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## Physical habitat attribute mediates biotic resistance to non-indigenous species invasion

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**Abstract** A soft-shelled non-indigenous clam, *Nuttallia obscurata*, has invaded coastal soft-sediment habitats of the northeastern Pacific. In a survey of 35 sites within the San Juan Islands, Washington, USA, *Nuttallia* was found almost exclusively in sandy substrates, higher in the intertidal than most native clams (>1 m above mean lower low water). The distinctive distribution of *Nuttallia* suggested that tidal height and sediment composition may be important physical factors that control its refuge availability, regulating its exposure to predation and ultimately the success of its invasion. I tethered *Nuttallia* for 24 h in the high intertidal where it is typically found and in the low intertidal at an elevation where it was never found. Clams restrained to the surface suffered high mortality from crab predation at both tidal heights, whereas control clams with unrestricted burrowing movement exhibited high mortality rates only in the low intertidal. In a second experiment, I transplanted sediment within and between the two intertidal heights to measure effects of tidal height and sediment type on survival and burial depth of *Nuttallia*. At both tidal heights all clams placed on mud-cobble substrate, naturally common in the low intertidal, suffered high mortality rates (>60% in 24 h). *Nuttallia* on loosely packed sand substrate, naturally found in the upper intertidal, survived much better, however, because they buried deeper than in the tightly packed mud. Caged control clams at both tidal heights suffered no mortality. Apparently native predators are mitigating community level impacts of an invader by excluding *Nuttallia* completely from some beaches with improper sediment characteristics or relegating it in others to a zone not often inhabited by native species, thereby

reducing potential competitive interactions. These findings show that a physical habitat characteristic can mediate biotic resistance to an invader and thus control invasion success and community-level impacts. Generally, such physical-biological interactions may explain some of the reported site-to-site variability in invasion success, as well as the patchy distribution of many soft-sediment infaunal species.

**Keywords** *Cancer productus* · Introduced species · Physical-biological coupling · Predator-free space · Soft-sediment communities

### Introduction

Non-indigenous species introduced to novel areas often experience reduced predation pressure that is frequently considered fundamental to their success and proliferation (Lawton and Brown 1986; Crawley 1987; Wilson 1989; Wells and Henderson 1993). This expectation of lower predation rates in novel habitats has certainly been useful as a heuristic guideline, but empirical support for it as a dominant characterization of non-indigenous species introductions has been variable. For example, in some systems, native predators do in fact prey minimally upon invaders (Trowbridge 1995). However, in others, native predators have been shown to strongly inhibit the success of invading species (Robinson and Wellborn 1988; Baltz and Moyle 1993). In still others, predators prey heavily on an invader, but have little overall influence on the invasion success, apparently due to life histories of the invader that compensate for the high predation rate, e.g., high growth rates or fast reproduction (Reusch 1998).

The variable influence of predators may be due, at least in part, to the availability of refuges, since predator influence is typically highly dependent on characteristics of the physical environment (Gause 1932; Menge and Sutherland 1976; Malmqvist and Sackmann 1996; Chalcraft and Andrews 1999; Leonard 2000). Implicit to

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this observation is the fact that alterations of the physical environment do not just modify biological processes of a species in isolation, but can also govern consequent biotic interactions between species (e.g., Sousa 1979; Williams 1994; Boulding et al. 1999; Byers 2000). For example, in the context of physical factors influencing predator-prey interaction strengths, Gardner (1981) demonstrated that increased water turbidity reduced prey-finding abilities of visually orienting zooplanktivorous fish, which consequently decreased zooplankton mortality. Similarly, physical stresses modify chemical production within seaweeds that in turn alter herbivore consumption rates (Renaud et al. 1990; Cronin and Hay 1996). In this study I demonstrate the importance of a physical habitat attribute governing biological interactions between an invasive bivalve and native predators. Recognition of such interactions is important because the outcomes of invasions, even of a single non-indigenous species among many novel sites, are often viewed as idiosyncratic and case-specific from site to site (e.g., Drake et al. 1989; Gilpin 1990). Interactions between physical and biological processes that determine invasion success may imply that more complex, yet deterministic factors underlie the seemingly idiosyncratic fate of invasions.

#### Study organism and system

A non-indigenous, thin-shelled clam, *Nuttallia obscurata*, has quickly and successfully become established in many intertidal areas of the northeastern Pacific. *N. obscurata*, the purple varnish clam, is native to northern Asia (Japan and Korea), and was first noted in the northeastern Pacific (Vancouver, British Columbia, Canada) in 1991 (Forsyth 1993; Mills 1998), most likely introduced via shipping ballast water (Coan et al. 2000). *N. obscurata* has spread rapidly within its introduced range and is presently found at least as far north as the Discovery Islands, British Columbia (50.1°N) and as far south as Alsea Bay, Oregon, USA (44.4°N) (Jamieson 1997; Coan et al. 2000). *N. obscurata*, a suspension feeder, is commonly found buried 8–10 cm deep (and up to 20–25 cm deep) and usually inhabits sandy sediments in the high intertidal. Its maximum longevity is apparently in the order of 5 years (Yates 1999). While almost no ecological data are available on *N. obscurata* in its native habitat, one of its highly similar congeners, *N. olivacea*, is described as very dense (up to 5,000/m<sup>2</sup>) and associated with sandy sediment (Tsutsumi and Sekiguchi 1996; Miyawaki and Sekiguchi 1999). Additionally, *N. obscurata* and its congeners are found subtidally to depths of 20 m and are often buried up to 20 cm (Kira 1965 ( $\approx N. solida$ ); Habe 1968; Yamada 1995; Miyawaki and Sekiguchi 1999).

The existence of many generalist and bivalve-specializing predators makes marine intertidal and shallow subtidal communities a seemingly unlikely environment for an invading clam species to find inherently predator-free. Major clam predators occur at a variety of taxo-

nomic levels. In the northeastern Pacific these include: crabs, carnivorous gastropods, echinoderms, fishes, and shorebirds. Crabs in particular have been shown to heavily impact infaunal and epifaunal organisms in these communities (Yamada and Boulding 1996; Smith et al. 1999; Grosholz et al. 2000). Many studies on clams have shown that refuges are essential for survival to escape sometimes massive rates of crab predation (Blundon and Kennedy 1982; Hines and Comtois 1985; Eggleston et al. 1992; Skilleter 1994; Ebersole and Kennedy 1995; Zaklan and Ydenberg 1997; Smith et al. 1999). In particular, *Cancer productus*, the red rock crab, is a major forager in the northeastern Pacific intertidal and shallow subtidal communities (Robles et al. 1989; Yamada and Boulding 1996). Based on my observations and predator trapping, *C. productus* is the most common large aquatic predator in soft-sediment intertidal areas of the San Juan Islands, Washington, USA, and readily consumed *Nuttallia* that I placed on the surface in shallow water.

This study examines the mechanisms that allow *Nuttallia* to successfully invade and persist in this non-native, predator-rich, nearshore environment of the northeastern Pacific. Specifically I address the ability of native predators to suppress *Nuttallia* by measuring how the strength of biotic resistance varies with such physical attributes as tidal height and sediment characteristics. I hypothesized that these physical habitat attributes might determine the availability of refuge for the otherwise vulnerable *Nuttallia*, and thus mediate the impact of predation on this invading bivalve.

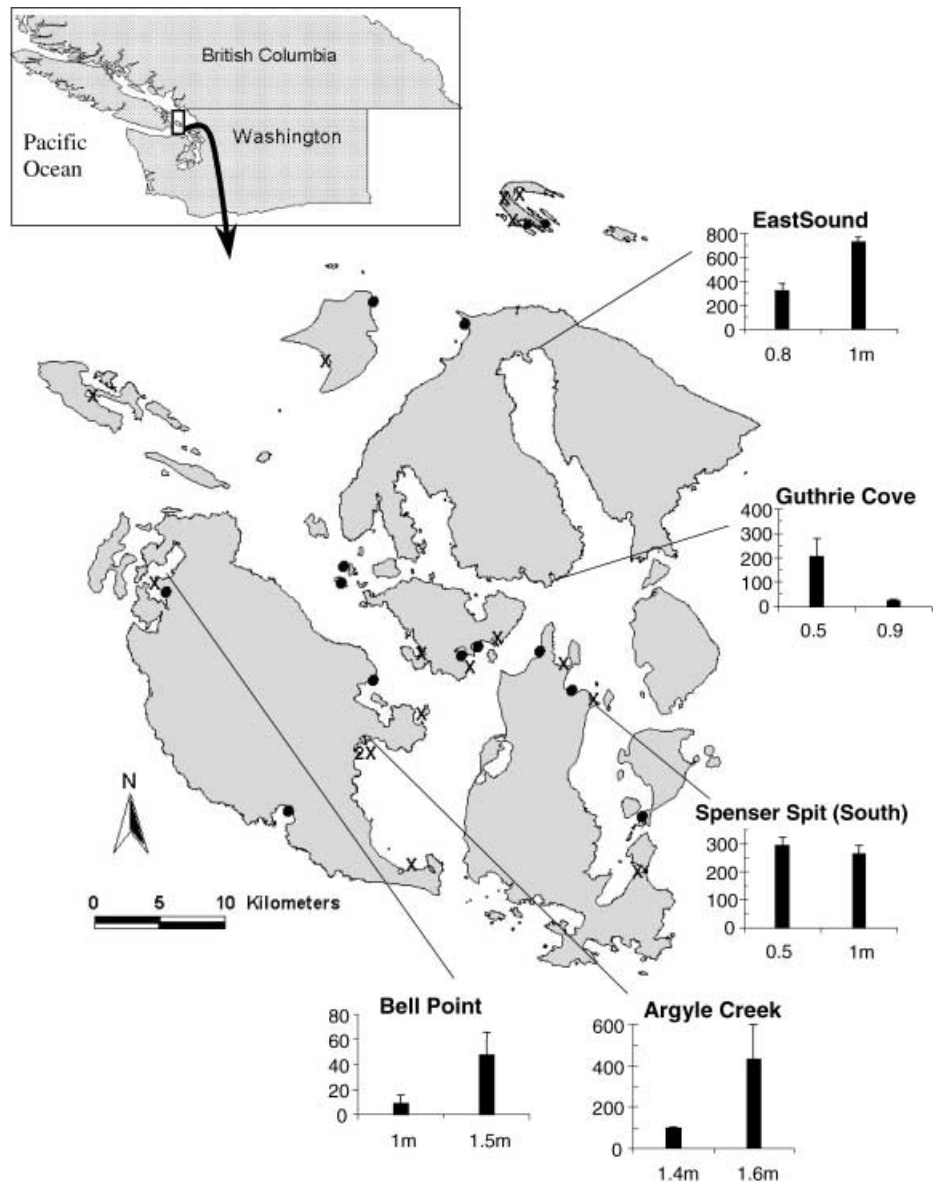
## Materials and methods

### Field survey

To sample the density and distribution of a recently invading bivalve, *Nuttallia obscurata*, I surveyed 35 intertidal sites within San Juan County, Washington (Fig. 1), a region with mixed, semi-diurnal tides. Soft-sediment sites were sampled that displayed characteristics generally associated with suitable clam habitat (e.g., calm water, a variety of sediment types). At the ten sites with the highest *Nuttallia* abundance, I extended at least three vertical transects perpendicular to the shoreline from the point of mean higher high water (MHHW) to the point of mean lower low water (MLLW) (U.S. datum MLLW=0 m). A cylindrical metal core of area 0.11 m<sup>2</sup> was pushed into the sediment 20 cm deep – a common maximum depth reported for this species (Mills 1998; Yates 1999; J.E. Byers, personal observation) – at chosen tidal heights along each transect. When possible, I included tidal heights 0.5 m and 1 m above MLLW to help maintain a standardized basis of comparison between sites (although sometimes topography, sediment characteristics, or water flow precluded exact matching). Because Argyle Creek samples were taken next to a flowing tidal creek, a MLLW reference point was difficult to establish. Thus, at that site tidal heights were approximated by referencing nearby Argyle Beach.

I removed and sieved sediment from inside each core, identified the clams, and measured their external dimensions to the nearest 0.1 mm. At the other sampled sites ( $n=25$ ), mostly where *Nuttallia* shells were sparse or absent from the surface, sampling was much less formal and consisted of digging several cores over a wide area at various tidal heights to establish the presence/absence of *Nuttallia*. Although competition is often thought to have limited power to

**Fig. 1.** Soft-sediment sampling locations and densities of *Nuttallia obscurata* within the archipelago of San Juan County, Washington (48°30'N, 123°00'W). Densities (individuals/m<sup>2</sup>) are depicted for the five sites where *Nuttallia* was found in highest abundance. Additional sampled sites that had only few *Nuttallia* are marked X; sampled sites that had no *Nuttallia* are marked O. Argyle Beach (a separate site from Argyle Creek) and Jackson Beach are separated by a tidal lagoon, but marked 2X for presentation clarity



structure distributions of suspension-feeding bivalves in soft-sediment communities (Peterson 1979), clams have been shown to emigrate away from areas with high densities of competitors (Peterson and Andre 1980; Peterson 1982). I examined the potential for interactions with resident clam species to influence the distribution of *Nuttallia* by conducting a linear regression of its density against the density of all other clams in cores where at least one *Nuttallia* was found. For this analysis, *Nuttallia* density was natural log-transformed and the combined density of the resident clams was natural log ( $x+1$ )-transformed.

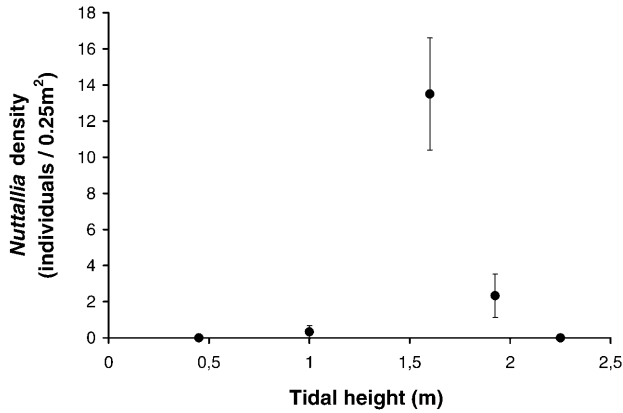
#### Field predation experiment 1

Because the field survey indicated that *Nuttallia* usually inhabits areas high in the intertidal, sometimes in a narrow band only a few meters wide, I wanted to explore possible mechanisms for this pattern. In lower reaches of the intertidal, longer submersion times typically afford aquatic predators more foraging time than in the high intertidal (Robles et al. 1989; Yamada and Boulding 1996; but see Micheli 1997a). To test whether heightened predation by aquatic predators in low intertidal areas may contribute to the

clam's almost universal absence from the low intertidal (<0.5 m), I conducted a transplant experiment. In addition to testing the effect of a clam's shoreline elevation on mortality, I also designed the experiment to test how a clam's freedom to burrow below the sediment surface might affect the survival of transplanted clams.

First, to determine the natural distribution of *Nuttallia* at the experimental site, I surveyed the intertidal at Argyle Beach, San Juan Island, a sheltered, moderately sloping soft-sediment beach. On 28 July 2000, three transect lines were placed perpendicular to the waterline, extending from the low to high intertidal. Transects were spaced 10 m apart and along each I placed a 0.25 m<sup>2</sup> quadrat at points corresponding to 0.45 m, 1 m, 1.6 m, 1.9 m, and 2.25 m above MLLW, which were surveyed with a mounted hand level and meter stick. Densities of *Nuttallia* were obtained by sampling quadrats to a depth of 20 cm. To provide a better estimate of the variance of *Nuttallia* density, at the tidal level of greatest clam density one extra quadrat was sampled at a random distance within 5 m to the side of each transect.

Sampling indicated that *Nuttallia* occupied a narrow band in the upper intertidal (Fig. 2). From this zone of high abundance, 180 *Nuttallia* (>15 cm in shell height) were collected and numbered on the shell with permanent marker (916 Brite-Mark paint pens,

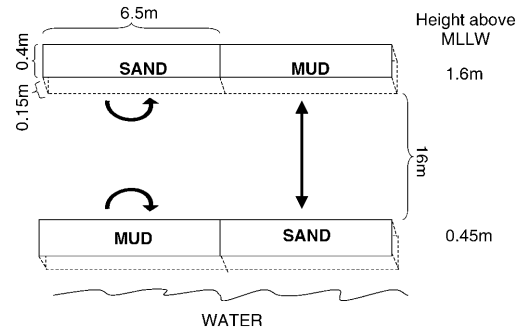


**Fig. 2.** Densities of *N. obscurata* at experimental study site (Argyle Beach) at five tidal heights along transects perpendicular to waterline. Tidal height represents distance above MLLW. Error bars represent 1 SE.  $n=3$  for each tidal height except for height 1.6 m where  $n=6$

Mark-Tex, Englewood, N.J., or Sharpie permanent marker, Sanford). The height of each clam was measured from the umbo to the ventral margin at an angle perpendicular to the length (anterior-posterior) axis. I assigned 60 clams to each of three treatments: a short tether of 2–3 cm designed to prevent the clam from burying and hold it on the surface; a long tether of 20 cm designed to control for the presence of a tether yet still allow the clam to bury up to its natural maximum burial depth; and a non-tethered clam control to which nothing was attached to control for mortality that may have been due to the tethering process. The use of already fairly sedentary species reduces artifacts typically associated with tethering experiments. Furthermore, employing the two tether controls (long tether and no tether) at each shoreline elevation allowed me to test explicitly for any artifactual enhancement of predation by tethering across habitat types. In the absence of a higher-order tethering artifact (i.e., an interaction between tethering effect and habitat) I could justify comparing relative rates of predation between the two tidal elevations (Peterson and Black 1994). Tethers were waxed dental floss and were attached to the clams with superglue (Krazy glue, Elmer's Products) near the umbo and reinforced with a small 0.25cm<sup>2</sup> piece of duct tape. The glue was left to dry for approximately 20 min. I then tied the tether to a 15-cm-long garden staple, with one short-tethered clam and one long-tethered clam tied to each staple.

I placed half of the clams in each treatment in the low intertidal (0.45 m), where no *Nuttallia* had been found in the transect sampling, and half in the high intertidal (1.6 m), where the maximum density of *Nuttallia* had been found during sampling. I pushed staples into the sediment spacing them ~20 cm apart in a row along these elevation contours. One “no tether” control clam was placed with each staple; thus, each staple had a clam from each of the three treatments associated with it.

The experiment was allowed to run for 24 h (submersion time for low zone=20 h; high zone=14.5 h; immersion observed directly, emergence estimated from a graph of the day's tidal cycle), at which point I recorded the status of each clam as dead, alive, or missing. Missing clams (19 out of 180) were assumed to be dead due to predation mortality, since this was the most logical explanation for their absence for at least two reasons. First, the clams were not strong enough to break their own tethers. This was supported by the fact that the tethers of missing tethered clams were always on the sediment surface and did not lead down into the sediment (the direction the clam would most likely pull against the tether). In contrast, I did observe one of the clam's major predators, the red rock crab (*C. productus*), putting a tremendous strain on a tether as it tried to pull the clam away, presumably to eat it in a more secluded spot. Second, all clams that were ripped off tethers, but subsequently found in the vicinity of the experiment, exhibited definitive charac-



**Fig. 3.** Design of experiment 2. Dashed lines represent dimensions below the sediment surface. Bold arrows represent directions of sediment transplants. Clams were planted in the center of each experimental trough. Control cages were implanted 3 m to side of each experimental row (not pictured). Note that drawing is not exactly to scale

teristics of crab damage, further suggesting crabs were responsible for broken tethers. Ultimately, whether I included the missing clams as dead or excluded them from analyses made no difference to the patterns or statistical significance of the results.

I recovered most of the non-tethered clams in the immediate area of the staple. In a few cases I dug for them over a wider area (1 m radius from staple). Only eight of the non-tethered clams were not recovered (dead or alive). Because all eight of these came from the low zone, where clam burial is more difficult (see Results section: experiment 2), and because no clams were missing from the high zone, where burial is easier, it is unlikely these clams evaded detection by burrowing far from their initial placement. Regardless, whether these clams were classified as dead or excluded from the analyses again had no influence on patterns or significance in the results.

I analyzed the effects of the factors shoreline elevation and tether treatment and the covariate clam size on clam mortality over this 24 h period using logistic regression (Proc catmod; SAS V6; SAS 1987). I first, however, examined the effect of long tethers versus no tethers on *Nuttallia* mortality within each tidal height. A significant difference would indicate that the application of a tether affected the clams. No significant difference would indicate that no-tether and long-tether clams could be combined to compare against short-tether clams for analyses.

#### Field predation experiment 2

Because experiment 1 indicated that *Nuttallia* restrained to the surface, especially in the low zone, were more susceptible to predation, I wanted to explore how the different substrates available at high and low zones might influence clam mortality. I collected *Nuttallia* ranging from 24 mm to 50 mm in shell length (=19–44 mm in shell height) from the upper intertidal band at Argyle Beach on 27 August 2000. The clams were taken back to the laboratory where the outer shell surfaces were allowed to dry in air. I measured the length of each clam (from anterior to posterior tip) with digital calipers and marked the clam with a corresponding number in large font with an oil-based paint pen (916 Brite-Mark by Mark-Tex) on the periostricum and with permanent ink on a small sandpapered area of shell near the umbo. After clams were measured and marked, I attached each clam to a 40 cm tether of waxed dental floss in the same manner as in experiment 1. The tether was tied as before to a 15-cm-long garden staple, with two clams tethered to each staple. The glue was left to dry for approximately 1 h, after which the clams were kept overnight in an aerated seawater table, and tethers were checked the next morning to ensure tight adhesion.

During low tide on 28 August, I dug a trough parallel to the waterline 6.5 m long×0.4 m wide×0.15 m deep at both the low (+0.45 m) and high tidal zones (+1.6 m) (Fig. 3). I placed the



sediment removed from these troughs into 5-gallon (22.7 l) buckets and then transferred it between the troughs in opposite zones. This resulted in one trough in the high intertidal containing mud-cobble sediment with few interstices transported from the low intertidal, and one trough in the low intertidal containing mostly sandy, porous sediment transported from the high zone. Adjacent to the end of each trough in the high and low zones I dug another identical trough. The sediment removed from these two troughs was placed into plastic buckets and poured back into the hole from which it was dug. This procedure did not change the sediment type in this second trough, but controlled for any effects of digging and pouring the sediment. I removed naturally occurring *Nuttallia* from the upper 5 cm of sediment in both troughs containing sediment that originated from the high zone. I quantified sediment characteristics of each tidal height by analyzing cores (depth 10 cm) using a combination of wet sieving for the sand fraction and pipette analysis for the silt and clay fraction as described in Buchanan (1984). Also, I extracted three cores (4 cm deep, 4.25 cm diameter) at each tidal height that I combusted for 4 h at 450°C to measure the percentage of organic material at each tidal height. Prior to organic analyses I removed rocks with the smallest dimension >1.25 cm by sieving.

After the sediment was prepared, I placed the garden staples (each with 2 clams) 20 cm apart down the middle of each sediment row with the number of clams per trough ranging from 62 to 68 (31–34 staples). With this arrangement, the density of clams on the surface was approximately the same between experiments 1 and 2 (although the absolute number was different). The longer (40 cm) tether employed in this experiment was to allow clams the potential to bury diagonally into a sediment type different from the one upon which it was initially placed. The clams were left on the surface to bury themselves. However, while waiting for the tide to rise, I poured water over the clams periodically to keep them and the sediment moist and facilitate their burial. Two people guarded the clams from birds, crabs, and other would-be predators while they were out of the water and for 1 h after submersion to allow the clams a chance to bury before giving predators access. More than two thirds of the clams extended their feet or attempted to start burying during this time period.

To examine clam mortality when predators were excluded, I inserted three 1.25 cm wire mesh (hardware cloth) cages (30×30×18 cm) into the sediment spaced 0.5 m apart at both tidal heights. I removed the sediment from inside each cage, placed it in buckets, and then poured it back inside the cage. Twenty marked clams with mock tethers (not tied to a staple) were added to each cage and the cage top was sealed with plastic cable ties to keep out predators.

After 24 h (submersion time for low zone=20.5 h; high zone=16.3 h), I ended the experiment by removing tethered clams and noting their status (dead, alive, or missing). If a clam was buried, I carefully dug down to it and measured its burial depth (the distance from the surface to the tip of its shell) with a measuring tape. I analyzed the effects of the factors tidal height and sediment type on clam mortality over this 24-h period using logistic regression (Proc catmod; SAS V6; SAS 1987). My design was technically pseudo-replicated for testing the interaction of sediment and tidal height because only one long trough of each sediment type was manipulated at each tidal height. While this design was necessitated by logistical considerations, clam responses to the interaction should still incorporate much small-scale variability because, compared to the size of a clam, each trough covered a relatively large linear distance (6.5 m). Nonetheless, statistical analysis of the sediment×tidal height interaction on mortality in the logistic regression analysis was precluded. The effect of clam size on mortality was tested with a separate logistic regression. Since data for the two logistic regressions outlined here utilized the same response data, I used a Bonferroni correction factor, which set the significance level for each test at 0.025 (0.05/2).

To analyze the effect of sediment treatment on burial depth of *Nuttallia*, I used one-way ANOVA with the two troughs of each sediment type (one at each tidal height) as replicates. Similarly I examined the effect of tidal height on *Nuttallia* burial depth using one-way ANOVA. Both of these tests separately analyze the

effects of different treatments on the same data. Therefore, I employed a Bonferroni correction, which again set the significance level for *P* values of both tests at 0.025 (0.05/2).

Because the clams in the experiment were guarded until submerged, no birds approached the clams. Also, the distinctive markings and cracks in dead *Nuttallia* shells make it reasonable to assume that all of the mortality during these experiments is attributable to aquatic predators—almost exclusively crabs. Aquatic predators can typically forage longer in the lower intertidal because it is submerged longer during the tidal cycle (Robles et al. 1989; Yamada and Boulding 1996). Therefore, to enable better comparison of mortality rates between tidal heights and between experiments 1 and 2, I standardized measured mortality rates by the submersion time of each zone to render hourly per capita instantaneous mortality rates (*Z*). Values of *Z* were calculated using the standard equation:  $N_t = N_0 \times e^{-Zt}$ , where  $N_0$  is the number of organisms at time=0;  $N_t$  is the number of survivors at time=*t*; *t* is the number of hours submerged; and *Z* is the instantaneous rate of mortality. With this standardization, mortality rates could be compared independent of the number of hours of access by aquatic predators.

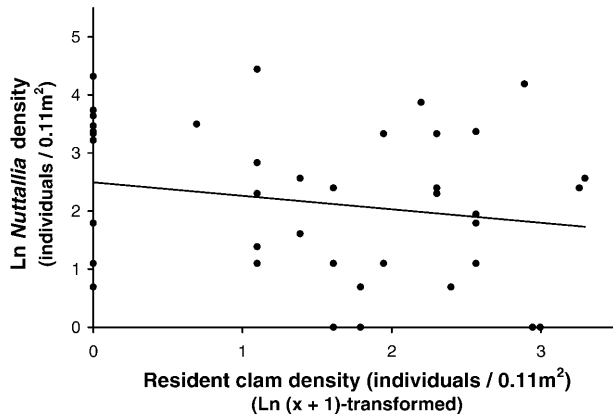
## Results

### Field survey

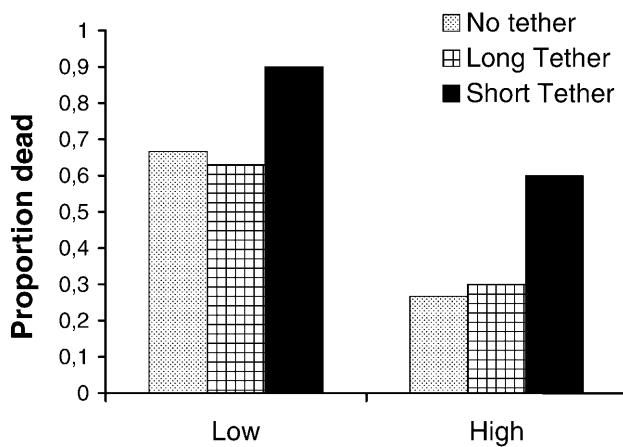
*Nuttallia* was highly abundant in five sites around San Juan County (Fig. 1) with adult densities at these sites higher than observed for any other infaunal bivalve (average max. density >340 *Nuttallia*/m<sup>2</sup>). (Other predominant bivalves included *Protothaca staminea*, *Venerupis philliparum* (≈*Tapes japonica*), *Mya arenaria*, *Saxidomus giganteus*, *Macoma nascuta*, and *Macoma inquinata*; rarely did any of their densities exceed 125/m<sup>2</sup>). At a sixth site, Argyle Beach, *Nuttallia* were moderately abundant with densities up to 54/m<sup>2</sup>, while in 16 of the other sampled intertidal sites *Nuttallia* was present, but in low numbers (<20/m<sup>2</sup>). At 13 sites no *Nuttallia* were observed. Consistently, *Nuttallia* was restricted to sandier sediment and was located high in the intertidal (≥ 0.5 m). Very often, especially in the higher reaches of the intertidal (>1.4 m above MLLW), *Nuttallia* was the only clam found. Among the 12 sites where *Nuttallia* was most abundant, i.e., where there were more than just a few thinly distributed individuals, the lower limit to its vertical distribution (mean±SD) was 0.92±0.41 m and the average of its upper vertical distribution was 1.50±0.30 m. Guthrie Cove, however, was an exception having low *Nuttallia* densities (mean±SD) extending down to 0.25 m (24±39.2 individuals/m<sup>2</sup>), and I even found two clams at 0 m (4.5±5.2 individuals/m<sup>2</sup>). The linear regression of *Nuttallia* density (ln-transformed) against the density of all other clams (ln(x+1) - transformed) within each core where at least one *Nuttallia* was found exhibited no significant relationship (*n*=41, *r*<sup>2</sup>=0.038, *P*=0.22) (Fig. 4).

### Field experiment 1

At Argyle Beach, *Nuttallia* were confined to a narrow range of shoreline elevation (Fig. 2) in a sandy band in



**Fig. 4** Relationship between *N. obscurata* density (Ln transformed) and the density of all other resident clams [Ln (x+1)]-transformed within field survey cores where at least one *Nuttallia* was found



**Fig. 5.** Mortality of *N. obscurata* over 24 h period due to tethering treatments at low (0.45 m) and high zones (1.6 m) in experiment 1. Long tethers were 20 cm and short tethers were 2 cm, which constrained clams to the surface.  $n=30$  for each treatment at each tidal height

**Table 1** Effects of tidal zone, treatment [short tether (2–3 cm) versus no tether and long tether (20 cm) controls combined], their interaction, and size (covariate) on mortality rate of *Nuttallia obscurata*. Results are presented for the reduced model from logistic regression for experiment 1. All higher-order covariate interaction terms were non-significant and sequentially removed

Effect	$\chi^2$	<i>P</i>
Intercept	0.08	0.78
Zone	17.41	<0.0001
Treatment	12.74	0.0004
Zone × Treatment	0.11	0.75
Size	1.02	0.31

the upper intertidal of approximately 6 m width. Even within this narrow area *Nuttallia* density peaked quite markedly in the center of this band and dropped off rapidly on either side. In the experiment the effect of the no-tether and long-tether treatments on clam mortality were

**Table 2** Sediment characteristics at low and high tidal heights of experimental site at Argyle Beach. Sediment that would not pass through a 32 mm ( $-5\phi$ ) square mesh sieve includes both cobble (64–80 mm) and large pebbles (32–64 mm) referred to collectively as “cobble”. “Gravel” represents sediment between 2–32 mm; “sand” is sediment between 0.0625–2 mm; and “fines” is everything <0.0625 mm. All percentages are calculated by weight. Sorting (SD) is an index of the dispersion of sediment grain sizes

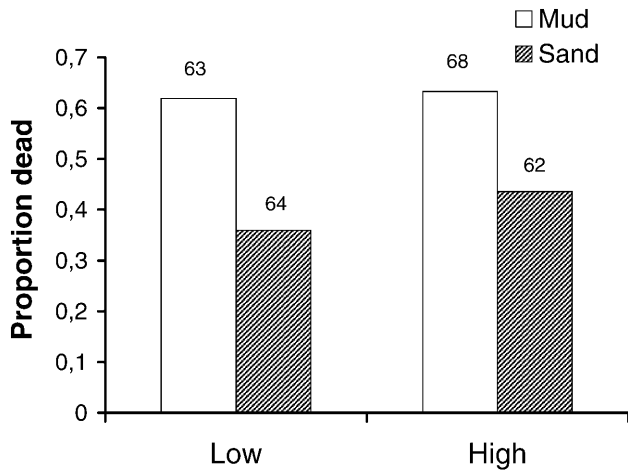
Sediment characteristics	Tidal zone	
	Low	High
% Cobble	52.7%	20.4%
% Gravel	27.4%	49.4%
% Sand	17.0%	29.3%
% Fines	2.9%	0.9%
Median grain size (mm)	34.3	6.1
% Fines (excluding cobble)	6.2%	1.2%
Excluding cobble and gravel		
Median grain size (mm)	0.21	0.55
Sediment category	Fine sand	Coarse sand
Sorting	1.33	1.43
Proportion organic ( $\pm$ SD)	0.026 $\pm$ 0.0049	0.015 $\pm$ 0.0059

not significantly different at either tidal height (high zone  $\chi^2=0.08$ ,  $P=0.77$ ; low zone  $\chi^2=0.07$ ,  $P=0.79$ ). Therefore, in subsequent analyses data from these two treatments were pooled to test for effects of short-tethered clams versus no tether and long tether control clams combined. Mortality of clams in the experiment was high, especially on short tethers and in the low zone (Fig. 5) and differed significantly by tidal height and tethering treatment (Table 1). Clam size did not significantly influence mortality. All dead clams exhibited cracking and chipping indicative of crab predation.

## Field experiment 2

Sediment characteristics between the high and low tidal elevations were substantially different (Table 2). More than 2.5 times as much cobble by weight was present in the low intertidal. The rest of the sediment in the low intertidal was much muddier and more tightly packed (as indicated by a higher percentage of fines and a lower median grain size of sands and fines) than the high zone. In contrast, sediment grain size in the upper intertidal was larger, which given the equal sorting of grain sizes creates greater interstitial space. Tethered *Nuttallia* had significantly higher mortality when placed on a mud-cobble substrate compared to sand (Fig. 6). Substrate type significantly affected clam mortality, while tidal zone did not (Table 3). Also, the interaction of tidal zone with substrate type appeared to have little, if any, influence on mortality (Fig. 6). Again, size was not a significant influence on clam mortality ( $\chi^2=2.72$ ,  $P=0.10$ ).

Substrate also exerted a significant effect on the depth of clam burial (ANOVA,  $F_{1,2}=73.9$ ,  $P=0.013$ ), while tidal height did not (ANOVA,  $F_{1,2}=0.043$ ,  $P=0.85$ ). A power analysis revealed that despite the non-significant



**Fig. 6.** Mortality of *N. obscurata* over 24 h period due to sediment type and tidal zone in experiment 2. *Mud* indicates sediment naturally found in the low zone; *sand* indicates sediment naturally found in the high zone. Numbers above each bar represent the number of *Nuttallia* exposed to that treatment

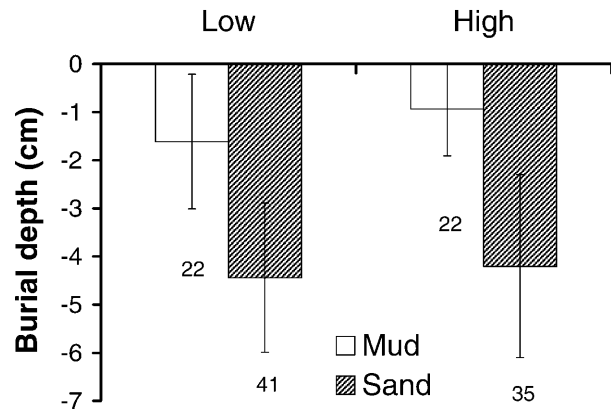
**Table 3** Logistic regression analysis of experiment 2 on the effects of tidal zone and substrate on mortality rate of *N. obscurata*. Although limited replication precluded testing of the substrate  $\times$  zone interaction, the data (Fig. 6) seem to reflect very little, if any, interactive effect

Effect	$\chi^2$	P
Intercept	0.13	0.71
Zone	0.53	0.47
Substrate	13.14	0.0003

result, this latter analysis had sufficient power ( $1 - \beta = 0.91$ ) to detect as little as a 1 cm difference in burial depth between tidal heights. Live *Nuttallia* placed on the sand substrate were on average 3 cm deeper at the conclusion of the experiment (Fig. 7). Clams on the mud-cobble substrate buried to extremely shallow depths, averaging only 1.3 cm (Fig. 7). In fact, of the 49 *Nuttallia* found alive that had been placed on the mud substrate, 22% were found entirely on the surface. *Nuttallia* in the low mud were found an average of 0.7 cm deeper than in the high mud (mean $\pm$ SD: low 1.61 $\pm$ 1.40; high 0.93 $\pm$ 0.98). *Nuttallia* in low sand were found an average of 0.2 cm deeper than in the high sand (low 4.44 $\pm$ 1.55; high 4.21 $\pm$ 1.90).

Mortality of *Nuttallia* due to sources other than predation over this 24-h period was essentially negligible, as clam survival rates in the wire mesh control cages were 100%. One *Nuttallia* in a control cage in the low zone, however, was slightly cracked (seemingly by a crab that reached through the cage mesh), but was still alive.

The instantaneous mortality rate ( $Z$ ) standardized by the number of hours that clams were submerged was higher in the high zone for experiment 2 (sand:  $Z=0.035$ ) than experiment 1 (long and non-tethered clams on sand:  $Z=0.023$ ). In the low zone the standardized per capita



**Fig. 7.** Burial depth (cm) of *N. obscurata* over 24 h period by tidal zone and sediment type in experiment 2. Error bars represent 1 SD. Numbers above each bar represent the number of live *Nuttallia* contributing to the estimate for each treatment

hourly mortality rates between the experiments were similar: experiment 2, mud:  $Z=0.047$ ; experiment 1, long and no tethers on mud:  $Z=0.0525$ .

## Discussion

Even after standardization for exposure time to predators, values of  $Z$  were highest for clams in the low intertidal on mud, emphasizing that the high rate of *Nuttallia* mortality was due to more than just increased hours of predator access in the low intertidal. Specifically, a physical site characteristic – the availability of large grained, loosely packed sandy sediment in the high intertidal – allows *Nuttallia* to persist despite otherwise high potential levels of predation. Soft-sediment characteristics are often well correlated with tidal height, with finer, muddier sediments found lower in the intertidal, and sandier, less packed grains found higher (Brown et al. 1989; Peterson 1991; Horn 1993). By independently manipulating sediment within tidal heights, I demonstrated that sediment characteristics (i.e., grain size, percent cobble, interstitial space) are an important influence on *Nuttallia* mortality and not tidal height per se. Specifically, sediment characteristics influence *Nuttallia* mortality by regulating the depth to which it can bury and presumably determining the ease with which it can be encountered and eaten by predators.

Elevation on shorelines has often been recognized as a major factor that directly controls predation rates by controlling the duration of predator access (e.g., Peterson 1991). In this system I have demonstrated that elevation is more important for its indirect effects on predation rates. Specifically, the elevation of a shore affects sediment qualities that in turn determine predation rates. I suggest that the interaction of the physical sorting of intertidal slopes and the consequent, sediment-grade dependent biological processes like predation may prove to be a widespread and important structuring component

of soft-sediment communities, perhaps helping to account for the patchy distributions of many infaunal species.

Many studies have documented the importance of refuges on bivalve survival (Arnold 1984; Lipcius and Hines 1986; Irlandi 1997), and deep burial is a common means for soft-sediment species, especially soft-shelled clams, to minimize mortality from predation (Blundon and Kennedy 1982; Hines and Comtois 1985; Zaklan and Ydenberg 1997; Smith et al. 1999). For example, Skilleter (1994) measured mortality of two native clams at 78–90% over 7 days, but while clams were in refuges (amidst shells and another bivalve *Rangia cuneata*) mortality dropped to 0–15%. Smith et al. (1999) noted that 5 cm was a critical burial depth for the soft-shelled clam, *Mya arenaria*, to escape predation by *C. productus*. Crabs foraging for clams shallower than this depth did not actually have to dig, but rather could simply pull clams out through the sediment with their chelipeds. This change in foraging mechanics decreased excavation times to as fast as 25 s. The present experiment confirms that burial depth also greatly increases the clam's chances of survival. In experiment 1, although *Nuttallia* on mud buried only to ~1 cm, they were nonetheless less vulnerable than when they were completely constrained to the surface. Further, *Nuttallia* on sand burrowed 3 cm deeper in a 24-h period than *Nuttallia* on mud-cobble substrate, and their chance of mortality decreased by 31–42%.

The mortality of *Nuttallia* on mud substrate was extraordinarily high. For example, in the high zone its chance of mortality on mud in experiment 2 compared to short-tethered clams in experiment 1 was essentially equal. That is, a *Nuttallia* high in the intertidal on mud had the same likelihood of mortality as one tied to the surface. In the low zone (experiment 2), mortality on mud was also extremely high, but slightly less than the rate for short tethered clams (experiment 1), presumably because longer submersion in the lower intertidal helps to facilitate clam burial to a small extent. Mud substrates, however, are not inherently inhospitable to clams. Certain native clams such as *Macoma nasuta* and *M. inquinata* can be found abundantly in muddy sediments in the lower intertidal, commonly inhabiting depths  $\geq 8$  cm (Kozloff 1996); J.E. Byers, personal observation

Artifacts could have affected absolute rates of mortality measured here, but in any event they should not affect the direction of effects used in comparisons. While the experiments demonstrated that the relative survival of *Nuttallia* is much higher in sand than mud, its mortality in sand – the substrate where it naturally occurs – was still high (35–40%). Since *Nuttallia* continues to persist at Argyle Beach, it is impossible that this predation rate is sustained daily. At least two factors account for the elevated rate measured in my experiments. First, I did not measure the mortality at the depth at which it normally occurs; rather I started these clams out on the surface to measure their ability to take refuge. Only 8

*Nuttallia*, or 3% of the total used in experiment 2 (6.7% of total live clams at experiment's conclusion), buried to their natural (and presumably safer) depth of at least 7–8 cm within the 24-h experimental period. Thus, mortality was almost certainly boosted by predation of clams that did not bury sufficiently, either because they stayed on the surface or were taken by predators quickly after the experiment started. Second, the high density of *Nuttallia* on or near the surface likely increased the predation rate due to an experimental artifact that induced apparent competition (sensu Holt 1977) between conspicuous and inconspicuous prey. Due to the aggregation of predators attracted to the high density of conspicuous and easily accessible prey (clams on short tethers or impenetrable substrate), even clams that normally would have had sufficient crypsis to escape predation (clams with long or no tethers on sand) may have been discovered by a high concentration of feeding predators, which often concentrate attention in patches of denser prey (Murdoch and Oaten 1975).

The higher hourly per capita rate of mortality in the high zone in experiment 2 compared to experiment 1 may also be explained by heightened predation on inconspicuous prey due to apparent competition. While overall *Nuttallia* densities between the two experiments were similar, in experiment 2 there were 126% more clams on or within ~1 cm of the surface ( $n=68$ ) compared to the number of clams tethered to the surface in the high zone of experiment 1 ( $n=30$ ). Thus, elevated densities of conspicuous prey may have increased the predation rate in the high zone in experiment 2. In contrast, in the low zone where the number of *Nuttallia* with restricted burial was more similar between experiments ( $n=90$  vs  $n=63$ ), Z values were also very similar between experiments. The higher mortality rate of clams on sand in the high zone in experiment 2 may also have been due to some differential effect of the tilling of the sand substrate during experimental setup. Also, although experiments 1 and 2 were separated by 1 month, crab predators may have retained an association of easily encountered prey in the high zone from “training” on tethered clams in experiment 1 (Micheli 1997b). This latter mechanism, however, would not explain why mortality rates stayed relatively constant in the low zone between experiments. Regardless of the reason for the difference between clam mortality rates on sand in the two experiments, in both experiments standardized rates in sand were much lower than the rates in mud.

#### Implications for invasion

Non-indigenous species that defend themselves similarly to native prey species will likely encounter predators in the non-native habitat that are capable of eating them. The abundance of bivalve predators in nearshore coastal and estuarine environments should make it an unlikely environment for an invader to find inherently “predator-free”. Consequently, successful bivalve invaders will



likely be species that readily exploit a spatial, temporal, behavioral, or physiological refuge to escape predators. *Nuttallia* in particular should be an ideal prey item because it is an extremely easy clam to crack; in fact it can be easily crushed by hand (J.E. Byers, personal observation). The thin shell of *Nuttallia* and its high ratio of tissue to shell size underscore its dependence upon refuges to minimize exposure to predators. Native crabs readily consume local hardshell venerid clams, e.g., *Protothaca staminea* and *Tapes japonica* (itself a non-native species) (Pearson et al. 1979, 1981; Boulding 1984; Juanes and Hartwick 1990), which live in similar habitats often contiguous to, or sometimes overlapping with, *Nuttallia*. These hardshell clams require up to 7–8 times the pressure to crack compared to a *Nuttallia* of equal tissue mass (J.E. Byers, unpublished data). Burying deeply and inhabiting high shoreline elevations are thus effective, and seemingly necessary, ways for *Nuttallia* to increase crab search time and thus decrease its otherwise extremely high relative profitability as prey. Because native clams are largely absent from the very high reaches of the intertidal (>1.4 m) where *Nuttallia* is often found, the effectiveness of its refuge may be enhanced by native crabs' lack of expectation (in an evolutionary sense) to find prey there. However, in experiment 2, virtually identical mortality rates of *Nuttallia* between the two tidal elevations for a given substrate suggest that sediment type, not elevation-associated expectations by crabs at shoreline levels of high native clam abundance, is the overriding factor influencing its distribution.

Physical control over predation intensity can account for variability in the height above MLLW at which *Nuttallia* is found, since grain size, which is normally well correlated with tidal height, can vary from site to site. For example, variation in the vertical distribution of grain sizes on a beach may explain the ability of *Nuttallia* to extend lower in the intertidal at Guthrie Cove and Spenser Spit South. Moreover, the spatially variable success of the invasion of *Nuttallia* in the northeastern Pacific exemplifies the influence that physical properties can have over biological resistance to species invasions. In this case physical characteristics of the areas being invaded mediate the invader's success by controlling burial depth, and thus its exposure to native predators. Specifically, *Nuttallia* is seemingly successful only at sites where it is able to inhabit a specific refuge in the loose sediments of the upper intertidal. Through burial, *Nuttallia* mitigates predator pressure, but if the physical characteristics are not accommodating the clam gets eaten at extremely high rates and the invasion is severely impeded or stopped.

Predators are apparently mitigating community-level effects of an invader by either excluding *Nuttallia*, or relegating it to a zone that is not often inhabited by natives, and reducing potential competitive interactions with native species for space and food. Food competition among suspension feeders is likely to extend over wide scales; however, it is most intense in the immediate

vicinity of high densities of other suspension feeders (Peterson 1982; Peterson and Black 1987; Skilleter and Peterson 1994). Native competitors themselves could be displacing *Nuttallia* to higher tidal elevations (i.e., unoccupied habitat); however, this mechanism must be relatively much less important than predation given that *Nuttallia* was found coexisting with native clams on beaches where loosely packed sediments extended lower in the intertidal. Furthermore, the regression of *Nuttallia* density against resident clam density suggests that the impact of resident clams on *Nuttallia* is not strong enough to reduce the overlap of their distributions (Fig. 4).

Because of the physical-biological interaction, predators only partially control the invasion of *Nuttallia*. If predator impact was strong, but the prey refuge did not exist, predators would have eradicated *Nuttallia* and there would be no invasion to study. Alternatively, if the prey could take refuge in any substratum, the invader, despite its otherwise vulnerability, might be ubiquitous throughout the intertidal and shallow subtidal, provided it had sufficient larval supply. In both of these scenarios the ubiquity or complete absence of *Nuttallia* would not imply any biological resistance to invasion, either operational or potential. The physical-biological interaction, however, produces a *Nuttallia* distribution that suggests a shaping influence by native predators. Thus, not only may physical controls mediate biological resistance, but sufficient variation in such physical controls may often make biological invasion resistance more readily apparent.

In addition to the strong influence of habitat refuge, prey and predator densities will also influence the persistence and population dynamics of *Nuttallia* in this system. It is possible, for example, that saturating predator functional response curves (i.e., types II and III) may boost per capita survival rates of *Nuttallia* at high densities. This mechanism may help *Nuttallia* maintain its high densities, particularly because crab foraging time is already severely limited by deep prey burial depths and by high shoreline elevations where mutual interference among foraging crab predators in such a narrow band of clam abundance is likely. At the opposite extreme, *Nuttallia* in low densities deep within the sand may also experience decreased per capita predation mortality due to decreased predator encounter rates. Type III functional responses appear typical for predators of deeply burrowing bivalves (Lipcius and Hines 1986; Mansour and Lipcius 1991; Eggelston et al. 1992; Seitz et al. 2001) and may help to ensure continued persistence of *Nuttallia* in a habitat that it is able to invade. Thus, while native predators greatly shape its distribution on a beach, they may be highly unlikely to eliminate it from the system.

In summary, local predation pressure on the thin-shelled *Nuttallia* in the novel non-native environment is extremely high except in a thin refuge in sandy sediment where it can escape predators. The availability of loose, sandy substrate which allows the clam adequate burial determines the degree to which the invader will be suppressed by the native fauna. Where these refuges exist *Nuttallia* does very well, achieving high densities

and producing propagules to enable fast regional spread (at least 20 km/year in the seven ensuing years after its discovery in an isolated British Columbia population). Importantly, such physical control of biotic resistance to invasion could explain the variation in the influence of native predators on non-indigenous species and thereby help explain the seemingly idiosyncratic nature of sites to resist invasion.

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