

Response of a native, herbivorous snail to the introduced seaweed *Sargassum muticum*

Kevin H. Britton-Simmons · Benjamin Pister ·
Iñigo Sánchez · Daniel Okamoto

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Abstract The role of native consumers in mediating biological invasions is poorly understood. In theory, there are reasons to expect both strong and weak effects of native consumers on non-native species. However, non-native ranges may include multiple regions or even continents, each with its own

suite of consumers and invader–consumer interactions may play out differently in different places and times. In this Washington State (USA) study we found that the common herbivorous snail *Lacuna vincta* was 2–9 times more abundant on the non-native seaweed *Sargassum muticum*, compared to native kelps. Choice feeding trials with fresh tissue and artificial foods both suggest that *S. muticum* is a preferred food for *Lacuna vincta*. Lab experiments indicated that *L. vincta* did not experience diminished predation by two common predators on *Sargassum muticum* compared to native kelp hosts. Our results suggest that *Sargassum* experiences considerable herbivory by *Lacuna vincta* in our study region, a conclusion that is consistent with previous work and our own field observations. In our system, *L. vincta* and *S. muticum* have been coexisting in the same habitats for at least 50 years and available data suggest that it acquired a preference for *S. muticum* more than 30 years after the initial invasion. Comparison of our results to recent work on *Sargassum*–herbivore interactions in Europe suggests that the response of native consumer communities to *S. muticum* varies both within and among regions. Geographic and temporal variation in the response of native consumers are likely to be hallmarks of many large-scale invasions.

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K. H. Britton-Simmons · B. Pister
Department of Ecology and Evolution, The University of
Chicago, 1101 E. 57th Street, Chicago, IL 60637, USA

I. Sánchez
Department of Biología de Organismos y Sistemas, The
University of Oviedo, Área de Ecología, C/Catedrático
Rodrigo Uria s/n, 33071, Oviedo, Spain

K. H. Britton-Simmons (✉) · D. Okamoto
Friday Harbor Laboratories, University of Washington,
620 University Road, Friday Harbor, WA 98250, USA
e-mail: aquaman@uw.edu

Present Address:
B. Pister
National Park Service, Cabrillo National Monument, 1800
Cabrillo Memorial Dr., San Diego, CA 92106, USA

Present Address:
D. Okamoto
Department of Ecology, Evolution and Marine Biology,
University of California, Santa Barbara, Santa Barbara,
CA 91036, USA

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Introduction

The capacity for native communities to resist invasion by non-indigenous species has been the subject of considerable work during the past two decades. The vast majority of biotic resistance studies have focused on the importance of competitors in generating invasion resistance (see reviews by Levine & D'Antonio, 1999; Levine et al., 2004). In contrast, the role of native consumers in mediating biological invasions is poorly understood.

In theory, there are reasons to expect both strong (increased susceptibility/biotic resistance; Darwin, 1859; Hokanen & Pimentel, 1989; Colautti et al., 2004; Parker & Hay, 2005) and weak (enemy release; Darwin, 1859; Elton, 1958; Williamson, 1996; Keane & Crawley, 2002) effects of native consumers on non-native species. However, the non-native range of many introduced species now includes multiple regions or even continents, each with its own suite of consumers. Although the release/resistance hypotheses are often framed as competing, it is more likely that invader-consumer interactions play out differently in different places and times. In this study we examine interactions between the key native herbivore *Lacuna vincta* (Montagu) and the invasive seaweed *Sargassum muticum* (Yendo) in the San Juan Islands of Washington State. We then compare our results to those from other regions/continents to assess geographic-scale spatial variation in *Sargassum*–herbivore interactions.

Since its initial introduction in the NE Pacific more than 50 years ago *S. muticum* has spread widely and its distribution on the west coast of North America now extends from Alaska to Baja California (Scagel, 1956; Setzer & Link, 1971). Available data indicate that it has colonized at least 18% of the shoreline in Washington State and 47% of the shoreline in San Juan County, WA, the location of our study (Near-shore Habitat Program, 2001). Overall, *Sargassum muticum* is widely distributed as a non-native species having colonized more than 10 countries in two different oceans in less than 100 years.

The purpose of this study was to investigate the field distribution and feeding preference of the native mesograzer *Lacuna vincta* with respect to *Sargassum muticum* and native kelp species. *Lacuna vincta* is a small, numerous, widely distributed herbivorous gastropod that is important for the ecology of subtidal communities because its grazing influences the

distribution, abundance, and biomass of kelps (Johnson & Mann, 1986; Duggins et al., 2001). In Washington State *Lacuna vincta* is a generalist herbivore found on a wide variety of algae. It is the most abundant herbivore in subtidal communities within this region (personal observation) and the only mesoherbivore we consistently find on *S. muticum* that is capable of inflicting severe grazing damage. Therefore, *L. vincta*'s response to *S. muticum* is important for understanding whether *S. muticum* encounters biotic resistance in our study area.

There is ample evidence demonstrating that native herbivores feed on and can regulate the distribution and abundance of non-native seaweeds (Trowbridge 2002; Sjutun et al., 2007; Lyons & Scheibling, 2008). However, it is also important to consider the broader food web context, because to the extent that predators influence the distribution and abundance of herbivores (e.g., Duggins, 1983; Duffy & Hay, 2002) they may indirectly mediate interactions between native herbivores and their non-native prey. We hypothesized that feeding preferences and predation would co-regulate the distribution and abundance of *Lacuna vincta* on native kelps and *Sargassum muticum* in our system.

The motivation for this project came from field observations we made while SCUBA diving in the shallow subtidal zone. We observed large numbers of *Lacuna vincta* on *Sargassum muticum* over many years. They appeared to be consistently more abundant on *S. muticum* than on nearby native kelp species, a pattern that is consistent with a previous report from our region (Giver, 1999). Our goal was to address three specific questions: (1) Is *Lacuna vincta* more abundant on *S. muticum* than native kelp species? (2) Does *L. vincta* prefer *S. muticum* over native kelps in choice feeding trials? (3) Does *Lacuna vincta* experience less predation on *S. muticum* compared to native kelps? We used a combination of field surveys and laboratory experiments to address these questions.

Materials and methods

Study areas

This work was based out of Friday Harbor Laboratories (FHL) on San Juan Island, WA, USA. Field sites were located on San Juan and Shaw Islands and

included the following locations: Colin's Cove (48.54961°N, 123.00558°W), Pt. George (48.56038°N, 122.98866°W), Snag Pt. (48.54644°N, 122.94991°W), Hick's Bay (48.54955°N, 122.96647°W), Pt. Caution (48.56213°N, 123.01686°W). All of our field sites were located in San Juan Channel, an area that is protected from wave exposure but experiences strong tidal currents. Shallow, subtidal communities in this region are dominated by kelps (Phaeophyceae, Laminariales) and understory red algae (Rhodophyta). The introduced alga *Sargassum muticum* is common in these habitats throughout the region (Nearshore Habitat Program, 2001; Britton-Simmons, 2004).

Distribution and abundance of *Lacuna vincta*

To test the hypothesis that *Lacuna vincta* was more abundant on *Sargassum muticum* than native kelp species we measured the abundance of *Lacuna vincta* on *Sargassum muticum*, and two native kelps, *Saccharina subsimplex* (Setchell & N.L. Gardner) (formerly *Laminaria bongardiana*) and *Agarum fimbriatum* (Harvey) at five sites in July of 2002. At each site we used SCUBA to lay a 20 m transect at a depth of 2–3 m below mean lower low water. At each of three randomly selected locations on the transect we collected one individual of each species by taking those closest to the randomly chosen transect points. Seaweeds less than 1 m in height were excluded a priori. Each alga was removed from the substratum and immediately placed in a plastic bag secured with a cable tie. Snails from each alga were then counted in the lab. Algal tissue was weighed before and after it was dried to a constant weight in a 60°C oven.

We calculated total blade area of the kelps collected in the above samples using mass to area regressions obtained in previous projects. *Saccharina subsimplex* blade area was estimated using wet mass ($\text{Area} = 19.037 * \text{WM} + 83.654$) and *Agarum fimbriatum* blade area was estimated using dry mass ($\text{Area} = 146.89 * \text{DM} + 277.97$). These blade areas were then used to calculate *L. vincta* density on the two kelp species.

Food preference experiments

We used choice experiments to test *Lacuna vincta*'s preference for *Sargassum muticum* versus two native kelp species, *Agarum fimbriatum* and *Saccharina*

subsimplex. *Sargassum muticum* has a relatively high surface area to volume ratio relative to native kelps and that could influence the feeding rate of snails in fresh tissue experiments. Therefore, in addition to a fresh tissue feeding trial we performed a second feeding experiment using artificial foods to control for morphology.

Fresh tissue feeding experiment

The experimental containers were 1 l plastic beakers that had two 7 × 7 cm mesh windows located on opposite sides (mesh size = 1.5 × 1.5 mm). Each container in the experimental treatment contained pieces of *Sargassum muticum*, *Saccharina subsimplex*, and *Agarum fimbriatum* as well as 20 *Lacuna vincta* that ranged in size from 4 to 11 mm in length. The snails were collected from a variety of subtidal algae during the week preceding the start of the experiment and were kept in a flow-through seawater tank stocked with fresh *S. muticum*, *S. subsimplex*, and *A. fimbriatum* tissue until the experiment began. Our control treatment consisted of identical containers in which we placed algae, but no snails, in order to account for algal growth during the experiment. Beakers were capped with 0.5 mm Nitex mesh cable tied over the top opening. The containers (12 per treatment) were evenly divided between two large, circular, outdoor aquaria (105 cm in diameter, 45 cm tall) supplied with flow-through seawater.

The algae used in the experiment were collected on the same day that the experiment began and kept in a tank with flow-through seawater until needed. In order to minimize variation in polyphenolic levels among the pieces of algae used in the experiment we did not use any reproductive tissue (i.e., sori or receptacles). We also used tissue at least 30 cm from the meristem region (apical in *Sargassum*, intercalary in the two kelp species). The pieces of algae were weighed at the beginning and end of the experiment. Prior to weighing each piece it was spun in a salad spinner for 20 s to remove any excess water on its surface. The pieces of algae ranged in size from 4.0 to 4.9 g at the beginning of the experiment.

Because there was no natural pairing of control and experimental replicates in our experiment we randomly paired each experimental replicate with one of the control replicates. We then calculated the amount of each species consumed in each experimental

replicate using the formula $[T_i(C_f/C_i)] - T_f$ where T_i and T_f are the initial and final algal masses in the treatment container and C_f and C_i are the initial and final algal masses in the randomly paired control container (Cronin & Hay, 1996).

Agar block feeding experiment

We constructed feeding containers for this experiment using petri dishes (9 cm diameter) that were divided in four equal compartments. A 6-cm diameter circular mesh (1.5 × 1.5 mm) window was created in the lid of each petri dish to allow water exchange between the petri dish and the surrounding seawater.

Clean, medium-sized adult specimens of *Agarum fimbriatum*, *Saccharina subsimplex*, and *Sargassum muticum* were collected and lightly brushed and rinsed to remove epiphytes. Tissues were removed from these species, excluding reproductive and meristematic regions of the thalli (see previous section for details). The excised tissues from each species were rinsed in deionized water and then pureed in a blender. We poured the blended tissue into clean petri dishes and froze them at -80°C . The frozen tissue was then freeze-dried and ground with a mortar and pestle until it could be sifted through 500 μm mesh.

Artificial tissues were created for each species by first making two solutions (Hay et al., 1994; Cronin & Hay, 1996): (1) a 3.6% agarose-reverse osmosis water solution, and (2) a 12.5% aqueous algal homogenate, made from ground seaweed tissue and reverse osmosis water. The agarose solution was brought to a boil in a microwave oven, quickly mixed with the algal homogenate solution, and poured into the petri dish wells. The two solutions were mixed in a 5:4 ratio (agarose solution:algal homogenate) to achieve final concentrations of 2% agarose and 5.5% algal powder. One well per petri dish contained artificial tissue from each species of algae. The fourth well in each petri dish was filled with a control solution containing 2% agarose but no algal homogenate. The spatial arrangement of the four treatments within each petri dish was varied so that each of the six possible arrangements was represented twice for a total of 12 replicate petri dishes. Once the agar blocks had cooled and solidified we removed the blocks from the wells, flipped them upside down and reinserted them into the petri dish (preserving the

relative positions of the treatments) exposing smooth, bubble-free surfaces for grazing.

Between their collection and use in the experiments the snails were fed fresh tissue from all three species of algae to avoid biasing their preferences. At the beginning of the feeding trial we placed 15 *L. vincta* in each feeding container. Snails were carefully placed in the container as follows: 4 *L. vincta* were placed on each of the three artificial algal tissues and the remaining 3 *L. vincta* were placed on the control block (agarose only).

After snails were added to the containers they were covered and placed in a sea table with a constant supply of fresh seawater. The experiment ran for a total of 23 h. We quantified consumption by placing a transparent 3 mm grid on top of the agar blocks and examining them under a dissecting microscope. Each square in the grid was scored by estimating the percentage of its surface that had been grazed using the following categories: 0% grazed, 25% grazed, 50% grazed, 75% grazed, 100% grazed. We then summed over all grid squares to calculate the percentage of each block's surface that had been grazed by *L. vincta*.

Predation experiments

We tested the hypothesis that *L. vincta* experience less predation when living on *S. muticum* compared to *A. fimbriatum* or *S. subsimplex* using two common predators of this snail, the kelp crab *Pugettia producta* and the sea star *Leptasterias hexactis*.

Leptasterias hexactis, *Lacuna vincta*, and the three seaweed species were collected using SCUBA. Prior to beginning the experiment *L. vincta* were fed scraps of all three experimental seaweeds. Individual *S. subsimplex*, *A. fimbriatum*, and *S. muticum* that were used in the experiment were collected on the same day the experiment was started. All animals were removed from the algae before the start of the experiment.

The sea star experiment was set up in three large circular plexiglass tanks (105 cm in diameter, 45 cm tall), each of which contained eight 19 l buckets. Each bucket was an experimental replicate, had its own seawater supply, and contained one individual *S. subsimplex*, *A. fimbriatum*, or *S. muticum*. Algae were anchored to the bottom of the buckets using pieces of bath mat with slits cut in them so the holdfast of the alga could be inserted into it. Replicates were assigned randomly to tanks and each

treatment had a total of seven replicates. At the beginning of the experiment 25 haphazardly chosen *Lacuna vincta* were placed on each alga. One hour later, two haphazardly chosen *Leptasterias hexactis* were placed on each alga. The experiment was terminated after 4 days and the remaining live snails were counted.

The predation experiment was repeated using the crab *Pugettia gracilis* as the predator. All experimental organisms were collected from the same sites used in the sea star experiment. We followed the same methods described above for the sea star experiment except that the number of *Lacuna vincta* in each replicate was reduced to 17. The experiment was terminated after 3 days when we discovered that an animal (probably a raccoon) had eaten the crabs in two of the *A. fimbriatum*, one of the *S. subsimplex*, and one of the *S. muticum* treatments during the previous night.

Both of these predators occur at low densities in the field ($\ll 1$ per plant) so the crab and sea star densities used in our experiments were relatively high to maximize the chance of generating a predation effect if one existed.

Statistical analyses

All statistical analyses were carried out using Systat (versions 10.2 and 13). We compared the number of *L. vincta* on the three species of algae across all five sites using a two-way ANOVA with site (random) and algal species (fixed) as main effects. Prior to analysis the data were \ln transformed to meet the homogeneity of variance assumption. Post hoc analysis of the *L. vincta* data was carried out using Dunnett's test to make pairwise comparisons of snail abundance on each of the two native seaweeds to snail abundance on *S. muticum* at each site (e.g., Goodsell & Underwood, 2008).

The fresh tissue and agar block feeding experiments were each analyzed using Quade's test, a non-parametric method based on ranks (Conover, 1999). Quade's test evaluates the null hypothesis that there was no preference among algal foods and includes a post hoc procedure for evaluating pairwise differences when the null hypothesis is rejected.

Data on the number of snails eaten in each of the predator experiments were analyzed using a one-way ANOVA. It was not necessary to transform the data

from either of these experiments to comply with the assumptions of ANOVA.

Results

Distribution and abundance of *Lacuna vincta*

A significant site by species interaction ($P = 0.013$, Table 1; Fig. 1) rendered the main effects uninterpretable. Nevertheless, *L. vincta* was more abundant on *S. muticum* compared to the two native kelps at all five sites (Dunnett's test, $P \ll 0.01$ for all comparisons).

Food preference experiments

Fresh tissue feeding experiment

Lacuna vincta showed a preference among the three species of algae (Quade test, $T_3 = 6.47$, $P < 0.01$,

Table 1 Results of mixed model ANOVA testing whether *Lacuna vincta* density varied among sites (random) and species (fixed) of algae

Source of variation	SS	Df	MS	F	P
Site	4.778	4	1.195	2.463	0.07
Species	58.027	2	29.013	19.692	0.001
Site \times Species	11.787	8	1.473	3.038	0.013
Error	14.550	30	0.485		

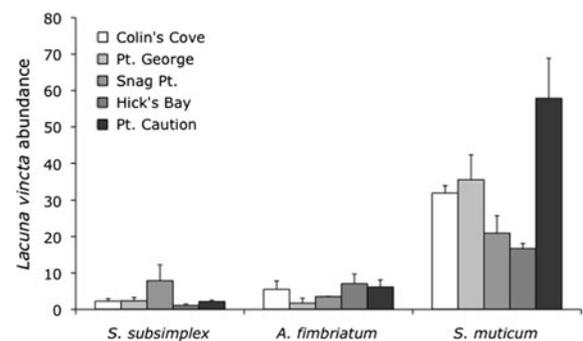


Fig. 1 *Lacuna vincta*. Number per gram of dry mass on *Sargassum muticum* and the two native kelps *Saccharina subsimplex* and *Agarum fimbriatum* at five sites in the San Juan Islands. *Lacuna vincta* was more abundant on *S. muticum* compared to the each native kelp at all five sites (Dunnett's test, $P \ll 0.01$ for all comparisons). Error bars are standard error

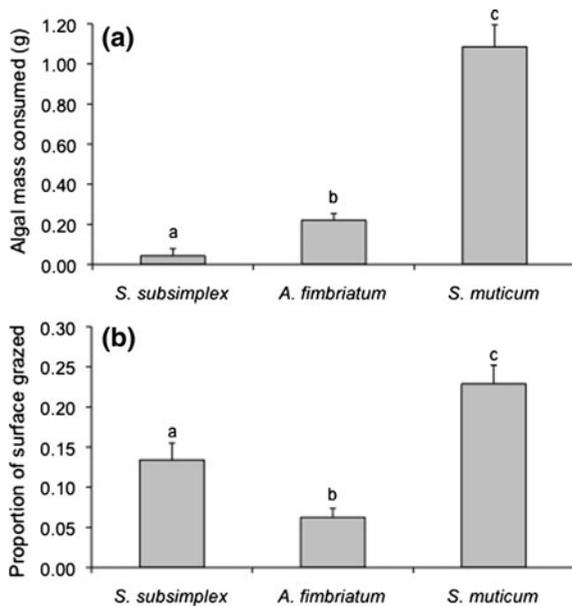


Fig. 2 **a** Mass of algae consumed by *Lacuna vincta* during a “choice” experiment in which it was simultaneously offered *Saccharina subsimplex*, *Agarum fimbriatum*, and *Sargassum muticum*. Letters indicate which means are significantly different from one another. Error bars are standard error ($N = 12$). **b** Proportion of artificial food surface grazed by *Lacuna vincta* in a “choice” experiment where it was simultaneously offered artificial foods made from *Saccharina subsimplex*, *Agarum fimbriatum*, and *Sargassum muticum*. Letters indicate which means are significantly different from one another. Error bars are standard error ($N = 12$)

Fig. 2a). *Sargassum muticum* was preferred over *A. fimbriatum* ($P < 0.01$) and *S. subsimplex* ($P < 0.001$). In addition, *L. vincta* preferred *A. fimbriatum* over *S. subsimplex* ($P < 0.025$).

Agar block feeding experiment

Lacuna vincta showed a preference among artificial foods made from the three species of algae was rejected (Quade test, $T_3 = 18.11$, $P \ll 0.01$, Fig. 2b). *Lacuna vincta* preferred *S. muticum* over both *S. subsimplex* ($P < 0.05$) and *A. fimbriatum* ($P < 0.001$), and that *S. subsimplex* was preferred over *A. fimbriatum* ($P < 0.01$).

Predation experiments

There was no evidence that predation on *Lacuna vincta* varied among species of algae in the *Pugettia producta* predation experiment ($F_{2,18} = 0.29$,

$P = 0.84$). The number of snails consumed by *Lepidasterias hexactis* did not vary significantly among the three algae treatments ($F_{2,21} = 0.02$, $P = 0.98$).

Discussion

Our results suggest that the invasive seaweed *Sargassum muticum* experiences considerable herbivory by the native herbivore *Lacuna vincta*. In this system, *L. vincta* is more abundant on *Sargassum muticum* than on the two most common native kelps *Saccharina subsimplex* and *Agarum fimbriatum* (Fig. 1). This result corroborates similar data collected from four additional sites in this region during 1997 (Giver, 1999) and is consistent with our field observations made during more than a decade of work in the San Juan Archipelago.

The hypothesis that *Lacuna vincta* feeding preference explains its distribution in the field was supported by choice feeding trials with both fresh algal tissue (Fig. 2a) and artificial foods (Fig. 2b). In both feeding trials *Lacuna vincta* preferred to consume *S. muticum* over *A. fimbriatum* or *S. subsimplex*, the two most common native kelp species in this shallow subtidal system. However, relative preference for the two native kelps was not consistent in the two feeding trials. Whereas *A. fimbriatum* was preferred over *S. subsimplex* in the fresh tissue feeding trial, this pattern was reversed in the agar feeding experiment. Although all three species of algae we studied contain polyphenolic compounds that are known to deter consumption by some herbivores (Hay, 1996; Targett & Arnold, 1998), the relative levels of these compounds are unlikely to explain the results of our feeding experiments. *Sargassum muticum* and *S. subsimplex* have roughly equivalent, low levels of polyphenolics (1–2% DW; Hammerstrom et al., 1998; Giver, 1999). In contrast, *A. fimbriatum* has relatively high polyphenolic levels (7–14% DW; Hammerstrom et al., 1998). Thus, if *L. vincta* was responding solely to algal chemical defenses then *A. fimbriatum* should consistently have been the least preferred seaweed. This result is consistent with previous work suggesting that phlorotannins may not function as a chemical defense against *L. vincta* (Toth & Pavia, 2002).

Saccharina subsimplex is known to be palatable to other grazers, such as sea urchins (*Strongylocentrotus* spp.; Vadas, 1977; Britton-Simmons, 2004) so why

did *L. vincta* avoid feeding on it during the fresh tissue feeding trial? During our study we noted that *S. subsimplex* releases copious amounts of thick mucilage when it is damaged. It is possible that this mucilage deters feeding by small herbivores such as *L. vincta*, but is ineffective against larger grazers such as urchins. For example, mucilage might clog *L. vincta*'s radula or make it difficult for the snail to stay attached to the algal blade. We hypothesize that the absence of *S. subsimplex* mucilage in the agar feeding trial was the reason why this kelp was more preferred in that trial, compared to the fresh tissue experiment.

Differential predation is an alternative explanation for the distribution of *L. vincta* on our focal seaweeds. One might expect that the substantial morphological differences between these species of algae could have consequences for the ability of predators to forage on them. For example, it might be difficult for sea stars to climb up *Sargassum*'s wiry axes in comparison to the large blades of the two kelp species. However, our lab experiments suggested that predation rates on *L. vincta* by *Pugettia producta* and *Leptasterias hexactis* did not differ on *S. muticum* compared to native kelp species, and both of these common predators readily climbed *S. muticum* in the lab. Nevertheless, it remains possible that other predators we did not consider play a role in generating the distribution pattern we observed in the field. Some fishes in this region are known to consume *L. vincta* (Norton, 1988), but such fish predators are either uncommon (pile perch) or are generalist predators for whom *L. vincta* composes a relatively small portion of their diet (spinynose sculpin).

One consequence of the radically different morphologies of *S. muticum* compared to the two native kelps is that they clearly differ in surface area to volume ratio (Giver, 1999). *S. muticum*'s highly branched, wiry morphology has a higher surface area to volume ratio than the single bladed morphology of both the native kelp species. Thus, an additional hypothesis that might explain why *L. vincta* is so abundant on *S. muticum* in the field (on a per g dm basis) is that the high surface area to volume ratio of this alga allows it to accommodate more snails per unit mass. This is a difficult hypothesis to test and we cannot rule out the possibility that it partly explains the high abundance of *L. vincta* on *S. muticum*. However, given that the mean density of snails per kelp blade area was relatively low for both

S. subsimplex (0.02 snails cm⁻²) and *A. fimbriatum* (0.03 snails cm⁻²), and that *L. vincta* feeding rate is density-independent (Britton-Simmons, unpublished), we think that surface area per se has little explanatory power. However, higher surface area could indirectly influence *Lacuna vincta* by providing more substrate for epiphytes, thereby increasing food availability (Viejo, 1999).

Release from natural enemies (i.e., predators, parasites, and pathogens) in their introduced ranges is one hypothesis proposed to explain the success of many non-native species. One tenet of the enemy release hypothesis is that generalist herbivores will have a greater impact on native competitors than on introduced species (Keane & Crawley, 2002). The green sea urchin (*Strongylocentrotus droebachiensis*) and the snail *Lacuna vincta* are both generalist consumers in this shallow, subtidal marine ecosystem. However, these two species respond very differently to the presence of *Sargassum muticum*. Green urchins avoid foraging in areas where *S. muticum* is present and food preference data indicate that urchins do not like to feed on it (Britton-Simmons, 2004). In contrast, this study and previous work (Giver, 1999) demonstrate that *L. vincta* either aggregates to or preferentially recruits onto *S. muticum*, and exhibits a strong feeding preference for *S. muticum* compared to native algae. Assuming that the grazing damage inflicted by *L. vincta* is proportional to its abundance these results suggest that *S. muticum* suffers 2–9 times more damage from *L. vincta* herbivory than does either native kelp species in our study (Fig. 1). It is very common to find many hundreds of *L. vincta* on a single *S. muticum* (maximum number recorded = 2,967 snails). We commonly observe individual *S. muticum* plants in the region that have suffered considerable damage from *L. vincta* (which leaves distinctive grazing scars that no other local mesoherbivore is capable of generating) particularly during late summer, when the snail populations are near their peak size.

It is not clear why *S. droebachiensis* and *L. vincta* have such different preferences for *Sargassum muticum* compared to native kelps. Although both are generalist herbivores, they differ greatly in size, feeding mode, reproductive biology, mobility, and other characteristics. Because *L. vincta* deposits egg masses on its host seaweed, it is possible that food preference and egg mass substrate preference are confounded in this and

other mesograzers species. Regardless of the explanation, the differential response of these grazers corroborates considerable previous work indicating that herbivore species respond very differently to algal defenses (Amsler & Fairhead, 2006).

Native consumers have been documented to prey on invaders in a variety of systems (Harding, 2003; Jensen et al., 2007; Levine et al., 2004; Griswold & Lounibos, 2004; Parker & Hay, 2005) and have been demonstrated to prefer non-native over native prey (Trowbridge, 1995; Reusch, 1998; Griswold & Lounibos, 2004; Parker & Hay, 2005). Such cases are likely to become more common because the longer an introduced species has been present, the more probable that some native consumer will begin to utilize it as a food resource. In our system, *L. vincta* and *S. muticum* have been coexisting in the same habitats since at least 1948. We know that *L. vincta* has been utilizing *S. muticum* since at least 1978, but it occurred on less than 5% of plants at that time (Norton & Benson, 1983). By 1997 *Lacuna vincta* was more abundant on *S. muticum* than on native kelps (Giver, 1999) and the present study shows that pattern has persisted. Therefore, it appears that *Lacuna vincta*'s preference for *Sargassum muticum* arose more than 30 years after the initial invasion of this area.

Although *Sargassum muticum* has been present in our study region since the 1940s (Scagel, 1956), its arrival in Europe is relatively recent, where the earliest occurrence was in 1973 on the Isle of Wight in Southern England (Critchley et al., 1983). Studies of food preference have been carried out in both Portugal and Ireland, both of which were invaded by *S. muticum* around the same time, in the early to mid 1990s (Engelen et al., 2008; Kraan, 2008). Although no herbivores were found to prefer *S. muticum* in Portugal (those tested included *Gibbula* spp., *Paracentrotus lividus*, *Aplysia punctata*; Monteiro et al., 2009), *S. muticum* is a preferred food for the abundant native amphipod *Dexamine spinosa* in Ireland (Strong et al., 2009). Like our system, field observations and lab experiments both suggest that a single mesograzers species exerts strong grazing pressure (and hence native biotic resistance) on *S. muticum* in Ireland (Strong et al., 2009). These results collectively indicate that the response of native consumer communities to *S. muticum*, and therefore the potential for consumer generated biotic resistance to invasion, varies over space and time.

Conclusion

Although *Sargassum muticum* may largely escape herbivory in some portions of its non-native range (Monteiro et al., 2009) our results suggest that it attracts and is a preferred food resource for the abundant native herbivore *Lacuna vincta*, an association that appears to have arisen more than 30 years after these species first encountered one another in our region. Our study contributes to a growing body of literature demonstrating that introduced species do not always escape consumption in their new ranges. Like *Sargassum muticum*, many non-native species have invaded multiple geographic regions (e.g., *Crassostrea gigas*, *Undaria pinnatifida*). Comparison of our results with herbivore–*Sargassum* studies from European shores indicates that herbivore communities vary in the extent to which they generate biotic resistance to *Sargassum* invasion. Widespread non-native species may simultaneously experience enemy release and encounter biotic resistance in different portions of their non-native range. Geographic and temporal variability in the response of native consumers are likely to be hallmarks of many large-scale invasions.

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