lagoon and Morro Bay, CA (Barrett 1963). Likewise, the disappearance of the oyster from Coos Bay, OR, may have been due to a tsunami or large fire followed by heavy rains, which caused heavy sedimentation that smothered *O. lurida* populations (Groth & Rumrill 2009). Interestingly, in Elkhorn Slough, CA, neither juvenile size nor density was significantly different between sites of high versus low sedimentation, although mortality was significantly higher ($P = 0.03$) in areas of high versus low sedimentation (85% versus 66%, respectively) (Wasson 2010).

Population declines of *Ostrea lurida* to the point of functional extinction have been observed over their entire distribution (Kirby 2004, Beck et al. 2011). The dearth of hard substrate providing settling sites may also be an important factor hindering the recovery of *O. lurida* (Groth & Rumrill 2009, see Brumbaugh & Coen 2009 for a full review). In addition, *O. lurida* also shows 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 over time (Groth & Rumrill 2009, Wasson 2010). Without sufficient hard substrate (rip-rap, shells, pilings, etc.) settling larvae may be forced to settle on driftwood, mud, or debris, which could be washed away, buried in settling sediment, or resuspended and deposited in unsuitable environmental conditions. Monitoring natural recruitment and survival on unenhanced (mud, debris) and enhanced (e.g., with shell bags or rip-rap) areas would help illuminate the importance of hard substrate in promoting recovery (Polson & Zacherl 2009).

In Coos Bay, OR, settlement has been observed on old marine batteries, logging cables, and a submerged shopping cart and motorcycle (Groth & Rumrill 2009). Recruits may also prefer hard and shell habitat to bare sediment, which in turn, may be preferred to eelgrass habitats (*Zostrea marina*) (Trimble et al. 2009). These recruitment patterns among substrate types could, however, have been an effect of survival rather than settlement preference. Among 32 sites observed in Elkhorn Slough, CA, 25 sites were characterized as mudflats, and seven were characterized as mudflats enhanced with anthropogenic hard substrate. At any sites characterized as mudflats, *Ostrea lurida* was not present and was only present at five of the seven sites where hard substrate was available (Wasson 2010). If settlement substrate is lacking, larvae may cope through one of two choices: (1) settle in a suboptimal 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 because of predation or larval wastage (Rumrill 1990, Morgan 1995). Therefore, it is essential for restoration sites to have sufficient settlement substrate.

In naturally occurring populations, the influence of environmental parameters in addition to the availability of settlement substrate on *Ostrea lurida* population size and health has been infrequently examined. In Elkhorn Slough, CA, populations of *O. lurida* were absent or at very low densities at locations with large ranges in water quality parameters, including temperature, salinity, turbidity, dissolved oxygen, and fluorescence, whereas sites with smaller ranges in these parameters tended to have larger populations (Wasson 2010). High-density oyster sites were also very closely clustered within a water quality nMDS plot, indicating a high level of similarity in these water quality parameters where oysters are found in high densities (Wasson 2010). Conversely, sites with oysters absent or found in low densities were loosely clustered in the nMDS plot, indicating a high level of variability in these water quality parameters where oysters were scarce. These data highlight the need for more information on the influence of water quality parameters and characteristics in limiting the natural recovery or future restoration of *O. lurida* populations.

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One last parameter that has been examined with *Ostrea lurida* is water pH. Having a shell composed primarily of calcium, bivalves may be particularly sensitive to future ocean acidification. Hettinger et al. (2012) investigated the effects of ocean acidification on larval and juvenile growth in *O. lurida*. Larvae were reared in treatments of 700 (control), 800, or 1100 ppm CO$_2$, corresponding to pH values of approximately 8.0, 7.9, and 7.8, respectively. These CO$_2$ concentrations were chosen to fall 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, whereas 800 and 1100 ppm CO$_2$ were chosen to simulate future mean conditions based on available projections. After 9 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 pH 7.8 had 7% smaller shells area at settlement relative to control larvae. Lastly, 7 days after settlement, juveniles reared in pH 7.8 had 41% slower shell growth compared with control juveniles.

Depending on the conditions to which they were exposed as larvae, this study concluded that persistent carryover effects influence juvenile shell growth rates. In a restoration context, therefore, this study suggests that site selection for restoration efforts should consider annual fluctuations in pH.

Even within a small area, some habitats are more suitable than others. For example, 115× more spat were found on the under-side of horizontal surfaces (settlement plates) compared with the upper, and 3× more on the underside of horizontal surfaces compared with vertical surfaces (Hopkins 1935). This is likely due to the swimming orientation of a larva, with the velum pointed upward (Hopkins 1935). Other hypotheses suggest settling on the underside of shell, plates, or rocks, prevents the animal from being smothered by sediment (Cole & Knight-Jones 1939, Michener & Kenny 1991). The oyster's preferential attachment is also not a negative phototrophic behavior, but the larvae may be negatively geotactic: a possible evolutionary adaptation to reduce exposure to direct sunlight and decrease thermal stress to the future recruit (Hopkins 1935). Working with settlement plates submerged for 3 mo, however, Hopkins (1935) recognized that these recruitment data might reflect survivorship and not settlement preference.

With little information regarding the locations of historical populations within estuaries, coupled with the slow recovery of present populations, it remains unknown under what conditions *Ostrea lurida* are most successful during different life history stages. It has been suggested that the earliest life stages in marine invertebrates are most sensitive to physiological stress (Bayne et al. 1976), but there is currently little information on the tolerances of larvae of *O. lurida* to temperature and salinity, or how variations in these parameters might influence growth, settlement, or mortality.
Although it is relatively straightforward 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 their small size and 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.

OTHER THREATS TO RECOVERING POPULATIONS

Declining populations of *Ostrea lurida* have also been due to land use changes (Clasen et al. 2010), sewage contamination (Galtsoff 1929), and long-term effects of sulfur liquor emissions from pulp mills in the early 1900s, which was shown to have negative effects on both reproduction and health (Hopkins et al. 1935, Odlaug 1949). Logging, mining, and high boat traffic could also be compromising bay water quality and thus, oyster habitats. Pollution from gasoline and motor oil are of concern, especially in areas of high boat traffic such as the Coos Bay estuary, OR, where shipping and commercial and recreational fishing are prevalent activities. It has been estimated that there is approximately a 10% loss of outboard fuel for each boat on the waterways (Clark et al. 1974). Although oysters may be able to tolerate brief exposure to motor oil and gasoline by closing their shell, up to 14% population mortality results after 10 days at even dilute concentrations (Clark et al. 1974). Other sources of anthropogenic disturbance, including sedimentation caused by topsoil runoff in areas of logging and mining, could cause clogging of gills and respiratory tracts in bay in low water movement and tidal flushing (Trimble et al. 2009). Dredging may also affect populations by changing hydrodynamics of bays, influencing dispersal (Pritchard et al. in preparation) and water quality parameters like salinity and temperature to which adults have adapted, genetically or phenotypically.

CONCLUSIONS

Regarding restoration efforts, location within the estuary appears to be an important factor influencing the success of attempts to reestablish populations of *Ostrea lurida*. First, water in the area needs to have residence times facilitating local retention of larvae of *O. lurida*. Second, restoration locations should occur midbay (not too far seaward or riverward). This is where high larval supply (García-Peteiro unpublished, Pritchard 2013), and recruitment (Kimbro 2008, Deck 2011, Rimler 2014) have been observed. These midbay sites also appear to have longer retention times than sites located close to the mouth of the bay, yet they are far enough away from fresh water that the large ranges in environmental parameters observed closer to the head of the bay are less extreme. At the head of the bay, ranges in environmental parameters are generally high because of the proximity to the river, and recruitment is low at these sites (Wasson 2010, Rimler 2014) despite ample larval supply, in some cases (Pritchard 2013). Third, in the northern part of their range, hard substrata should be available in the low intertidal or high subtidal to allow the water to buffer and protect oysters from desiccation and freezing temperatures. Fourth, tidal flushing must be sufficient to allow for food resources and oxygen delivery. Lastly, summer temperatures at restoration sites must reach critical reproductive temperatures; this will facilitate spawning and increase the probability that populations will become self-sustaining. If restoration efforts were initiated at sites where the minimum temperature never rose above the minimum threshold for spawning, the site would be completely dependent on management-supplied spat.

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