Ecology, 86(2), 2005, pp. 487–500

MARINE RESERVES ENHANCE ABUNDANCE BUT NOT COMPETITIVE IMPACTS OF A HARVESTED NONINDIGENOUS SPECIES

JAMES E. BYERS[1]

Friday Harbor Laboratories, University of Washington, 620 University Road, Friday Harbor, Washington 98250 USA

Abstract. Marine reserves are being increasingly used to protect exploited marine species. However, blanket protection of species within a reserve may shelter nonindigenous species that are normally affected by harvesting, intensifying their impacts on native species. I studied a system of marine reserves in the San Juan Islands, Washington, USA, to examine the extent to which marine reserves are invaded by nonindigenous species and the consequences of these invasions on native species. I surveyed three reserves and eight non-reserves to quantify the abundance of intertidal suspension-feeding clam species, three of which are regionally widespread nonindigenous species (*Nuttallia obscurata*, *Mya arenaria*, and *Venerupis philippinarum*). Neither total nonindigenous nor native species' abundance was significantly greater on reserves. However, the most heavily harvested species, *V. philippinarum*, was significantly more abundant on reserves, with the three reserves ranking highest in *Venerupis* biomass of all 11 sites. In contrast, a similar, harvested native species (*Protothaca staminea*) did not differ between reserves and non-reserves.

I followed these surveys with a year-long field experiment replicated at six sites (the three reserves and three of the surveyed non-reserve sites). The experiment examined the effects of high *Venerupis* densities on mortality, growth, and fecundity of the confamilial *Protothaca*, and whether differences in predator abundance mitigate density-dependent effects. Even at densities 50% higher than measured in the field survey, *Venerupis* had no direct effect on itself or *Protothaca*; only site, predator exposure, and their interaction had significant effects. Analyses incorporating environmental variables tracked at each site indicated that crab biomass most heavily influenced clam responses, causing lower growth of both species and higher mortality of *Venerupis*, whose annualized loss rate was 50% when exposed to predators. A laboratory prey choice experiment indicated that *Cancer productus*, an influential intertidal crab predator, favored small adult *Venerupis* at least 1.7 times over *Protothaca*. *Venerupis*' high susceptibility to excavating crab and human predators, as well as its faster growth compared to *Protothaca* can be explained by its shallower burial depth. By growing quickly and residing near the surface, *Venerupis* apparently absorbs the brunt of harvest pressure while *Protothaca* maintains high biomass even outside of reserves.

Key words: *apparent competition; clams; exotic species; fisheries; marine protected areas; mixed effects models;* Nuttallia obscurata; Protothaca staminea; *San Juan Islands, Washington (USA); spatially replicated experiments;* Tapes japonica; Venerupis philippinarum.

INTRODUCTION

Marine reserves, or marine protected areas, have emerged as a prominent conservation tool to protect exploited marine species (Ballantine 1991, Lauck et al. 1998, Murray et al. 1999, Wilder et al. 1999). These reserves are intended to provide a refuge that both protects a minimum number of individuals of a species, and also maximizes the potential that the species' propagules can disperse and replenish other unprotected areas. While marine reserves are often established with a principal goal of protecting or restoring one or a handful of target fishery species, comprehensive prevention of harvesting by humans affects nontarget species as well (Edgar and Barrett 1999). Effects on nontarget species could be both direct, through reduction of mortality due to bycatch or destructive harvesting techniques (e.g., bottom trawling), and indirect, through alterations of ecological interactions due to recovery of target (often predatory) species (Babcock et al. 1999, Eisenhardt 2001).

One seldom explored, yet potentially important change in nontarget species is the proliferation of nonindigenous species and their subsequent impact on native species within marine reserves. In combination with habitat loss, interactions with nonindigenous species have been identified as the primary cause of endangerment of native species (Czech and Krausman 1997, Wilcove et al. 1998), and the number of marine invasions continues to increase each year (Carlton and Geller 1993, Lodge 1993, Cohen and Carlton 1998).

Manuscript received 2 September 2003; revised and accepted 9 July 2004. Corresponding Editor: J. R. Bence.

[1] Present address: Department of Zoology, University of New Hampshire, 46 College Road, Durham, New Hampshire 03824 USA. E-mail: jebyers@unh.edu

PLATE 1. Four of the numerically dominant clams surveyed in this study. Clockwise from bottom: *Nuttallia obscurata*, *Mya arenaria*, *Venerupis philippinarum*, and *Protothaca staminea*. *Protothaca* is the only clam of these that is native to the study region. For scale, mesh size is 1.25 cm. Photo credit: J. Byers.

While almost nothing is known about the extent of nonindigenous species in marine reserves, in terrestrial systems nonindigenous species are readily and increasingly found within reserve boundaries (Brockie et al. 1988, Loope et al. 1988, Macdonald and Frame 1988, Usher 1988, Smallwood 1994, Lonsdale 1999). To date, the focus of marine reserves has emphasized their design, placement, and enforcement (e.g., Francour et al. 2001, Shanks et al. 2003). However, if marine reserves protect nonindigenous species that are normally affected by harvesting, nonindigenous species could diminish benefits to native species that would otherwise accrue within reserves (Simberloff 2000). Particularly if nonindigenous species strongly affect natives, merely setting aside protected areas may be an insufficient strategy to bolster populations of native marine species. Rather, to safeguard native biota within reserves nonindigenous species may need to be controlled.

In this study I use a system of intertidal reserves in northern Puget Sound, Washington, USA to address the issue of nonindigenous species in marine reserves. Specifically I focus on nonindigenous clam species and the resultant impact of these species on native clams within and outside of reserves throughout the archipelago. I first explore the pattern of invasion through field surveys to address whether the abundance and biomass of nonindigenous clam species varies as a function of reserve/non-reserve status. Second, through field and laboratory experiments I explore potential mechanisms of impact of one of the heavily harvested nonindigenous clams, *Venerupis philippinarum*. Specifically, I address (1) whether protecting clams or clam predators from removal on reserves differentially benefits the nonindigenous clam species, and (2) whether a reduction in predation intensifies competitive impacts of the nonindigenous clam on natives. In sum, this investigation informs whether blanket protection of species within a reserve may increase nonindigenous species and their subsequent impacts on natives.

Study system

Since 1990 the University of Washington and the Washington Department of Fish and Wildlife have jointly overseen a small system of intertidal and shallow subtidal marine reserves in the San Juan Islands of northern Puget Sound (Tuya et al. 2000). Within the reserves fishing and collections of marine organisms are prohibited, except for herring and salmon and except for scientific purposes as permitted by the director of the Friday Harbor Laboratories, University of Washington. Also in the San Juan Islands, the National Park Service oversees British Camp Historical Site that includes an area (BCC) that has been closed to shellfishing since ~1977.

Three nonindigenous suspension-feeding clam species, *Nuttallia obscurata*, *Mya arenaria*, and *Venerupis philippinarum*, have become abundant and widespread throughout large regions of the western coast of Canada and the United States, including the San Juan Islands (Carlton 1979, Haderlie and Abbott 1980, Kozloff 1996, Byers 2002; see Plate 1). All three prefer partly sandy, low wave energy environments. *Nuttallia obscurata*, the purple varnish clam, is native to northern Asia (Japan and Korea) and was first recorded in the northeastern Pacific in 1991 (Forsyth 1993; C. E. Mills, *unpublished*), most likely introduced via shipping ballast water (Coan et al. 2000). *N. obscurata* is commonly found buried 8–10 cm deep (and up to 20–25 cm deep) and usually inhabits sandy sediments in the high intertidal (Byers 2002). *Mya arenaria*, native to the Atlantic coast of North America, was introduced accidentally in imported seed oysters in the late 1800s to the Pacific coast of North America, and was subsequently spread intentionally for human consumption (Carlton 1979, 1992). *Venerupis philippinarum* (=*Paphia philippinarum*, =*Protothaca philippinarum* =*Venerupis japonica*, =*Venerupis semidecussata*, =*Ruditapes philippinarum*, =*Tapes japonica*, =*Tapes semidecussata*), the Japanese littleneck clam, was accidentally introduced to the eastern Pacific in the 1930s with imported oyster seed from Japan and is now found from British Columbia to southern California (Quayle 1941, Haderlie and Abbott 1980). It is the most prolific of these introduced clam species in the San Juan Islands and accounts for 50% of the annual commercial landings of hard-shell clams in Washington (*available online*).[2] The species is also cultivated within intertidal beds at several aquaculture facilities throughout the state.

Several native clam species inhabit this region and most of the Pacific coast of North America and were common in my surveys. *Macoma nasuta* and *M. in-*

[2] ⟨http://wdfw.wa.gov/fish/shelfish/beachreg/1clam.htm#manila⟩

quinata are capable of both suspension and deposit feeding and often associated with sheltered bays and a variety of sediment types. *Clinocardium nuttallii*, *Saxidomis giganteus*, *Tresus capax*, and *T. nuttalli* are larger, deeper dwelling bivalves associated with sand or mud sediments. Finally, *Protothaca staminea* is a common, harvested clam that was particularly prominent in this study (Appendix A).

The clams' longevity (5–10 years) provides a demographic buffer to temporal fluctuations in abundance and helps isolate the effect of reserves using even a single sample in time. Not only are these clams common, tractable species, but bivalves in general can compete strongly (Peterson 1982, Weinberg 1998, Talman and Keough 2001). In particular, the nonindigenous *Venerupis* shares a number of life history and ecological attributes with the native confamilial species, *Protothaca staminea* (Family: Veneridae), and thus may be especially likely to compete with it for resources. Both are suspension-feeding species that occupy similar sediment types and intertidal height. Importantly, *Venerupis* is popular with human clammers, potentially indicating that its abundance and resultant impact on native species may differ substantially inside and outside protected areas. Also, other clam predators [e.g., Dungeness crab (*Cancer magister*); red rock crabs (*Cancer productus*); starry flounder (*Platichthys stellatus*); rock, sand, and English sole (*Lepidopsetta bilineata*, *Psettichthys melanostictus*, *Parophrys vetulus*); and pile perch (*Rhacochilus vacca*)], which may prey differentially on the clam species, likely vary in abundance between protected and non-protected areas. I examine in detail whether reserve attributes (increased clam and clam predator abundance resulting from harvest restrictions) affect the competitive influence of nonindigenous *Venerupis* on the native *Protothaca*.

Methods

Field survey

In June 2000, I surveyed 11 soft-sediment intertidal sites (three reserves, eight non-reserves) that were selected on the basis of suitable sediment characteristics, limited wave exposure, and a minimum combined *Protothaca* and *Venerupis* density of 16 individuals/m^2 (Fig. 1). This latter biological criterion directly ensured the selected reserve and non-reserve sites were suitable habitat for these focal species. The San Juan archipelago is dominated by rocky shores, so I was able to initially spot check essentially all intertidal soft-sediment areas. The formally surveyed sites represent all that met the selection criteria. With the exception of harvest restrictions, reserve and non-reserve sites were otherwise similar. Measurements of environmental variables at many of the sites (see *Methods: Quantifying site-level physical and biological covariates*) confirmed that while harvest-influenced variables (e.g., crab abundance) differed between reserves and non-reserves, general physical variables (e.g., chlorophyll, salinity, temperature) were similar. Based on the area of each site, I sampled 7–11 replicate cores (0.125-m^2 metal cylinders 18 cm deep) spaced at haphazard intervals at 0.5 and 1.0 m above mean lower low water tidal elevation (MLLW; U.S. datum MLLW = 0 m). This replication was sufficient to characterize clam density at a site because after only 4–6 replicates, the mean density and its variance had always leveled off to within a few percent of their final values. All clams were sieved from cores through a 5-mm mesh, identified to species, and measured for length (maximum from anterior to posterior edge of shell) and height (from the umbo to the ventral margin).

I determined empirical relationships between shell measures (length and height) and dry masses of tissue and shell. The strongest relationships were used to estimate biomass (r^2 values all >0.95) from at least 25 total individuals of each common species collected from several surveyed sites. I then used these relationships to calculate the biomass of the field-surveyed clams. The biomass of rare species ($<1\%$ of clams surveyed) was approximated using relationships derived for morphologically similar common clam species.

I evaluated variation in average core biomass between reserves and non-reserves for both native and nonindigenous clams using *t* tests. Using biomass as a response variable more heavily weights older (and thus larger) individuals compared to density measurements. Thus, biomass naturally integrates reserve effects over longer time periods. Data were log-transformed [$x' = \ln(x)$ or $x' = \ln(x + 1)$] as needed to meet *t* test assumptions. For all *t* tests reported in this paper (biomass and other variables as well), equality of variances was tested using PROC TTEST (SAS Institute 1999). If variances between treatments were not equal, *t* tests with Welch-Satterthwaite approximations for unequal variance were used (Stewart-Oaten et al. 1992). If equal, then regular *t* tests on pooled variances were reported.

Because of particularly high nonindigenous biomass at one reserve site, the effect of reserves on nonindigenous biomass was also analyzed with a nonparametric Mann-Whitney test. Additionally, I analyzed separately the density and biomass of the native *Protothaca* and the nonindigenous *Venerupis* (both species are the most commonly harvested species in their category) as a function of reserve status. As further evidence of the degree to which nonindigenous clam patterns were driven by *Venerupis*, I performed a *t* test on the combined biomass of the two nonindigenous clams besides *Venerupis* (i.e., *Nuttallia* and *Mya*) as a function of reserve status. Finally, to calculate whether reserves differentially affected the demography of *Venerupis* and *Protothaca*, I examined with a *t* test the average difference in the size (length) of the clam species between reserve and non-reserve sites that had at least

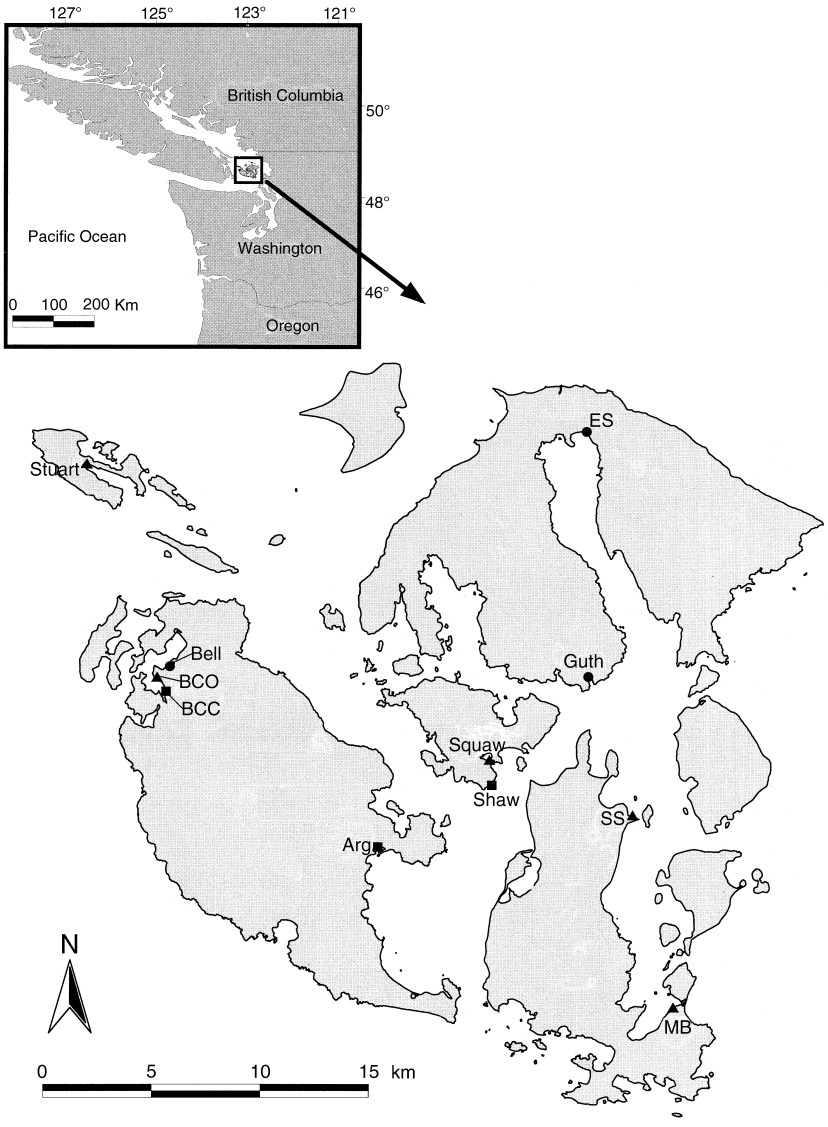

FIG. 1. Map of survey and experimental sites in the San Juan Islands, Washington, USA. Non-reserve (solid circles) and reserve sites (solid squares) were used in both the survey and the field experiment. Two of the reserve sites (Argyle and Shaw) are under University of Washington jurisdiction; the third (British Camp Closed) is overseen by the National Park Service. Additional non-reserve sites used in the field survey are depicted as solid triangles. Abbreviations for the sites are: Arg, Argyle Creek; BCC, British Camp Closed; BCO, British Camp Open; Bell, Bell Point; ES, Eastsound; Guth, Guthrie Cove; MB, Mud Bay; Shaw, Shaw Island Preserve; SS, Spenser Spit; Squaw, Squaw Bay; Stuart, Stuart Island State Park.

10 clams of each species (three reserves and four non-reserve sites).

Experimental investigation of nonindigenous clam impacts

Experimental setup.—Marine reserves may influence the abundance and size of potential competitors, particularly the often-harvested, nonindigenous *Venerupis philippinarum*, as well as clam predators. Therefore, to simulate reserve and non-reserve attributes at each experimental site, I manipulated *Venerupis* density and predator exposure in an orthogonal design to quantify their effects on the mortality, growth, and fecundity of *Protothaca*. I used the three intertidal reserves (Argyle, BCC, Shaw) and three non-reserve control sites (ES, Bell, Guth). The three non-reserve sites were selected haphazardly from the original eight surveyed areas, with emphasis placed on sites where I could best safeguard the experiment over its duration. The site at Bell provided the added benefit of being adjacent to a reserve site. I collected all clams used in this experiment from the same site (Bell) to reduce the effects of potential genetic variability on outcomes. Both species have similar allometric relationships, so

I selected small adult clams from a size range of 36–40 mm in length (*Protothaca*, 38.2 ± 3.7 mm; *Venerupis*, 37.4 ± 2.2 mm, mean ± 1 SD).

In late July 2000 at the six sites I inserted hardware cloth enclosures (0.3×0.3 m = 0.09 m^2, 1.25-cm mesh size) 17 cm into the substrate so that they extended 1 cm above the sediment surface in a single line along a tidal height contour of ~0.8 m above MLLW. The depth of these enclosures extended well beyond typical maximum burial depths (~8 cm) for these species (Haderlie and Abbott 1980), thus serving to prevent lateral migration of the clams out of the experimental plot (Peterson and Andre 1980). Enclosure bottoms were composed of naturally occurring hard clay and lined with a few centimeters of cobble to further prevent clams from burrowing deeper (and potentially out of) the enclosed area. Prior to initiating the experiment I excavated and sieved the sediment within each enclosure to remove all clams >5 mm. The excavated sediment was filled back into the enclosure to within 5 cm of the surface, at which point 10 *Protothaca* and a specified number of *Venerupis* were added. I measured and marked all 10 *Protothaca* and 10 *Venerupis* (for nonzero *Venerupis* density treatments) before adding them. I then added and lightly packed the remaining sediment into the enclosure until it was flush with the surrounding ambient sediment. Clam predators (e.g., fish, crabs, and birds) were excluded from half the enclosures by completely covering them with hardware cloth tops (1.25-cm mesh).

Three densities of *Venerupis* (0, 10, 20 individuals per enclosure) were crossed with exposure to predators (presence or absence of enclosure tops) for a total of six treatments. These six treatments were replicated in three contiguous blocks within each of the six sites (18 enclosures per site). Blocks were used solely to ensure adequate interspersion of treatments. Enclosures were spaced 6–8 cm apart to enhance the homogeneity of environmental conditions between them. To reduce potential biases from predators foraging in open-topped enclosures and spilling over onto an adjacent open-topped enclosure, I systematically interspersed topped and topless treatments. Assignment of density treatments was randomized within each predator treatment within each block.

The density of 10 *Protothaca*/0.09 m^2 was chosen because, for the size of the clams used in the experiment, the biomass matched closely the average *Protothaca* biomass found in the field surveys in areas where it predominated. Also, having a minimum of 10 *Protothaca* per enclosure provided acceptable resolution for quantifying its mortality response. The levels of *Venerupis* density were chosen to bracket (and augment by 50%) the range of its biomass quantified in the field survey. Treatments containing no *Venerupis* simulated the maximum effect of clam reductions that can occur in harvested, non-reserve areas. Higher density treatments simulated the effect of potential population expansions where they are unchecked by either human or aquatic predators. *Venerupis* density was treated as a ''pulse'' manipulation (sensu Bender et al. 1984) to test if predation reduces and thus mitigates density-dependent competitive effects. Enclosures were cleaned every 2 wk for 10.5 mo (312 d) to keep the mesh free of fouling organisms, and I scoured the surrounding area for dead clams from the experiment. No substantive effects of enclosures on clam responses were observed (Appendix B).

Quantifying growth, fecundity, and burial depth.—I measured burial depths of each clam species at the end of the experiment. To complement these field measurements, more precise burial depths were measured with a ruler on 150 individuals (42–60 mm length) of both *Venerupis* and *Protothaca*, held in the laboratory for 10 d in running seawater tanks lined with 15 cm of sediment, and compared with a *t* test. In the field, clams were sieved from the enclosures, counted, measured, and frozen for later dissection. I measured the marked clams' final shell dimensions and dissected them to extract their somatic and gonadal tissue, which I dried for 9 h at 75°C to obtain a dry tissue mass following the methods of Peterson (1982).

At the beginning of the experiments, I had estimated initial dry tissue mass and dry gonad mass of each marked clam using empirically determined relationships between external shell measurements and dry tissue mass. These relationships were calculated by haphazardly selecting clams of both species over a range of sizes from the source collection (Bell), measuring their external shell dimensions, removing the tissue from the shells, drying the tissue for 9 h at 75°C, and weighing it. For *Protothaca* I regressed dry tissue mass against shell length (total tissue, $R^2 = 0.93$; gonad, $R^2 = 0.87$); for *Venerupis* I regressed dry tissue mass against shell height (total tissue, $R^2 = 0.82$; gonad, $R^2 = 0.67$). I calculated the change in total dry tissue mass (somatic and gonad) and change in gonadal dry tissue mass of each clam as: final dry tissue mass − estimated initial dry tissue mass. The change in gonad dry mass served as a proxy for a clam's investment in reproduction. Although change in dry tissue mass is a highly sensitive measure of growth, I also examined changes in other growth metrics (shell length, height, thickness, wet tissue mass, relative dry tissue mass [(final mass − initial mass)/initial], and total shell plus tissue dry mass) to ensure that species-specific differences in growth form or allocation between shell and tissue did not lead to any discrepancies in results that could alter conclusions drawn from dry tissue growth rates (Appendix C).

Growth of gonad and somatic dry tissue were highly correlated for each species (*Protothaca*, $R = 0.84$; *Venerupis*, $R = 0.96$). These strong correlations are consistent with the tight coupling of size and fecundity in venerid clams in general (Ansell 1967, Yap 1977, Pe-

terson 1986). Thus, statistical analyses of fecundity produced similar results to those I present for growth.

Quantifying mortality.—Mortality of clams was tallied periodically during the year when cracked shells were found during enclosure maintenance and thoroughly at the end of the experiment when enclosures were excavated. For experimental clams that were recovered with my identification markings I could typically discern the source of mortality, i.e., cracked shells = crab predation; empty valves intact and blackened = anoxia, disease, or starvation (although starvation is unlikely due to flexible physiology and development [Peterson 1982]). Clams that were unable to be recovered (mostly *Venerupis* from topless enclosures) were assumed dead. Biologically this is the most realistic assumption since the most likely explanation for a missing clam is that it was excavated and carried off by a predator. Since <1% of clams were missing from topped enclosures, the surface was the only feasible direction of escape, and clams that expose themselves by coming to the surface are highly vulnerable to predators (e.g., Smith et al. 1999, Seitz et al. 2001, Byers 2002). Mortality proportions for each species within each enclosure were Anscombe transformed to normalize their distributions for statistical analyses (Zar 1996). To explore differential effects of predator exposure on the two species, I regressed *Venerupis*' mortality against *Protothaca*'s mortality at each site for both topped and topless enclosures.

Quantifying site-level physical and biological covariates.—I quantified several environmental variables at each site throughout the experiment to use as site-level covariates in analyses. These physical and biological properties associated with each experimental site may influence clam responses directly, or through interactions with the predator and density treatments. These properties were measured approximately every two weeks during daytime low tides and conducted at all sites as concurrently as possible (typically within 48 hours). For use in analyses, averages and standard deviations (to reflect seasonal variability) were computed for each covariate at each site for the entire sampling period. I measured temperature and salinity using a thermometer and handheld refractometer. Potential bird predators (i.e., crows [*Corvus caurinus*], gulls [*Larus* sp.], and oystercatchers [*Haematopus bachmani*]) were quantified at each site along a transect band centered over the enclosures. I also quantified additional predator abundance (crabs), competitor biomass (ambient clams), and food availability (chlorophyll, sediment organic matter) at each site. Details on collection methods of these variables are presented in Appendix D.

Statistical analysis of field experiment.—As a preliminary step, mixed-effects ANOVAs were used to analyze clam growth and mortality responses due to the effects of *Venerupis* density and predator exposure (fixed factors) and site (random factor). These analyses demonstrated evidence for effects of predator exposure, site, and their interaction (Appendix E). Consequently, I analyzed the effect of density and predator exposure on the mortality and growth of each clam species while incorporating the physical and biological covariates measured at each site, using a mixed-effects linear model (SAS proc mixed, Kenward-Rogers degrees of freedom method). The mixed-effects model is useful to examine spatially replicated experiments by fitting a covariance structure to account for the correlation of data from a common cluster, i.e., site (SAS Institute 1999). Because experimental enclosures at each site experience the same environmental conditions, each replicate at a site should be treated as a repeated measure relative to the site-level covariates. Thus, a random intercept is fitted for each site, which causes observations within a site, even after adjusting for fixed effects, to be correlated (a variance components model). I treat these effects as random because I am not interested in the specific effect of site, but rather treat site as being randomly selected from all possible sites within the region. This process can thereby identify specific attributes of a site (environmental variables) that might underlie the significant effect of site on clam responses, while still allowing sites to differ due to other intrinsic variables.

The fixed factors predator exposure and density comprised the baseline model, and I first added the interaction of the two main factors into the baseline model. If the interaction was not significant, I proceeded to add each covariate (including interactions with main factors) one at a time into the baseline model. Because there were far more covariance parameters than sites (i.e., degrees of freedom), I used a combination of forward and backward stepwise selection processes (Cooper et al. 2002). I report all variables that were significant when entered alone into the original baseline model, but I emphasize the largest model where all included covariates and covariate interactions were significant. If no covariate or covariate interaction was significant, I retained the variable that resulted in the smaller P values of the fixed factors.

Finally, for a more detailed analysis of the effects of crab predators, the most influential covariate, I compared the average growth of each clam species as a function of crab biomass density at each site. Specifically, to examine how tactile cues or other sublethal effects of crabs (e.g., siphon nipping or withdrawal) might have influenced clam growth, for each clam species I regressed the difference in dry tissue growth in the topped and topless enclosures at each site against crab biomass.

Prey choice/susceptibility experiments

To examine in detail the extent to which differential predation by a major intertidal clam predator, the red rock crab (*Cancer productus*), contributes to observed patterns of native and nonindigenous species biomass observed in the field, I conducted a prey choice ex-

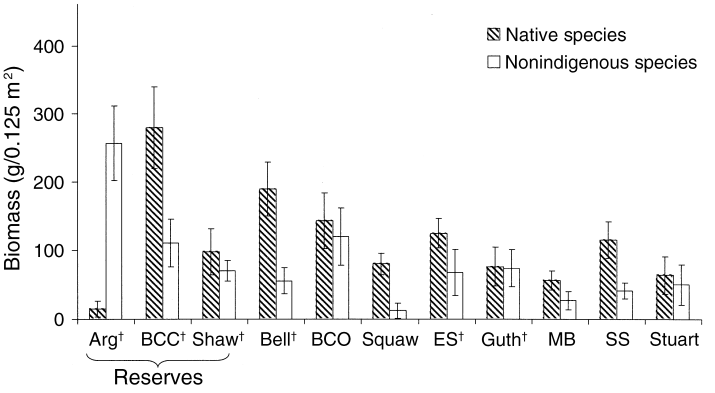

FIG. 2. The biomass (mean ± 1 SE) of native and nonindigenous clams by site in the field survey. Biomass is the combined dry shell and dry tissue mass. The three reserve sites are grouped together on the left. Abbreviations for sites are the same as in Fig. 1. Dagger symbols indicate survey sites used in the subsequent field experiment.

periment using *Protothaca* and *Venerupis*. During late summer and fall 2000 I filled four indoor seawater tray tables (60 × 50 cm) with 6 cm of natural sand, mud, and gravel substrate, which I sieved to remove macroorganisms (e.g., worms and clams). Running seawater was added to each tank and kept at a depth of 17 cm. Tanks were covered on the outside with black plastic and a wooden lid was placed over the top to darken each tank. Large crabs were collected by divers and traps in the immediate vicinity of Friday Harbor Laboratories and held in tanks without food for several days before their use in choice trials.

To eliminate clam size as a confounding variable in prey selection, I used clams between 29 to 32 mm in length. The burrowing depth of these small adult clams rarely exceeds 4 cm (*personal observation*); however *Protothaca* may have been slightly constrained by the sediment depth provided. If full burial of *Protothaca* was restricted, results of this experiment may conservatively underestimate differences in prey selection by crabs in natural settings. Four marked clams of each species were alternately placed ~6 cm apart in a 4 × 2 array in the center of the tank, and pushed down several millimeters below the sediment surface. Clams were allowed to acclimate and burrow to desired depths for one hour before a single crab was added. Each crab usually spent several days acclimating to its enclosure during which time it did not forage.

Enclosures were examined twice a day, roughly 12 hours apart in the early morning and evening. When I discovered a clam was eaten (i.e., broken shell fragments noted on surface), I removed the crab, recovered the broken shell, and replanted another clam of the same species several millimeters deep in the center of the tank. After one hour the crab was reintroduced. Each crab was used until it had eaten a minimum of 12 clams. At the end of the trial series for each crab, the tank was drained and the sediment sieved carefully to verify that the proper number of clams remained. Over the course of the experiment 10 crabs were active consumers. One crab died before it ate any clams. Three crabs had not eaten any clams after two weeks and were subsequently replaced.

I performed individual χ^2 tests on each replicate crab to compare the preference of each crab for *Venerupis* and *Protothaca*. To determine whether crab preference was homogeneous among replicates I conducted a heterogeneity χ^2 analysis of data for all 10 crabs. This test revealed that replicates were homogeneous (heterogeneity $\chi^2 = 4.22$; df = 9; $P > 0.75$) and could thus be pooled to test the null hypothesis of no preference by *Cancer productus* for either species of clam. Pooled frequencies for each prey species were compared with a χ^2 goodness-of-fit test using Yates' correction for continuity (χ^2_C) (Zar 1996).

RESULTS

Field survey

Similar numbers of clam species were present at each surveyed site (7.4 ± 1.75 species, mean ± 1 SD). Nonindigenous clam species were present at all sites, and *Venerupis* specifically was found at all but one site (Figs. 2 and 3). The reserve at Argyle was the most heavily invaded site, where 75% of the clam species (three out of four) were nonindigenous, representing 94% of clam biomass. Of the 11 sites, the three reserves had the first, third, and fifth highest biomass of nonindigenous species (Fig. 2). For *Venerupis*, the reserves ranked 1, 2, and 4 in highest *Venerupis* density and 1, 2, and 3 in *Venerupis* biomass (Fig. 3).

Although the average density of nonindigenous biomass was more than three times higher inside reserves than outside, this difference was not significant (Welch-Satterthwaite t test: $t = -1.55$, df = 2.17, $P = 0.25$; Mann-Whitney $U = 21$, $P = 0.066$; Fig. 2). While there may have been a substantial real difference in biomass density within and outside of reserves, high among site variability led to low statistical power. The large difference in average biomass density was substantially influenced by a high value at Argyle, but this was interpreted by the t test procedure as potentially due to naturally high variability at the reserve sites, and was given less weight by the U test based on ranks. Native species biomass did not vary significantly as a function of reserve status ($t = 0.31$, df = 2.13, $P = 0.78$).

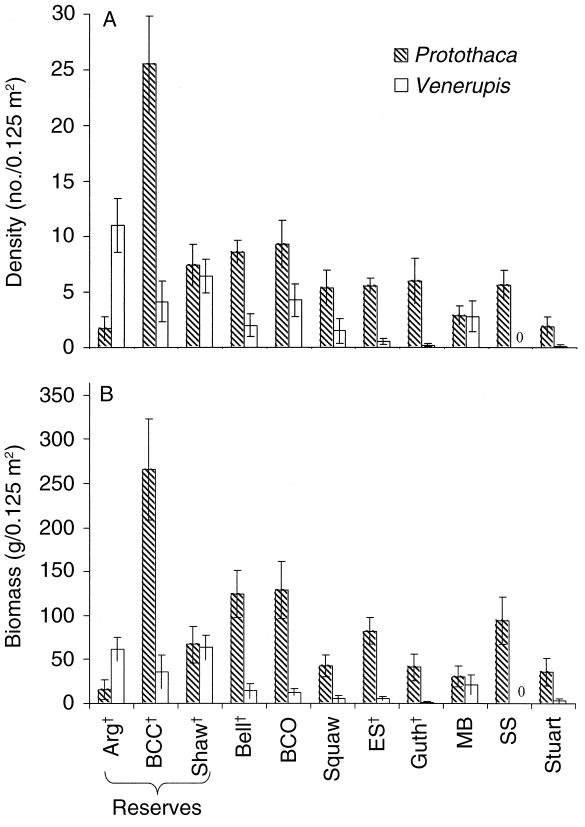

FIG. 3. The (A) density and (B) biomass of *Prothothaca staminea* (native) and *Venerupis philippinarum* (nonindigenous) by site in the field survey. Because of their commercial and recreational value, these two species were a primary focus of this study. As in Fig. 2, biomass is the combined shell and dry tissue mass. Error bars indicate ±1 SE. Abbreviations for sites are the same as in Fig. 1.

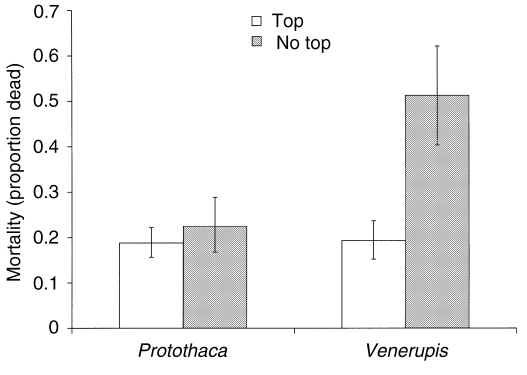

FIG. 4. Mortality rate of *Protothaca* and *Venerupis* in the main field experiment (spanning 312 days) as a function of exposure to predators. Enclosure tops prohibited access by macropredators. Data are averages, and error bars are 95% confidence intervals computed with Anscombe transformation and back-transformed.

TABLE 1. Status of shells of experimental clams and the mortality source suggested by each.

Species, predator exposure treatment	Status of shells (mortality source)		
	Undamaged shells (e.g., anoxia or starvation)	Cracked shells (definitively crab-killed)	Missing clams (probably predator-killed)
Protothaca, topped	96	0	1
Protothaca, no top	86	9	26
Venerupis, topped	96	5	7
Venerupis, no top	22	45	203

Notes: Each predator treatment for each species (i.e., each row) began with a total of 540 clams. Mortality from anoxia, disease, parasitism, or starvation is indicated by empty, intact, and often blackened valves. Designation of definitively crab-killed clams was based on recovery of crab-cracked shell pieces with my identification markings. See *Methods: Experimental investigation . . .* for fuller explanation.

The native clam, *Protothaca*, did not differ significantly between reserves and non-reserves in either density ($t = -0.38$, df = 2.24, $P = 0.74$) or biomass ($t = -0.04$, df = 2.26, $P = 0.97$; Fig. 3). In contrast, nonindigenous *Venerupis* was significantly higher inside reserves in both density ($t = -3.35$, df = 9, $P = 0.0085$) and biomass ($t = -3.43$, df = 9, $P = 0.0075$; Fig. 3). (Argyle was not a statistical outlier in these analyses.) Finally, the biomass of nonindigenous species excluding *Venerupis* (i.e., the biomass of *Mya* and *Nuttallia*) was high, but was highly variable (reserves, CV = 1.03; non-reserves, CV = 0.69) and did not differ significantly with reserve status ($t = -0.79$, df = 2.19, $P = 0.51$).

Reserve status differentially affected the demographics of each clam species. *Venerupis* was on average 9 mm smaller than *Protothaca* at non-reserve sites, but was only 1 mm smaller on reserves. This size differential as a function of reserve status was significant (one-tailed t test, $t = 2.19$, df = 5, $P = 0.04$).

Experimental investigation of nonindigenous clam impacts

Mortality.—Predator exposure affected *Protothaca* and *Venerupis* differently (Fig. 4). Protecting *Protothaca* from predators with enclosure tops decreased its mortality rate by only a few percentage points (Fig. 4). However, *Venerupis*' mortality dropped significantly, from 50% to 21%, from the exposed to the protected enclosures (Fig. 4). In topped enclosures very few clams were missing or cracked by crabs, and approximately the same number of *Protothaca* and *Venerupis* died from causes other than crab predation (e.g., anoxia, disease, senescence) (Table 1). However, in topless enclosures 92% of *Venerupis* mortality was attributable to crab and other macropredators, compared to only 29% for *Protothaca* (Table 1). When clams were protected from predators, overall mortality rates at each

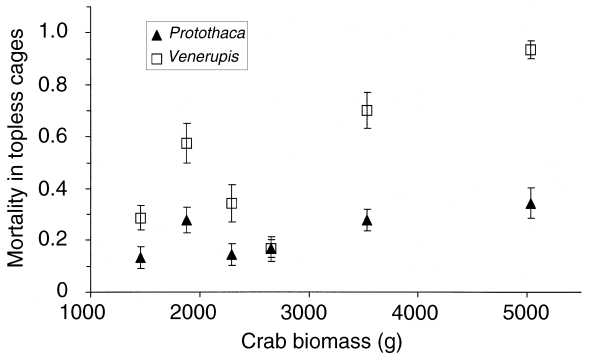

FIG. 5. Mortality (mean ± 1 SE) for both clam species in topless enclosures as function of crab biomass at the six experimental sites.

site were uncorrelated between the clam species ($R^2 = 1.8 \times 10^{-6}$; $P = 0.998$). However, when exposed to macropredators, mortality was highly and significantly correlated ($R^2 = 0.84$; $P = 0.010$; Appendix F).

Not only did *Venerupis* experience higher mortality than *Protothaca* in enclosures exposed to predators, but this difference increased as crab biomass density increased (Fig. 5). *Cancer productus* was the most abundant crab throughout the sites, while *C. gracilis* was sampled in moderate abundance at two sites, and *C. magister* only rarely. For *Venerupis*, in the final model the interactions of predator exposure with crab biomass and with temperature both significantly affected mortality (Table 2). For *Protothaca*, although crabs in particular were not implicated, predator exposure interacted with organic content to significantly influence mortality (Table 2). The recurrence of predator exposure as an interaction term in nearly all of the significant covariates emphasizes its influential role in driving clam mortality (Appendix G). In contrast, *Venerupis* density had almost no effect on either clam's mortality (Table 2; Appendix G). Likewise, the covariates salinity, temperature, and chlorophyll had no significant effect on mortality (Appendix G).

Growth, fecundity, and burial depth.—Dry tissue and gonad growth rates of both species were highly site specific and *Venerupis* grew significantly more than *Protothaca* at all sites except one (Fig. 6; Appendix E). Faster growth by *Venerupis* was consistent across all growth metrics (Appendix C). In the final models, *Venerupis* density had no effect on the growth of either clam (Table 2).

The growth of both species of clam was negatively affected by exposure to predators, particularly when crab biomass was high. Specifically, tissue growth of both clams was significantly affected by predator exposure × crab biomass (Table 2). For *Venerupis*, the interaction of predator exposure × number of crabs also significantly affected growth (Table 2). As further evidence of the large effect of crabs, as crab biomass increased, the growth of predator-exposed clams decreased relative to predator-protected clams (*Protothaca*, $R^2 = 0.88$, $P = 0.0055$; *Venerupis*, $R^2 = 0.63$, $P = 0.059$; Appendix H). For *Protothaca*, although no other covariate (or covariate interaction) was significant when predator exposure × crab biomass was included in the model, many interactions of predator exposure with other covariates (except birds, temperature, and salinity) were significant in initial exploratory models (Appendix G). In alternate, exploratory models for *Venerupis*, only covariates relating to ambient clam biomass and crab metrics (and their interactions with predator exposure and density) were significant when added to the baseline model (Appendix G).

In the laboratory tanks *Protothaca* buried nearly 3 cm deeper than *Venerupis* on average (3.8 vs. 1.0 cm; *t* test, $t = 18.3$, df = 248, $P < 1 \times 10^{-15}$). Although both clams overall buried more deeply in the field, *Protothaca* in both laboratory and field was consistently 2–4 cm deeper than *Venerupis* on average—a finding further corroborated by other studies (Haderlie and Abbott 1980, Richardson 1985, Lee 1996, Sakurai et al. 1996).

Prey choice/susceptibility experiments

In the laboratory, *Cancer productus* given same-sized, small adult clams significantly chose *Venerupis* over *Protothaca* by a factor of 1.7. Not one of the 10 crabs used in the trials selected *Protothaca* more than *Venerupis*, and four crabs chose *Venerupis* at rates of 2 to 1 or greater (Appendix I). The heterogeneity χ^2 analysis indicated that the data were consistent with a homogeneity assumption (heterogeneity $\chi^2 = 4.22$, df

TABLE 2. Effects of predator exposure, density, and site-level covariates on the mortality and dry-tissue growth of *Protothaca staminea* and *Venerupis philippinarum* in mixed-model analyses.

Source	df	*F*	*P*
Protothaca staminea			
Mortality (transformed)			
Predation	1, 98	6.23	0.014
Density	2, 98	0.89	0.42
Predation × organic content	2, 9.56	3.97	0.056
Dry tissue growth			
Predation	1, 98	5.59	0.020
Density	2, 98	0.93	0.40
Predation × crab biomass	2, 9.56	5.50	0.026
Venerupis philippinarum			
Mortality (transformed)			
Predation	1, 62	9.01	0.0040
Density	1, 62	0.32	0.58
Predation × crab biomass	2, 6.94	29.10	0.0004
Predation × temperature	2, 6.94	10.75	0.0075
Dry tissue growth			
Predation	1, 59.2	4.25	0.044
Density	1, 59.3	0.16	0.69
Predation × crab biomass	2, 6.9	88.6	<0.0001
Predation × crab numbers	2, 6.9	72.9	<0.0001

Note: A random site effect was specified for the intercept.

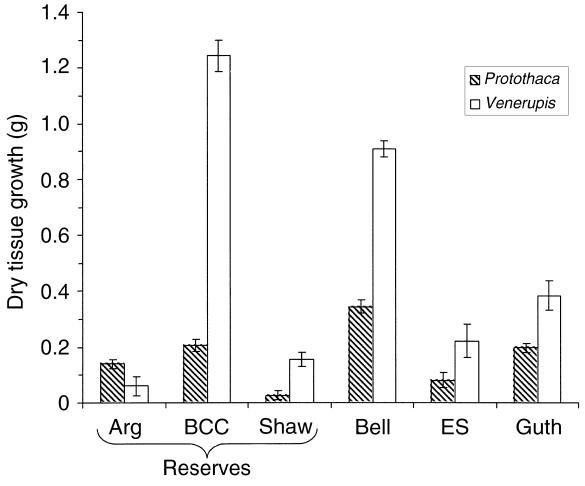

FIG. 6. Dry tissue growth (mean ± 1 SE) of *Protothaca* and *Venerupis* over the course of the experiment (312 days) at each experimental site calculated from enclosure averages. Abbreviations for sites are the same as in Fig. 1.

= 9, $P = 0.89$), thus pooling of the data across crabs was justified. Overall, *Cancer productus* demonstrated a highly significant preference for *Venerupis* (pooled $\chi^2_C = 8.20$, df = 1, $P < 0.005$).

DISCUSSION

Marine reserves substantially augmented the density, biomass, and size structure of *Venerupis philippinarum*, a heavily harvested nonindigenous species. In contrast, the two nonindigenous clams with little to no harvest pressure (*Mya arenaria* and *Nuttallia obscurata*) (see footnote 2), although abundant, demonstrated no consistent pattern in abundance with reserve status. Native clams in general also exhibited no significant pattern between reserves and non-reserves, including a harvested native species (*Protothaca staminea*) that is morphologically and ecologically similar to *Venerupis*. The moderate to high densities of *Protothaca* in most sampled areas underscore that these areas provided suitable habitat for the similar confamilial clam, *Venerupis*. Hence, the observed differences between reserve and non-reserve sites for *Venerupis* are most likely not driven by natural habitat differences, but instead by factors related to reserve status, such as harvest pressure. While occasional poaching within reserves is possible, a strong reserve effect still emerged for *Venerupis*.

In addition to density, reserves also differentially affected the average sizes of *Protothaca* and *Venerupis*, emphasizing the disparate effect of reserve status and subsequent harvest pressure on the two species. Both species exhibit similar allometries and have the same legal harvest size (38 mm length). Despite *Venerupis*' faster growth rate, it averaged 9 mm smaller than *Protothaca* at non-reserve sites, but differed negligibly on reserves. Based on the size–fecundity relationship quantified by Yap (1977), the larger size of *Venerupis* on reserves translates into an approximate 75% increase in per capita fecundity. Coupled with the higher densities of *Venerupis* found on reserves, these areas may contribute disproportionately to the regional production of *Venerupis*' broadcast larvae. Because *Venerupis* is a heavily harvested species, its increase in abundance and size inside reserves is intuitive; however, the fact that the only species consistently benefiting from protection was nonindigenous highlights a potential, unintended consequence of marine reserves.

Venerupis' shallow burial depth, and not its nonindigenous status per se, best explains why it so heavily benefited from reserve status compared to *Protothaca*. Because *Venerupis* burrows several centimeters shallower than *Protothaca*, it can be excavated more easily by human predators (in addition to possibly being simply preferred [Chew 1987]). In all areas crabs also mitigate high *Venerupis* density, preying on them differentially more than *Protothaca*, presumably because crabs excavate the shallowly burrowing *Venerupis* more easily. While *Protothaca* and *Venerupis*' shells exhibit similar resistance to cracking (*unpublished data*), search and handling times of crabs are decreased for a shallower clam (Smith et al. 1999, Seitz et al. 2001). In general, annualized crab predation rates >50% are characteristic of *Venerupis* in its native and introduced regions (Yap 1977, Lee 1996).

Not surprisingly, *Venerupis* was most abundant on reserves where protected from humans, especially when these areas were also low in crab biomass density, e.g., BCC, Argyle. While not a formal part of the analyses, crab biomass was lower at reserve sites than the experimental non-reserve sites (reserves, 2.00 ± 0.61 kg; non-reserves, 3.62 ± 1.37 kg, mean ± 1 SD). This trend could stem from the fact that the two most common crabs sampled (*C. productus* and *C. gracilis*) experience limited harvest pressure themselves and benefit from removal of other more heavily harvested predator and competitor species from non-reserve areas. In particular, the Dungeness crab, *Cancer magister*, which does not generally forage for intertidal clams, is heavily harvested in the region and is known for its highly agonistic interactions (Fernandez et al. 1993).

Although high densities of *Venerupis* may rarely occur naturally because of its vulnerability to predation, even relatively higher densities, such as in reserves and in experimentally augmented treatments, did not directly affect the ecologically similar, confamilial clam, *Protothaca*. Even within predator exclosures that experienced no density mitigation by predators, *Protothaca* showed little discernable response to high *Venerupis* density. Although *Venerupis* densities in the experiment bracketed and even enhanced ambient densities, these apparently still did not extend high enough to result in substantial interspecific or intraspecific competition.

While deeper burial depths do increase *Protothaca*'s protection from human and crab predators, deeper depths also expose clams to a more reducing, i.e., anoxic, environment. In fact, *Protothaca* exhibited greater mortality indicative of anoxia (i.e., undamaged, blackened shells) than *Venerupis*. Sites where *Protothaca* experienced a higher incidence of such mortality in the field experiment (Argyle, ES) also had lower natural densities of *Protothaca* in surveys. *Venerupis* died from anoxia at a rate equal to *Protothaca* when crab predation was prevented by the topped enclosures. When exposed to predators, crab predation on *Venerupis* increased, but its effect on overall mortality was partially offset by a decrease in mortality by anoxia, suggesting these mortality sources for *Venerupis* were compensatory (Table 1).

Although predators caused little mortality of *Protothaca* (Table 1), the interaction between predator exposure and organic content was marginally significant (Table 2). *Protothaca*'s overall mortality increased with decreasing organic content in the topless enclosures, but was nearly constant in topped enclosures (Appendix J). However, *Protothaca* mortality attributable solely to non-predation deaths (undamaged shells) was not different between topped and untopped enclosures (Table 1). So tops were not simply trapping organic matter and helping *Protothaca* avoid starvation where organic content was naturally lower. Rather, the significance of predator exposure $\times$ organic content on *Protothaca* mortality is likely due either to an increase in crabs' dependence on clams as a prey source when the environment is oligotrophic, or more likely, clams exhibiting riskier behavior when organic content is low (such as slow withdrawal of siphons), that renders them more susceptible to discovery by predators. The interaction between predator exposure and organic content was enhanced by a negative correlation of crab biomass with organic content, such that crabs were also more abundant at sites where organic content was low.

While crab biomass did not directly influence *Protothaca*'s mortality, it did decrease the growth rates of both clams (Table 2; Appendix H). At high crab sites, clams in topped enclosures not only survived better, but also grew better. Presumably, enclosure tops reduced the amount of physical contact between clams and crabs that would cause siphons to withdraw and reduce feeding time. A limited laboratory trial corroborated that in the absence of crabs, *Protothaca* and *Venerupis* grew up to two times faster compared to clams that were exposed (nonlethally) to crabs (*unpublished data*). Studies of sublethal effects of predators on clams have generally confirmed that predator presence significantly decreases clam growth (Irlandi and Peterson 1991, Nakaoka 2000).

Regardless of crab abundance, *Venerupis* is a highly productive clam with a tissue growth rate up to six times faster than that of *Protothaca* (Fig. 5). The energetic efficiency of feeding with a siphon decreases with burial depth (Zaklan and Ydenberg 1997), at least partially explaining why the more deeply burrowing *Protothaca* does not grow as fast as *Venerupis*. With a shallower burial depth, *Venerupis* can filter food particles more quickly (Zaklan and Ydenberg 1997) and can invest less in the development of its siphon compared to a deeper clam with a longer siphon.

Although *Venerupis* is productive and attains relatively higher biomass in reserves, its absolute biomass in all areas is still typically much lower than *Protothaca*. Thus, *Venerupis*' high mortality–high growth trade-off, stemming in part from shallow burial, is seemingly not as conducive for maintaining large populations as the low mortality–low growth trade-off manifested by *Protothaca*. *Venerupis*' trade-off helps explain why it is overwhelmingly favored over *Protothaca* by aquaculturists who can benefit from *Venerupis*' high growth rate while artificially protecting it from predators with nets and other exclusion devices (e.g., Spencer et al. 1992). In natural settings, *Venerupis*' trade-off explains why areas with low natural and anthropogenic sources of mortality (e.g., reserves) are prone to enhanced aggregations of larger, more fecund clams that consequently contribute disproportionately to *Venerupis* populations within the region.

Even when human harvest pressure and crab biomass are both high, as they are on non-reserves, *Protothaca* biomass is still on par with reserves where both factors are low. The absence of a reserve effect on *Protothaca* implies that in non-reserve areas *Venerupis* may be largely satiating the demand of human harvesters and intertidally foraging crabs. Given the clam species' similar shell strength and caloric value, *Venerupis*' shallower burial depth translates into a higher energy gain per unit handling time for an excavating predator. Thus, the more profitable and vulnerable *Venerupis* may play a sacrificial role that at least partially protects *Protothaca* from predator mortality. With *Venerupis* apparently taking the brunt of predator pressure, even at open harvest sites *Protothaca*'s abundance is no different than reserves.

However, a larger, negative effect of *Venerupis* on *Protothaca*, and especially other prey species eaten by crabs, may occur at larger temporal and spatial scales. In the field experiment *Venerupis* was seven times more likely to be taken than *Protothaca* when exposed to predators (Table 1). Even in conservative laboratory prey choice trials, *Venerupis* was favored 1.7 times over *Protothaca*. By growing quickly and by serving as an easy prey source for crabs, this nonindigenous prey species may be boosting regional crab abundance and productivity. Given how widespread *Venerupis* is throughout the west coast of North America, this crab food subsidy could be substantial. In addition, the thin shelled, nonindigenous *Nuttallia obscurata* is also an easy, novel prey item for crabs when it occurs in areas without appropriate physical refuges (Byers 2002). Because *Cancer* crabs are omnivorous predators, their in-

crease (particularly non-harvested sizes, sexes, and species [*Cancer gracilis* and *C. productus*]) potentially affects many other native species that serve as crab prey, including other bivalves, worms, fish, and crustaceans (Butler 1954, Gotshall 1977, Stevens et al. 1982). Subsidies of native predators may in fact be a largely disregarded means by which nonindigenous species that are consumed heavily by native predators enhance apparent competition, and thus escalate the impact of predators on native species (Courchamp et al. 2000, Byers 2002). Furthermore, if *Venerupis* boosts populations of a mobile, omnivorous predator, protecting broadcast spawning clams like *Venerupis* from substantial harvest reductions within reserves may fuel an impact that transports well beyond the boundaries of the reserves themselves (Lenihan et al. 2001).

In summary, although marine reserves strongly enhance the nonindigenous clam, *Venerupis philippinarum*, its increase did not affect native populations of one of its most likely competitor species, *Protothaca staminea*. Negative impacts on *Protothaca* resulting from the productivity and increase of *Venerupis* are small and indirect, with crabs that track *Venerupis* abundance slightly affecting *Protothaca*'s growth and size-dependent fecundity. A potential positive effect of *Venerupis* may stem from it being more readily consumed (by both humans and crabs) and thus decreasing predation on *Protothaca*. However, by serving as a more accessible food resource, *Venerupis* may boost regional crab abundance and productivity, thereby influencing nearshore community structure and food web dynamics. Terrestrial reserve managers routinely apply control measures for nonindigenous species; the findings presented here suggest a similar proactive approach for marine reserves as well.

Acknowledgments

I thank D. Byers, T. Byers, and J. Meyer for help in the field. Taylor Shellfish and M. Billington at Westcott Oyster Farms allowed access to their operations and clams. Friday Harbor Seafood donated crab bait. This work benefited from interactions with J. Bence, A. Cooper, A. Davidson, M. Dethier, J. Grabowski, E. Kozloff, E. Noonburg, J. Shima, R. Strathmann, M. Tyrell, G. Vermeij, and L. Whitlow. Access to various field sites was granted by the National Park Service, San Juan Preservation Trust, and San Juan County Land Bank. Support was from Friday Harbor Labs Postdoctoral Fellowship; Marine Ecosystem Health Program through the Wildlife Health Center, School of Veterinary Medicine, University of California at Davis; and Washington Sea Grant.

Literature Cited

Ansell, A. D. 1967. Egg production of *Mercenaria mercenaria*. Limnology and Oceanography **12**:172–176.

Babcock, R. C., S. Kelly, N. T. Shears, J. W. Walker, and T. J. Willis. 1999. Changes in community structure in temperate marine reserves. Marine Ecology Progress Series **189**:125–134.

Ballantine, W. J. 1991. Marine reserves—the need for networks. New Zealand Journal of Marine and Freshwater Research **25**:115–116.

Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. Ecology **65**:1–13.

Brockie, R. E., L. L. Loope, M. B. Usher, and O. Hamann. 1988. Biological invasions of island nature reserves. Biological Conservation **44**:9–36.

Butler, T. H. 1954. Food of the commercial crab in the Queen Charlotte Islands region. Fisheries Research Board of Canada, Progress Reports of the Pacific Coast Stations, report number **99**:3–5.

Byers, J. E. 2002. Physical habitat attribute mediates biotic resistance to non-indigenous species invasion. Oecologia **130**:146–156.

Carlton, J. T. 1979. History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America. Dissertation. University of California, Davis, California, USA.

Carlton, J. T. 1992. Introduced marine and estuarine mollusks of North America: an end-of-the-20th-century perspective. Journal of Shellfish Research **11**:489–505.

Carlton, J. T., and J. B. Geller. 1993. Ecological roulette: the global transport of nonindigenous marine organisms. Science **261**:78–82.

Chew, K. 1987. Littleneck clam aquaculture in the Pacific Northwest. Pages 99–102 *in* Fourth Alaska Aquaculture Conference. Sitka, Alaska, USA.

Coan, E. V., P. V. Scott, and F. R. Bernard. 2000. Bivalve seashells of western North America; Marine bivalve mollusks from Arctic Alaska to Baja California. Santa Barbara Museum Natural History, Santa Barbara, California, USA.

Cohen, A. N., and J. T. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. Science **279**:555–558.

Cooper, A. B., J. C. Pinheiro, J. W. Unsworth, and R. Hilborn. 2002. Predicting hunter success rates from elk and hunter abundance, season structure, and habitat. Wildlife Society Bulletin **30**:1068–1077.

Courchamp, F., M. Langlais, and G. Sugihara. 2000. Rabbits killing birds: modelling the hyperpredation process. Journal of Animal Ecology **69**:154–164.

Czech, B., and P. R. Krausman. 1997. Distribution and causation of species endangerment in the United States. Science **277**:1116–1117.

Edgar, G. J., and N. S. Barrett. 1999. Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. Journal of Experimental Marine Biology and Ecology **242**:107–144.

Eisenhardt, E. P. 2001. Effect of the San Juan Islands Marine Preserves on demographic patterns of nearshore rocky reef fish. Thesis. University of Washington, Seattle, Washington, USA.

Fernandez, M., D. A. Armstrong, and O. Iribarne. 1993. First cohort of young-of-the-year Dungeness crab, *Cancer magister*, reduces abundance of subsequent cohorts in intertidal shell habitat. Canadian Journal of Fisheries and Aquatic Sciences **50**:2100–2105.

Forsyth, R. G. 1993. *Nuttallia obscurata*, an introduced bivalve (Psammobiidae) in British Columbia. Vancouver Shell News for 1993 **14**:7, 9–12.

Francour, P., J. G. Harmelin, D. Pollard, and S. Sartoretto. 2001. A review of marine protected areas in the northwestern Mediterranean region: siting, usage, zonation and management. Aquatic Conservation Marine and Freshwater Ecosystems **11**:155–188.

Gotshall, D. W. 1977. Stomach contents of northern California dungeness crabs, *Cancer magister*. California Fish and Game **63**:43–51.

Haderlie, E. C., and D. P. Abbott. 1980. Bivalvia: the clams and allies. Pages 355–411 *in* R. H. Morris, D. P. Abbott, and E. C. Haderlie, editors. Intertidal invertebrates of Cal-

ifornia. Stanford University Press, Stanford, California, USA.
Irlandi, E. A., and C. H. Peterson. 1991. Modification of animal habitat by large plants: mechanisms by which seagrasses influence clam growth. Oecologia **87**:307–318.
Kozloff, E. N. 1996. Seashore life of the Northern Pacific coast. University of Washington Press, Seattle, Washington, USA.
Lauck, T., C. W. Clark, M. Mangel, and G. R. Munro. 1998. Implementing the precautionary principle in fisheries management through marine reserves. Ecological Applications **8**:S72–S78.
Lee, S. Y. 1996. Distribution pattern and interaction of two infaunal bivalves, *Tapes philippinarum* and *Anomalocardia squamosa* (Bivalvia: Veneridae). Journal of Experimental Marine Biology and Ecology **201**:253–273.
Lenihan, H. S., C. H. Peterson, J. E. Byers, J. H. Grabowski, G. W. Thayer, and D. R. Colby. 2001. Cascading of habitat degradation: oyster reefs invaded by refugee fishes escaping stress. Ecological Applications **11**:764–782.
Lodge, D. M. 1993. Biological invasions: lessons for ecology. Trends in Ecology and Evolution **8**:133–137.
Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology **80**:1522–1536.
Loope, L. L., P. G. Sanchez, P. W. Tarr, W. L. Loope, and R. L. Anderson. 1988. Biological invasions of arid land nature reserves. Biological Conservation **44**:95–118.
Macdonald, I. A. W., and G. W. Frame. 1988. The invasion of introduced species into nature reserves in tropical savannas and dry woodlands. Biological Conservation **44**: 67–93.
Murray, S. N., et al. 1999. No-take reserve networks: sustaining fishery populations and marine ecosystems. Fisheries Management **24**:11–25.
Nakaoka, M. 2000. Nonlethal effects of predators on prey populations: predator-mediated change in bivalve growth. Ecology **81**:1031–1045.
Peterson, C. H. 1982. The importance of predation and intra- and interspecific competition in the population biology of two infaunal suspension-feeding bivalves, *Protothaca staminea* and *Chione undatella*. Ecological Monographs **52**: 437–475.
Peterson, C. H. 1986. Quantitative allometry of gamete production by *Mercenaria mercenaria* into old age. Marine Ecology Progress Series **29**:93–97.
Peterson, C. H., and S. V. Andre. 1980. An experimental analysis of interspecific competition among marine filter feeders in a soft-sediment environment. Ecology **61**:129–139.
Quayle, D. B. 1941. The Japanese ''little neck'' clam accidentally introduced into British Columbia waters. Progress Report of the Fisheries Research Board of Canada Pacific Coast Station **48**:17–18.
Richardson, H. 1985. Availability of buried littleneck clams (*Venerupis japonica*) to northwestern crows (*Corvus caurinus*). Journal of Animal Ecology **54**:443–457.
Sakurai, I., M. Seto, and S. Nakao. 1996. Effects of water temperature, salinity, and substrata on burrowing behaviors of the three bivalves, *Pesudocardium sachalinensis*, *Mactra chinensis*, and *Ruditapes philippinarum*. Nippon Suisan Gakkaishi **62**:878–885.
SAS Institute. 1999. SAS onlinedoc, version 8. SAS Institute, Cary, North Carolina, USA.
Seitz, R. D., R. N. Lipcius, A. H. Hines, and D. B. Eggleston. 2001. Density-dependent predation, habitat variation, and the persistence of marine bivalve prey. Ecology **82**:2435–2451.
Shanks, A. L., B. A. Grantham, and M. H. Carr. 2003. Propagule dispersal distance and the size and spacing of marine reserves. Ecological Applications **13**:S159–S169.
Simberloff, D. 2000. No reserve is an island: marine reserves and nonindigenous species. Bulletin of Marine Science **66**: 567–580.
Smallwood, K. S. 1994. Site invasibility by exotic birds and mammals. Biological Conservation **69**:251–259.
Smith, T. E., R. C. Ydenberg, and R. W. Elner. 1999. Foraging behaviour of an excavating predator, the red rock crab (*Cancer productus* Randall) on soft-shell clam (*Mya arenaria* L.). Journal of Experimental Marine Biology and Ecology **238**:185–197.
Spencer, B. E., D. B. Edwards, and P. F. Millican. 1992. Protecting Manila clam (*Tapes philippinarum*) beds with plastic netting. Aquaculture **105**:251–268.
Stevens, B. G., D. A. Armstrong, and R. Cusimano. 1982. Feeding habits of the Dungeness crab, *Cancer magister*, as determined by the index of relative importance. Marine Biology **72**:135–145.
Stewart-Oaten, A., J. R. Bence, and C. W. Osenberg. 1992. Assessing effects of unreplicated perturbations: no simple solutions. Ecology **73**:1396–1404.
Talman, S. G., and M. J. Keough. 2001. Impact of an exotic clam, *Corbula gibba*, on the commercial scallop *Pecten fumatus* in Port Phillip Bay, south-east Australia: evidence of resource-restricted growth in a subtidal environment. Marine Ecology Progress Series **221**:135–143.
Tuya, F. C., M. L. Soboil, and J. Kido. 2000. An assessment of the effectiveness of marine protected areas in the San Juan Islands, Washington, USA. ICES Journal of Marine Science **57**:1218–1226.
Usher, M. B. 1988. Biological invasions of nature reserves: a search for generalisations. Biological Conservation **44**: 119–135.
Weinberg, J. R. 1998. Density-dependent growth in the Atlantic surfclam, *Spisula solidissima*, off the coast of the Delmarva Peninsula, USA. Marine Biology **130**:621–630.
Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. BioScience **48**:607–615.
Wilder, R. J., M. J. Tegner, and P. K. Dayton. 1999. Saving marine biodiversity. Issues in Science and Technology **15**: 57–64.
Yap, W. G. 1977. Population biology of the Japanese littleneck clam, *Tapes philippinarum*, in Kaneohe Bay, Oahu, Hawaiian Islands. Pacific Science **31**:223–244.
Zaklan, S. D., and R. Ydenberg. 1997. The body size–burial depth relationship in the infaunal clam *Mya arenaria*. Journal of Experimental Marine Biology and Ecology **215**:1–17.
Zar, J. H. 1996. Biostatistical analysis. Third edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

APPENDIX A

A plate showing four of the numerically dominant clams surveyed in this study: *Nuttallia obscurata*, *Mya arenaria*, *Venerupis philippinarum*, and *Protothaca staminea* is available in ESA's Electronic Data Archive: *Ecological Archives* E086-025-A1.

APPENDIX B

A description of the test for potential effects of enclosures on clam responses is available in ESA's Electronic Data Archive: *Ecological Archives* E086-025-A2.

APPENDIX C

A table of exploratory analysis of numerous growth metrics of *Venerupis* and *Protothaca* is available in ESA's Electronic Data Archive: *Ecological Archives* E086-025-A3.

APPENDIX D

Additional details on measurements of environmental covariates at each experimental site are available in ESA's Electronic Data Archive: *Ecological Archives* E086-025-A4.

APPENDIX E

A table showing two separate mixed-effects ANOVAs for each clam species to examine the effects of site, predator exposure, and density on mortality and day tissue growth is available in ESA's Electronic Data Archive: *Ecological Archives* E086-025-A5.

APPENDIX F

A figure showing the relationship of *Protothaca* mortality and *Venerupis* mortality at each experimental site for topped and untopped enclosures is available in ESA's Electronic Data Archive: *Ecological Archives* E086-025-A6.

APPENDIX G

A table of significant site-level covariates that were significant in exploratory analyses when added individually to the baseline mixed model examining mortality and dry tissue growth responses of each species is available in ESA's Electronic Data Archive: *Ecological Archives* E086-025-A7.

APPENDIX H

A figure showing the effect of crab biomass on the average growth at each site in topped minus untopped enclosures for *Protothaca* and *Venerupis* is available in ESA's Electronic Data Archive: *Ecological Archives* E086-025-A8.

APPENDIX I

A table showing the number of clams (*Venerupis philippinarum* and *Protothaca staminea*) eaten by each replicate adult red rock crab, *Cancer productus*, in prey choice trials is available in ESA's Electronic Data Archive: *Ecological Archives* E086-025-A9.

APPENDIX J

A figure showing mortality of *Protothaca* in topped and topless enclosures as a function of sediment organic content is available in ESA's Electronic Data Archive: *Ecological Archives* E086-025-A10.