# Positive effects of a dominant invader on introduced and native mudflat species

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ABSTRACT: Many introduced species have negative impacts on native species, but some develop positive interactions with both native species and other invaders. Facilitation between invaders may lead to an overall acceleration in invasion success and impacts. Mechanisms of facilitation include habitat alteration, or ecosystem engineering, and trophic interactions. In marine systems, only a handful of positive effects have been reported for invading species. In an unusual NE Pacific marine assemblage dominated by 5 conspicuous invaders and 2 native species, we identified positive effects of the most abundant invader, the Asian hornsnail *Batillaria attramentaria*, on all other species. *B. attramentaria* reached densities >1400 m$^{-2}$, providing an average of 600 cm of hard substrate per m$^2$ on this mudflat. Its shells were used as habitat almost exclusively by the introduced Atlantic slipper shell *Crepidula convexa*, the introduced Asian anemone *Diadumene lineata*, and 2 native hermit crabs *Pagurus hirsutiusculus* and *P. granosimanus*. In addition, manipulative experiments showed that the abundance of the mudsnail *Nassarius fraterculus* and percentage cover of the eelgrass *Zostera japonica*, both introduced from the NW Pacific, increased significantly in the presence of *B. attramentaria*. The most likely mechanisms for these facilitations are indirect grazing effects and bioturbation, respectively. Since the precise arrival dates of all these invaders are unknown, the role of *B. attramentaria's* positive interactions in their initial invasion success is unknown. Nevertheless, by providing habitat for 2 non-native epibionts and 2 native species, and by facilitating 2 other invaders, the non-native *B. attramentaria* enhances the level of invasion by all 6 species.

KEY WORDS: Biological invasion impacts · Positive interactions · Facilitation · Ecosystem engineering · Pacific Northwest

## INTRODUCTION

The impacts of introduced species are generally reported in terms of negative effects on native species (e.g. Parker et al. 1999, Grosholz 2002). In some cases, however, an invader may have positive effects on native species (e.g. Crooks 2002) or other invaders (Simberloff & Von Holle 1999, Richardson et al. 2000, Ricciardi 2001). Positive interactions, namely mutualisms (+/+) and 1 side of both commensal (+/0) and exploitative (+/–) relationships, have thus far only rarely been reported between marine invaders (Crooks 2002, Levin et al. 2002, Wonham 2003). As the prevalence and ecological importance of positive interactions are increasingly recognized in marine systems (Peterson & Heck 2001, Stachowicz 2001, Bruno et al. 2003, Mouritsen 2004), we anticipate an increase in reports of facilitative interactions with invaders as well. Based on observations in other systems (Simberloff & VonHolle 1999, Richardson et al. 2000) these facilitations will likely include pairs of introduced species that were previously associated in their native ranges, and non-co-evolved species in their new regions of sympatry.

Mechanisms of facilitation between invaders and resident (introduced or native) species in terrestrial communities are primarily plant pollination and dispersal by animals, mycorrhizal relationships, and habitat alteration by both animals and plants (D'Antonio & Vitousek 1992, Simberloff & VonHolle 1999, Davis et al. 2000, Richardson et al. 2000). In aquatic systems, where the first of these relationships are less relevant, habitat alteration or ecosystem engineering (Crooks 2002, Lambert & Lambert 2003, Castilla et al. 2004) and trophic interactions (e.g. Alpine & Cloern 1992, Kitchell et al. 1997, Ricciardi 2003) may be the most important mechanisms of invader impacts, including facilitation. The same likely holds for marine communities.

In the present study, we identify an unusual marine assemblage consisting almost entirely of 6 macroinvertebrates and 1 vascular plant, of which all but 2 are introduced species. The introduced Asian hornsnail *Batillaria attramentaria* (Crosse 1862) (previously referred to as *B. zonalis* and *B. cumingi* in Pacific coast literature) is by far the most abundant animal in this system. As a diatom grazer and bioturbator (Whitlatch & Obrebski 1980, Byers 2000, Kamimura & Tsuchiya 2004), we expected that it could influence sediment chlorophyll levels and the abundance of other grazers through grazing; the abundance of shell epibionts and occupants through habitat provision; sediment particle size through bioturbation; and eelgrass percentage cover through bioturbation and pseudofecal deposition. We used field surveys and experimental manipulations to evaluate these potential relationships.

## MATERIALS AND METHODS

**Study system.** We conducted our study in Padilla Bay, a shallow sheltered ~14 km long bay in northern Puget Trough, Washington, USA (48° 40′ N, 122° 50′ W). (Site maps available in O'Connor et al. 2002 and Wonham & Carlton 2005.) In the upper-mid intertidal mudflats, the Asian hornsnail *Batillaria attramentaria* (hereafter *Batillaria*) and Asian eelgrass *Zostera japonica* Aschers. & Graebn. are highly abundant, and the Asian mudsnail *Nassarius fraterculus* (Dunker 1860) (hereafter *Nassarius*) is present but less common. *Batillaria* shell surfaces are colonized primarily by the introduced Atlantic slipper shell *Crepidula convexa* Say 1822 (hereafter *Crepidula*) and the introduced Asian anemone *Diadumene lineata* (Verrill 1869) (hereafter *Diadumene*). Empty shells are used by native hermit crabs *Pagurus hirsutiusculus* and *P. granosimanus*, which were counted together for the purposes of this study (hereafter, *Pagurus* spp.). *Batillaria*, *Nassarius*, *Crepidula*, and *Z. japonica* are reported from Padilla Bay since 1970 (Penttila 1971, D. Penttila,

Washington Department of Fish and Wildlife, pers. comm. to M. J. Wonham). All 5 non-native species were introduced with commercial oyster shipments in the late 1800s to early 1900s; *Diadumene* may also have been transported on ship hulls (Carlton 1979, 1987, 1992, Gollasch & Riemann-Zürneck 1996, Byers 2000, Wasson et al. 2001). No other mudflat snails are reported from Padilla Bay or similar habitats in the region (Sylvester & Clogston 1958, Jeffrey 1976, Carlton 1979), or were seen during this study (authors' pers. obs.). The native snails *Lacuna vincta*, *Littorina* spp., and *Nucella* spp. are found in nearby habitats, but their shells are rarely found on the mudflat. For further details of site and methods see O'Connor et al. (2002).

**Spatial distribution surveys.** In a series of surveys, we estimated *Batillaria* abundance and size, the abundance of empty *Batillaria* shells, *Nassarius*, and *Pagurus* spp., the percentage cover of *Zostera japonica*, and the abundance of *Batillaria* shell epibionts. Since the bay is wide and shallow, we measured distance from shore rather than intertidal height. A distance of 100 m, where *Batillaria* tends to be most abundant (authors' pers. obs.), corresponds to approximately 45 cm above Mean Lower Low Water.

We estimated *Batillaria*, *Nassarius*, and *Pagurus* spp. abundances at 100 m from shore in 5 surveys at 12 sites 0.5 to 1 km apart, in September and November 1999 and January, March, and November 2000 (Survey 1). To quantify the broader distribution of *Batillaria* and *Zostera japonica*, we estimated *Batillaria* abundance and size and *Z. japonica* percentage cover at 50, 100, and 150 m from shore at the same sites on 1 occasion in August 1999 (Survey 2). At a local scale, we used intensive surveys to estimate *Batillaria* and empty shell abundance, shell size, and *Z. japonica* percentage cover at 0 to 150 m from shore at a 13th, central site (Survey 3). These last data were collected by 4 University of Washington undergraduate classes from July 1999 to October 2000.

For Surveys 1 and 2 we established a transect running perpendicular to shore from the high water mark. At each distance we haphazardly placed three 25 × 25 cm quadrats, 0.25 to 1 m apart (Survey 1) or one 50 × 50 cm quadrat (Survey 2) on the mudflat surface at low tide. We counted all shells in each quadrat and measured shell lengths in one per site. Sampling methods for Survey 3 were as for Survey 1, but with 1 to 4 transects at least 10 m apart and 1 to 3 quadrats per transect at 0, 50, 100, and 150 m from shore. *Batillaria* shell lengths were measured in all quadrats. *Nassarius* and *Pagurus* spp. were present at this site, but were too rare to analyze their abundance.

In all surveys, snails and hermit crabs were detected by sight and touch from the surface to a sediment depth of 5 cm. We found no additional individuals of these

species in sediment samples retained on a 250 µm mesh sieve, confirming the reliability of this field collection method (O'Connor et al. 2002). *Zostera japonica* percentage cover was estimated using a 50 point grid on the sampling quadrats. *Batillaria* shell lengths were measured from apex to aperture to the nearest mm.

**Epibiont abundance and distribution.** To quantify the use of *Batillaria* shells as habitat, we surveyed shell epifauna at 3 sites in March 2001. At each site, approximately 100 shells were collected at each distance 0, 50, 100 and 150 m from shore. Shell occupants (*Batillaria*, *Pagurus* spp., or empty) and epibionts were identified and counted.

**Batillaria manipulation.** To experimentally evaluate *Batillaria* impacts on *Nassarius* and *Pagurus* spp. abundance, *Zostera japonica* percentage cover, sediment chlorophyll level, and sediment grain size, we manipulated snail densities at 1 survey site with high *Batillaria* densities (1441 ± 353 m$^{-2}$, n = 8). Twenty-seven plots were established in a 9 × 3 array parallel to the shore, 100 m from shore. Plots were haphazardly assigned to 3 treatments: snail removal (cage with all live *Batillaria* removed, n = 8), snail enclosure (cage enclosing ambient density *Batillaria*, n = 11), and open (ambient snail densities in a marked plot with no cage, n = 8). The initial abundance of *Nassarius* (16 ± 23 m$^{-2}$) and *Pagurus* spp. (21 ± 28 m$^{-2}$), which were able to climb in and out of the cages, was not manipulated. Empty *Batillaria* shells (1.8 ± 5.0 m$^{-2}$) were not manipulated and did not differ significantly in abundance at the end of the experiment.

Cages consisted of circular roofless fences, 30 cm tall and 56 cm in diameter, made of 3 mm galvanized mesh. They were buried 10 cm into the sediment and anchored with 50 cm stakes. Plots were established in early April 2000 and stray *Batillaria* were evicted from the removal cages after 2 and 10 wk. After 18 wk, we counted all snails and hermit crabs and estimated eelgrass abundance, chlorophyll levels, and sediment size in each plot.

Eelgrass percentage cover was photographed and subjectively estimated from 35 mm slides (following Dethier et al. 1993) without observer knowledge of treatment. For chl *a*, multiple 0.5 cm deep sediment samples were pooled to a 3 ml volume and stored at –10°C. Chlorophyll was determined by fluorometry following a 24 h extraction at 4°C in 80% methanol and correcting for phaeopigments (following Marker et al. 1980). For particle size analysis, sediment was pooled and homogenized from 3 cores, 3 cm deep and 1 cm in diameter. Silt:sand ratios were determined by placing subsamples of 1 to 2 ml in a 2 m tall glass cylinder filled with water (following Emery 1938). Settled particle volumes were recorded after 4 min (sand, diameter >63 µm) and 12 h (silt, diameter < 63 µm). The remain-

ing volume of suspended clay constituted <1% of the particles by volume in trial runs.

**Data analysis.** Count and size data were ln(*x*)-transformed and proportion data were arcsin-square-root-transformed to improve normality. To test for relationships between the abundance of empty *Batillaria* shells, *Pagurus* spp., and *Nassarius* vs. *Batillaria* abundance, we used repeated measures regressions (Survey 1). To examine the spatial distribution of *Batillaria*, we used 1-way ANOVA (Survey 2) and repeated measures ANOVA (Survey 3) for abundance vs. distance from shore. To test for relationships between empty *Batillaria* shell abundance, *Batillaria* shell length, and *Zostera japonica* percentage cover vs. *Batillaria* abundance and distance from shore, we used ANCOVA (Survey 2) and repeated-measures ANCOVA (Survey 3), after determining that, in all cases, the interaction effect between *Batillaria* abundance and distance was nonsignificant.

All data from the *Batillaria* removal experiment were analyzed with 1-way ANOVA by treatment. Significant results were explored with post-hoc pairwise Student's *t*-tests. Shell epibiont distribution was analyzed with 1-way ANOVA and Chi$^2$ tests. Analyses were conducted in JMP Version 3.2.6 for Macintosh (©SAS Institute 1988–1999) using a significance level of α = 0.05. All mean values in the text are presented ±1 SD.

## RESULTS

### Spatial distribution surveys

In Survey 1, empty *Batillaria* shell and *Nassarius* abundances increased significantly with live *Batillaria* abundance (Survey 1, Fig. 1A,B, Table 1). *Pagurus* spp. abundance tended to increase as well, but this relationship was weak (Survey 1, Fig. 1C, Table 1). The total abundance of *Batillaria* shells in this survey averaged 833 ± 1052 m$^{-2}$, of which live *Batillaria* constituted 88.7% (mean abundance 738 ± 1029 m$^{-2}$) and empty shells constituted 8.8% (73 ± 152 m$^{-2}$). *Pagurus* spp. (mean abundance 21 ± 47 m$^{-2}$) occupied the remaining 2.5% of all *Batillaria* shells, or 22% of snail-less shells. *Nassarius* abundance averaged 21 ± 28 m$^{-2}$; all shells were <1 cm long and were occupied by live snails. We found no other macrofaunal species in the survey quadrats.

Species distributional patterns varied with distance from shore in some but not all surveys (Tables 2 & 3). Across all sites, live *Batillaria* abundance averaged 429 ± 407 m$^{-2}$ and did not vary with distance (Survey 2, Table 2). At the single site, however, it decreased significantly with distance from 2293 ± 576 m$^{-2}$ at 0 m to 1483 ± 572 m$^{-2}$ at 50 m, 959 ± 314 m$^{-2}$ at 100 m, and 480 ± 284 m$^{-2}$ at 150 m (Survey 3, Table 3). Empty shell
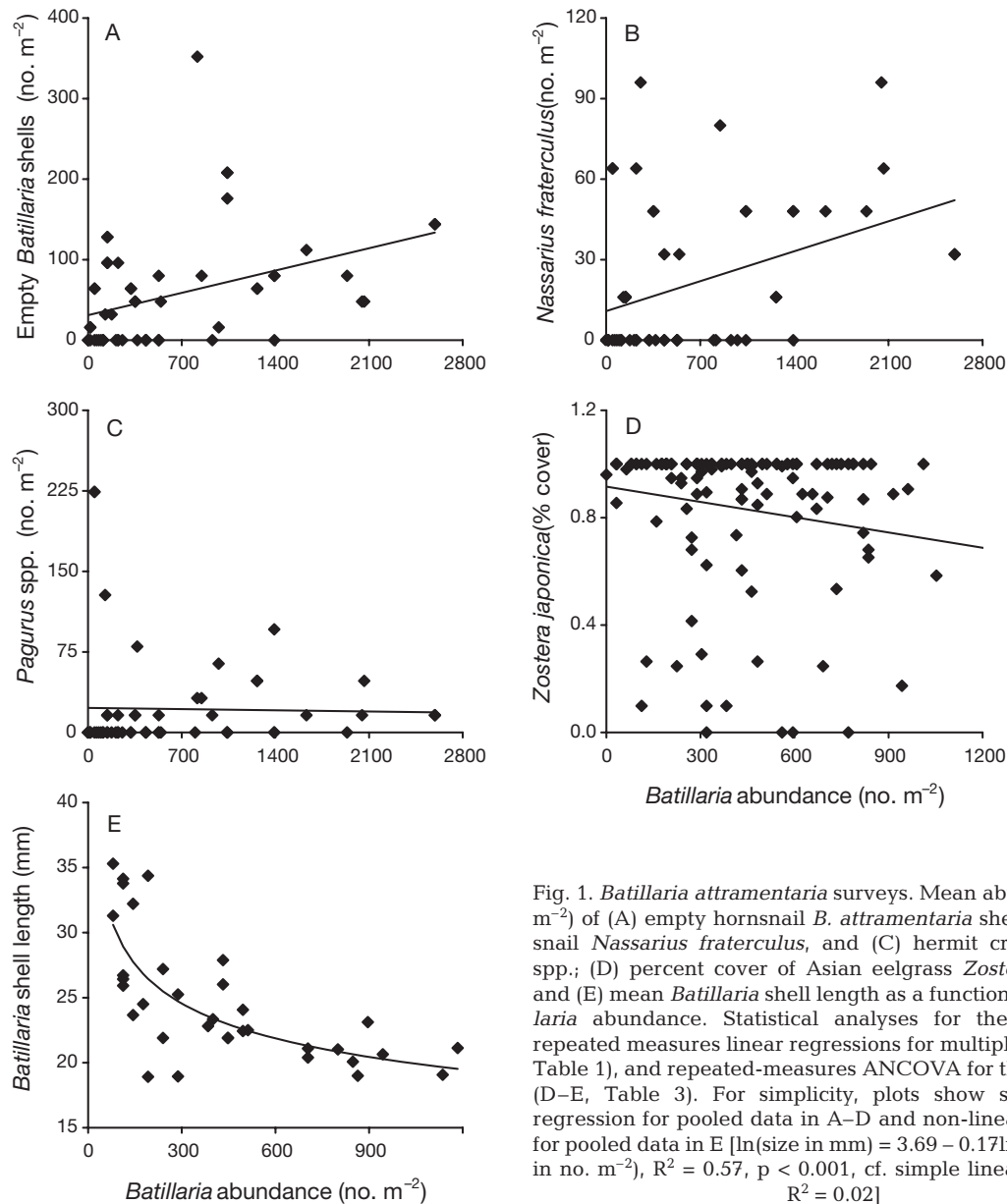
Fig. 1. *Batillaria attramentaria* surveys. Mean abundance (no. m$^{-2}$) of (A) empty hornsnail *B. attramentaria* shells, (B) mud-snail *Nassarius fraterculus*, and (C) hermit crabs *Pagurus* spp.; (D) percent cover of Asian eelgrass *Zostera japonica*, and (E) mean *Batillaria* shell length as a function of live *Batillaria* abundance. Statistical analyses for these data are repeated measures linear regressions for multiple sites (A–C, Table 1), and repeated-measures ANCOVA for the single site (D–E, Table 3). For simplicity, plots show simple linear regression for pooled data in A–D and non-linear regression for pooled data in E [ln(size in mm) = 3.69 – 0.17ln(abundance in no. m$^{-2}$), $R^2$ = 0.57, p < 0.001, cf. simple linear regression $R^2$ = 0.02]

abundance increased significantly with increasing *Batillaria* abundance, but showed no effect of distance across all sites or at the single site (Tables 2 & 3).

*Zostera japonica* percentage cover averaged 27.7 ± 40.6 across all sites, or 47.7 ± 43.5 (n = 6) excluding the sites with no *Z. japonica*, and did not vary with distance or *Batillaria* abundance (Table 2). At the single site, *Z. japonica* percentage cover decreased significantly with increasing distance and tended to decrease with increasing *Batillaria* abundance (Table 3, Fig. 1D).

*Batillaria* shell lengths decreased significantly with increasing *Batillaria* abundance across all sites and at the single site, where it also increased significantly with distance (Tables 2 & 3, Fig. 1E).

## Epibiont abundance and distribution

Given mean *Batillaria* shell densities of approximately 400 m$^{-2}$, and an average shell area of 3.06 cm$^2$ (based on half the surface area of a cone 24 mm tall and 8 mm across at the base), we estimate that *Batillaria* provides 600 cm$^2$ of hard substratum per m$^2$ of mudflat. Not all this substratum was visibly exploited: of 1205 *Batillaria* shells, only 72 (6%) carried 1 or more epibionts (Table 4).

Shells occupied by *Pagurus* spp. were colonized by epibionts significantly more frequently than were live *Batillaria* or empty shells (Table 4; 1-way ANOVA *F* = 5.95, df = 2, p = 0.007). Epibionts consisted almost

Table 1. Repeated-measures regressions for the abundance of empty *Batillaria attramentaria* shells, hermit crabs *Pagurus* spp., and the mudsnail *Nassarius fraterculus* vs. abundance of live *Batillaria* 100 m from shore at 13 sites over 5 sampling dates (4 dates for *Pagurus* spp. and *Nassarius*) (Survey 1). All relationships with *Batillaria* abundance were positive (See Fig. 1). SS: sum of squares; df: degrees of freedom; *F*: *F*-ratio; p: probability (p < 0.05 in **bold**, p < 0.1 in *italics*); $R^2$: proportion of total variance explained by model

| Response | Factor | SS | df | *F* | p | $R^2$ |
|---|---|---|---|---|---|---|
| Empty *Batillaria* shells | *Batillaria* (+) | 32.60 | 1 | 8.32 | **0.006** | 0.222 |
| | Date | 14.82 | 3 | 1.26 | 0.301 | |
| *Pagurus* spp. | *Batillaria* (+) | 10.35 | 1 | 3.01 | *0.089* | 0.083 |
| | Date | 5.73 | 4 | 0.42 | 0.796 | |
| *Nassarius fraterculus* | *Batillaria* (+) | 16.82 | 1 | 5.06 | **0.030** | 0.145 |
| | Date | 16.82 | 4 | 0.61 | 0.615 | |

Table 2. One-way ANOVA for the abundance of *Batillaria attramentaria* abundance vs. distance from shore, and ANCOVA for empty shell abundance, shell length, and eelgrass *Zostera japonica* percent cover vs. *Batillaria* abundance and distance from shore, in bay-wide surveys (Survey 2: 12 sites; 50, 100, and 150 m from shore; 1 sampling date). Significant positive (+) and negative (–) relationships indicated for *Batillaria* (continuous) and distance (categorical) factors. Abbreviations as per Table 1

| Response | Factor | SS | df | *F* | p | $R^2$ |
|---|---|---|---|---|---|---|
| Live *Batillaria* | Distance | 11.99 | 2 | 2.11 | 0.126 | 0.039 |
| Empty *Batillaria* shell abundance | *Batillaria* (+) | 46.60 | 1 | 15.20 | **<0.001** | 0.137 |
| | Distance | 8.37 | 2 | 1.36 | 0.260 | |
| *Zostera japonica* (all sites) | *Batillaria* | 0.02 | 1 | 0.11 | 0.742 | 0.030 |
| | Distance | 0.14 | 2 | 0.42 | 0.659 | |
| *Z. japonica* (sites where present) | *Batillaria* | 0.07 | 1 | 0.33 | 0.573 | 0.060 |
| | Distance | 0.16 | 2 | 0.40 | 0.673 | |
| Live *Batillaria* shell length | *Batillaria* (–) | 0.54 | 1 | 34.15 | **<0.001** | 0.554 |
| | Distance | 0.02 | 2 | 0.55 | 0.583 | |

Table 3. Repeated-measures ANOVA for the abundance of *Batillaria attramentaria* abundance vs. distance from shore, and RMANCOVA for empty shell abundance, shell length, and eelgrass *Zostera japonica* percent cover vs. *Batillaria* abundance and distance from shore, in repeated surveys at a single site (Survey 3: 1 site; 0, 50, 100, and 150 m from shore, 4 sampling dates). Significant positive (+) and negative (–) relationships indicated for *Batillaria* (continuous) and distance (categorical) factors. Abbreviations as per Table 1

| Response | Factor | SS | df | *F* | p | $R^2$ |
|---|---|---|---|---|---|---|
| Live *Batillaria* | Distance (–) | 4.94 | 3 | 2.95 | **0.036** | 0.109 |
| | Date | 3.49 | 3 | 2.09 | 0.106 | |
| Empty *Batillaria* shells | *Batillaria* (+) | 8.06 | 1 | 5.70 | **0.019** | 0.328 |
| | Distance | 2.44 | 3 | 0.80 | 0.632 | |
| | Date | 64.63 | 3 | 15.23 | **<0.001** | |
| *Zostera japonica* percent cover | *Batillaria* (–) | 0.44 | 1 | 3.57 | *0.062* | 0.364 |
| | Distance (–) | 3.33 | 3 | 8.98 | **<0.001** | |
| | Date | 3.34 | 2 | 13.50 | 0.126 | |
| Live *Batillaria* shell length | *Batillaria* (–) | 0.06 | 1 | 4.22 | **0.042** | 0.632 |
| | Distance (+) | 2.49 | 3 | 55.18 | **<0.001** | |
| | Date | 0.11 | 3 | 2.39 | *0.072* | |

exclusively of *Diadumene* and *Crepidula*, which were differently distributed (Table 4). *Crepidula* was more abundant on *Pagurus* spp. and empty shells than on *Batillaria*, whereas *Diadumene* was more abundant on *Batillaria* than on empty or *Pagurus* spp. shells. These host-epifaunal associations were distributed significantly differently from uniform in contingency table analyses (2 epibionts × 3 shell types) for both the number of fouled shells ($\chi^2$ = 13.15, df = 2, p = 0.001) and the number of epibiont individuals ($\chi^2$ = 64.8, df = 2, p < 0.001). Only 1 shell was fouled by both *Crepidula* and *Diadumene*, compared to 40 shells colonized by *Crepidula* alone and 30 by *Diadumene* alone.

Table 4. Frequency and distribution of epifaunal species on *Batillaria attramentaria* shells. Frequency of fouling given for shells occupied by live snails, by hermit crabs *Pagurus* spp., or empty (SD: 1 standard deviation; N: number of samples of 100 to 120 shells each). Distribution of epibionts given for introduced Atlantic slipper shells *Crepidula convexa* and introduced Asian anemones *Diadumene lineata* (number of individuals followed by number of shells in parentheses). Shells sampled at 12 locations in Padilla Bay, Washington, 2000

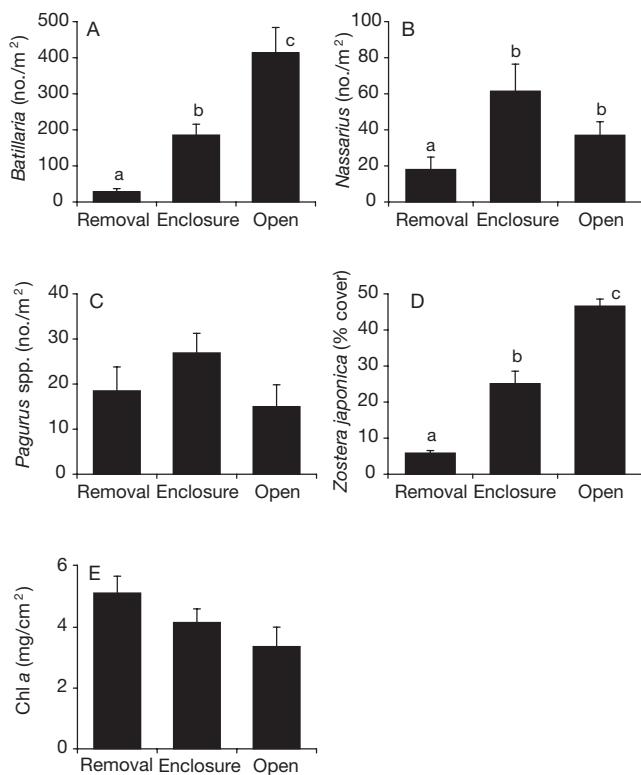| Epifauna | *Batillaria* | *Pagurus* spp. | Empty |
|---|---|---|---|
| Frequency | | | |
| Total shells | 1062 | 61 | 82 |
| Mean proportion fouled | 0.037 | 0.470 | 0.131 |
| SD (N) | 0.059 (12) | 0.454 (9) | 0.205 (12) |
| Distribution | | | |
| No. *Crepidula* (shells) | 9 (6) | 26 (12) | 22 (14) |
| No. *Diadumene* (shells) | 33 (7) | 0 (0) | 2 (2) |



Fig. 2. *Batillaria attramentaria* removal experiment. Mean (A) hornsnail *B. attramentaria* abundance, (B) mudsnail *Nassarius fraterculus* abundance, (C) hermit crabs *Pagurus* spp. abundance, (D) eelgrass *Zostera japonica* percentage cover, and (E) sediment chlorophyll levels at the end of the experiment. When *Batillaria* densities were reduced, *Nassarius* abundance and *Zostera* cover were significantly increased, *Pagurus* spp. showed no effect, and chlorophyll level tended to decrease. Error bars show 1 SE; letters above bars indicate significantly different groups in post-hoc analysis

Additional shell and epibiont species were rare. Other epibionts consisted of mussels *Mytilus* sp., unidentified eggs, and brown macroalgae on 4 live *Batillaria* shells, and spirorbid polychaetes on 4 *Pagurus* spp. shells. We also found 4 *Nassarius* shells with *Crepidula*, *Diadumene*, and *Pagurus* spp., and 1 *Lacuna* sp. shell occupied by a *Pagurus* sp.

### *Batillaria* manipulation

*Batillaria* density treatments differed significantly from each other at the end of the experiment (Fig. 2A; ANOVA $F = 43.4$, df = 2, p < 0.0001). The higher abundance in open plots than in enclosures indicates a net snail emigration from the cages. Comparison of removals to enclosures therefore illustrates the effect of *Batillaria*, and comparison of enclosures to open plots illustrates the combined *Batillaria* and cage effect. Both *Nassarius* and *Zostera japonica* increased with increasing *Batillaria* abundance. *Nassarius* abundance was significantly greater in *Batillaria* enclosures and open plots than in removals (Fig. 2B; ANOVA $F = 4.92$, df = 2, p = 0.016). *Z. japonica* percentage cover was significantly higher in open plots than in enclosures, and in enclosures than in removals (Fig. 2C; ANOVA $F = 57.9$, df = 2, p < 0.0001). *Pagurus* spp. abundance did not differ significantly among treatments (Fig. 2D; ANOVA $F = 1.21$, df = 2, p = 0.32). Sediment chl *a* concentration tended to decrease from removal to enclosure to open treatments, but this was not statistically significant (Fig. 2E; ANOVA $F = 2.53$, df = 2, p = 0.101). Sand:silt ratios did not differ significantly among open (0.41 ± 0.03, n = 7), enclosure (0.40 ± 0.02, n = 11), or removal treatments (0.41 ± 0.02, n = 8).

### DISCUSSION

The intertidal mudflat assemblage of Padilla Bay is dominated by 7 conspicuous species. The most abundant of these is the introduced hornsnail *Batillaria*, which reaches densities averaging 429 $m^{-2}$ and exceeding 1400 $m^{-2}$. The significant negative relationship we report between *Batillaria* abundance and size may indicate some density-dependent limitation in this population. Notably, these observed high densities are attained despite a nearly 90% prevalence of infection by the castrating trematode parasite *Cercaria batillariae* (J. Byers, University of New Hampshire, and M. Torchin, National Center for Ecological Analysis and Synthesis, pers. comm. to M. J. Wonham).

*Batillaria* significantly affects the abundances of 2 epibionts, 3 other grazers, and 1 eelgrass species. For epibionts, *Batillaria* shells provide on average 600 cm

m$^{-2}$ of hard substratum in a mudflat system. The 2 dominant epibionts, the Asian anemone *Diadumene* and the Atlantic slippershell *Crepidula*, are rarely, if ever, found free-living on the mudflat surface. In the absence of *Batillaria*, neither would find much available habitat, as there are no other native snail shells present, and shells of the other introduced snail, *Nassarius*, are smaller and much less abundant. The relative abundance of unfouled *Batillaria* shells suggests, however, that this resource is not fully exploited in Padilla Bay.

Although we found no significant effects of *Batillaria* on sediment chlorophyll levels, this species alters diatom community structure and sediment organic carbon in other mudflat systems (Byers 2000, Kamimura & Tsuchiya 2004). If *Batillaria* reduced grazer resources, other grazers might be expected to segregate spatially from *Batillaria* as a result of competition. Alternatively, they could aggregate with *Batillaria* if they were attracted to the same diatom resources, or if selective grazing by *Batillaria* (Whitlatch & Obrebski 1980, Byers 2000) enhanced the abundance of the other grazers' preferred diatoms. In addition, hermit crabs might be expected to aggregate to empty shells, the abundance of which is positively correlated with live *Batillaria* abundance. We found no significant evidence of positive or negative association in abundance between *Pagurus* spp. and *Batillaria*. We therefore suggest that the primary influence of *Batillaria* on the *Pagurus* spp. population in this system is simply habitat provision. The other grazing snail, *Nassarius*, was positively associated with *Batillaria* in both surveys and experimental studies. We suggest that selective grazing by *Batillaria* may indirectly enhance the preferred diatom resources of *Nassarius*, leading to aggregation of the 2 species.

Shells occupied by *Pagurus* spp. were more exploited by *Crepidula* and less by *Diadumene* than shells occupied by live *Batillaria*, indicating indirect as well as direct effects of *Batillaria* on the 2 epibionts. This association among snail, crab, and epibiont species from different ocean basins is strikingly similar to associations of analogous native species in both the Atlantic and Pacific (e.g. Morton 1980, Karlson & Cariolou 1982, McDermott 2001). Thus, *Batillaria* appears to affect native grazers and introduced epibionts through habitat provision, and the introduced grazer through indirect trophic effects.

*Batillaria* enhanced the percentage cover of eelgrass *Zostera japonica* in the manipulative experiment. Across sites there was no significant relationship between these species, although at the single site there was a negative trend in their association. Differences between the bay-wide and single-site results may partially reflect the absence of samples at 0 m from shore in Survey 2, which is where the smallest and most abundant *Batillaria* were found in Survey 3. In addition,

minor site differences in topography, wave energy and sediment composition mean that distance from shore is not a perfect proxy for intertidal height, and may have contributed to variation among sites. In similar soft-sediment habitats, bioturbation and pseudofecal deposition affect oxygen and nutrient levels in the sediment and water (e.g. Reise 2002, Kamimura & Tsuchiya 2004). These factors are known to affect eelgrass growth (e.g. Peterson & Heck 2001). We suggest that by modifying oxygen and nutrient levels, *Batillaria* indirectly facilitates *Z. japonica*, and that these mechanisms are more readily observed in enclosed cages than in the more diffuse system of the open bay. These hypothesized mechanisms of facilitation for *Pagurus* spp., *Nassarius*, and *Z. japonica* remain to be investigated in future work.

We provisionally define *Batillaria*'s impacts on all 6 species as positive. For the 4 other non-native species, this illustrates multiple positive effects of a marine invader. We note, however, that a complete determination of *Batillaria's* impacts and an assessment of the associated process of invasional meltdown (Simberloff & Von Holle 1999) requires an understanding of *Batillaria*'s net effects on these other invaders, and the role of each invader's local population as a sink or source in the larger region. In addition, since exact arrival dates of each invader are unknown, the importance of positive interactions in their early establishment vs later spread cannot be determined. Nonetheless, *Batillaria* appears to increase the invasibility of this mudflat, as well as the potential population size, and therefore the chance of persistence and the total impacts, of 6 other species. The mechanism of enhancement for 5 of these species is habitat provision, or ecosystem engineering (Crooks 2002), in a manner consistent with the conceptual model of increased resource availability enhancing community invasibility (Sher & Hyatt 1999, Davis et al. 2000). The mechanism for the 6th species (*Nassarius*) may be indirect trophic interactions. This suite of *Batillaria* impacts is a central component of the combined invasion of over 25 species to the NE Pacific via commercial shipments of both Pacific and Atlantic oysters (Carlton 1979, 1987, 1992, Wonham & Carlton 2005). To fully appreciate the consequences of this larger invader assemblage, the direct and indirect impacts of the majority of these species remain to be assessed.

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