



Padilla Bay

National Estuarine Research Reserve

Technical Report No. 25

**Quantifying the Impacts of an Invader:
The Asian mud snail *Batillaria attramentaria*
on the mud flats of Padilla Bay, Wa.**

**Mary O'Connor
Marjorie Wonham
and
Christopher Harley**

December 2001

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Batillaria attramentaria on the mud flats of Padilla Bay, Wa.**

December, 2001

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ABSTRACT

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The impacts of biological invasions are costly to human economy and global biodiversity. It is important to measure and understand the ecological impacts of alien species in order to work toward the development of a predictive science of invasions. This study seeks to experimentally quantify the impact of the nonindigenous Asian Mud Snail *Batillaria attramentaria* on the soft sediment community of Padilla Bay, Washington. In order to do so, we studied the range, abundance and ecological effect of the invader. Mud snails were excluded from areas of the mud flat using small fences. Two experimental designs were employed, one that included sites throughout most of the bay, and one with replicated treatments concentrated at one site to minimize habitat heterogeneity. Response variables were sediment chlorophyll *a* concentration, sediment particle size, per cent cover of eelgrass and macrofauna densities. *Batillaria* removal led to a decrease in *Z. japonica* cover after five months. Particle size distributions, chlorophyll *a* concentrations and infauna populations did not change significantly, but apparent patterns suggest complex interactions with the mud snail. Study site data describe parts of Padilla Bay in detail.

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INTRODUCTION

Understanding the distributional patterns and effects of biological invasions is one of the most important questions facing conservation ecologists today (D'Antonio and Vitousek 1992, Parker et al 1999). According to Wilcove et al. (1998), the cumulative number of successful invasions has skyrocketed since the late 18th century when global trade and travel began, and the rate of invasions continues to increase in habitats exposed to known and effective mechanisms of species introduction (Cohen and Carlton 1998). Conditions facilitating the transport of individuals from their native habitats are relatively new, common and completely anthropogenic (Hanna 1966, Carlton 1989). Agents of species introduction continue to operate and alien species continue to become established in new systems, changing ecological interactions in native communities.

Nonindigenous species have the potential to restructure the communities they invade through mechanisms such as competitive displacement (e.g. Brenchley and Carlton 1983, Race 1982, Abrams 1996, Berman and Carlton 1991), habitat modification (e.g. Bertness 1984, Creese et al. 1997, Herbert et al. 1991) and predation (e.g. Zaret and Paine 1973, Rodda and Fritts 1992). For example, invading species can alter the physical structure of a habitat, as when the cord grass *Spartina alterniflora* invades cobble beaches (Bruno 2000) and mud flats (Zipperer 1996) and can affect the chemical quality of the environment as done by the nitrogen fixing plant *Myrica faya* in Hawaii (Vitousek and Walker 1989). Invasions by alien species can also have direct implications for humans in the form of disease (Native Americans and smallpox), economically useful species such as corn and livestock, and environmentally damaging invaders such as the pathogen causing chestnut blight in New England (Anagnostakis 1987). Often the impact of invasive species is costly, both economically (Pimentel et al. 2000) and in terms of local and global species diversity (D'Antonio and Vitousek 1992). Wilcove et al. (1998) show that the spread of alien species is the second greatest threat to biodiversity after habitat destruction. The problem of species introduction will continue, and human systems as well as native ecosystems will continue to change as a result. In order to understand these changes and attempt to minimize species loss and economic cost, we must study invading species, invaded ecosystems, and the patterns of invasion. If we are familiar enough with these interactions that we can identify patterns and begin to predict the

impacts and extent of invasions, we have the potential to develop effective policy to preserve ecosystems and delay the reduction in global species diversity (Carlton 1989).

To date relatively little research has experimentally quantified the impacts of invasions (Parker et al. 1999, Karieva 1996, Abrams 1996, Berman and Carlton 1991). Studies that measure impacts at multiple spatial and temporal scales and multiple levels of organization are needed to appreciate the ecological effects of an invader. In their framework for assessing the ecological impact of invasive species, Parker et al. (1999) describe the impact of an invader as comprised of three fundamental parts: range, abundance and per-capita ecological effect. The authors argue the importance of understanding impacts of invasions to making theoretical and practical generalizations about the level of impact so that research and management efforts may be efficiently focused.

In this study, we quantify the impact of the introduced Asian mud snail *Batillaria attramentaria* (hereafter, *Batillaria*) to a tidal mudflat community in Puget Sound, Washington. As outlined by Parker et al., we describe the range, abundance and distribution of *Batillaria* in Padilla Bay, WA, and experimentally manipulate the density of *Batillaria* to elucidate potential community effects on several spatial and temporal scales. The ecological impact of an invader may be direct, i.e. through consumption, or indirect through competition, habitat modification or facilitation. We address direct impact through estimation of the standing biomass of the primary food source (benthic diatoms) of *Batillaria*, potentially affected by snails through grazing or disturbance, using sediment chlorophyll *a* concentrations. Indirect effects of *Batillaria* are less easily assessed. Other epifaunal and infaunal organisms are counted in experimental areas with and without *Batillaria* to identify those species potentially experiencing negative effects, such as competition or habitat disruption, by the presence of the mud snail. In addition, we quantify the effect of habitat modification through analysis of particle size distributions in several different habitats containing *Batillaria*.

This study is the first explicit experimental application of the theoretical framework (range, abundance and ecological effect) described by Parker et al. (1999) for estimating the impacts of an invasion. It is also the first experimental study of the ecological role of *Batillaria* in Padilla Bay. Few studies to date have focused on the

benthic ecology of Padilla Bay, and baseline ecological data provided here will be useful to the science based management of the study site, the Padilla Bay National Estuarine Research Reserve (NERR).

Natural History of Batillaria

Batillaria attramentaria (Sowerby) (= *B. zonalis* (Bruguère)) is a native of temperate western Pacific coastal regions including Japan. Cultivation of the Japanese oyster *Crassostrea gigas* in the Pacific Northwest U.S. facilitated the introduction of *Batillaria* to the region in the early 20th century (Quayle 1964). *Batillaria* remains abundant in many areas where Japanese oysters were introduced, and is one of only two Potamidid gastropods and the only member of the *Batillaria* genus present in the northeastern Pacific Ocean. Although it is a conspicuous invader, introduced populations of *Batillaria* have been minimally studied beyond a few surveys in salt marshes and mud flats in Puget Sound and southwestern British Columbia, (e.g. Behrens Yamada 1982, Cooper 1997, Whitlatch 1974) and one experimental study in Bolinas Lagoon in central California (Byers 2000).

Batillaria is a deposit feeder thought to selectively consume small, round benthic diatoms from soft sediments (Cooper 1997). Occasionally snails have been observed highly aggregated on and under drift algae and on dead eelgrass blades, although no damage from grazing has been observed on the algae. This pattern suggests possible grazing for epiphytes on the algae and plant surfaces. Gut content studies have revealed benthic diatoms to be the bulk of ingested material, along with some detrital material surrounding clay sized particles and only very small portions of dead and decaying vascular plant material (Cooper 1997, Whitlatch and Obreski 1980). Comparisons of chlorophyll *a* content of diatoms in the sediment with those in freshly collected fecal pellets led Whitlatch and Obreski (1980) to the conclusion that microphytes are an important food source for *Batillaria*. They also showed that snails selectively ingest certain diatom sizes based on diatom body size.

Like other deposit feeding mud snails, *Batillaria* lives on the surface of the sediments. At low tide, the snail moves its proboscis back and forth across the mud surface as it advances, leaving a trail of displaced particles behind it in the substrate. In

the winter, many snails bury under the surface of the mud up to 2 cm (*personal observation*, Whitlatch 1974).

There is no pelagic larval stage in the life cycle of *Batillaria* (Behrens Yamada and Sankurathi 1977). Studies have found *Batillaria* to reach a length of 35 mm in about 8 years in Tomales Bay, CA, (Whitlatch 1974) and size reached an asymptote around 20 mm in Montague Harbor, BC, after 11 years (Behrens Yamada, 1982). In Padilla Bay, WA, we observed *Batillaria* up to 41 mm long. In Montague Harbor and in Tomales Bay, CA, *Batillaria* has been described as patchily distributed and highly aggregated in marsh pans and drainage ditches. However, in central California and Padilla Bay, WA, these mud snails are by far the most conspicuous epifaunal species in almost all upper intertidal areas of the mudflat (Whitlatch 1974, *personal observation*).

Although *Batillaria* is the only epifaunal gastropod present in densities above 20/m² (reaching densities of over 1600 individuals/m²) in Padilla Bay, it coexists in high densities in central California with another deposit feeding gastropod (Whitlatch and Obreski 1980). Byers (2000) has recently shown that this apparent coexistence of *Batillaria* and a native ecological equivalent, *Cerithidea californica*, is now thought to be part of a long-term (approximately 50 year) process of competitive exclusion of the native snail. The only other mud snail in Padilla Bay is *Nassarius fraterculus*, which is also an invader from Japan and occurs in densities of 0 – 20 individuals / m² (*present study*). No native mud snails have been documented in the bay, and the periwinkle *Littornia sitkana* was infrequently observed. The only specialized predator of *Batillaria* observed in Padilla Bay is a parasitic fluke residing in the stomach of the snail. We found some empty shells with drill holes, suggesting predation by drilling snails (possibly the moon snail, *Polinices lewisii*) and others with a chipped aperture that may indicate crab predation. *Batillaria* represents a small percentage of the gut contents of seasonal predators such as Northern Pintail ducks and Mallards which migrate through Padilla Bay in the late fall (Baldwin and Lovvorn 1994b).

METHODS

Study site

All fieldwork was carried out in Padilla Bay, located in northern Puget Sound, WA (48° 40' N, 122° 50' W). The shallow bay encompasses approximately 5868 ha, bounded on the east and south by diked farmland, to the west by Guemes Island and to the north by Samish Island (Figure 1). Tides are mixed semidiurnal, and the mean range is 1.55 m. Nearly 60% of the bay is exposed at mean lower low water, and only a small area in the center of the bay exceeds 15 feet in depth. There is no river outlet into the bay, and most freshwater input consists of runoff from surrounding slopes and farmland (Jeffrey 1976). Turbidity of the water is usually low, and salinities range from 15 – 30 ‰. Water temperatures in the bay range from 7°C in December to 25°C in tide pools on the mud in the summer (Thom and Kennedy 1995).

The benthic environment of Padilla Bay is predominantly soft sediment deposited historically by the Skagit River. Particles range in size from clay to gravel and are unevenly distributed throughout the bay. The sediments of the south end of the bay are a more homogeneous mix of smaller grain size, while along the eastern shore there are several areas with homogeneous sandy particles and highly heterogeneous mixes (*present study*). Padilla Bay has been described as having the most mixed substrate of the several nearby soft sediment bays (Jeffrey 1976).

Eelgrasses (*Zostera marina*, *Zostera japonica*) are the dominant vegetation, covering approximately 3200 ha, or 53% of the bay (Bulthuis 1991). *Z. marina* is native to Padilla Bay, and grows in the lower intertidal regions, while *Z. japonica* is invasive and grows at higher tidal elevations than its local counterpart. Eelgrass beds harbor rich communities of invertebrates (Posey 1988) and *Z. japonica* beds have been shown to be important feeding areas for migrating fish and birds such as dabbling ducks and brant (Baldwin 1994a). Marine algae and diatoms are associated with the eelgrass beds, and are also present on the mud surface outside the eelgrass beds.

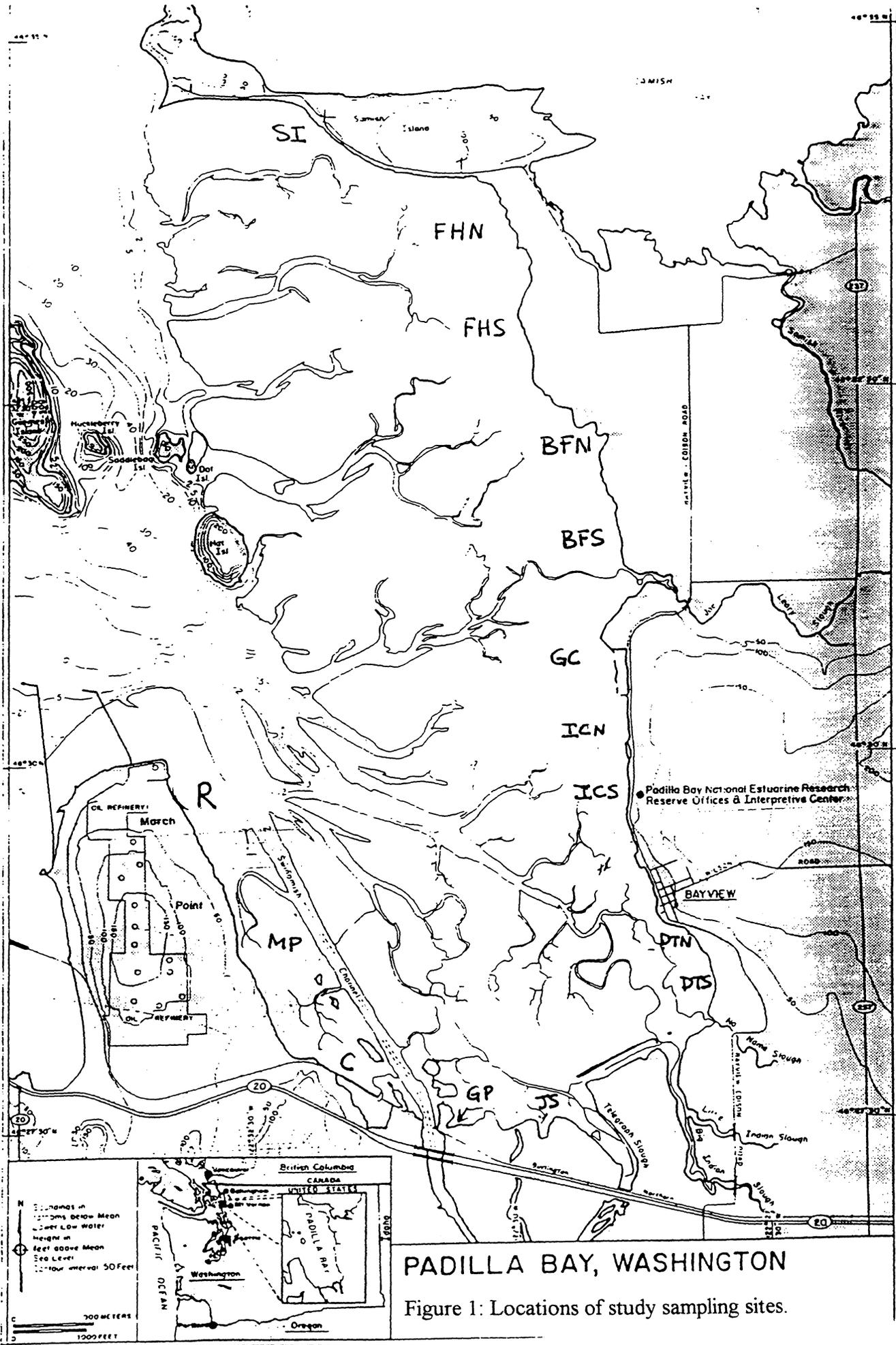
Padilla Bay is host to many resident and migratory fish and bird species. Several species of juvenile salmon migrate through the bay, which also provides a secure habitat for maturing herring (*Clupea harengus*) and a nursery for many species of flatfish

(Jeffrey 1976, Simenstad et al. 1988). Great Blue Herons (*Ardea herodias*), Bald Eagles (*Haliaeetus leucocephalus*), and Band-tailed Pigeons (*Columba fasciata*) are known to nest on the shores of the bay, and over 100,000 ducks of various species migrate through the bay annually (Jeffrey 1976). These resident and temporary vertebrates represent a largely unquantified consumer pressure on their intertidal prey.

Human use of Padilla Bay includes recreational boating and commercial shipping. On the west side of the bay are two oil refineries, Tesoro Northwest and Equilon, and oil tankers pass very near the mouth of the bay to dock at the refineries. Saddlebag Island in the northwest region of the bay is a state park frequented by day and overnight visitors during the summer months, and Bay View State Park hosts visitors all year round. Historically, parts of the bay have been used for growing oysters, and oysters are continually planted for recreational use at the state park. Padilla Bay was designated a NOAA National Estuarine Research Reserve in 1980.

Experimental Design

To examine the effect of *Batillaria* on the physical habitat and biological community on several spatial scales, we carried out two *Batillaria* exclusion experiments. In the first manipulation, one set of three treatments was installed at twelve different locations throughout Padilla Bay. We considered each site a replicate within the bay, and therefore there was no within-site replication. Upon analysis, we found that this design did not consider the high degree of heterogeneity within the mudflat habitat and we were unable to detect differences among treatments above the variation in site character. Although this design did not serve to sufficiently answer our initial questions about the ecological role of *Batillaria*, it did provide information on *Batillaria* in several different types of mudflat habitat. To better study specific aspects of the ecology of *Batillaria*, we modified the first experimental design to minimize habitat heterogeneity among replicates and therefore to provide more powerful results.



PADILLA BAY, WASHINGTON

Figure 1: Locations of study sampling sites.

Experiment #1

Batillaria survey

The first experiment began in August of 1999. Initially we surveyed the entire bay and recorded *Batillaria* size, frequency and density at 15 different sites (Table 1, Figure 1). At each site, we sampled at 50, 100, and 150 m along a transect perpendicular to the shore from the high water mark. At each sampling point, a 1/16 m² quadrat was haphazardly tossed down three times and snails in the quadrat were counted. The height of each snail from apex to siphonal canal was measured for snails in the second of the three sampling quadrats.

Table 1: Sampling site characteristics for *Batillaria* study in Padilla Bay, WA

Site Abbrev.	Location	Average Particle Size	Substrate Cover
R	Refinery	silt	cobbles
MP	March Point	silt	mud
C	Casino	silt	mud
GP	Gravel Pit	silt	diatom mat
JS	Swinomish Gun Club	silt*	mud, diatoms
DTS	Dike Trail - South	silt*	mud
DTN	Dike Trail - North	silt*	eelgrass (Z.j.)
ICS	Interpretive Center - S	sand*	eelgrass (Z.j.)
ICN	Interpretive Center - N	sand*	eelgrass (Z.j.)
GC	Gun Club Trail	sand*	gravel / mud
BFS	Big Field South	sand	sand
BFN	Big Field North	silt	mud
FHS	Prairie Gardens S	silt	mud
FHN	Prairie Gardens N	sand	sand
SI	Samish Island	sand	eelgrass (Z.m.)

* = analyzed using settlement method, no * indicates description based on observation. Z.j. = *Zostera japonica*, Z.m. = *Zostera marina*.

Design

Batillaria density manipulation began in August, 1999, and was monitored until March of 2000. At the 12 survey sites where we found *Batillaria*, we installed one set of experimental treatments consisting of a *Batillaria* removal area, a caged area enclosing *Batillaria* at ambient density, and an open reference area with no fence. Fences were 0.25

m² circular plots fenced with 1/8" galvanized mesh wire 30 cm tall. Galvanized mesh was used as cage material because it has been found to provide a physical and chemical barrier to marine snail migration (Bertness 1984). The cages were set 7 cm into the sediment to prevent snail and predator migration, and anchored with three 50 cm aluminum or stainless steel dowels bent into U's. At each site, treatments were placed 100 m offshore from the high water mark. Plots were established one meter apart parallel to the shore with the cage control in the middle. The slope of the substrate is extremely gradual and we assume equivalent tidal height for each treatment within a site in the first experiment. This assumption is supported by the observation that treatments flooded at the same time.

Data were collected and cages were maintained in August, September and November, 1999, and January and March, 2000. At each sampling time, all *Batillaria* and other surface macrofauna were identified and counted in each plot. Specifically, hermit crabs (*Pagurus spp.*) were counted because they primarily inhabit discarded *Batillaria* shells, and *Nassarius fraterculus* was counted because it is the only other mud snail present in consistent numbers. In the exclusion plots, *Batillaria* were counted and removed. Densities of *Batillaria* in the inclusion treatment were not manipulated. Over the two months between sampling only a few *Batillaria* per square meter managed to enter the removal treatments (with the exception of BFS). Cages were quite effective in consistently excluding *Batillaria*, although inclusion densities were not always consistent with open reference densities. At these sampling times, sediment samples were collected from each plot for chlorophyll *a*, grain size and infauna analysis.

Sediment chlorophyll *a*

We analyzed sediment samples for chlorophyll *a* in September of 1999 and January of 2000. Three samples from the surface mud of each treatment at every site were collected in small scoops from the surface mud (top 0.5 cm). Samples were stored at -10°C until analysis. We analyzed sediment chlorophyll *a* concentration using a Perkin Elmer spectrophotometer. Chlorophyll was extracted for 24 hours at 4°C from approximately 0.5 g thawed sediment in 10 ml 90% acetone with one drop of MgCO₃ added. We centrifuged each sample for five minutes, and then recorded the absorption

spectra from 400–780 nm before and after acidification of the supernatant. We converted absorption peaks to chlorophyll *a* concentrations following the calculations outlined in Lorenzen (1967).

Sediment particle size

Two samples of 120 ml were collected from each treatment, each consisting of three samples of 40 ml. Samples were collected using a round cookie cutter pressed 2 cm into the sediment to ensure equal depth and volume of each sample. All samples were collected from the inner half of the cage area in attempt to minimize edge effects. To construct particle size distributions for each site, we analyzed sediment samples using the standard sedimentation rate calculations for particle size analysis of soils (SSSA Book Ser: 5) using American Society for Testing and Materials (ASTM) standard hydrometers (ASTM no. 152H). Particles were classified according to the Canada Soil Survey Committee (CSSC) system. Pretreatment of soils consisted of dispersion by soaking in sodium hexametaphosphate (HMP) on a horizontal shaker overnight.

Statistical analyses consisted of student's t-tests and regression analysis.

Experiment #2

Design

The second experiment began in April of 2000, and data were collected through the end of September 2000. We chose the site ICS (Interpretive Center South) for the second design because it is easily accessible and because, with abundant *Zostera japonica*, we could explore *Batillaria*'s relationship with eelgrass. Three replicates of an additional treatment type containing snails at twice the ambient density were added, and there were 8 sets of treatments identical to those in the first experimental design (*Batillaria* removal, ambient density, no fence and double ambient density). Cages were constructed using the same materials and measurements as in Experiment 1. Treatments were placed at the same location as in Experiment 1, at 100 m from the high water mark at a tidal elevation of approximately +45 cm.

Vegetation cover

We photographed each replicate of each treatment on the final date of the experiment in September, 2000, and analyzed the slides to estimate percent cover of vegetation using visual observation methods based on those described in Dethier et al. (1993). Percent cover of the eelgrass *Zostera japonica* (the most common vegetation) was estimated to the nearest 5% by two independent observers.

Sediment chlorophyll *a*

At the end of the experiment in September of 2000, we used a syringe with a bore of .33 cm² to collect three 1 ml samples of surface mud to a depth of 1 cm from each treatment. We extracted chlorophyll *a* for 24 hours at 4°C in a known volume of methanol. We determined sediment chlorophyll *a* corrected for phaeopigments by fluorometry (Marker et al. 1980).

Meiofauna

Meiofauna were sorted and categorized in September of 2000. Three 10 mL samples of mud were collected to a depth of 3 cm from each treatment using a syringe core to ensure equal volume and depth of sampling. We then sorted samples according to size, and invertebrates retained in a 250 µm sieve were counted and identified to phylum in most cases. We identified Arthropods to subclass, and annelids to family.

Sediment particle size

We found the ratio of silts (particles larger than clay with diameters < 63 µm) to sands ($d > 63 \mu\text{m}$) in each treatment in September of 2000 according to methods described by Emery (1938). Samples were collected using small coring devices to a depth of 3 cm, and sorted by size in a tall glass cylinder filled with water. Sediment samples were untreated prior to analysis in order to record sediment as it occurs in nature, including aggregations due to organic matter or dried saline. We allowed samples to settle for 12 hours, and measured the silts as those particles that had settled, and considered clays to be those that remained in suspension. Four trial runs showed that less

that one percent of particles by volume remain in suspension after twelve hours, and this small amount is well within the accepted error of the method.

RESULTS

Experiment #1

Abundance and Distribution

Batillaria were found on the southern and eastern intertidal regions of Padilla Bay, and no *Batillaria* were found west of Swinomish Slough. In general, low *Batillaria* densities (40 snails/m²) occurred on the southern mudflats and densities increased northward along the eastern shore to a maximum of over 1100 snails/m² at BFS. Densities then decreased along the shore to the northeastern part of the bay where they were lowest (25 snails/m²). *Batillaria* density at a given site varies with distance from shore (Table 2). We found *Batillaria* at every site that we found *Z. japonica* or *Z. marina* (DTN, ICS, ICN, SI, see Table 1). The variance in *Batillaria* density in eelgrass habitats was 100 – 800 snails/m², narrower than the range of densities in habitats where there is no vegetation (0 – 1400 snails/m²). Generally, densities of *Batillaria* were higher at sites with mostly sand-sized particles than at sites dominated by coarse silts and clays (student's t-test, $\alpha < .01$). The two sites with much larger grain size, BFS and Gun Club, had the highest densities of *Batillaria*.

Table 2 : Mean *Batillaria* density (individuals / square meter) and standard error at each sampling site. Sampled Aug '99.

Site	50m		100m		150m	
	mean	s.e.	mean	s.e.	mean	s.e.
BFN	549.3	26.7	474.7	6.0	1157.3	224.7
BFS	261.3	9.5	1152.0	7.6	1221.3	5.9
DTN	282.7	20.8	160.0	18.1	101.3	23.0
DTS	128.0	16.0	186.7	10.0	128.0	6.0
FHN	864.0	9.8	954.7	20.9	1045.3	27.2
FHS	192.0	9.2	437.3	24.7	469.3	29.0
GC	986.7	23.4	645.3	9.7	560.0	18.8
GP	0.0	0.0	69.3	15.2	0.0	0.0
ICN	405.3	16.7	272.0	8.3	117.3	27.3
ICS	842.7	25.4	496.0	19.2	298.7	19.8
JS	144.0	26.4	170.7	11.1	96.0	32.3
SI	346.7	17.0	192.0	32.3	26.7	10.9

A negative relationship exists between shell height and *Batillaria* density (Figure 2). This pattern was present across all habitat types in the bay, but was less clear at densities below 200 individuals/m², suggesting a threshold density level for growth limitation. Average height of *Batillaria* ranged from 20 mm at the most densely populated areas to 35 mm in the most barren areas on the southern mudflats (Table 3).

Because of the large range of variation in *Batillaria* density with location throughout the bay, snail densities in the control and inclusion treatments vary widely (see Appendix A) and prohibit a meaningful comparison of these treatments across sites.

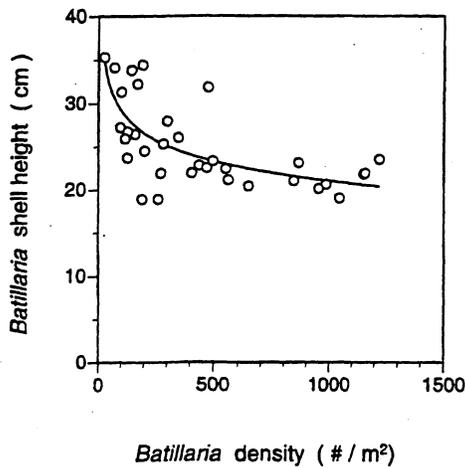


Figure 2: Shell height vs *Batillaria* density in August, 1999. Data include all populations sampled at three distances from shore (50m, 100m, and 150m). Statistical analysis indicates that variation in snail shell height is related to variation in snail density ($F = 28.03$, $p < .0001$).

Table 3 : Mean shell height (mm) and standard error of *Batillaria* at each sampling site. Sampled Aug. '99.

Site	50m		100m		150m	
	mean	s.e.	mean	s.e.	mean	s.e.
BFN	22.4	0.3	24.1	0.4	21.9	0.8
BFS	18.9	0.7	19.1	0.3	21.1	0.2
DTN	25.3	1.2	38.5	0.4	31.3	1.9
DTS	23.7	0.7	24.5	1.0	26.7	0.9
FHN	23.1	0.2	20.1	0.5	19.0	0.6
FHS	18.9	2.7	22.8	0.6	22.5	0.8
GC	20.6	0.2	20.4	0.4	21.1	0.6
GP	0.0	0.0	34.1	1.8	0.0	0.0
ICN	21.9	0.3	21.9	0.9	25.9	0.7
ICS	21.0	0.3	23.3	0.5	27.9	0.7
JS	33.8	1.3	32.2	2.9	27.2	0.9
SI	26.0	0.8	34.4	1.3	35.3	1.2

Sediment chlorophyll a

The average sediment chlorophyll *a* concentrations of removal and enclosure treatments are not statistically different from each other in September or in January (student's t-test) (Table 4). The difference in chlorophyll *a* between snail removal and reference areas varies among sites and sampling times (Table 5). In September, removal treatments had greater chlorophyll *a* concentrations than enclosures in three of twelve sites, removals had lower chlorophyll *a* concentrations in four of twelve sites, and at the remaining five sites there was no difference between treatments. In January, five of eleven sites showed increases in chlorophyll *a* concentration with *Batillaria* removal, three sites showed a decrease in chlorophyll *a* with removal, and there was no change in the remaining three sites. See Appendix C for mean chlorophyll *a* concentrations and standard errors.

**Table 4: Experiment 1
Mean and standard error of chlorophyll *a* concentrations**

mg chl _a /g dry sediment	mean	+ s.e.
Sept. (n=12)		
removal	7.77	+ 1.72
enclosure	7.39	+ 3.07
Jan. (n=11)		
removal	3.65	+ 2.99
enclosure	3.74	+ 3.32

**Table 5: Patterns of change in chlorophyll *a* values in first experiment
Trends are insignificant.**

Increase in Chla with removal		Decrease in Chla with removal			No change	
September	January	September	January	January	September	January
FHS	FHS	GP	GP	GP	ICN	ICN
DTS	DTS	JS	JS	JS	SI	SI
GC	BN	BFS	GC	GT	BFN	BFS
	ICS	DTN			ICS	FHN
	DTN					

Sediment particle size

Particle size distributions were constructed for six of the twelve sites, both at the initiation of the experiment in August and in January. At five of the six sites, all particles had a diameter less than 2 mm; the Gun Club Trail site had some gravel mixed with mud. Each site had a unique ratio of particle size classes (Figure 3), although three sites were mostly sand and the other three sites were mostly medium to coarse silts with some clay. Approximate median particle diameter for sampled sites in August ranged from 18 μm at the southwest part of the bay to 122 μm on the central west shore.

We made three comparisons among particle size distribution curves: exclusion treatments in August versus exclusions in January, exclusion versus inclusion treatments in August, and exclusion versus inclusion treatments in January. Kolmogorov-Smirnov one-sample tests indicated that in every comparison the particle size distributions were not different ($p > .2$).

Meiofauna

We detected no correlation between *Batillaria* removal and *Nassarius fraterculus* density. *Nassarius* was inconsistently distributed at low densities throughout the bay. Densities ranged from 0 to 36 individuals/ m^2 , and *Nassarius* was only present at nine of the twelve experimental sites. Appendix A lists densities of *Batillaria* and *Nassarius* at each sampling site at five dates between August 1999 and March 2000.

There was a significant increase in hermit crab (*Pagurus spp.*) density inside both caged treatments relative to the open reference plot. The density of empty *Batillaria* shells remained constant across all three treatments, indicating that hermit crabs entering the cages brought their shells with them.

Traces of predation by generalist predators such as crabs and drilling gastropods did not vary with treatment, and were few relative to *Batillaria* density.

Experiment #2

The exclusion treatments successfully maintained *Batillaria* densities close to zero (Figure 4). *Batillaria* densities in enclosure treatments were significantly higher than in the exclusion treatments, but also much lower than in the open controls at the end

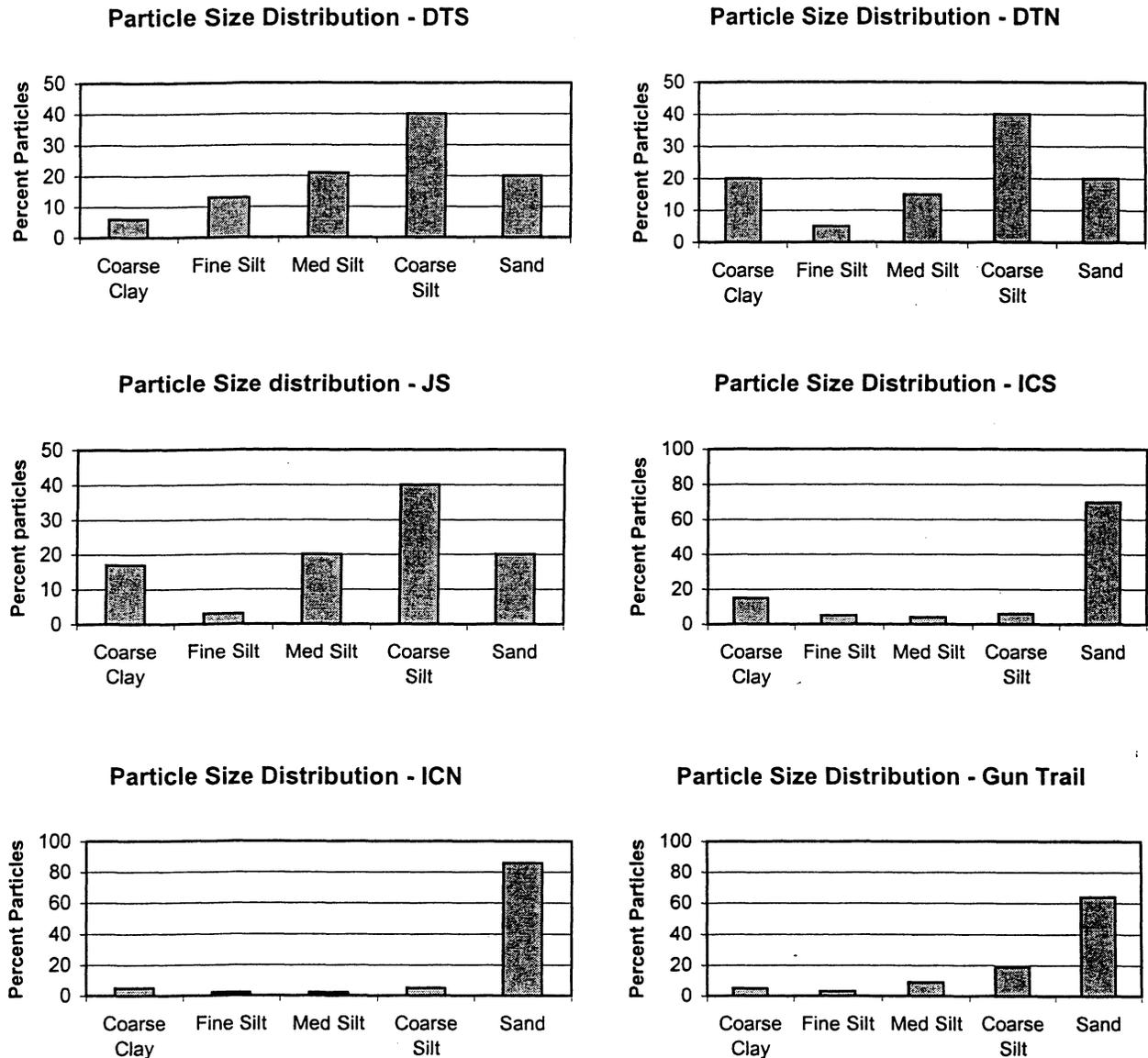


Figure 3: Particle size distributions according to CSSC (Canada Soil Survey Committee) classifications. Coarse Clay = < 2um d, fine silt = 2 - 5 um d, med silt = 5 - 20 um d, coarse silt = 20 - 50 um d, sand = 50 - 200 um diameter. Samples taken from exclusion areas before fences were set up in August. Note the difference in scale of y-axes of sand dominated sites vs silt dominated sites.

of the experiment. Treatments designated as double inclusions, with initially twice the ambient density of *Batillaria*, by the end of the experiment were no different from the ambient inclusions. We therefore chose to consider both ambient and double inclusion treatments as one treatment type for our analyses.

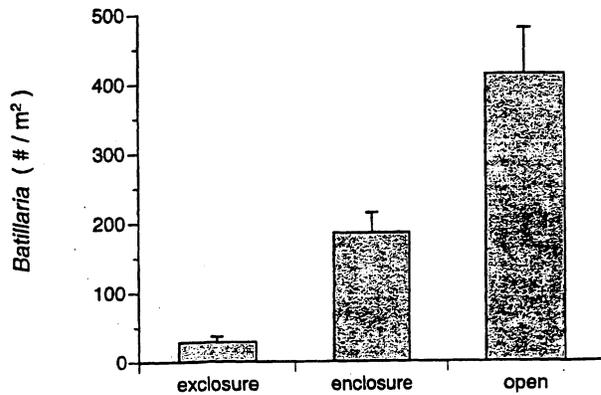


Figure 4. Density of *Batillaria* in exclosure, enclosure and open control treatments at end of five month experimental period, September 2000. $F = 43.36$, $p < .0001$, ANOVA of \ln transformed data. Tukey-Kramer HSD post hoc shows these relationships are significant ($\alpha = .05$).

Vegetation cover

In the second experiment, *Z. japonica* was the only species of vegetation present in the treatments. Percent cover of the eelgrass was reduced in *Batillaria* removal areas (Figure 5). Two visual estimations of percent cover made by independent observers were highly correlated ($r^2 = .91$), and the mean values of the cover estimates were analyzed. These values for percent cover were transformed with a $\sqrt{\text{arcsine}}$ transformation for statistical analysis.

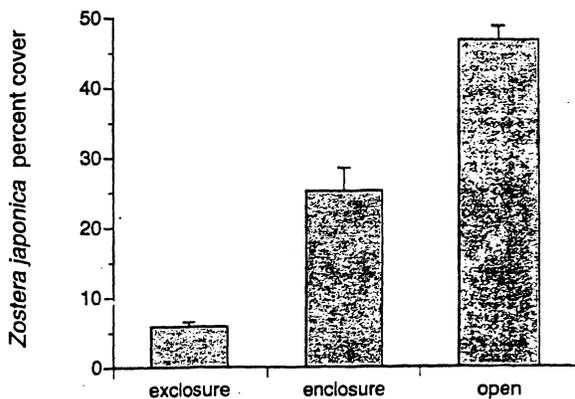


Figure 5. Percent cover of the eelgrass *Zostera japonica* in *Batillaria* exclosure, enclosure and open control treatments at end of five-month experimental period, September 2000. A one-way ANOVA produced an F-ratio of 57.84 ($p < .0001$). A post hoc Tukey-Kramer HSD test indicates that these relative percent cover values are significant.

Sediment chlorophyll a

Mean values for chlorophyll *a* concentration per unit area did not vary with treatment (Table 6).

Table 6: Mean chlorophyll a values for Experiment 2

Treatment	N	mean mg/cm ²	(+ s.e.)
Removal	8	30.7	(+ 1.87)
Inclusion	11	34.5	(+ 5.18)
Open Control	8	28.7	(+ 3.64)
ANOVA	F = .57	df = 26	p = .57

Samples were collected to a depth of 2mm.

Sediment particle size

Ratios of silt to sand from sediment cores at the end of the second experiment were similar in all treatments (Table 7). Sediment from several treatments was aggregated in flakes and settled slowly, but the samples with flakes were not related to treatment.

Table 7: Mean ratio of silt to sand (\pm standard error) for each treatment type in Experiment 2.

Treatment	n	mean ratio \pm s.e.
Exclusion	8	2.41 \pm .2
Inclusion	10	2.15 \pm .15
Open control	8	2.78 \pm .64

Meiofauna

We did not detect any direct relationships between infaunal population densities and *Batillaria* presence (Table 8). Sabellid and Spionid polychaete worms were common, and most of the families identified were characterized by elaborate feeding appendages suggesting deposit or suspension feeding mechanisms. There was no correlation, however, between the number of individuals with external feeding

appendages and snail density. Appendix B lists mean densities, standard error and frequency of detection for each invertebrate class sampled.

Nassarius responded negatively to *Batillaria* removal (Figure 6). Hermit crabs appeared to respond positively to the double snail density treatments, but a t-test with $p = .09$ shows this result isn't convincing. Although the differences are not significant, the pattern in relative hermit crab density among treatments is suggestive of both a positive reaction to *Batillaria* removal and the cages themselves.

Table 8: ANOVA values for meiofauna in Experiment 2

	F ratio	P-value
Nematodes	0.8396	0.4861
Nemerteans	0.7308	0.5441
Annelids		
Polychaetes		
f. Cirratulidae	2.3048	0.1036
f. Maldanidae	2.006	0.1412
f. Oweniidae	0.0756	0.9725
f. Sabellidae	0.6106	0.615
f. Spionidae	0.1111	0.9527
unidentified polychaete A	0.8813	0.4653
unidentified polychaete B	2.0593	0.1336
unidentified polychaete C	0.698	0.5628
worms with feed appendages	0.6883	0.5684
all tube building worms	0.7478	0.5347
Arthropods		
Amphipods	0.5066	0.6816
Copepods	0.1056	0.9559
Isopods	0.5049	0.6827
Ostracods	1.6528	0.2049
Hermit Crabs	1.3151	0.2936
Crabs (<i>Hemigrapsus spp.</i> <i>Cancer spp.</i>)	1.567	0.2244
Molluscs		
Batillaria, live	28.5103	0.0001
Batillaria, dead	0.8373	0.4872
Batillaria shells, broken	0.1804	0.9086
Batillaria shells, chipped	1.2908	0.3013
Nassarius, live	3.6085	0.0286
Nassarius, dead	2.101	0.1279

ANOVAs for infauna group by treatment (E,O,I,2I). Worms with feeding appendages include Sabellidae, Spionidae, Oweniidae, Maldanidae, Cirratulidae, and unknowns A and B. Tube building worms are Sabellidae, Spionidae, Cirratulidae.

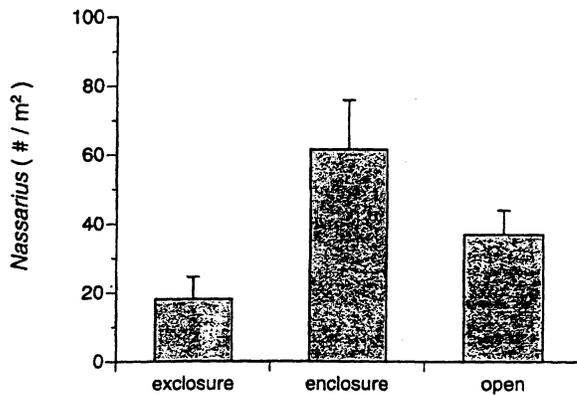


Figure 6. Density of mud snail *Nassarius fraterculus* in *Batillaria* exclosure, enclosure and open control treatments at end of five month experimental period, September 2000. One-way ANOVA: F ratio = 3.6085, $p = .0286$ ln transformed.

Design Artifacts

Several complicating features of this study arise from the experimental design itself. Experimental manipulations involving cages in soft sediment habitats inherently disturb the environment. Cages may slow the flow of water, affecting particle transport and deposition, as well as hydrodynamic stress within the cage. At least one organism, the hermit crabs, appeared to respond directly to the treatment, rather than to the manipulated *Batillaria* densities. Chlorophyll *a* concentrations seem to be affected slightly by the cages at several sites (GP, GT, FHS, JS and BFN) in the first experiment.

DISCUSSION

There are two aspects of the process of quantifying the impact of an invasion which require attention: *measuring* the impact of the invader and *understanding* the impact of an invader. In order to *measure* the impact of an invader, we need to know its density and distribution in the invaded habitat. We also need to know the time frame of the invasion, and have some idea of the per capita effects of the invader. Ideally, we will also know how those per capita effects vary with density, location, and time. After measuring the impact, we then seek to *understand* the impact, which requires knowledge of the mechanisms by which the per capita effects occur. In surveying a conspicuous but largely unstudied mud flat invader, we have quantified its density and distribution, and some aspects of its temporal variation. We have further identified several effects that the invader may have on its new environment. Several potential mechanisms exist for these effects, which we discuss in the context of the literature on other grazing mud flat snails.

Density and Distribution

We found *Batillaria* at all 12 sites sampled east of Swinomish Channel. The absence of a pelagic larval stage in *Batillaria* might make the deeper channel an impassable boundary for snail dispersal, and *Batillaria* may have never crossed in sufficient numbers to establish a population on the western mudflats. On the eastern mudflats, snail density range includes two orders of magnitude (25 – 1200 / m²). Average density in the southern bay is approximately 116 snails / m², in the central bay 584 snails / m², and 503 snails / m² in the northern bay. A conservative estimate that viable habitat extends 200 m offshore leads to a minimum total estimate on the order of 1.42 billion *Batillaria* snails in the bay. It is likely, then, that even if the per capita ecological effect of *Batillaria* is weak, the overall effect of this invader is worth attention considering the extreme numbers of *Batillaria* in the bay.

These extraordinary densities of *Batillaria* may in part reflect the apparent absence of competitors and specialized predators in the invaded ecosystem. As a new member of this community, *Batillaria* is not the primary food source of any major

resident consumer. Evidence of reduced size at high densities suggests that intraspecific competition may limit *Batillaria* density under certain conditions. It remains unclear what factor, or combination of factors, controls the density of *Batillaria* in Padilla Bay. We found no distinct correlation between snail density and particle size or vegetation cover, suggesting that other elements of the habitat are important to the robustness of snail populations.

Temporal Variation

Response variables based on population cycles vary in space and time across trophic levels, therefore an estimate of the impact of an invader may change with time (Parker et al. 1999, Berman et al. 1992). This quality of trophically complex systems such as the soft sediment community potentially results in an inaccurate assessment of overall, relative change among different community levels when sampling is infrequent and instantaneous. For example, successional colonization and community development may occur in a disturbed area (e.g. snail removal area) on scales of weeks to months for microorganisms, while species distribution within the community varies with time until the stable community is reached (Levinton and Stewart 1982). Long intervals between sampling (2 - 4 months) in our experiment may have allowed us to miss stages of community development associated with the removal of *Batillaria*, especially within the infaunal community. Also, the limited time of our study tested for population changes by migration for some species (*N. fraterculus*, *Pagurus spp.*), but allowed others with shorter generation times (diatoms, sabellid worms) the opportunity to reproduce and recruit to the treatment areas.

In order to quantify the current impact of *Batillaria* on the Padilla Bay ecosystem, we must quantitatively compare the equilibrium communities with and without the mud snail. However, we need to acknowledge that small-scale removals of the invasive species will perhaps give an assessment of the current ecological role in this invaded system, but we cannot conclude that this current impact is the same as the initial impact of the species during establishment in the new habitat. For example, the invader may have caused the local extinction of certain species through competition (e.g. Byers 1999) or predation (e.g. McCoid 1991) and the extinct species will certainly not return when

the invader is removed from a small experimental area. The invader may have caused permanent changes in habitat quality or structure that may not reverse with small-scale removal. It is also possible that the invader facilitated the invasion or expansion of another species, but upon removal of the first invader the second species remains persistent in the community. Few studies provide a detailed profile of an invasion from the beginning. This reflects the paucity of studies that thoroughly describe invaded communities before the arrival of the invader (Brenchley and Carlton 1983), and the challenge of obtaining complete and appropriate data for the assessment of impact. Rarely do researchers have the opportunity to obtain appropriate data on a native system both before and after an invasion (but see Grosholz and Ruiz 1995), since invasion studies focused on invasive species usually only occur after the invasion has taken place and the community is substantially altered. In summary, our assessment of the current ecological role of *Batillaria* contributes to the understanding of long term impacts of an invader, but does not provide a complete picture of the impact of the invasion from the beginning.

Mechanisms of effect

Several mechanisms of ecological impact have been frequently studied in the soft sediment community. We explore common impacts of mud snails, such as bioturbation and consumption, as possible mechanisms of *Batillaria*'s impact in Padilla Bay.

Physical disturbance is a significant structuring agent of soft sediment communities (Woodin 1983, Snelgrove and Butman 1994). The foraging and burrowing of mud snails can be a consistent and important disturbance to the soft sediment community. Brenchley and Carlton (1983) discuss the strong effects of the bioturbation by the eastern mud snail *Ilyanassa obsoleta* on mudflat community structure. In addition to bioturbation, snails may manipulate the average particle size of the surface sediments through the ingestion of small clay particles with food, and later egesting them as aggregated in fecal pellets, thus increasing the effective particle size of the sediments (Wilson 1991, Lopez and Levinton 1978 and sources cited therein). Bioturbation and pelletization by mud snails are habitat modifying processes that have been found to influence the distribution of other benthic organisms such as amphipods (DeWitt and

Levinton 1985), oligochaetes (Levinton and Stewart 1982), and diatoms (Connor and Teal 1982). Responses of certain organisms to sediment disturbance can also be important in determining community structure. For example, Woodin (1983) demonstrated that the tubes of the polychaete *Diopatra cuprea* create a spatial refuge from bioturbation, thus increasing species diversity in the area immediately surrounding the tubes. Also, diatom communities have been found to exhibit both positive and negative responses to bioturbation by mud snails. Connor and Teal (1982) found that the level of bioturbation caused by low densities of *Ilyanassa obsoleta* in a given soft sediment habitat actually contribute to an increase in diatom productivity. Increased mud snail densities in the same habitat caused a decrease in diatom productivity, possibly in part due to intolerable levels of sediment perturbation.

It is likely that *Batillaria* disturbs the surface sediments in a manner comparable to that of *I. obsoleta* and other mud snails. In areas of *Batillaria* removal, percent cover of the eelgrass *Z. japonica* was reduced, and the existing blades were covered with a thin layer of mud. In control areas, the eelgrass was relatively free of a mud covering. This pattern illustrates the physical effects of *Batillaria*'s bioturbation: consistent sediment disturbance prevents the accumulation of finer, more volatile sediments on substrate surfaces and maintains a well mixed layer of surface sediments. Other evidence of bioturbation might lie in the response of sediment chlorophyll *a* concentration to the removal of *Batillaria* in the first experiment. Although results were insignificant overall in this study, small-scale directional responses provoke further inquiry. It is possible that at certain sites in the bay, levels of bioturbation are detrimental to diatom productivity, while at other sites under different habitat conditions levels of bioturbation are a positive factor for diatoms. Further research is necessary to quantify bioturbation by *Batillaria*, and examine the effects of snail-induced disturbance on the community in Padilla Bay.

Another important mechanism of mud snail impact on the soft sediment community is through consumption and the resulting competition for food (Fenchel 1976, Lopez and Levinton 1978, Nichols and Robertson 1979). Benthic diatoms are a major food source for many mud flat organisms, and effects of sharing the resource depend on the strength and character of diatom grazing by potential competitors for the food source. Nichols and Robertson explained the increase in nematode populations following the

removal of *I. obsoleta* as a competitive release response. Consumption of diatoms can also have direct effects such as diatom community restructure (Connor and Teal 1982, Bianchi and Levinton 1981, Bianchi and Rice 1988). Connor and Teal showed that grazing by *I. obsoleta* affects diatom communities by increasing the proportion of non-migratory diatoms to migratory diatoms. In addition, selective grazing by mud snails based on size and shape of diatoms leads to the removal of certain diatom species or sizes, changing microalgal community dynamics and in some cases increasing diatom community production (Connor and Teal 1982, Fenchel 1976, Bianchi and Rice 1988). However, high densities of mud snails can overgraze diatom populations and suppress primary production (e.g. Cranford 1988).

One other mechanism of interaction between mud snails and the basic trophic levels of the community is through fertilization. Mud snails add ammonium to the system through the deposition of feces and acceleration of nutrient cycling (Lopez and Levinton 1978, Connor and Teal 1982). Fertilization might explain, at least in part, the more robust presence of *Z. japonica* in the presence of *Batillaria*.

The possible interactions between *Batillaria* and the diatom community are many and the character of the overall interaction remains unclear. Several studies have shown that *Batillaria* selectively consumes diatoms by size and shape (Cooper 1997, Whitlatch and Obreski 1980), and therefore potentially influences diatom community structure in a manner similar to that of other mud snails. Our results suggest different directional responses of sediment chlorophyll *a* concentrations to the removal of *Batillaria* in different habitats. If real, this pattern indicates that the presence of *Batillaria* does affect productivity of the diatom community, and that the effect varies with time and space. A possible explanation for this variability is that multiple mechanisms of impact occur between snails and diatoms, and the relative importance of each mechanism varies with habitat. For example, Connor and Teal (1982) showed that low densities of *I. obsoleta* exert a net positive effect on diatom community production through a combination of fertilization and low levels of disturbance and consumption. However, increased densities of the mud snail result in a net negative effect for primary production when the problems of overgrazing and disturbance outweigh the positive effects. It is possible, then, that there exists a threshold density of snails that tips the balance between net

positive and net negative effects on primary production in a specific habitat. Should a similar situation exist with *Batillaria* in Padilla Bay, the varying direction of chlorophyll response to snail removal may reflect the density of snails at that microhabitat relative to the threshold density. Further research is necessary to determine the factors limiting *Batillaria* density within the bay and how these factors vary on spatial and temporal scales.

A broader impact of *Batillaria*'s invasion may be the facilitation of *Z. japonica* establishment and growth. *Z. japonica* is native to Japan, and is thought to have been, like *Batillaria*, an incidental transplant to North America along with the Japanese oyster beginning in the 1930s (Harrison and Bigley 1982). Areas with the most robust *Z. japonica* beds are locales of historic oyster aquaculture, and also places where *Batillaria* is established (e.g. Padilla Bay, Boundary Bay). It is possible then that *Batillaria* modifies the habitat in some way that encourages *Z. japonica* growth. Further research is necessary to clarify this relationship.

Per capita effects

As the numerically dominant surficial macrofauna, *Batillaria* likely affects the structure of macrofaunal communities. However, due to the complexity of the mudflat habitat and the high variability on small spatial scales, our experimental design was inappropriate to determine *per capita* ecological effects of the invader. To determine *per capita* impact, more research is necessary, particularly experiments specifically focused on certain aspects of *Batillaria*'s ecology.

Conclusions

This report successfully illustrates the range, abundance and aspects of the ecological effect of *Batillaria attramentaria* in the mudflat community of Padilla Bay. Results in the large scale experiment (Experiment 1) do not indicate any significant directional responses in measured ecological parameters to the removal of *Batillaria*, suggesting that the effects of removing *Batillaria* from the surface community are not detectable above the natural variation in the system when considering the entire benthic

habitat of Padilla Bay. However, when effects of mud snail removal are examined on a smaller spatial scale, some interesting trends become apparent. After the removal of *Batillaria*, sediment chlorophyll levels changed and the eelgrass *Zostera japonica* decreased in abundance. Populations of the mud snail *Nassarius fraterculus* also suffered with the removal of *Batillaria*. Not surprisingly, effects of snail removal vary with habitat type, and appear to vary with season. This study highlights the importance of quantifying the effects of an invader over a broad spatial and temporal scale.

We have learned a little about the ecological role of *Batillaria* in Padilla Bay. Future research should explore mechanisms of the mud snail's interaction with *Z. japonica*, and study effects on the infaunal and diatom community on shorter time scales. Results presented here will be useful as baseline data for future work with the Padilla Bay ecosystem.

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APPENDIX A: Mean density (individuals / square meter) of meiofauna in Experiment 1

Live Batillaria	August			September			November			January			March			
	Site	E	I	O	E	I	O	E	I	O	E	I	O	E	I	O
BFN	0	448	474.7	16	112	92	40	516	288	152	300	260	164	184	452	
BFS	0	1152	1152	408	668	280	440	812	692	460	1408	1612	-	-	-	
DTN	0	160	160	12	140	232	0	164	88	8	148	152	4	148	64	
DTS	0	192	160	12	132	44	8	92	40	4	60	20	0	24	28	
FHN	0	948	954.7	100	148	132	20	456	648	-	-	-	-	-	-	
FHS	0	424	437.3	8	80	16	140	408	36	88	128	136	268	292	484	
GC	0	480	645.3	-	-	-	32	328	260	24	168	200	24	244	204	
GP	0	64	69.3	0	8	24	0	52	56	0	28	52	0	8	48	
ICN	0	204	272	32	116	348	12	276	316	4	224	512	0	228	516	
ICS	0	496	496	12	332	244	4	488	348	16	460	408	8	444	392	
JS	0	44	170.7	0	24	40	0	28	108	0	44	132	0	24	132	
SI	0	192	192	0	0	0	16	96	12	112	76	32	-	-	-	
Empty Batillaria shells																
BFN	10.7	10.7	10.7	4	0	0	16	32	32	120	36	52	152	4	24	
BFS	21.3	21.3	21.3	4	0	0	36	84	16	4	12	16	-	-	-	
DTN	0.0	0.0	0.0	0	0	0	4	0	12	0	0	0	4	4	0	
DTS	16.0	16.0	16.0	0	4	8	0	8	4	0	0	0	4	0	0	
FHN	10.7	10.7	10.7	8	12	20	0	36	36	-	-	-	-	-	-	
FHS	0.0	0.0	0.0	0	4	0	32	44	24	76	52	16	40	52	20	
GC	112.0	112.0	112.0	-	-	-	44	40	52	92	136	324	44	204	88	
GP	0.0	0.0	0.0	0	0	0	0	0	0	12	0	0	0	4	0	
ICN	10.7	10.7	10.7	0	0	0	0	8	16	20	8	12	0	0	12	
ICS	0.0	0.0	0.0	0	0	4	12	12	20	36	8	36	4	16	20	
JS	5.3	5.3	5.3	0	0	0	4	8	0	0	4	0	4	4	0	
SI	0.0	0.0	0.0	0	0	0	8	20	16	56	44	8	-	-	-	
Hermit Crabs																
BFN	0	0	0	4	20	20	148	60	0	52	16	0	12	16	4	
BFS	0	0	0	0	0	0	24	0	0	0	0	0	-	-	-	
DTN	0	0	0	48	16	4	20	0	4	0	0	0	0	4	0	
DTS	0	0	0	0	0	0	12	4	0	0	4	0	0	0	0	
FHN	0	0	0	0	0	0	4	36	4	-	-	-	-	-	-	
FHS	0	0	0	0	0	0	0	28	4	0	28	0	24	40	0	
GC	0	0	0	-	-	-	20	32	0	64	68	0	76	52	8	
GP	0	0	0	0	0	0	4	0	0	0	0	0	8	0	0	
ICN	0	0	0	8	20	24	16	36	12	8	28	8	0	72	12	
ICS	0	0	0	4	8	16	36	132	0	8	84	4	0	12	8	
JS	0	0	0	0	0	0	60	48	0	0	12	0	8	4	4	
SI	0	0	0	0	0	0	84	100	56	56	80	36	-	-	-	
Nassarius fraterculus																
BFN	4	0	0	-	-	-	36	44	4	28	16	0	8	4	16	
BFS	0	0	0	-	-	-	0	0	0	0	0	0	-	-	-	
DTN	3	0	0	-	-	-	12	16	12	12	12	12	0	0	24	
DTS	0	0	0	-	-	-	0	0	0	0	0	0	0	0	0	
FHN	0	0	0	-	-	-	4	16	8	-	-	-	-	-	-	
FHS	0	0	0	-	-	-	0	4	4	0	0	8	4	8	12	
GC	15	12	2	-	-	-	16	28	12	4	0	0	4	20	0	
GP	0	0	0	-	-	-	0	0	0	0	4	0	0	0	0	
ICN	0	0	0	-	-	-	8	16	4	0	60	24	0	12	16	
ICS	17	0	0	-	-	-	4	24	12	16	24	12	0	8	20	
JS	0	0	0	-	-	-	0	4	0	0	0	0	12	4	0	
SI	0	0	0	-	-	-	8	0	16	4	8	4	-	-	-	

APPENDIX C: Mean chlorophyll a values for Experiment 1

Experiment 1

January	E mean	(s.e.)	I mean	(s.e.)	O	(s.e.)
BFN	2.383	0.805	2.001	0.490	0.718	0.396
BFS	1.967	0.427	2.196	2.115	2.895	0.940
DTN	2.068	0.456	1.187	0.554	1.117	0.548
DTS	10.332	3.397	4.256	0.657	5.472	0.758
FHS	3.622	2.009	1.345	0.500	2.996	0.966
GP	8.411	1.363	12.221	3.931	9.348	5.870
GT	2.439	0.806	4.710	0.569	5.698	1.140
ICN	1.880	0.246	1.977	0.591	1.378	0.569
ICS	2.210	0.155	1.796	0.196	2.006	0.353
JS	4.124	1.411	5.123	0.240	4.322	0.282
SI	0.714	0.345	0.725	0.358	0.929	0.268
mean of all sites	3.650	2.996	3.738	3.323	3.713	2.853

August	E mean	(s.e.)	I mean	(s.e.)	O	(s.e.)
BFN	4.125	0.941	3.924	2.406	4.373	0.333
BFS	8.305	0.302	9.108	0.422	7.373	0.824
DTN	5.521	1.529	10.118	3.198	6.909	2.425
DTS	11.967	3.075	6.278	0.475	6.946	2.458
FHS	17.282	1.847	9.277	9.791	13.909	0.362
GP	6.273	3.876	8.203	1.439	17.732	-
GT	8.125	5.440	6.520	5.238	4.002	1.285
ICN	5.274	1.164	5.456	1.284	4.627	0.392
ICS	4.835	0.928	4.845	3.173	4.037	0.775
JS	9.355	4.109	13.059	6.637	14.820	5.861
SI	2.295	0.296	2.750	0.775	2.173	0.940
mean of all sites	7.772	1.721	7.388	3.067	8.109	5.030

dry wt approximately 3g. Experiment 1 values are mg chla / g dry sediment

