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FACTORS PREVENTING THE RECOVERY OF A HISTORICALLY OVEREXPLOITED SHELLFISH SPECIES, *OSTREA LURIDA* CARPENTER 1864

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ABSTRACT The Olympia oyster, *Ostrea lurida* Carpenter 1864,† in estuaries along the Pacific coast of North America, experienced overexploitation throughout its range in the late 1800s, resulting in commercial extinction before 1930. Significant harvest restrictions and marine reserves were established in Washington State by 1897 to protect new recruits, and harvest pressure has been negligible for the past 80 y. Nevertheless, *O. lurida* remains locally rare. This study focuses on the contemporary dynamics of the remnant population of *O. lurida* in Willapa Bay, Washington, historically home to the largest native oyster fishery on the coast, with a broad focus on factors preventing recovery. Failed recovery could be because of reproductive limitation, or to poor postrecruitment performance. In this case, reproductive limitation seems unlikely, because historical (1947 to 1983) and modern (2002 to 2006) records reveal 5-fold higher annual spatfall for *O. lurida* than introduced Pacific oysters (*Crassostrea gigas*.) However, *O. lurida* remains rare and *C. gigas* is commercially exploited from natural recruitment. To evaluate the effects of abundant *C. gigas* in intertidal areas on *O. lurida* settlement patterns, strings of *C. gigas* shell were placed at two tidal elevations in three habitat types—open mud, eelgrass beds of *Zostera marina*, and *C. gigas* reefs. Settlement of *O. lurida* was significantly higher on the shell strings placed in the *C. gigas* reefs at both tidal heights. To evaluate postrecruitment demography, juvenile *O. lurida* were outplanted at three tidal elevations at five sites, and fouling organisms were manipulated to test for competition. Short emersion times (8% greater exposure) reduced survival by 80% relative to subtidal treatments, but did not affect growth rates of survivors. Naturally-setting competitors, mostly nonindigenous, depressed survival by 50% and growth by 20%. In a third experiment, manipulating the density and stability of shell substrate, *O. lurida* was easily moved or buried when outplanted in a thin, unconsolidated layer. These results indicate that recovery has been hampered by the removal of dense subtidal native oyster shell accumulations during exploitation, by direct competition from exotic species, and by the appearance of novel introduced oyster shell settlement substrate in the intertidal zone. This altered web of interactions influencing *O. lurida* serves as a model for beginning to explore the failed recovery of overfished species in rapidly changing coastal systems.

KEY WORDS: Olympia oyster, *Ostrea lurida*, *Crassostrea gigas*, competition, oysters, recruitment, introduced species, Willapa Bay

INTRODUCTION

About seventy-five percent of currently fished stocks worldwide are fully or over-exploited (UNFAO 2004). These data do not include historical fisheries that no longer exist, such as the native oyster fisheries of the entire Pacific Coast of the United States, parts of the Atlantic and Gulf coasts of the United States, parts of Eastern Australia, and throughout much of the North Sea in Europe (Korringa 1976, Kirby 2004). In these and many contemporary cases, although fishing pressure eventually stops, stocks fail to recover. Scientists have speculated about the factors that hold remnant populations at low levels in the absence of direct exploitation, including poor per capita reproduction at low population size (depensation or Allee effects; Myers et al. 1995), predator pits (Bakun 2006), and alternative community states (Choi et al. 2004). In most systems, testing the factors that prevent recovery is intractable because of difficulties in directly manipulating populations, and because many marine organisms have complex life histories and open populations. Also, most collapses have been relatively recent, so data on recovery trajectories is of short duration (Myers et al. 1995). Here we examine recruitment and post-recruitment growth and survival to determine their role in preventing recovery of the once common oyster species native to estuaries of western North America, the Olympia oyster (*Ostrea lurida*), nearly a century after the collapse of the fishery.

The native oyster fishery in Willapa Bay, WA State ended in the early 1900s, and, despite little subsequent exploitation, *O. lurida* has failed to recover. This fishery began in 1851 with exports to San Francisco and other markets peaking at over one hundred million live adult oysters per year from the mid-1860s to 1907 (Fig. 1), arguably the largest fishery for native oysters in the Eastern Pacific region. Harvest rates declined after 1910 and the fishery was abandoned after successful introduction of Pacific Oysters (*Crassostrea gigas*) in 1928. The total harvest of native oysters from Willapa Bay approached four billion live adults including approximately seventy-seven million kilograms of shell material between 1851 and 1933 (Swan 1857, Collins 1892, Townsend 1896, Kincaid 1968). Today, fewer than 1,200 *O. lurida* are harvested from Willapa Bay for commercial sale annually (W. Cowell, pers. comm.).

The early oyster fishers in Willapa Bay recognized signs of overexploitation as early as 1855 when they decided to outlaw harvest from June 1 to August 1, during the main reproductive period (Steele 1957). These restrictions were enacted four years after the first commercial harvest and 30 years prior to Statehood (1889). Oyster laws defining tideland ownership, harvest restrictions and licensing were started at Statehood and eventually led to a system of Oyster Reserves, established in 1897.

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†The taxonomy of the Olympia oyster has been in dispute since Harry (1985) proposed synonymy of *Ostre lurida* Carpenter 1864 and *Ostrea conchaphila* Carpenter 1857. Polson et al. 2009 provide molecular evidence that the Olympia oyster refers to the nominal species, *Ostrea lurida* Carpenter 1864. In view of their genetic data and for consistency, the original taxon, *Ostrea lurida*, is used throughout this volume to refer to the Olympia oyster, which is distributed from approximately Baja California(Mexico) to southeast Alaska.

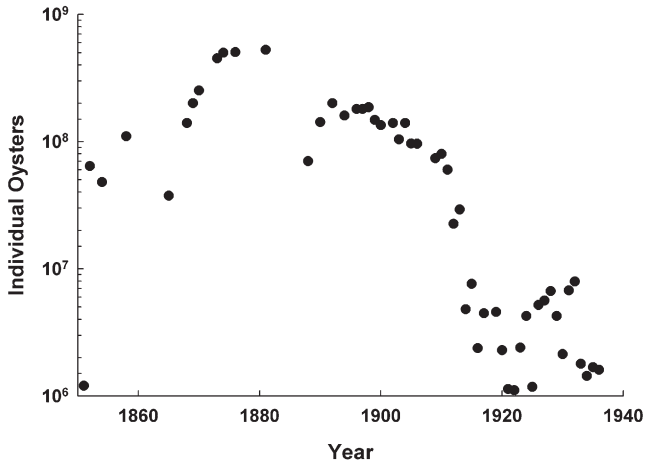

Figure 1. Commercial catch of native oysters *Ostrea lurida* from Willapa Bay, 1851–1934. Data were collated from Swan 1857, Collins 1892, Townsend 1896, Kincaid 1968, and computed based on the following conversions: 1 bushel = 4,000 oysters = 0.5 sacks (Brennan 1939, Hopkins 1937).

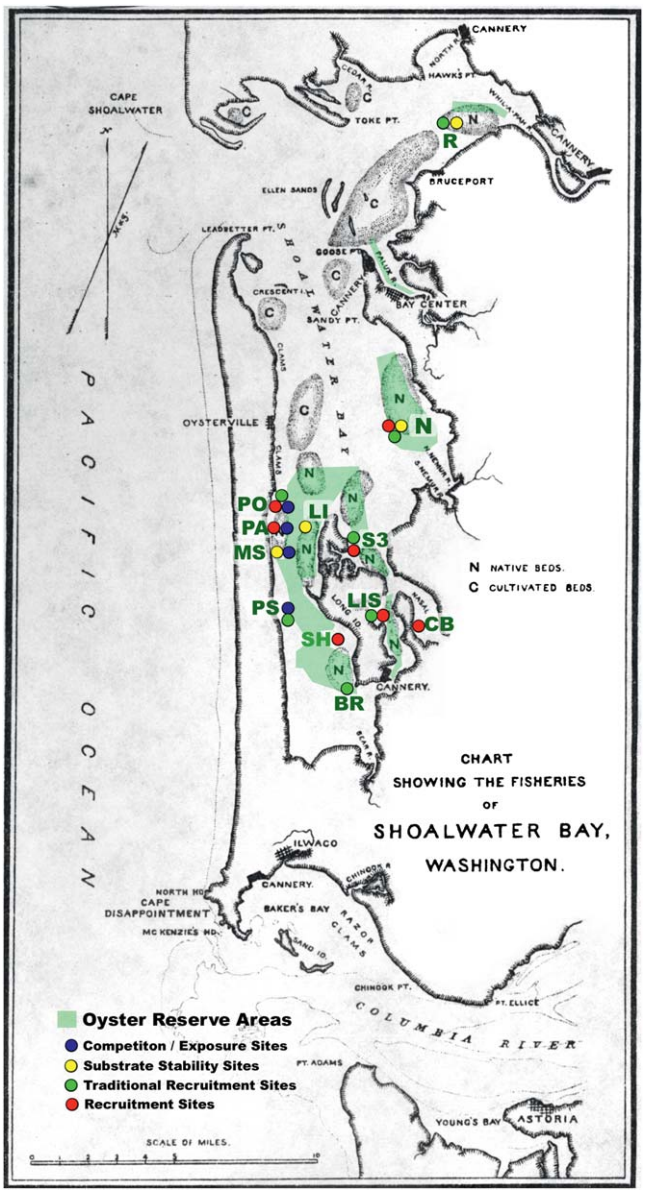

Figure 2. Map of Willapa Bay, showing study sites (colored circles), the boundaries of the Oyster Reserves (shaded green areas), and areas where native oysters formerly recruited in abundance, according to Collins (1896).

The reserves in Willapa Bay remain in force (most of the reserves in the rest of Washington have been sold to aquaculture interests) and encompass more than 4,600 hectares, approximately 13% of the estuary (Fig. 2). The reserves were designed to overlap natural populations of native oysters, from which fishers could collect limited numbers of small oysters and move them to private land for grow-out. The reserves were largely unsuccessful at maintaining either sources of oyster seed for transplantation or natural oyster bed (spawner) habitat. Possibly, the species was already overfished, or the removal of small oysters continued to erode the shell habitat necessary for recruitment.

Whereas *O. lurida* was ephemerally listed as threatened in the 1970s in Washington State, it was finally recognized as a species of concern by the Washington Department of Fish and Wildlife in 2000 because it remained at low density (Cook et al. 2000.) However, minimal funding has been allocated for research and restoration. In addition, although Baker (1995) reviewed more than 300 documents relevant to *Ostrea lurida*, including abstracts, agency publications, and early reports; only 63 items appeared in our literature search (Aquatic Sciences and Fisheries Abstracts, accessed 5/6/2005, Key words (*Ostreola* or *Ostrea*) and (*lurida* or *conchaphila*), compared with 2,848 concerning *Crassostrea virginica*. This ratio suggests that almost two orders of magnitude more scientific attention has been paid to the native (Eastern) oyster of the United States east coast.

Several hypotheses concerning failed recovery of *Ostrea lurida* have been suggested, including predation by introduced snails (Hopkins 1937) or flatworms (Woelke 1959), competition from other space occupants (Loosanoff 1955), water pollution (McKernan et al. 1949), habitat loss (Steele 1957), and disease (Bower et al. 1997, Friedman et al. 2005). As protective measures for native oysters failed, commercial oystering activities were maintained through the importation of several other oyster species. *Crassostrea gigas* rapidly naturalized after introduction in Willapa Bay, and commercial harvest has been sourced from wild recruitment, imports of seed from Japan (1929–1977), and local hatchery production since 1978. In addition, four other nonindigenous oysters have been planted: Eastern oysters (*Crassostrea virginica*), which were regularly transported by railcar from Chesapeake Bay from 1893–1917 and continue to be outplanted from local hatchery stocks, European flat oysters (*Ostrea edulis*), Kumamoto oysters (*Crassostrea sikamea*), and Suminoe oysters (*Crassostrea ariakensis*) are also outplanted from hatcheries for growout (B. Blake, Washington Department of Fish and Wildlife, pers. comm.) Many of these introductions occurred prior to concern about "hitchhiking" species, and oyster-associated organisms contribute to the almost 40 nonindigenous species reported for Willapa Bay (Cohen et al. 2001). The combined effects of introduced species on the recovery trajectory of *O. lurida* are unknown, and we specifically tested for competitive impacts in this study. Whereas these interactions are clearly significant,

they do not necessarily constitute the entire mechanism for failed recovery throughout *O. lurida's* native range. It is likely that studies concerning disease, upland development, timber harvesting, and other factors will reveal roles for these factors as well, but to date none have been published. In addition, we have not observed clear evidence of disease as currently being a strong inhibitor to native oyster population growth in Willapa Bay, because it is easy to maintain stocks for long periods with low mortality in many areas of the Bay (unpub. data).

Ostrea lurida provides a model system for exploring mechanisms that maintain previously exploited species at low abundance. The pattern of the Willapa oyster fishery boom and bust is similar to patterns of oyster fisheries worldwide (Kirby 2004). Peak harvest of *Crassostrea virginica* in Chesapeake Bay, and *Ostrea edulis* in Europe occurred in the mid-1800s. No country was apparently able to develop a sustainable fishery for wild oysters, although some have replaced their fishery with aquaculture of native species (New Zealand temporarily, much of Asia; Dinamani 1991, Kusuki 1991).

The ecological importance of oysters stems from their construction of habitat, high filtration rate, and role in estuarine food webs and biogeochemistry (Kennedy 1996, Jackson et al. 2001, Ruesink et al. 2005). However, different oyster species are unlikely to be plug-and-play ecological replacements for each other. In this case, native (and currently listed as endangered) salmonids coevolved with extensive *O. lurida* populations. These native oyster populations have been replaced with other species, and no locations exist where the interactions between salmon and intact, extensive native oysters can be studied. Economically, farmed *Ostrea lurida* continues to command high prices in a niche market as a "boutique" oyster. Because of their possible but unknown ecological roles and retained economic value, substantial restoration of native oysters in at least one location should be a high priority. In fact, a few small restoration efforts are happening along the west coast of North America in San Francisco and Tomales Bays, California (P. Olin, pers. comm.), Siletz, Netarts, and Coos Bays, OR (D. VanderShaff pers. comm.), and Puget Sound, WA (B. Peabody, pers. comm.). These involve outplanting hatchery-set *O. lurida* or adding hard substrate; however, most efforts are not set up or monitored as experiments.

For *O. lurida* in Willapa Bay, there is no evidence that the species will recover on its own, and methods for restoration are lacking scientific guidance. In this study we tested the following 4 hypotheses: (1) low recruitment prevents densities from increasing; (2) recruitment to intertidal (*vs.* subtidal) habitat results in poor-post-recruitment growth and survival; (3) interactions with competitors, particularly nonindigenous species, reduce postrecruitment growth and survival; and (4) postrecruitment performance is sensitive to stability and density of shell substrate. The goal of this study is to provide partial advice for recovery efforts of *O. lurida* and evaluate effectiveness of interventions to improve recovery.

METHODS

Species

Ostrea lurida was originally described by Carpenter in 1864 and later synonomized with *Ostrea conchaphila* (Carpenter 1857) to include specimens along the entire coast from Alaska to Panama (Harry 1985, Coan et al. 2000, Carriker & Gaffney 1996; but also see Baker 1995 and Polson et al. this issue). It is the only estuarine native oyster species to occur from Baja California to Alaska. *O. lurida* is relatively small, reaching a shell length of only 5 cm after four years (Hopkins 1937). However, it begins reproducing within a year. An alternating hermaphrodite, it may produce several broods of 250,000 offspring annually between May and September (Hopkins 1936, 1937). *Ostrea lurida* broods larvae within its shell for about 10 days after fertilization (Hopkins 1936), and free-swimming larvae subsequently spend several weeks feeding and growing in the water column until competent to settle at a size of about 300 μm (Loosanoff et al. 1966). When competent, the larvae select hard substrates such as shell or concrete for attachment (Hopkins 1935) and can be distinguished from other oyster spat at settlement by shell morphology (Loosanoff et al. 1966).

Based on maps prepared by 19th-century fisheries biologists, *O. lurida* occurred subtidally in Willapa Bay, WA (Collins 1892, Townsend 1896). Not surprisingly, these areas also overlap Oyster Reserves that were initially established to protect native oysters where they recruited reliably (the Reserves are no longer used for this purpose; Fig. 2). No quantitative data on densities exist from this period, but *O. lurida* was clearly a conspicuous estuarine resident for thousands of years, because subfossil deposits (10,000 y BP) uplifted on the eastern shore of Willapa Bay contain multiple thick layers of shell (10–20 cm; Clifton 1983). The original harvest method, in which fishers stood on flat boats at high tide and collected oysters with long-handled tongs, suggests that *O. lurida* grew in unconsolidated layers in shallow subtidal areas (Collins 1892, Townsend 1896). Today, *Crassostrea gigas* forms consolidated reefs or "hummocks" in the same regions of the bay where native oysters were recorded historically. However, most of these naturalized oysters inhabit the intertidal rather than subtidal zone (pers. obs.).

Study sites

Willapa Bay (46°40′N, 124°0′W), located on Washington state's southwest coast (USA), is a shallow estuary with extensive intertidal flats (140 km^2) comprising about half of the bay's total area (Hedgpeth & Obrebski 1981, Borde et al. 2003). The Bay experiences semidiurnal tides with an amplitude ranging between 3 and 4 m (NOAA/NOS/CO-OPS Station 9440910, Toke Point, WA). Secondary productivity, specifically growth of introduced Pacific oysters (*Crassostrea gigas*), generally improves towards the marine end of the estuary (Ruesink et al. 2003), whereas oysters recruit towards the freshwater end. Willapa Bay currently produces about 10% of the United States oysters, almost exclusively *C. gigas*. Yield has remained steady since about 1950 (although the proportional contribution to the United States production has increased) (Ruesink et al. 2006).

Multiple sites in Willapa Bay were selected for 4 separate studies (Fig. 2), as follows:

(1) Recruitment was monitored from 2002 to 2005 at up to 8 sites where native oysters historically occurred. Many of the same sites were studied from 1942 to 1983 as part of long-term monitoring for recruitment of Pacific oysters by the Washington Department of Fish and Wildlife;

(2) The response of recruitment to tidal elevation and substrate type was studied at one site (Mill Channel) where spatfall has historically been high;
(3) The response of growth and survival to tidal elevation and competition was tested at five sites in the middle of the bay, which were in close proximity because we required regular access to maintain experimental manipulations;
(4) The response of growth and survival to substrate characteristics was studied at four sites broadly spaced throughout the bay to include variation in wind, wave, and flow conditions.

The substrate elevation at these sites was at or below mean lower low water (MLLW; the mean height of the lowest of diurnal daily low tides, 0.88 m above the lowest recorded tidal level at Toke Point, Willapa Bay, Washington). Native eelgrass, *Zostera marina*, was common, and scattered individual native oysters were present nearby.

Oyster Recruitment Over Time

Recruitment limitation is one possible explanation for continued low abundance of native oysters, and we examined this hypothesis by comparing historical and modern recruitment. In 1942, scientists at the University of Washington and Washington Department of Fisheries (now Fish and Wildlife; WDFW) began a sampling program to determine the magnitude and timing of Pacific oyster recruitment (spatfall) in Willapa Bay. These samples were taken with similar techniques to parallel projects in Puget Sound (Hood Canal, WA DFW) and British Columbia (Ladysmith Harbor and Pendrell Sound, Canadian DFO). Each week, they placed two sets of 20 shells of *Crassostrea gigas*, strung together on a wire with the inner face down, just above the substrate, at several sites. One set was retrieved a week later (weekly shellstrings), and the other set left to accumulate recruits until early fall (seasonal shellstrings). Biologists scanned the inner face of these shells for new recruits under a dissecting microscope. The sampling program focused primarily on the species of interest to aquaculture (*C. gigas*) and therefore often missed early recruitment of *O. lurida*; native oysters often begin recruiting in May, but the first shellstrings were deployed between late June and early August. Also, in some years, particularly when Pacific oysters recruited well, native oysters received little scrutiny and their recruitment was not reported. Nevertheless, these historical data provide an index of the relative magnitude of recruitment of native and Pacific oysters. We compiled these data from various sources, specifically descriptions in weekly oyster bulletins (1947 to 1956), quantitative data from summary reports (1957 to 1962), and original data sheets on file at the Willapa Bay field station, WDFW (1963–1983).

In the years 2002 to 2006, we reinitiated sampling for recruitment by deploying weekly shellstrings from May to August at many of the same sites previously selected by WDFW. At each site and for each year, we determined the maximum seasonal spatfall per shellface (or cumulative, if only weekly shellstrings were available) for *O. lurida* and *C. gigas*, then calculated an average across sites to represent spatfall of each species for the bay as a whole. Identification to species was performed by visual inspection with a dissecting microscope by morphology using Loosanoff et al. 1966 as a reference (see Fig. 3). Based on this time series, we tested whether the magnitude of recruitment differed between the two species and was changing directionally over time (analysis of covariance, with species as a fixed factor and year as covariate). To account for heterogeneity of variances, data were log-transformed prior to analysis.

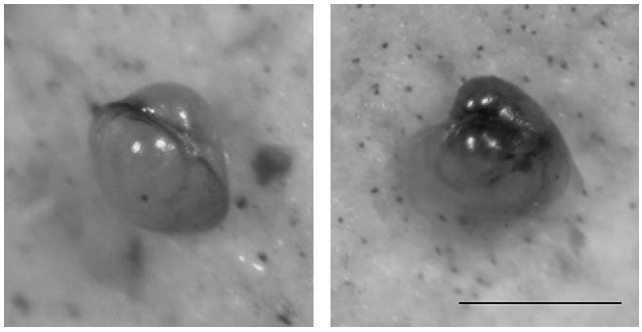

Figure 3. Photographs of newly settled oysters, less than 48 h old, on a *C. gigas* shellface from a shellstring deployed to measure weekly spatfall. Image on left is *Ostrea conchapila*. Image on right is *Crassostrea gigas*. Each valve of *O. lurida* is characteristically symmetrical and the spat are nearly transparent (note eyespot still visible), whereas *C. gigas* exhibits obvious "twisted" asymmetry and dark coloration to the shell and internal anatomy. Scale bar = 300 microns.

Recruitment Preference

Native oyster shell no longer exists in areas where it was historically present (Fig. 2), and instead reefs of *Crassostrea gigas* occur intertidally. We tested whether this shift in the location of shell could influence recruitment patterns of native oysters, and addressed the same issue for Pacific oysters for comparison. Field experiments have shown that *O. lurida* preferentially selects shell for settlement over other substrates, with a slight but nonsignificant trend to select live adult congeners *versus* other shell types (White et al. this volume).

We modified the "shellstring" approach to provide a consistent settlement surface across treatments. Stacks of 11 Pacific oyster shells, held just above the sediment substrate, were placed near the center of existing patches (>10 m^2) of three types of habitat: bare sediment, eelgrass (*Zostera marina*), and *C. gigas* reef. Three or four replicate patches of each habitat type were selected at two tidal elevations (+0.2 m and MLLW) adjacent to the Mill Channel recruitment site (Fig. 2). Shell stacks were placed on May 21, 2004 and retrieved four weeks later on June 17, after the peak *O. lurida* spatfall of the season. We counted all recruits of *O. lurida* on 10 shellfaces (not the bottom shell) per stack under a dissecting microscope as described above (see Fig. 3). New shell stacks were placed in identical locations from July 18 to August 14, 2004 to record recruitment of *C. gigas*. We tested for effects of tidal elevation (above and at MLLW) and surrounding substrate (oysters, eelgrass, mud) on recruitment with analysis of variance. Counts of recruits were log-transformed prior to analysis to improve homogeneity of variances (necessary for *O. lurida* but not *C. gigas*).

Post-Recruitment Response to Tidal Elevation and Fouling Organisms

Juvenile *O. lurida* experience a dramatically altered web of interactions caused by numerous species that have been introduced to Willapa Bay (Cohen et al. 2001). In addition to

intertidal reefs formed by *C. gigas*, numerous introduced soft-bodied fouling organisms (ascidians, hydroids, sponges) occur at lower tidal elevation. We compared growth and survival of *O. lurida* at three tidal elevations, with and without competitors. We reduced competition by periodically removing fouling organisms from half of the replicates.

Ostrea lurida larvae from Willapa Bay broodstock were settled onto unglazed ceramic tiles (11 × 11 cm) at the Pt. Whitney Shellfish Laboratory, WDFW (Brinnon, WA), in July 2002. Initially, tiles harbored 50–250 juvenile *O. lurida*. When the juvenile oysters attained shell lengths of ~2 mm (August 8, 2002), they were outplanted to five sites (Long Island, Port, Mill Channel, Middle Sands, Peterson; Fig. 2). At each site, 10 tiles were suspended from a moored float and remained continuously submerged, 10 tiles were attached to PVC stakes just above the sediment surface at –0.3 m MLLW, and 10 tiles were attached to PVC stakes 0.6 m above the substrate at the same place, achieving a tidal elevation of +0.3 m MLLW. Tiles at –0.3 m and +0.3 m remained submerged for 98% and 90% of the time over the study period, based on water levels recorded August 8, 2002 to 2025 August 2003 (NOAA Toke Point station 9440910; http://co-ops.nos.noaa.gov/).

Hard and soft-bodied organisms other than *O. lurida* were removed from half of the tiles on August 24, September 3 and 17, October 7, 2002, February19, April 20, May 20, 2003. Tiles were photographed initially and on August 24, October 7, 2002, February 19, July 2 (moorings only), and August 26, 2003. Soft-bodied organisms only were removed from most control tiles (with competitors) on October 7, 2002 to improve the photographic record. At the end of the experiment on August 26, 2003 (July 2, for moorings), we collected all tiles and recorded percent cover of major fouling taxa, counted all *O. lurida*, and measured the shell length (largest diameter, regardless of hinge orientation) of the largest five individuals, if present. We used photographs to document the seasonal pattern of growth for oysters on cleaned tiles (oysters were too fouled to count or measure on other tiles). We statistically analyzed only the final data, specifically the number (or log-transformed proportion surviving) and mean size of the five largest *O. lurida*, cover of barnacles, and cover of ascidians (analysis of variance). Site was considered a random factor; tidal elevation and competitor removal were fixed factors. Unfortunately, one mooring (Long Island) was removed by a winter storm before the experiment ended, so we assumed the final data for that site were the average of all other moorings.

Post-Recruitment Response to Substrate Characteristics

Ostrea lurida may be faring poorly in Willapa Bay because of the removal of shell habitat that used to provide substrate for settlement at low intertidal and subtidal elevations. We explored how different substrate characteristics influence performance of *O. lurida*. Insufficient native oyster shell exists to recreate historic habitat, so we substituted shell of *C. gigas* and altered two properties: its stability (whether it was held in place) and its density. *Ostrea lurida* larvae from Willapa Bay broodstock was settled onto shells (cultch) of *C. gigas* at Pt. Whitney Laboratory in July 2002. This cultch was outplanted in four treatments. In the "bag" treatment, cultch was held in large mesh bags just above the sediment (high density, stable). In the "rosette" treatment, cultch were strung on wires and attached in groups of 10 to wooden posts, again held just above the sediment (low density, stable). In the "ground" treatment, about 500 cultch (2 bags) were spread in an area of 2 m^2 directly on the sediment (low density, unstable). Finally, in the "ground + shell" treatment, the sediment surface was entirely covered with two bushels of loose *C. gigas* shell before the cultch were spread across a 2 m^2 area (high density, unstable). Because this study did not require frequent visits, we selected four sites across a broad area of Willapa Bay (~250 km^2) in the eastern and southern arms (Fig. 2).

Treatments were set up on September 4, 2002, when oysters were at densities of 33.4 per cultch (4.1 SE) and average lengths of 7.2 mm (0.2 SE). A subset of cultch was collected the following May 16, 2003 to measure density and size of *O. lurida*, and the experiment ended August 27, 2003. We counted all *O. lurida* and measured the shell length (largest diameter, regardless of hinge orientation) of the largest five individuals on 10 haphazardly selected cultch from each treatment. Many of the unstable treatments entirely disappeared over winter; presumably water motion swept cultch and shell away. Therefore we were unable to examine the consequences of all treatments at all sites. We used ANOVA to compare bag and rosette treatments (fixed factor) across all sites (random factor) and to compare all treatments between Rogers and Mill Channel sites. In all analyses, each shell was a replicate, with oyster count and average size per cultch as dependent variables.

RESULTS

Recruitment Over Time

Despite the sparse densities of adult *Ostrea lurida* in Willapa Bay, seasonal recruitment exceeded that of introduced Pacific oysters throughout much of the past six decades (Fig. 4). On average, 9.9 recruits accumulated per shellface for native oysters, and just 2.4 recruits per shellface for Pacific oysters. Nevertheless, *C. gigas* remained the dominant oyster species in the south end of Willapa Bay even without aquaculture planting (many areas of feral *C. gigas* exist outside of aquaculture properties). In analysis of variance, the main effect of species was significant ($F1, 68 = 12.05$, $P = 0.0009$), but neither date ($F1, 68 = 0.35$, $P = 0.56$), nor its interaction with species ($F1, 68 = 1.86$, $P = 0.18$) was significant. Because of substantial interannual variation in recruitment, the overall model explained a small amount of total variation (adjusted $r2 = 0.13$, $n = 72$). The time series is being continued, however, because introduced oysters out-recruited natives in two of the past three years when shellstrings were reinstated after a 15-y hiatus (Fig. 4).

Recruitment Preference

In 2004, recruitment of *O. lurida* to the underside of oyster shells varied according to where the shells were placed on the tideflat (Fig. 5). Analyses were performed on log-transformed data, which solved problems of nonhomogeneity of variances (Bartlett's test). More than twice as many oysters recruited below than above MLLW (ANOVA $F_{1,16} = 11.5$, $P = 0.004$), and recruitment also varied among habitat types (ANOVA $F_{2,16} = 3.6$, $P = 0.05$). In posthoc tests, shell habitats attracted more native oyster recruits than eelgrass, with bare habitats intermediate (Tukey HSD: shell > bare > eelgrass). There was no statistical interaction among factors ($F_{2,16} = 0.1$, $P = 0.9$).

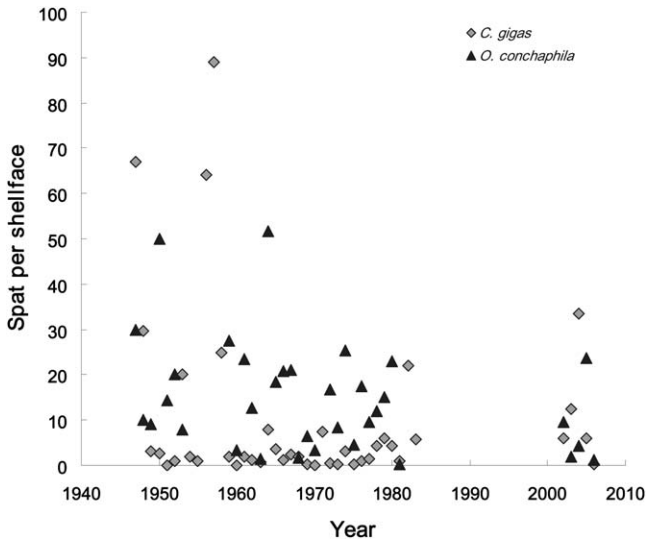

Figure 4. Average seasonal recruitment of *Ostrea lurida* and *Crassostrea gigas* recorded on shellstrings (smooth downward-facing surfaces of shells) at 3–8 sites in Willapa Bay, 1947 to 1983 and 2002 to 2003.

Introduced oysters showed the same tendency to recruit to shell stacks placed among shell as opposed to other habitats (Fig. 5; $F_{2,12} = 20.7$, $P = 0.0001$; Tukey HSD: shell > bare = eelgrass), but there was no tidal height effect ($F_{1,12} = 0.3$, $P = 0.6$) or interaction ($F_{2,12} = 1.1$, $P = 0.4$).

Post-Recruitment Response to Competition and Tidal Elevation

Initial densities of newly-metamorphosed *O. lurida* were high on tiles (>100 in 11 × 11 cm), but these dropped rapidly in the first few months even when tiles were continuously submerged and regularly cleaned (Fig. 6A). Over winter, tiles lost few additional oysters, but loss increased again in the next summer, probably caused by intraspecific competition because tiles became completely covered. This seasonal pattern of survival was mirrored by growth. From an initial size of 2 mm on tiles, juvenile oysters grew rapidly and reached 20 mm by the end of summer 2002. Overwinter growth was slow, but growth accelerated again in spring, and shell lengths reached 30 mm after one year (Fig. 6B). For comparison, *Crassostrea gigas* grown on tiles over the same period reached twice this length (C. Harvey, B. Feist, J. Ruesink, A. Trimble, unpublished data).

Fouling organisms reduced survival and growth of *O. lurida* on tiles (Fig. 7A, B, Table 1). Competitors reduced average survival across all elevations from 15% to 7%. They reduced final size of *O. lurida* by 2% to 35%, depending on site (generating significant site × treatment effects in ANOVA, Table 1, Fig. 7B).

Tidal elevation had a dramatic influence on survival of *O. lurida* but not growth (Fig. 8A, B, Table 2). Annual survival was approximately 20% on tiles continuously submerged on moorings, generally <10% just below mean lower low water, and <5% just above mean lower low water. In ANOVA, the site × elevation interaction was significant: oysters fared particularly poorly at Parcel A overall, but oysters just below MLLW survived relatively well at Middle Sands. Short emersion times (2% to10%) were sufficient to kill many oysters even though those that survived suffered no reduced growth. After one year, oysters reached 30 mm at all elevations.

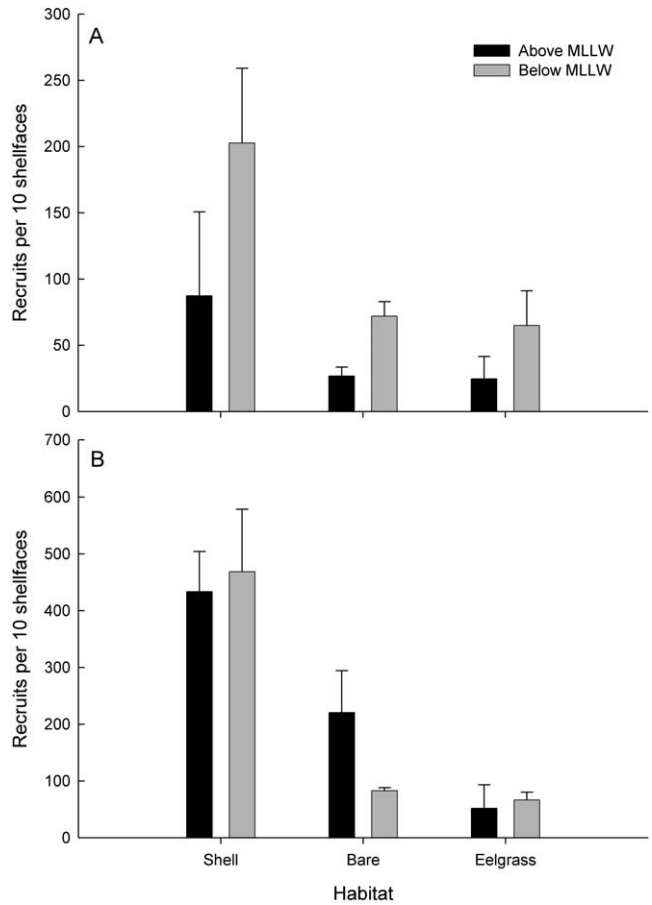

Figure 5. Recruitment of (A) *Ostrea lurida* from May 21, 2004 to June 17, 2004 and (B) *Crassostrea gigas* from July 18, 2004 to August 14, 2004 on 10 shells placed at two tidal elevations in three habitat types.

Post-Recruitment Response to Substrate Characteristics

The stable "bag" and "rosette" treatments persisted for one year at all sites where cultch was placed. However, unstable treatments disappeared at Long Island between September 2002 and May 2003 and from Mill Channel sometime thereafter. This differential success of treatments already implies site differences, but it made analysis difficult, because two treatments were missing from two sites. We focused statistical analyses on the two remaining treatments at all four sites. There were significant differences in survival among sites, with relatively high final numbers at Rogers (Fig. 9A, Table 3). Site and treatment differences existed for oyster size (Fig. 9B, Table 4). Shell length was higher for low-density stable outplants (rosettes) than for high-density stable outplants (staples), and oysters at Rogers and Nemah generally grew well. Overall, final sizes of *O. lurida* on cultch were similar to the tile experiment (about 30 mm, Fig. 9B), particularly tiles with competitors. Indeed, stable treatments had substantial cover of fouling organisms after one year.

DISCUSSION

In Willapa Bay, native oysters (*Ostrea lurida*) have failed to return to pre-exploitation densities despite almost a century of negligible fishing. Our results suggest that recruitment has been

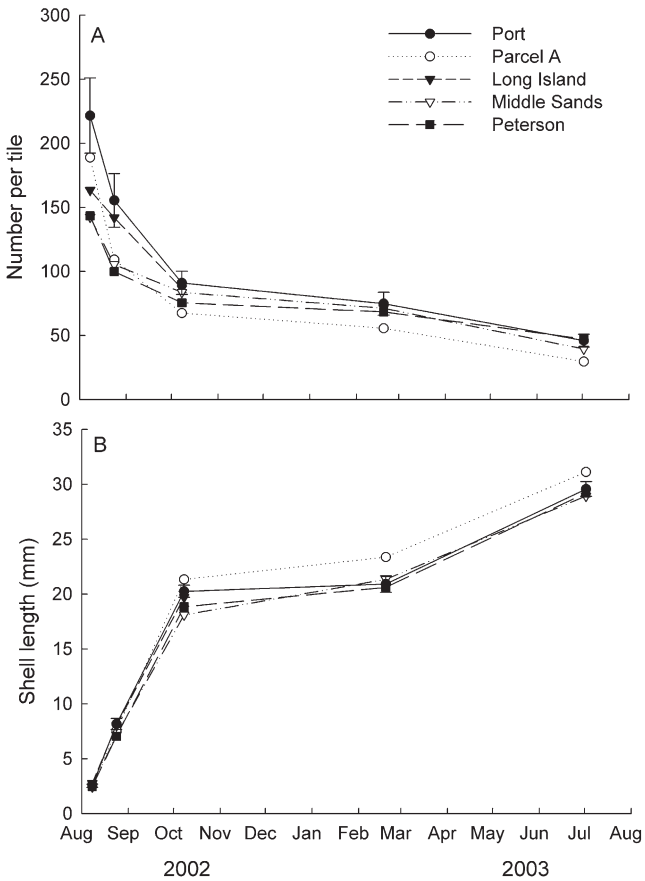

Figure 6. (A) Number and (B) size of native oysters *Ostrea lurida* on ceramic tiles at 5 sites in Willapa Bay, August 8, 2002 to July 2, 2003. Data were compiled only from tiles on moorings that were regularly cleaned of fouling organisms, to generate a best-case scenario of growth and survival. Error bars show standard error of 5 replicates. Each replicate is the average length of the five largest oysters per tile. Measurements taken from photographs.

high and persistent for at least five decades throughout the southern portion of the bay, which implicates poor postrecruitment survival and growth as the weak demographic link in the life cycle. We found four factors with large impacts on the performance of juvenile oysters: increased mortality from aerial exposure, competition from fouling organisms, many of which are introduced, recruitment preference for *C. gigas* reefs, and outplanting technique.

O. lurida has long been known to be sensitive to exposure to air. Townsend (1896) reported that native oysters died when exposed to freezing weather during low tides in midwinter. Early techniques for culturing native oysters were successful in regions where extensive dikes were constructed to hold intertidal oysters underwater at low tide (Korringa 1976). In the present study, at least some of the mortality was likely caused by high temperature stress. At three sites, more than half of the tiles at +0.3 m MLLW had lost 90% of their oysters by the time photographs were taken in October 2002. In any case, juvenile oysters fare poorly when exposed to air for even short periods of time (2–10%, Fig. 8), with survival dropping by half or more. Although it is possible that some of the additional mortality relative to moorings is caused by other factors, such as predation on-bottom relative to off-bottom, these alternative hypotheses cannot explain why tiles on poles above the substrate had lower oyster survival than tiles just above the substrate. The small amounts of emersion at –0.3 m and +0.3 m were not sufficient to affect growth. If anything, oysters that were continually submerged tended to grow slower, possibly because of intraspecific competition on these crowded tiles.

Removal of fouling organisms doubled the chance that native oysters would survive and improved their growth significantly (Fig. 7). On plates with no cleaning, ascidian cover reached 60%, particularly on tiles below MLLW, and barnacle cover exceeded 60% at some sites. These taxa and others may have smothered oysters, killing them outright, or restricted food access to stunt growth. We started this experiment after spatfall of Pacific oysters so direct competition between these species for space was not measured. However, growth rates of *C. gigas* on tiles is approximately twice as fast as *O. lurida* (unpublished data), and we would therefore expect *C.gigas* to overgrow native oyster spat sharing settlement space within a distance of 5 cm within one year.

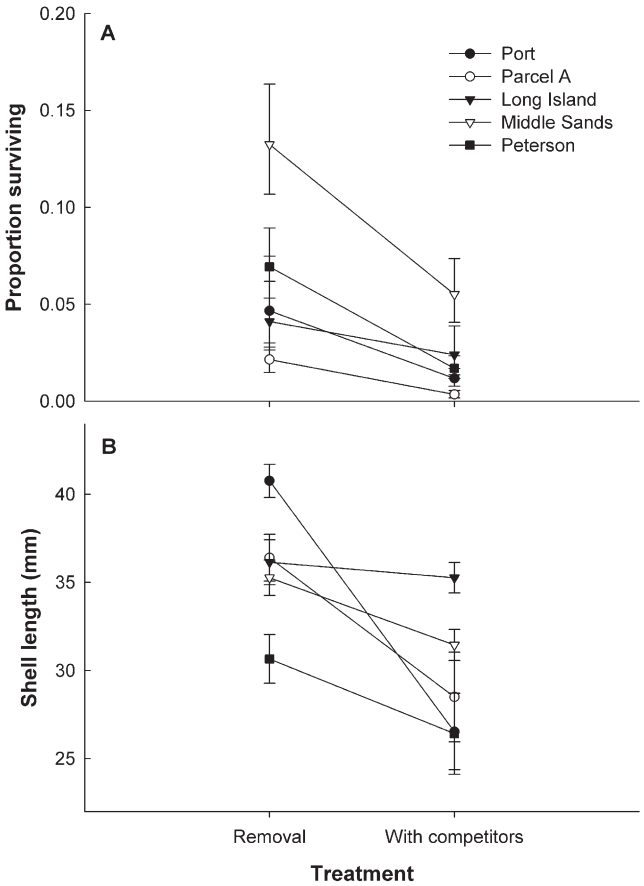

Figure 7. Effects of competitors on (A) survival and (B) size of native oysters *Ostrea lurida* at 5 sites in Willapa Bay. Fouling organisms were regularly removed from half of the tiles (Removed) but not from the remainder (with Competitors). Points show mean and standard error of 10 tiles on poles (no moorings). Proportion surviving is back-transformed from ln-transformed data, generating slightly asymmetric standard error bars.

TABLE 1.

Analysis of variance of ln-transformed survival of *Ostrea lurida* on tiles. Treatment refers to cleaning fouling organisms from half of the tiles. Missing values for the Long Island mooring were substituted by average values for other cleaned and uncleaned tiles on moorings.

	Sum of Squares	df	F	P
Site (S)	20.7	4	13.4	0.001
Elevation (E)	73.1	2	94.3	0.001
Treatment (T)	16.4	1	42.4	0.001
S × E	8.7	8	2.8	0.007
S × T	0.5	4	0.3	0.88
E × T	0.3	2	0.4	0.65
S × E × T	3.0	8	1.0	0.46
Residual	43.4	112		

TABLE 2.

Analysis of variance of size of *Ostrea lurida* on tiles. Tiles on poles were included, but not tiles on moorings.

	Sum of Squares	df	F	P
Site (S)	489.9	4	6.5	0.001
Elevation (E)	24.2	1	1.3	0.26
Treatment (T)	700.8	1	37.4	0.001
S × E	45.2	4	0.6	0.66
S × T	415.5	4	5.5	0.001
E × T	14.7	1	0.8	0.38
S × E × T	94.1	4	1.3	0.30
Residual	1,143.0	61		

Treatment differences were evident despite high mortality of small oysters even under the best conditions (Fig. 5), and also despite evidence of density dependent mortality at the end of the experiment. The oysters that we measured (5 largest) were generally the least crowded on the tiles; others were much smaller and grew up from the tile. Sometimes crowded oysters would flake off as we handled them. Increased mortality in the second summer likely occurred because rapidly-growing oysters ran out of room (Fig. 5).

Outplanting native oysters on Pacific oyster cultch was designed to mimic current restoration techniques. However, all of the methods that we used were less than satisfactory. Unstable substrates remained large but light (in contrast to

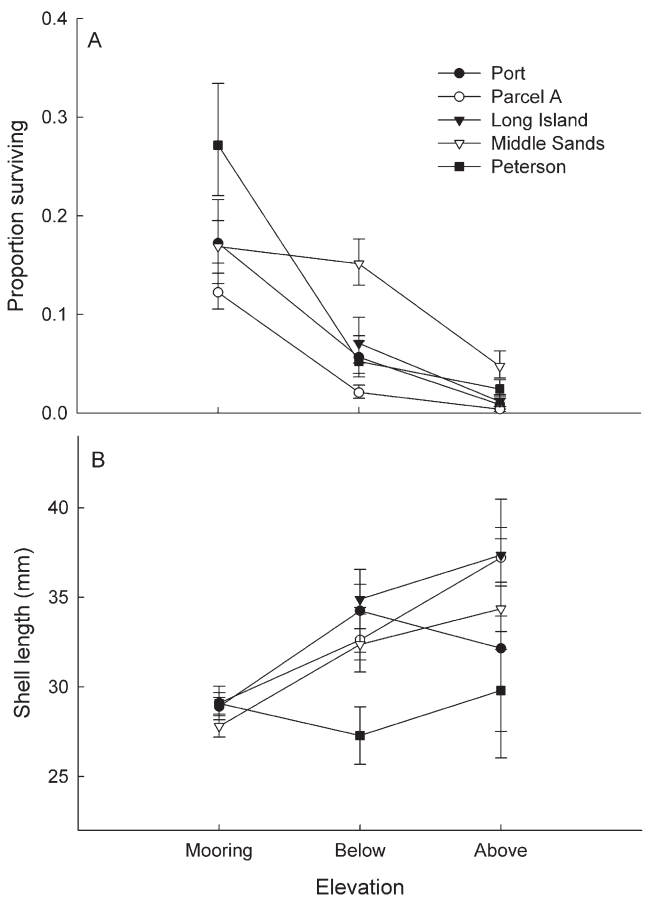

Figure 8. Effects of tidal elevation on (A) survival and (B) size of native oysters *Ostrea lurida* at 5 sites in Willapa Bay. Mooring = continuously submerged; Below = –0.3 m mean lower low water (MLLW), out of water 2% of the time; Above = +0.3 m MLLW, out of water 10% of the time. Points show mean and standard error of 10 tiles with and without competitors. Proportion surviving is back-transformed from ln-transformed data, generating slightly asymmetric standard error bars. The mooring at Long Island was destroyed by storms over winter.

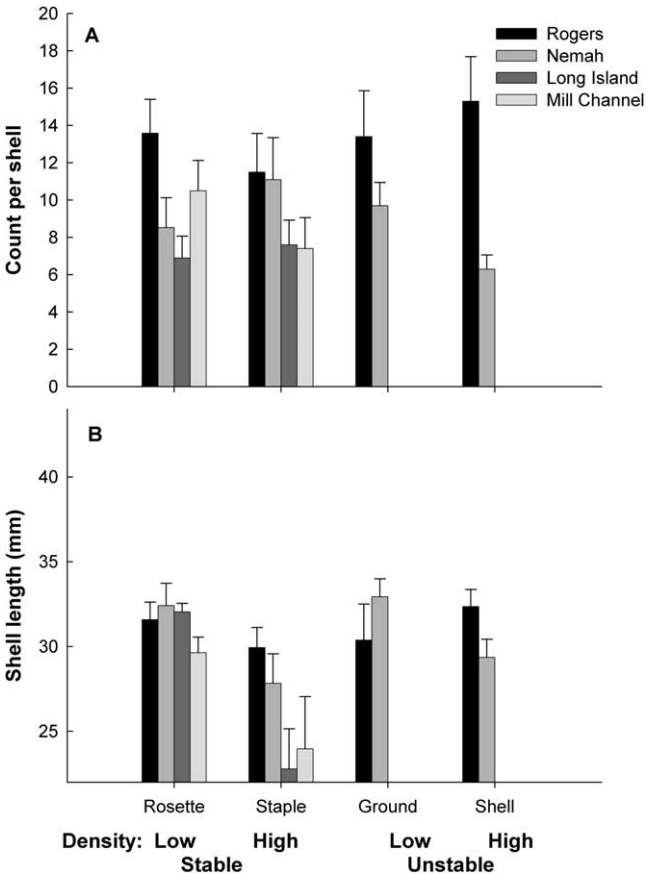

Figure 9. Effects of different outplant techniques on (A) density and (B) size of native oysters *Ostrea lurida* at 4 sites in Willapa Bay. Points show mean and standard error of 10 cultch (20 cultch for rosettes).

TABLE 3.

Analysis of variance of density of *Ostrea lurida* on cultch. All 4 sites are included, but only 2 treatments (rosettes and staples) that persisted at all sites.

	Sum of Squares	df	F	P
Site (S)	386.1	3	2.97	0.035
Treatment (T)	6.0	1	0.14	0.71
S × T	132.9	3	1.02	0.39
Residual	4772.4	110		

cultch used for Pacific oyster culture, because Pacifics grow much larger and eventually provide enough mass to prevent being moved by water motion). At half of the study sites, treatments in which cultch was placed directly on-bottom disappeared altogether, whereas naturally occurring adult native oysters in these areas remained. Stable treatments of rosettes and bags stayed in place better over one year. However, bags became extremely fouled, and oyster densities were high enough that individuals were stunted. We collected cultch from the outside, near the mesh, and problems were even more severe within the bag. No grower would ever attempt to produce a crop by packing oysters in a huge mass, and restoration is unlikely to be aided that way either. Finally, rosettes were a huge amount of work to deploy, impractical for large-scale restoration efforts. We are currently exploring whether small pieces of (crushed) shell can be used to restore native oysters more effectively. Remnant populations in Willapa Bay tend to include clumps of 3–5 native oysters that have settled on an original shell <3 cm long. These clumps, scattered in eelgrass beds (*Zostera marina*), remain on intertidal flats and are not lost to deep sedimenting channels.

Willapa Bay clearly has lost an enormous amount of biogenic shell habitat that formerly occurred in shallow subtidal areas. This shell was removed in the process of collecting *O. lurida* for export beginning in 1851. Data on these habitats are so scarce that we do not know what to try to recreate—presumably some sorts of shell accumulations actually helped hold live oysters in place, but the thin layers of Pacific cultch clearly were insufficient. More importantly, we believe, the absence of these subtidal shell accumulations means that native oyster larvae have few places that remain underwater and allow good postrecruitment survival, to recruit. Instead, they seem to be attracted to extensive intertidal *C. gigas* shell and recruit too high, where they desiccate or freeze and generally die. Our results suggest that intertidal Pacific oysters are a "recruitment sink" for natives (Fig. 4), because larvae of *O. lurida* tend to be attracted to large reefs, which today primarily occur above MLLW. Our quantitative results agree with decades of observation by aquaculturists that "…in Willapa Bay there has been in most years a good natural set of native oysters on Pacific oyster shells. However, once they grow to approximately 1 cm, the native oysters died" (Chew & Neil 1981).

TABLE 4.

Analysis of variance of size of *Ostrea lurida* on cultch. All 4 sites are included, but only 2 treatments (rosettes and staples) that persisted at all sites.

	Sum of Squares	df	F	P
Site (S)	290.8	3	3.45	0.019
Treatment (T)	704.2	1	25.04	0.001
S × T	179.9	3	2.13	0.10
Residual	2,953.0	105		

Today, there is a tremendous amount of discussion about the release of nonnative oyster species into Chesapeake Bay and other east coast estuaries, because the native Eastern oyster (*Crassostrea virginica*) has been severely depleted by overexploitation and new diseases (NRC 2004). Washington State (as did British Columbia, OR and California) made the decision a century ago to introduce new oyster species (including *C. virginica*) without discussion of the risks of nonindigenous species, as the potential risks were totally unknown at that time. These introductions did result in tremendous success for the shellfish industry, and are the basis for a large percentage of total production of shellfish in the United States today. Unfortunately, we show evidence that the commercial species introduced to replace *O. lurida*, in addition to hitchhiking species, may in fact be contributing to the inability of the native oyster to return to its former abundance. This new web of interactions includes nonindigenous species that directly compete for food and space, and a large, reef-forming oyster species (*C.gigas*) that builds different habitat from *O. lurida*. It is reasonable to believe that these competitive interactions can also occur outside Willapa Bay, in all areas where native oysters were historically present and culture of *C. gigas* is practiced. The impacts of this new habitat on salmonid populations as compared with the original native oyster dominated habitat are not possible to determine. Successful restoration of the native oyster of the west coast of North America, and subsequent studies on it's ecological roles may only be possible in restricted areas where these new interactors are either not yet present or can be managed effectively. Unfortunately, cultivation of nonnative shellfish and the presence of numerous other alien species are pervasive throughout *O. lurida's* native range and therefore suitable sites where these competitive interactions will not occur are difficult to imagine.

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