

## IMPACTS OF INVASIVE OYSTER DRILLS ON OLYMPIA OYSTER (*OSTREA LURIDA* CARPENTER 1864) RECOVERY IN WILLAPA BAY, WASHINGTON, UNITED STATES

ERIC R. BUHLE<sup>†\*</sup> AND JENNIFER L. RUESINK

Department of Biology, University of Washington, Box 351800, Seattle, Washington 98195

**ABSTRACT** The Olympia oyster (*Ostrea lurida*)<sup>‡</sup> was historically abundant in Willapa Bay, WA, but populations were decimated by overexploitation in the mid to late-1800s and have failed to recover. We investigated the potential role of two introduced predatory gastropods, the Japanese drill (*Ocenebrina inornata*) and the eastern drill (*Urosalpinx cinerea*), in limiting Olympia oyster recovery. We quantified the bay-wide distribution, local abundance, and per capita effects of drills, and asked how each of these three components of total invasion impact might be influenced by another dominant introduced species, the Pacific oyster (*Crassostrea gigas*). Bay-wide sampling revealed differences in spatial distribution of the two drill species, with *U. cinerea* more abundant toward the head of the estuary and *O. inornata* more abundant toward the mouth. Individual feeding trials indicated that both drill species preferred Pacific oysters to Olympia oysters of similar size, and preferentially attacked smaller oysters. We used field enclosures to quantify the direct effects of Japanese drill predation on Olympia and Pacific oysters, intra and interspecific competition, and indirect effects mediated by the shared predator. Predation reduced the survival of both oyster species, but the per capita impact of Japanese drills declined with increasing density of either Olympia or Pacific oysters, consistent with a type II functional response. This positive indirect effect of Pacific oysters on Olympia oysters was offset by asymmetric competition, in which Pacific oysters reduced Olympia oyster growth and survival but not *vice versa*. Despite the large drill impacts seen in these experiments, Olympia oysters transplanted to intertidal sites throughout the bay experienced low and variable rates of drill predation compared with other mortality sources. Introduced drills may be only one of a suite of factors that prevent rebuilding of Olympia oysters in the intertidal zone in Willapa Bay.

**KEY WORDS:** Olympia oyster, *Ostrea lurida*, invasion, predator-prey, indirect effect, *Ocenebrina inornata*, *Urosalpinx cinerea*, *Crassostrea gigas*

### INTRODUCTION

Biological invasions have had important consequences for coastal ecosystems and fisheries around the world (Carlton 1989, Grosholz 2002). Invasions rarely occur in isolation, so managing the impacted species requires understanding direct and indirect interactions among native and exotic species, harvest, and other human activities. A simple conceptual model (Parker et al. 1999) describes the impact of an invasive species as the product of its geographic range, density, and per capita effect, each of which may be influenced by biotic or abiotic attributes of the invaded community. In this paper we apply this framework to understand the impact of two introduced predators on a native bivalve in a highly modified estuary.

The Olympia oyster (*Ostrea lurida* Carpenter 1864) is a historically widespread, locally abundant, and commercially important species that has experienced major, persistent declines throughout its range. Native to the west coast of North America from Alaska to Baja California (Coan et al. 2000), this small ( $\leq 6$  cm) oyster supported commercial harvest beginning in the mid to late-1800s. In Willapa Bay, Washington, United States, where our research was conducted, Olympia oysters

occurred naturally in the low intertidal and subtidal. Exploitation by European colonists began in 1851 and wild stocks were rapidly depleted, with significant commercial catches ending by the early 1900s (Baker 1995, Cook et al. 2000). Initial declines were caused by overexploitation and unsustainable harvest practices, such as export of adult oysters in the shell and the consequent loss of both spawning stock and larval settlement substrate (Sayce 1976, Cook et al. 2000). Nonnative species were imported to sustain the industry, beginning with the Eastern oyster (*Crassostrea virginica* [Gmelin, 1791]) and later the Pacific oyster (*Crassostrea gigas* [Thunberg, 1793]). The latter species established a naturalized population in Willapa Bay and now comprises the majority of commercial oyster harvest in the Pacific Northwest (Sayce 1976).

Commercial shellfish introductions provided a pathway for the invasion of dozens of nontarget organisms, including two predatory gastropods: the Eastern drill (*Urosalpinx cinerea* [Say, 1822]) and the Japanese drill (*Ocenebrina inornata* [Récluz, 1851]; synonyms include *Ocenebrellus inornatus*, *Ceratostoma inornatum*, and *Tritonalia japonica*). The Eastern drill, *U. cinerea*, was introduced to Willapa Bay before 1948, probably with imported eastern oysters in the early 1900s, and *O. inornata* was introduced before 1965 with shipments of Pacific oysters (Carlton 1979). Both drill species are now established and widespread in Willapa Bay. *O. inornata* in particular is an economically significant pest of oyster aquaculture that is particularly damaging to juvenile (seed) oysters. Drills consume barnacles, oysters, mussels, and other bivalves. Oyster growers attempt to control drills by manually removing adults and egg capsules, but even local eradication has proven elusive and growers have abandoned some beds because of intense predation.

Despite the impact on cultivated Pacific oysters, little is known about the role of drills in limiting Olympia oyster recovery.

\*Corresponding author. E-mail: eric.buhle@noaa.gov

<sup>†</sup>Present address: Northwest Fisheries Science Center, 2725 Montlake Blvd. E, Seattle, Washington 98112.

<sup>‡</sup>The taxonomy of the Olympia oyster has been in dispute since Harry (1985) proposed synonymy of *Ostrea 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.

Cook et al. (2000) suggested that predation by *O. inornata* might contribute to the slow recovery of native oyster populations after initial declines, and *O. inornata* causes localized high mortality of *Olympia* oysters in Puget Sound (Chapman & Banner 1949, Buhle [unpublished data]). Muricid gastropods in general often have important top-down effects on intertidal prey populations and benthic community structure (Connell 1970, Navarrete & Menge 1996, Katz 1985).

We assessed the impact of drills on native oysters in Willapa Bay by quantifying the distribution, density, and per capita effects of *O. inornata* and *U. cinerea*. We also considered how *C. gigas*, now one of the dominant intertidal organisms in the bay, might modify each of these components of drill impact. Drills occur on intertidal hard substrates, particularly Pacific oyster reefs and aquaculture beds. *Olympia* oysters recruit into these habitats, but mortality is high and adults are uncommon (Trimble et al. 2009). Drills are direct developers with crawl-away juveniles emerging from benthic egg capsules, so natural dispersal is limited and the distribution of drills within the bay reflects the history of aquaculture transfers as well as possible ecological limiting factors. Pacific oysters could influence local drill density by creating complex habitat structure (Crooks 2002) or *via* bottom-up pathways (drills consume oysters as well as oyster epifauna such as barnacles), which could lead to apparent competition (Holt & Lawton 1994) between Pacific and *Olympia* oysters. We sampled sites throughout the bay over several years to map drill distributions and densities in relation to the presence of Pacific oyster aquaculture and reefs. Pacific oysters could also modify the per capita effect of drills on *Olympia* oysters by providing alternative prey. If drills have a saturating functional response, then an increase in Pacific oyster density is predicted to have a short-term indirect positive effect on *Olympia* oysters by reducing their mortality rate caused by predation (Abrams & Matsuda 1996). The possible outcomes are complex, however, if Pacific oysters also directly compete with *Olympia* oysters for food or space. We conducted feeding experiments to measure the per capita predation rates and preferences of drills on Pacific and *Olympia* oysters of a range of sizes. We also performed a field experiment to quantify the direct and indirect interactions among Japanese drills and the two oyster species. Finally, we measured predation impacts in an unmanipulated setting using *Olympia* oysters transplanted into several intertidal habitat types.

## METHODS

### *Drill Abundance and Distribution*

Drill densities were measured in three ways: mark-recapture, quadrats, and catch per unit effort. Mark-recapture generates the most accurate estimates of population size, but such studies were only carried out at three sites where quadrat data were also available. Mark-recapture indicated that detectability is inversely related to drill size (unpublished data), so the other methods likely underestimate the contribution of small drills to the population. All three methods generate information on presence/absence and on relative abundance of the two introduced drill species. However, abundances of drills cannot easily be compared across methods. Furthermore, catch per unit effort cannot be compared across habitat types if detectability differs between open tideflats and dense oysters. We report

quadrat data from all sites where available but include additional sites sampled *via* catch per unit effort (CPUE) because this improves our picture of the distribution of the two drill species throughout Willapa Bay. Sample methods, habitats, sites, dates, numbers of drills, median and maximum size (anterior-posterior shell length, mm) are reported in Table 1 and Table 2. Sites were characterized as on-bottom Pacific oyster aquaculture beds, naturally formed Pacific oyster reefs, or bare tideflat. One collection was made from bags of shell covered with small oysters (cultch) at the Port site.

### *Drill Feeding Rates and Preferences*

Single oyster drills were placed in enclosures with oysters, and counts of drilled oysters were recorded over time. The enclosures had dimensions of 15 × 5 × 10 cm and were made of translucent plastic with 1-mm mesh on two sides. They were kept continuously submerged in the field (Port site). We carried out four separate feeding experiments, each with 20 replicates (enclosures) for Japanese drills and 10 replicates for eastern drills. Each individual drill was used only once. The experiments were as follows: (1) From May 21 to June 28, 2002, each drill was offered small (15 mm shell length) Pacific oysters growing on a dead adult oyster shell (cultch). We compared feeding rates by different sizes and species of drills by analysis of covariance (ANCOVA) with drill shell length as the covariate; (2) From May 21 to June 28, 2002, each drill was offered 10 Pacific oysters ranging from 9–76 mm in shell length. We compared the average size of eaten *versus* uneaten oysters (paired *t*-test for each drill species) as an indicator of which sizes were drilled first; (3) From July 29 to August 24, 2002, each drill was offered one adult *Olympia* oyster and a Pacific oyster of similar size (~50 mm shell length). Because few oysters were drilled, we analyzed these data as contingency tables to determine if drilling frequency differed between drill or oyster species; (4) From September 7 to October 8, 2002, each drill was offered 2–6 small individuals of each oyster species, allowing us to determine preference between oyster species of ~15 mm shell length.

We calculated Manly's  $\alpha$ , adjusted for prey depletion throughout the feeding trial (Krebs 1999). This index of preference was designed for cases with at least 10 items of each prey remaining uneaten at the end of the experiment, an assumption that we clearly violated by beginning with fewer prey items than this. We adjusted this index to accommodate cases of complete prey removal as:

$$\alpha_i = \frac{\log(p_i + 0.01)}{\sum_{j=1}^m \log(p_j + 0.01)} \quad (1)$$

where  $\alpha_i$  is Manly's alpha for prey type  $i$ ,  $p_i$  is the proportion of prey type  $i$  uneaten at the end of the trial, and  $p_j$  is the proportion of each of the  $m$  prey types, including  $i$ , uneaten. For individual drills,  $\alpha_i$  was not necessarily restricted to the range (0, 1) but never exceeded this range by more than 0.03, suggesting that the average preference calculated for the whole trial was not substantially biased. Final sample sizes for all four feeding trials were less than initial numbers caused by loss of drills from the enclosures.

### *Direct and Indirect Effects—Enclosure Experiment*

We conducted a field experiment to estimate the direct effects on *Olympia* oysters caused by competition from Pacific

TABLE 1.  
 Distribution and abundance of Japanese and eastern oyster drills sampled in quadrats (usually 0.25 m<sup>2</sup>) in Willapa Bay, organized by habitat from north to south.

Habitat/Site	Lat/ Long	Date	No. quads	Mean (SD) Density (m <sup>-2</sup> )		Mean (max) Shell Length (mm)	
				Japanese	Eastern	Japanese	Eastern
BARE							
Bay Center	46.633 123.942	10/6/02	9	0.44 (1.3)	0		
Mid Sands	46.479 124.018	8/20/02 10/5/02	9	0	0		
Nemah	46.54 123.94	10/5/02	6	0	0		
Peterson	46.438 124.008	8/24/02 10/6/02	3	0	0		
AQUACULTURE							
Bay Center	46.633 123.942	8/22/02 10/6/02	101	2.2 (5.3)	0	30.1 (43.0)	
Stackpole	46.6 124.0	7/3/06	59	0.7 (1.2)	0		
Mid Sands	46.479 124.018	8/20/02 10/5/02	26	4.0 (7.8)	0		
Nahcotta Channel W	46.46 124.016	3/29/02 5/6/03	77	1.1 (2.8)	1.09 (4.0)	26.6 (48.0)	21.1 (34.9)
PACIFIC OYSTER REEFS							
Parcel A	46.495 124.027	8/1/01 3/29/02	13	10.7 (7.1)	0	23.2 (42.8)	
Mid Sands	46.479 124.018	8/20/02 10/5/02	29	46.4 (66.6)	0	19.5 (33.0)	
Nemah	46.54 123.94	8/21/02 10/5/02 5/3/03	20	17.0 (17.8)	0		
Nahcotta Channel W	46.46 124.016	5/6/03	15	6.9 (14.5)	0	27.5 (41.8)	
Long I Lewis Slough	46.469 123.95	3/30/02	5	0	0		
Sunshine Pt	46.46 123.926	3/30/02	6	0	0		
Long I Slough N	46.445 123.944	3/30/02	5	0	0		
Peterson St House	46.439 124.01	5/02	11	0	25.4 (32.6)		22.4 (28.0)
Peterson	46.438 124.008	5/02 8/24/02 10/6/02	19	10.1 (10.5)	8.4 (11.2)		
Long I Slough S	46.414 123.938	4/29/02	8	0	10.5 (11.3)		24.2 (29.0)
Refuge HQ	46.414 123.935	3/30/02	12	0	0		

oysters and predation by Japanese drills, as well as possible indirect effects between the two oyster species *via* their shared predator. The experiment was carried out in open-topped cylindrical enclosures with sheet copper walls to prevent drills from entering or leaving. The walls were 30 cm tall with the lower 15 cm buried in the sediment, and enclosed 0.25 m<sup>2</sup> of substrate. We manipulated densities of all three species in a fully crossed design with three replicates of each treatment combination. There were four levels of Pacific oyster density (~18, 207, 393, and 771 m<sup>-2</sup>), two levels of Olympia oyster density (~171 and 328 m<sup>-2</sup>), and two levels of Japanese drill density (0 and 12 m<sup>-2</sup>). Juvenile Pacific (mean shell length and SD, 26.1 ± 10.3 mm) and Olympia (10.3 ± 2.3 mm) oysters were settled on separate pieces of Pacific oyster cultch (i.e., dead shell). We varied the densities of the two oyster species by adding different amounts of cultch to each enclosure. The number of individual oysters was estimated based on the number of cultch pieces and the average number of individuals per shell counted on a subsample of cultch. In addition to cultch settled with live oysters, bare cultch was added as necessary so that the bottom of each enclosure was completely covered with a single layer of shell, ensuring that habitat complexity was constant across treatments. Because it was logistically impossible to follow the fate of every oyster in the experiment, a subset of cultch pieces was marked and used to estimate survival and predation rates. There were four marked cultch pieces for each oyster species in each enclosure, with the exception of the lowest Pacific oyster density treatment (one marked piece of Pacific oyster cultch) and the low Olympia oyster density treatment (three marked pieces of Olympia oyster cultch). We measured all individuals

on one of the marked cultch pieces for each species at the beginning and end of the experiment to test for density dependence in oyster growth rates.

Japanese drills (mean shell length and SD, 25.7 ± 3.1 mm) were measured and individually marked with numbered tags to measure growth. Drills and oysters were added to the enclosures on July 25, 2002. We then sampled the enclosures at approximately 2-wk intervals until September 4, 2002, recording the fate of oysters on marked cultch and replacing any dead or missing drills.

We analyzed the data from this experiment by fitting simple theoretical models of a one-predator, two-prey interaction web to the observed oyster fates, that is, the number of individuals alive, drilled, and dead from other causes at the end of the experiment, under different initial combinations of predator and prey density. The models were written as a coupled system of ordinary differential equations, and different specific model structures were used to represent alternative hypotheses about the drill functional response and intra and interspecific competition in the two oysters. Our general strategy was to construct a set of alternative models, fit each one to the data using maximum likelihood (Hilborn & Mangel 1997), and then use information-theoretical model selection methods (Burnham & Anderson 2002) to compare the relative strength of evidence for different models in light of the data. This approach offers several advantages over a more traditional analysis using linear statistical models such as ANOVA. First, it explicitly links our experimental results to basic food web theory that includes realistic nonlinearities and biologically interpretable parameters (e.g., handling time). Second, it can deal appropriately with nonnormal error structure in the data (in this case, discrete

counts of living, drilled, and dead oysters). Third, by numerically solving continuous-time models we account for the fact that prey densities (and in turn, the strength of species interactions) are changing throughout the experiment, producing a network of reciprocal causation that would be ignored by static models.

The basic model represents a single predator with fixed density  $P$  feeding on two prey with densities  $N_1$  and  $N_2$ . The predator's functional response, or *per capita* feeding rate on prey species  $i$  as a function of the densities of both prey, is  $F_i(N_1, N_2)$  (Holling 1965, Murdoch & Oaten 1975). The prey also experience nonpredatory mortality at some density-independent baseline rate. If intra or interspecific competition occurs, we assume that it causes a linear density-dependent increase in this mortality rate, as in the standard logistic and Lotka-Volterra models. Because drill predation leaves a recognizable mark, the model separately tracks the densities of prey eaten and dead of other causes ( $E_i$  and  $D_i$  respectively, for species  $i$ ) in addition to the density remaining alive. Thus the basic model for prey  $i$  is

$$\begin{aligned}\frac{dN_i}{dt} &= -F_i(N_1, N_2)P - (m_i + a_{i1}N_1 + a_{i2}N_2)N_i \\ \frac{dE_i}{dt} &= F_i(N_1, N_2)P \\ \frac{dD_i}{dt} &= (m_i + a_{i1}N_1 + a_{i2}N_2)N_i\end{aligned}\quad (2)$$

The baseline nonpredatory mortality rate for species  $i$  is  $m_i$ , and the competition coefficients  $a_{ij}$  represent the per-capita effect of species  $j$  on species  $i$ . Note that there is no recruitment of prey or predators over the time scale of our experiment. We compared alternative model structures designed to ask three questions about this interaction web: (1) Is there evidence of intraspecific density-dependence in the survival of one or both oyster species? We tested this by comparing the full model to models with one or both intraspecific competition coefficients ( $a_{ii}$ ) set to zero. (2) Is there evidence of interspecific competition between *Olympia* and Pacific oysters? Likewise, we tested this by setting one or both of the  $a_{ij}$ 's ( $i \neq j$ ) to zero. (3) Do the data indicate that drills have a linear (type I) or saturating (type II) functional response (Holling 1965)? This question is especially critical. A type II response leads to indirect facilitation between prey as an increase in the density of one prey species lowers the risk that other prey will be attacked (Abrams & Matsuda 1996, Wootton 2002), whereas this behavior-mediated indirect effect does not occur with a type I response. The type I functional response is given by

$$F_i(N_1, N_2) = c_i N_i \quad (3)$$

and the type II functional response is

$$F_i(N_1, N_2) = \frac{c_i N_i}{1 + c_1 h_1 N_1 + c_2 h_2 N_2}, \quad (4)$$

where the predator's attack rate on prey  $i$  is  $c_i$  and the handling time for prey  $i$  is  $h_i$ . We used the estimated attack rate parameters to calculate the preference of drills for each oyster species (Manly's  $\alpha$ ; Chesson 1983). Preference for prey species  $i$  is given by  $\alpha_i = c_i / (c_1 + c_2)$ .

Fitting the models requires an appropriate likelihood function for the data. The counts of live, drilled, and other dead individuals of oyster species  $i$  in enclosure  $k$  ( $n_{ik}$ ,  $e_{ik}$ , and  $d_{ik}$ , respectively) are a sample from a multinomial distribution. The log-likelihood of the model parameters  $\theta$ , given the data, is therefore

$$L(\theta | n_{ik}, e_{ik}, d_{ik}) = n_{ik} \ln \left( \frac{N_{ik}}{T_{ik}} \right) + e_{ik} \ln \left( \frac{E_{ik}}{T_{ik}} \right) + d_{ik} \ln \left( \frac{D_{ik}}{T_{ik}} \right), \quad (5)$$

where the expected probabilities are the model predictions  $N_{ik}$ ,  $E_{ik}$  and  $D_{ik}$ , expressed as proportions of the total number of individuals  $T_{ik} = N_{ik} + E_{ik} + D_{ik}$ . We calculated these values by numerically solving Eq. 2 for the duration of the experiment ( $t = 41$  d) using a fourth-order Runge-Kutta algorithm in MATLAB (MathWorks 1999), starting from the known initial densities in each enclosure. For treatments where drills were present, we took predator density  $P$  to be the average drill density over the course of the experiment, accounting for drill mortality and replacement. The total log-likelihood, summing across oyster species and replicates, is then

$$L(\theta | n, e, d) = \sum_{i=1}^2 \sum_{k=1}^{48} n_{ik} \ln \left( \frac{N_{ik}}{T_{ik}} \right) + e_{ik} \ln \left( \frac{E_{ik}}{T_{ik}} \right) + d_{ik} \ln \left( \frac{D_{ik}}{T_{ik}} \right). \quad (6)$$

The parameter values that maximize this quantity are the maximum-likelihood estimates  $\hat{\theta}$ . We ranked the strength of evidence for alternative model structures by calculating the sample size-corrected version of Akaike's information criterion ( $AIC_c$ ) for each model (Burnham & Anderson 2002).  $AIC_c$  is a measure of parsimony that reflects the tradeoff between goodness of fit and the number of parameters in a model. We obtained standard errors for all parameters in the best-supported model by bootstrapping the dataset (2,000 bootstrap resamples of enclosures, keeping treatment replication balanced).

#### Drill Impacts in the Field—*Olympia* Oyster Transplants

To examine patterns of drill predation pressure and other mortality sources in the field, we transplanted *Olympia* oysters into intertidal habitats at four sites in Willapa Bay (Bay Center, Nemah, Middle Sands, and Peterson Station; see Table 1). Transplants were classified by habitat type as Pacific oyster reefs, Pacific oyster aquaculture beds, or open mud. We attempted to find examples of all three habitat types at each site, but this was not always possible. Each transplant consisted of a PVC stake driven into the substrate. Four cultch pieces settled by juvenile *Olympia* oysters (mean shell length and SD =  $12.4 \pm 3.3$  mm) were attached to the stake with plastic cable ties so that they rested on the adjacent substrate. Transplants were deployed on August 20–24, 2002 and retrieved on October 5–6, 2002. The fate of all oysters (live, drilled, or dead from other causes) was recorded and a subset of individuals was measured at the beginning and end of the study to test for variation in growth rate as a function of site and habitat type. We also tested the influence of the local community on oyster survival and growth by measuring drill and alternative prey abundance. At the beginning and end of the study, we haphazardly placed three  $0.25\text{-m}^2$  quadrats near each transplant and recorded Japanese and Eastern drill densities and percent cover of Pacific oysters, barnacles, and mussels.

## RESULTS

#### Drill Abundance and Distribution

Distribution and abundance of oyster drills were determined at 30 sites spanning four habitat types (Pacific oyster reefs,

aquaculture, open mud, cultch pile) in Willapa Bay between 2001 and 2006 (Table 1). There were 23 quadrats per site on average (range 3–101). At some sites, we did not sample in quadrats but rather counted all drills encountered in a given time (mean 2.8 person-hours, range 0.3–6, Table 2). Both methods (quadrats and CPUE) were applied at six sites. Overall, drills were entirely absent from the northeast and southeast corners of Willapa Bay (Fig. 1). We also rarely encountered them on open tideflats in the absence of any hard structure such as shell: Japanese drill density (mean  $\pm$  SD) was  $0.11 \pm 0.11 \text{ m}^{-2}$  ( $n = 4$ ), and the eastern drill was not found on bare tideflat at either of two sites within its broader range. Both drill species co-occurred in the midlatitude region (north Long Island to Peterson Station) in similar proportions, eastern drills represented 57% of drills at these sites on average (range 35–55%,  $n = 5$ ). From this region of overlap, the range of Japanese drills extended to the north and eastern drills to the south.

Within the range occupied by Japanese drills, their density was nearly an order of magnitude higher in Pacific oyster reefs ( $18.2 \text{ m}^{-2}$ , SE = 7.2,  $n = 5$ ) than in aquaculture beds ( $2.0 \text{ m}^{-2}$ , SE = 0.7,  $n = 4$ ). Despite different densities, catch per unit effort of Japanese drills was similar in the two habitat types (reefs: 46 person-hr<sup>-1</sup>, SE = 20,  $n = 5$ ; aquaculture: 53 person-hr<sup>-1</sup>, SE = 29,  $n = 4$ ). Japanese drills became significantly larger with latitude (linear regression of shell length on latitude:  $F_{1,10} = 9.95$ ,  $P = 0.01$ ). Mean shell length was  $\sim 20$  mm at the southern end of the range in Willapa Bay and  $\sim 30$  mm at the northern end.

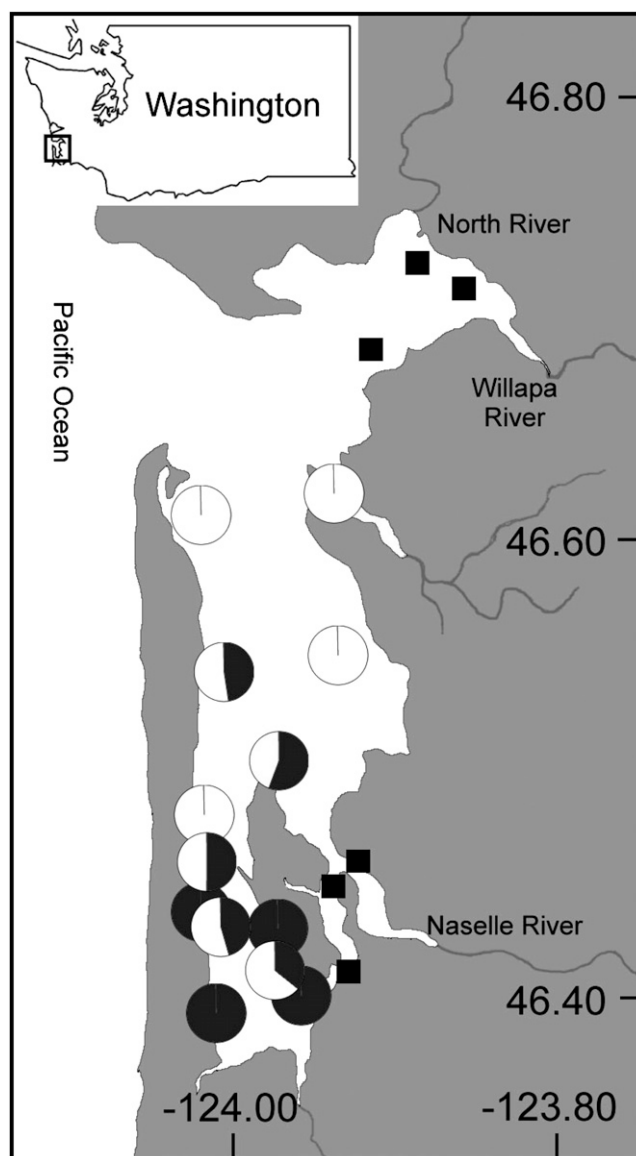
Because eastern drills occur primarily in south Willapa Bay, they have little overlap with aquaculture, which is concentrated in the north. Consequently, for this species, our results emphasize its distribution in hummocks. Mean density was  $26.2 \text{ m}^{-2}$  (SE = 14.8,  $n = 3$ ) and CPUE was 36 person-hr<sup>-1</sup> (SD = 12,  $n = 8$ ). Eastern drill size showed no latitudinal trend ( $F_{1,9} = 1.41$ ,  $P = 0.27$ ) but was relatively small (22 mm mean shell length) compared with Japanese drills.

#### Drill Feeding Rates and Preferences

Feeding rates of Japanese and Eastern drills on juvenile Pacific oysters were similar (Japanese drills: mean  $2.0 \text{ wk}^{-1}$ , SE = 0.2,  $n = 20$ , eastern drills: mean  $1.7 \text{ wk}^{-1}$ , SE = 0.1,  $n = 8$ ). There was no statistically significant difference between species or across drill size (Fig. 2; species  $F_{1,25} = 0.09$ ,  $P = 0.76$ ; size  $F_{1,25} = 0.42$ ,  $P = 0.5$ ).

Small oysters were clearly preferred over larger individuals. When Japanese drills were offered a range of sizes of Pacific oysters over 5 wk, drilled oysters had an average shell length of 28 mm, whereas undrilled individuals averaged 37 mm. Similarly, Eastern drills drilled oysters of an average shell length of 22 mm versus 38 mm left undrilled. These size differences were highly significant in a paired *t*-test ( $t = 5.15$ ,  $df = 23$ ,  $P < 0.0001$ ) and did not differ between species ( $F_{1,23} = 3.0$ ,  $P = 0.1$ ).

Concerns have been raised that the smaller size of native oysters relative to introduced Pacific oysters would make natives more susceptible to drill predation. However, our feeding trials involving oysters of comparable size indicated that drills preferred Pacifics over natives. In trials with larger (50 mm) oysters, Japanese drills consumed 8 of 18 Pacific oysters and just 1 of 17 Olympia oysters. Eastern drills showed a similar trend (2 of 8 Pacifics, 0 of 8 Olympias). Contingency table analysis showed a significant difference between oyster species

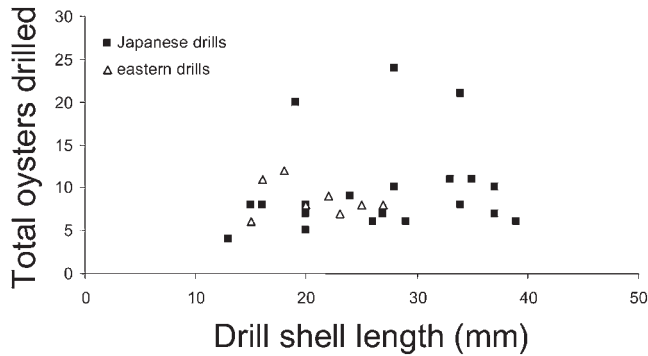


**Figure 1.** Distribution of two introduced oyster drills in Willapa Bay, WA. Centers of pie charts approximate locations of samples and show proportion of eastern (dark grey) and Japanese drills (white). Black squares indicate areas where no drills were found. All samples came from oyster hummocks or on-bottom aquaculture, and some similar nearby sites are not shown to reduce overlap in pie charts.

( $\chi^2 = 10.8$ ,  $P = 0.001$ ) but not between drill species ( $\chi^2 = 1.3$ ,  $P = 0.25$ ). In trials with juvenile oysters, 12 of 19 Japanese drills fed only on Pacific oysters, and most other individuals preferred this species, generating an average preference (Manly's  $\alpha$ ) of 0.87 (SE = 0.07,  $n = 19$ ). Similarly, 5 of 8 Eastern drills fed only on Pacific oysters, and Manly's  $\alpha$  averaged 0.82 (SE = 0.11,  $n = 8$ ). Among all individuals tested, only one Japanese drill fed exclusively on native oysters over  $\sim 4$  wk.

#### Direct and Indirect Effects—Enclosure Experiment

Predation by Japanese drills reduced the overall survival of Olympia oysters (mean and SE without drills,  $0.89 \pm 0.02$ ; with drills,  $0.83 \pm 0.02$ ) and Pacific oysters (without drills,  $0.83 \pm 0.03$ ;

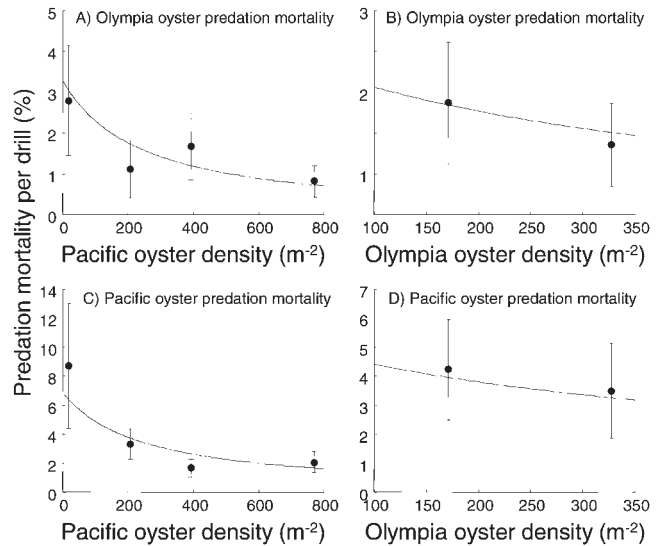


**Figure 2.** Number of juvenile oysters drilled by individual drills over 5 wk (May 21 to June 28, 2002) in feeding trials.

with drills,  $0.76 \pm 0.03$ ). When drills were present, they killed on average  $0.33$  ( $SE = 0.08$ ) Pacific oysters per drill per wk and  $0.16$  ( $SE = 0.04$ ) Olympia oysters per drill per wk. The *per capita* effect of drills on oyster survival was not constant, but rather depended on prey density. For example, as Pacific oyster density increased, the *per capita* effect (i.e., the mean percent mortality per drill) on Pacific and Olympia oysters declined hyperbolically (Fig. 3A, C). Increasing Olympia oyster density also diminished the *per capita* effect of drills on both oyster species, albeit more weakly (Fig. 3B, D). This decline in predator *per capita* effect with increasing prey density, and the resulting indirect facilitation between prey species, is indicative of a saturating functional response. Indeed, the predator-prey model with the strongest support from the data (lowest  $AIC_c$  value) included a type II functional response (Table 3). In every pairwise comparison between models that differed only in the functional response, the difference in  $AIC_c$  between the type I and type II models was  $>7$ , representing strong evidence in favor of the type II model (Burnham & Anderson 2002). The estimated prey handling times were 9.8 d for Pacific oysters and 10.3 d for Olympia oysters. The data indicated that Japanese drills preferred Pacific oysters as prey (Manly's  $\alpha = 0.69$ ,  $SE = 0.06$ ). The estimate of  $\alpha$  is fairly precise despite the fact that bootstrapped estimates of the attack rate parameters themselves were highly variable. The uncertainty in attack rates was probably because of the scarcity of experimental treatments in the range of low oyster densities where the drill functional response curve changes most rapidly (see Fig. 3).

Interspecific competition reduced Olympia oyster survival. The  $AIC_c$ -selected best model included an effect of Pacific oyster density on the mortality rate of Olympia oysters unrelated to predation (Table 3). The data overwhelmingly favored models that included this effect over those that did not ( $AIC_c$  differences  $> 35$ ). The effect of competition was also visible in Olympia oyster growth. Mean relative growth rate declined significantly as Pacific oyster density increased ( $F_{1,39} = 20.7$ ,  $P < 0.0001$ ,  $R^2 = 0.35$ ; Fig. 4). Because of interspecific competition, overall Olympia oyster survival was negatively related to Pacific oyster density in the absence of drills (Fig. 5). When drills were present, however, Olympia oyster survival initially improved slightly with increasing Pacific oyster density because of indirect facilitation (i.e., shared predation risk) before declining because of competition (Fig. 5).

Competition between the two oyster species was asymmetric; there was essentially no evidence that Olympia oysters affected



**Figure 3.** The effect of prey density on the *per capita* impact of Japanese drills (i.e., mean prey mortality rate per drill  $\pm 1$  SE) in a field enclosure experiment. Panels show diminishing *per capita* impacts on Olympia and Pacific oysters as Pacific oyster density (A, C) or Olympia oyster density (B, D) increases. Curves represent fitted values from the most strongly supported predator-prey model with parameters estimated from the entire oyster fate dataset.

Pacific oyster mortality. Although the model with the lowest  $AIC_c$  included both interspecific competition coefficients, this model differed negligibly ( $\Delta AIC_c = 0.7$ ) from a more parsimonious model that omitted the effect of Olympia oysters on Pacific oysters (Table 3). Likewise, there was no effect of Pacific or Olympia oyster density on Pacific oyster relative growth rate ( $P > 0.79$ ). The data also consistently failed to support intraspecific density-dependence in either oyster species (Table 3).

Over the course of the experiment, 55% of the experimental drills died or disappeared from the enclosures. As a result, too few of the initially marked individuals survived to permit an analysis of drill growth rates. At least 13 of the 15 dead drills that were recovered showed evidence of crab predation (cracked or chipped shells), and juvenile dungeness crab (*Cancer productus*) were occasionally found in the enclosures. Drills were never observed climbing enclosure walls.

#### Drill Impacts in the Field—Olympia Oyster Transplants

Drill predation on transplanted Olympia oysters was low on average but highly variable; only 7 of the 28 transplant stations had drilled oysters, but at these stations up to 33% of individuals were drilled. The overall mean mortality caused by drill predation was 4.0%. Predation did not differ detectably across habitat types (Kruskal-Wallis ANOVA,  $H = 1.07$ ,  $df = 2$ ,  $P = 0.59$ ) and was not significantly correlated with drill density (Spearman rank correlation,  $r_s = 0.16$ ,  $P = 0.40$ ). Total density of both drill species differed significantly among habitat types (Kruskal-Wallis ANOVA, ( $H = 19.5$ ,  $df = 2$ ,  $P = 0.0001$ ), with the highest densities in Pacific oyster reefs (mean and SE,  $33.6 \pm 16.6$   $m^{-2}$ ), followed by aquaculture beds ( $4.5 \pm 2.4$   $m^{-2}$ ) and open mud ( $0.0 \pm 0.0$   $m^{-2}$ ). Although no drills were observed at transplant stations in open mud, up to 32% of Olympia oysters at these stations were drilled, suggesting that drills

**TABLE 2.**  
**Distribution and abundance of Japanese and eastern oyster drills sampled by catch per unit effort (person-hrs searching) in Willapa Bay, organized by habitat from north to south.**

Site	Lat/ Long	Date	Effort (person-hrs)	CPUE (person-hr <sup>-1</sup> )		Mean (max) Shell Length (mm)	
				Japanese	Eastern	Japanese	Eastern
<b>AQUACULTURE</b>							
Stony Pt	46.69 123.925	4/1/02	3	0	0		
Stackpole	46.6 124.0	5/11/02	6	135.7	0	33.9 (56.0)	
Bay Center	46.633 123.942	5/1/02	6	52.2	0	32.4 (49.0)	
Nemah-Anderson		8/21/02	1	5	0		
Oysterville	46.538 124.014	7/14/02	0.5	20.0	18.0	26.5 (36.0)	21.4 (25.0)
<b>PACIFIC OYSTER REEFS</b>							
North River	46.72 123.89	4/1/02	3	0	0		
Willapa River	46.71 123.86	4/1/02	0.3	0	0		
Nemah	46.54 123.94	7/14/02	6	41.3	0	20.8 (35.0)	
Long I N Diamond	46.515 123.99	4/29/02	3	12.3	15.3	24.7 (44.0)	21.2 (25.0)
Mid Sands	46.479 124.018	7/9/02	1.5	125.3	0	20.5 (34.0)	
Peterson St house	46.439 124.01	8/23/02	2	0	107.0		22.7 (36.0)
Peterson	46.438 124.008	7/13/02	6	27.2	11.5	20.8 (33.0)	19.4 (27.0)
Smoky Hollow	46.43 123.98	5/02	2	0	51.0		23 (29.0)
Shoalwater NE	46.414 123.992	4/28/02	1	25.0	14.0	21 (35.0)	21.8 (24.0)
Shoalwater	46.406 123.987	4/28/02	1	0	15.0		22.5 (29.0)
Tarlatt	46.408 124.023	6/29/02	2	0	56.5		22 (29.0)
<b>CULTCH</b>							
Port	46.505 124.023	2/15/03	4	41.0	0.25	28.6 (40.2)	

aggregated to prey patches, fed, and dispersed. The mean mortality from sources other than drill predation was 16.9% and did not differ significantly across habitats (Kruskal-Wallis ANOVA,  $H = 0.85$ ,  $df = 2$ ,  $P = 0.65$ ). Habitat type also did not significantly affect the mean relative growth rate of transplanted oysters (Kruskal-Wallis ANOVA,  $H = 1.43$ ,  $df = 2$ ,  $P = 0.49$ ).

**DISCUSSION**

Our results illustrate the potential impact of invasive oyster drills on threatened native *Olympia* oysters in Willapa Bay.

Both Japanese and eastern drills readily consume *Olympia* oysters, and drills are widely distributed and abundant in intertidal habitats where *Olympias* historically occurred. Drill impacts are variable, however, and our results show that the three basic components of impact—distribution, local density, and per capita effect (Parker et al. 1999)—are modified by Pacific oysters, a dominant nonnative ecosystem engineer and the major aquaculture species in this estuary.

Natural dispersal of drills is limited, so spatial spread within Willapa Bay is largely the result of transfers of oysters and shell by growers. However, the complementary distribution of the

**TABLE 3.**  
**Predator-prey models for enclosure experiment data, ranked by AIC<sub>c</sub>. Interspecific competition includes the effect of Pacific oyster density on *Olympia* oyster survival (P → O) and the reverse (O → P). Models with intraspecific density-dependence in only one oyster species are not shown, as intraspecific competition was not supported by the data.**

Functional Response	Competition		No. parameters	-2L	ΔAIC <sub>c</sub>
	Intraspecific	Interspecific			
Type II	no	O → P, P → O	8	2,804.80	0.00
Type II	no	P → O	7	2,807.70	0.70
Type II	yes	O → P, P → O	10	2,804.80	4.20
Type I	no	O → P, P → O	6	2,816.50	7.40
Type I	no	P → O	5	2,819.30	8.10
Type I	yes	O → P, P → O	8	2,816.50	11.60
Type II	no	O → P	7	2,842.10	35.10
Type II	no	no	6	2,845.20	36.10
Type II	yes	no	8	2,845.20	40.30
Type I	no	O → P	5	2,853.70	42.50
Type I	no	no	4	2,856.80	43.50
Type I	yes	no	6	2,856.60	47.50

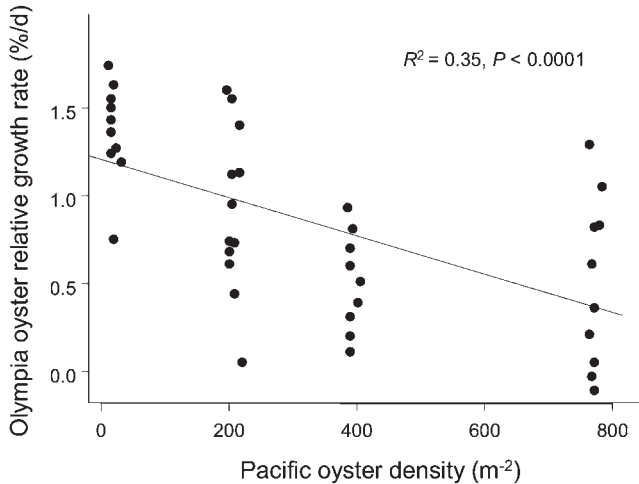


Figure 4. The effect of Pacific oyster density on Olympia oyster relative growth rate. Each point is the mean relative growth rate of measured oysters in a single enclosure. Least squares regression line is shown.

two drill species (Japanese drills relatively more abundant in the north, eastern drills in the south) suggests that local invasion success depends on abiotic or biotic limiting factors. These might include salinity (both species are absent from the northeast and southeast corners of the bay, close to major riverine inputs; Chapman & Banner 1949), temperature (*U. cinerea* is restricted to the warmer head of the estuary), interspecific competition, or predation. Drill mortalities observed in our field enclosures, as well as the results of a tethering study (unpublished data), suggest substantial rates of crab (*Cancer* spp.) predation on drills. Crab predation might present biotic resistance (Levine et al. 2004) to drill invasion, potentially limiting bathymetric distribution and local abundance.

Local drill densities were also affected by Pacific oysters. Both drill species were most abundant in naturally formed

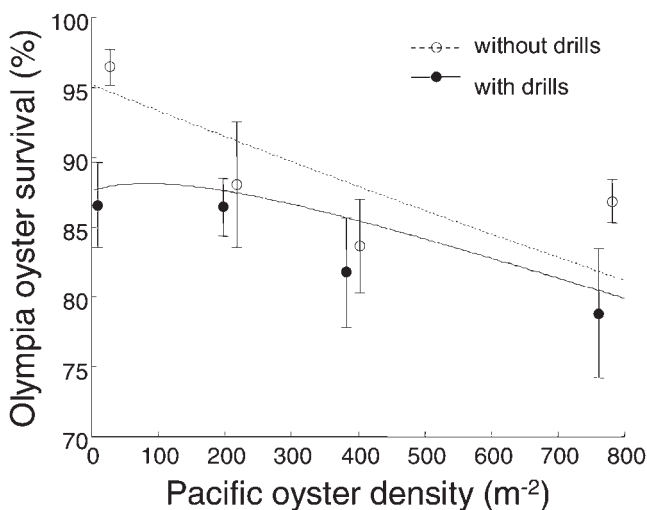


Figure 5. The net effects of Pacific oyster density and Japanese drill predation on Olympia oyster survival (mean  $\pm$  1 SE) in a field enclosure experiment. Curves represent fitted values from the most strongly supported predator-prey model with parameters estimated from the entire oyster fate dataset.

Pacific oyster reefs, followed by cultivated oyster beds and finally open areas without hard substrate. Pacific oysters likely benefit drills by providing complex habitats that offer a refuge from predation, as well as an abundant food resource. The disparity in drill density between reefs and aquaculture beds might reflect the greater abundance of juvenile oysters and other prey items such as barnacles on reefs, the more complex three-dimensional habitat structure of reefs, the relatively frequent disturbance of aquaculture beds by harvest and deliberate drill control efforts, or some combination of these factors.

*Per capita* effects of drills on native oysters varied with prey abundance and size structure. Both drill species preferentially attacked Pacific oysters rather than Olympia oysters of similar size, with a ratio of 2:1–7:1 for Japanese drills in feeding trials and field enclosures, and 5:1 for eastern drills in feeding trials. Because Japanese drills are sympatric with Pacific oysters in their native range but eastern drills are not, this preference likely reflects learned specialization for the dominant prey type in the system rather than adaptive coevolution. Indeed, ingestive conditioning, or an effect of diet history on prey preference, has been demonstrated in several muricid gastropods, including *U. cinerea* (Wood 1968, Murdoch 1969, West 1986, Wieters & Navarrete 1998). Drills selected smaller oysters of both species, which is consistent with the general importance of shell thickness in determining muricid prey preferences (Hughes & Dunkin 1984, Chew 1960). Over the life cycle, this may confer an advantage to Pacific oysters, which can escape in size from drill predation, whereas even large adult Olympia oysters remain vulnerable. The effect of prey size may also help to reconcile our results with those of Chew (1960), who reported that *O. inornata* from Puget Sound preferred smaller ( $\sim$ 35 mm) Olympia oysters to larger ( $\sim$ 55 mm) Pacific oysters. Alternatively, drills collected from Puget Sound might have encountered Olympia oysters more frequently than Pacifics.

The effects of prey density on drill per capita impacts are mediated by drills' strongly nonlinear functional response. We found that the functional response of Japanese drills saturates rapidly over a range of fairly low densities ( $<200 \text{ m}^{-2}$ ) of juvenile Pacific and Olympia oysters. This rapid saturation is caused by the long estimated handling times, on the order of 10 d for both prey species. Type II functional responses have been found for other muricids (Murdoch 1969), including *U. cinerea* (Katz 1985). A type II functional response leads to inversely density-dependent (depensatory) mortality in the prey because the per capita risk of predation declines as increasing prey density swamps the predator's ability to feed more rapidly. This destabilizing density-dependence can cause local extirpation of low-density prey patches unless recruitment is high enough to balance mortality from predation (Katz 1985, Seitz et al. 2001, Gascoigne & Lipcius 2004). In fact, Sinclair et al. (1998) argued that depensatory consumption by introduced generalist predators could drive rare native prey species extinct or prevent their escape from a persistent low-density state. This scenario could apply to Olympia oysters in Willapa Bay faced with nonnative drills that reach high densities supported by Pacific oysters, an abundant nonnative prey resource. However, another consequence of drills' type II functional response is indirect facilitation between prey species (Abrams & Matsuda 1996), an interaction modification (Wootton 2002) that arises when predator numbers are limited by some factor other than prey density. This indirect facilitation appeared as a diminishing per capita effect of



Japanese drills on Olympia oyster survival with increasing Pacific oyster density (Fig. 3) in our enclosure experiment where drill density was fixed. It is not known how drills respond numerically to changes in prey abundance; a strong numerical response would lead to a negative indirect effect of Pacific oysters on Olympia oysters (apparent competition; Holt & Lawton 1994, Noonburg & Byers 2005), which could outweigh the positive indirect effect mediated by the functional response.

In sum, the net impact of invasive drills and Pacific oysters on Olympia oysters in intertidal habitats depends on (1) geographic and bathymetric distributional overlap, (2) local drill abundance, (3) the numerical response of drills to changes in Pacific oyster density (apparent competition), (4) the non-linearity of drill functional responses to alternative prey (indirect facilitation), and (5) competition from Pacific oysters for space or food. We detected asymmetric competition between Pacific and Olympia oysters in the enclosure experiment, which was strong enough to overwhelm the positive effect on survival *via* shared predation risk (Fig. 5). Although it is possible that cage artifacts created unnatural conditions of food limitation in this study, in another sense our demonstration of competition is extremely conservative: the two oyster species were not grown on the same substrate, and space competition strongly affects Olympia oyster survival (Trimble et al. 2009).

Do locally high drill densities and the predation impacts we measured in small-scale experiments translate into large impacts on Olympia oysters in the field? Some anecdotal evidence suggests that they do—Olympia oysters outplanted to three sites in the bay for research or restoration purposes have been decimated by Japanese drills (Stackpole), eastern drills (Long Island Slough), or both (Diamont Point on Long Island). Also, we have observed drilled Olympia oysters at one of the few sites (South Mill Channel) where adults can be found intertidally. However, predation rates in our transplant study were inconsistent, even in reef habitats where drills are generally abundant. This might reflect fine-scale patchiness in drill density (where predation did occur, up to 33% of oysters were drilled), high availability of alternative prey in reefs and aquaculture beds, or reduced foraging rates during late August to October as seen in our feeding trials. Transplanted oysters also experienced considerable nonpredatory mortality (up to 63% over 45 d);

although the cause is unknown, it suggests possible desiccation, temperature, or other abiotic stress.

Olympia oyster larvae recruit heavily into intertidal Pacific oyster reefs (Trimble et al. 2009), but very few survive to sizes detectable in field sampling. Many factors, including physiological stress, competition, and predation, likely contribute to this high mortality, but the overall consequence seems to be that reefs are sink habitats for native oysters. It is unlikely that any efforts to reduce drill predation could significantly improve survival on a relevant scale for management; controlling drills entails major ongoing labor costs, even in aquaculture areas where adults and egg capsules are relatively apparent (Buhle et al. 2005). Thus attempts to rebuild intertidal native oyster populations in the bay may be restricted to areas where drills and naturalized Pacific oysters do not occur.

Our results highlight the importance of understanding the factors that drive variation in the impact of particular invasive species across the landscape (Byers et al. 2002). Although variability in occurrence and local density are generally recognized, local differences in per capita effect may also play an important role. We found that per capita effects of invasive drills on native oysters varied nonlinearly with native oyster density and with the density of nonnative alternative prey. A combination of field observations, experiments, and models can help to identify these sources of variability and design effective monitoring, control, and restoration strategies.

#### ACKNOWLEDGMENTS

The authors thank the organizers of the 2006 West Coast Native Oyster Restoration Workshop for coordinating this Special Issue. Lee McCoy, Nehemiah Richardson, Jon Adler, Heather Tallis, Brice Semmens, and Geoff Hosack provided invaluable help with the field work. This research was supported by grant #NA16RG1044 from the National Oceanic and Atmospheric Administration to Washington Sea Grant Program, University of Washington, and by a National Science Foundation Graduate Research fellowship and an Achievement Rewards for College Scientists fellowship to ERB. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or its subagencies.

#### LITERATURE CITED

- Abrams, P. A. & H. Matsuda. 1996. Positive indirect effects between prey species that share predators. *Ecology* 77:610–616.
- Baker, P. 1995. Review of ecology and fishery of the Olympia oyster, *Ostrea lurida* with annotated bibliography. *J. Shellfish Res.* 14:501–518.
- Buhle, E. R., M. Margolis & J. L. Ruesink. 2005. Bang for buck: cost-effective control of invasive species with different life histories. *Ecol. Econ.* 52:355–366.
- Burnham, K. P. & D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. New York: Springer-Verlag. 488 pp.
- Byers, J. E., S. Reichard, J. M. Randall, I. M. Parker, C. S. Smith, W. M. Lonsdale, I. A. E. Atkinson, T. R. Seastedt, M. Williamson, E. Chornesky & D. Hayes. 2002. Directing research to reduce the impacts of nonindigenous species. *Conserv. Biol.* 16:630–640.
- Carlton, J. T. 1979. History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America. Ph.D. dissertation. University of California, Davis. 904 pp.
- Carlton, J. T. 1989. Man's role in changing the face of the ocean: biological invasions and implications for conservation of near-shore environments. *Conserv. Biol.* 3:265–273.
- Chapman, W. M. & A. H. Banner. 1949. Contributions to the life history of the Japanese oyster drill, *Tritonalia japonica*, with notes on other enemies of the Olympia oyster, *Ostrea lurida*. *Washington Dep. Fish. Biol. Rep.* 49A:168–200.
- Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. *Ecology* 64:1297–1304.
- Chew, K. K. 1960. Study of food preference and rate of feeding of Japanese oyster drill, *Ocenebra japonica* (Dunker). Special Scientific Report Fisheries 365. Washington, DC: United States Fish and Wildlife Service. 27 pp.
- Coan, E. V., P. V. Scott & F. R. Bernard. 2000. Bivalve seashells of western North America: marine bivalve mollusks from Arctic Alaska to Baja California. Santa Barbara, CA: Santa Barbara Museum of Natural History. 764 pp.

- Connell, J. H. 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. *Ecol. Monogr.* 40:49–78.
- Cook, A. E., J. A. Shaffer, B. R. Dumbauld & B. E. Kauffman. 2000. A plan for rebuilding stocks of Olympia oysters (*Ostreola conchaphila*, Carpenter 1857) in Washington State. *J. Shellfish Res.* 19:409–412.
- Crooks, J. A. 2002. Characterizing ecosystem-level consequences of biological invasions: The role of ecosystem engineers. *Oikos* 97:153–166.
- Gascoigne, J. C. & R. N. Lipcius. 2004. Allee effects driven by predation. *J. Appl. Ecol.* 41:801–810.
- Grosholz, E. 2002. Ecological and evolutionary consequences of coastal invasions. *Trends Ecol. Evol.* 17:22–27.
- Hilborn, R. & M. Mangel. 1997. The ecological detective. Princeton, NJ: Princeton University Press. 315 pp.
- Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Canadian Entomological Society* 45:1–60.
- Holt, R. D. & J. H. Lawton. 1994. The ecological consequences of shared natural enemies. *Annu. Rev. Ecol. Syst.* 25:495–520.
- Hughes, R. N. & S. D. Dunkin. 1984. Behavioural components of prey selection by dogwhelks, *Nucella lapillus* (L.) feeding on mussels, *Mytilus edulis* (L.), in the laboratory. *J. Exp. Mar. Biol. Ecol.* 77: 45–68.
- Katz, C. H. 1985. A nonequilibrium marine predator-prey interaction. *Ecology* 66:1426–1438.
- Krebs, C. J. 1999. Ecological methodology. Menlo Park, CA: Benjamin/Cummings. 620 pp.
- Levine, J. M., P. B. Adler & S. G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecol. Lett.* 7:975–989.
- MathWorks. 1999. MATLAB: the language of technical computing. Natick, MA: MathWorks.
- Murdoch, W. W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecol. Monogr.* 39:335–354.
- Murdoch, W. W. & A. Oaten. 1975. Predation and population stability. *Adv. Ecol. Res.* 9:1–131.
- Navarrete, S. A. & B. A. Menge. 1996. Keystone predation and interaction strength: Interactive effects of predators on their main prey. *Ecol. Monogr.* 66:409–429.
- Noonburg, E. G. & J. E. Byers. 2005. More harm than good: when invader vulnerability to predators enhances impact on native species. *Ecology* 86:2555–2560.
- Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva, M. H. Williamson, B. V. Holle, P. B. Moyle, J. E. Byers & L. Goldwasser. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biol. Invasions* 1:3–19.
- Sayce, C. S. 1976. The oyster industry of Willapa Bay. In: R. D. Andrews, III, editor. Proceedings of the symposium on terrestrial and aquatic ecological studies of the Northwest. Cheney, WA: Eastern Washington State College Press. pp. 347–356.
- Seitz, R. D., R. N. Lipcius, A. H. Hines & D. B. Eggleston. 2001. Density-dependent predation, habitat variation, and the persistence of marine bivalve prey. *Ecology* 82:2435–2451.
- Sinclair, A. R. E., R. P. Pech, C. R. Dickman, D. Hik, P. Mahon & A. E. Newsome. 1998. Predicting effects of predation on conservation of endangered prey. *Conserv. Biol.* 12:564–575.
- Trimble, A. C., J. L. Ruesink & B. R. Dumbauld. 2009. Factors preventing the recovery of a historically overexploited shellfish species. *J. Shellfish Res.* 28:97–106.
- West, L. 1986. Interindividual variation in prey selection by the snail *Nucella emarginata*. *Ecology* 67:798–809.
- Wieters, E. A. & S. A. Navarrete. 1998. Spatial variability in prey preferences of the intertidal whelks *Nucella canaliculata* and *Nucella emarginata*. *J. Exp. Mar. Biol. Ecol.* 222:133–148.
- Wood, L. 1968. Physiological and ecological aspects of prey selection by the marine gastropod *Urosalpinx cinerea* (Prosobranchia: Muricidae). *Malacologia* 6:267–320.
- Wootton, J. T. 2002. Indirect effects in complex ecosystems: Recent progress and future challenges. *J. Sea Res.* 48:157–172.