

# *Lacuna vincta* (Mollusca, Neotaenioglossa) herbivory on juvenile and adult *Nereocystis luetkeana* (Heterokontophyta, Laminariales)

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**Abstract** Herbivory can be an important factor structuring coastal algal communities. Herbivores may preferentially graze particular algal species or tissue types. Mesograzers, despite their small size, can critically weaken kelp thalli and impact entire kelp beds. We propose that when kelp beds are composed of several kelp cohorts, mesograzers will selectively choose to inhabit younger plants and grazing activities will have a greater impact on younger plants. This study investigated the effects of grazing by the littorinid gastropod, *Lacuna vincta*, on different age classes of the bull kelp, *Nereocystis luetkeana* by (1) testing food preference of *L. vincta* on juvenile, first-year adult, and second-year adult *Nereocystis* blades in the laboratory, (2) determining substrate (blades of different ages) preference of *L. vincta* in the laboratory, and by (3) estimating in-situ herbivore abundances and densities on juvenile and adult *Nereocystis*. Results demonstrated that grazing by *L. vincta* produced greater damage on juvenile than older *Nereocystis* tissues. Although *L. vincta* did not select juvenile versus older kelps as substrate in the laboratory, in situ surveys showed that differences existed between age classes with

higher *L. vincta* densities on juvenile than adult kelp. We conclude that at a local scale, *L. vincta* can be an important structuring factor in *Nereocystis* populations due to its high density and grazing ability.

**Keywords** *Nereocystis luetkeana* · *Lacuna vincta* · Herbivory · Juvenile and adult kelp · Feeding and substrate

## Introduction

The dynamics of kelp communities result from complex interactions between various biotic and abiotic factors. Herbivory is a major ecological factor that influences kelp bed structure (Leighton, 1971; Duggins, 1980; Lubchenco & Gaines, 1981; Dayton, 1985; Vadas, 1985). Herbivory can dramatically alter the fitness, growth, and survival of individual algae (Steinberg, 1984; Johnson & Mann, 1986) as well as influence plant abundance, distribution, diversity, and succession at the population and community levels (e.g. Lubchenco & Gaines, 1981). Many organisms, including echinoderms, polychaetes, crustaceans, mollusks, and fishes graze on benthic algae (for review see, North, 1971; Foster & Schiel, 1985; O'Clair & Lindstrom, 2000). In temperate and high latitude algal communities, sea urchins, snails, and amphipods are particularly important (Vadas, 1985).

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Sea urchins are known to overgraze kelp beds (Mann & Breen, 1972; Duggins, 1980; Estes et al., 1998), however other grazers, such as isopods, amphipods, gastropods, echinoderms, and fishes have also been reported to critically affect algal communities (Jones, 1971; Leighton, 1971; North, 1979; Harris et al., 1984; Foster & Schiel, 1985; Vadas, 1985; Padilla, 1993; Leonard, 1994; Van Alstyne et al., 1999; Toth & Pavia, 2002a, b). Large grazers, such as urchins, can often damage large macrothalli by decreasing photosynthetic tissue, limiting development and growth, or shortening their life span (e.g. Lubchenco & Gaines, 1981; Thomas & Page, 1983; Johnson & Mann, 1986; for review see North, 1971; Foster & Schiel, 1985). Despite their smaller size, mesograzers also can impact the fitness, survival, and community structure of macroalgae (Tegner & Dayton, 1987; Brawley, 1992; Duffy & Hay, 2000).

*Lacuna vincta* (Montagu) is a small gastropod mesograzer commonly found in the low intertidal to subtidal zone of the northeastern Pacific (e.g. Fralick et al., 1974; Johnson & Mann, 1986; Martel & Chia, 1991a, b; Martel & Diefenbach, 1993; Padilla, 2001). It is rarely observed on benthic substrata (Padilla, 2001) and instead uses kelp for habitat and food (Padilla, 1998; Toth & Pavia, 2002a). In British Columbia, it is the dominant grazer found on canopies of *Macrocystis integrifolia* Bory de Saint Vincent and *Nereocystis luetkeana* (Mertens) Postels & Ruprecht (hereafter *Nereocystis*) (Martel & Chia, 1991a; Carney et al., 2005). On *Nereocystis*, *L. vincta* represented 94% of all grazers in the San Juan Archipelago (Duggins et al., 2001) and 98% in Kachemak Bay, Alaska (Chenelot, unpublished data). In Alaska, high numbers of *L. vincta* can have detrimental effects on *Nereocystis* sporophytes (Chenelot, 2003), the dominant canopy-forming species in southcentral Alaska and thus an important habitat former. As such, it is important to understand interactions between *Nereocystis* and its common grazer, *L. vincta*. To date, most studies on grazer feeding preference have been conducted with either *L. vincta* feeding on kelp species other than *Nereocystis* (Johnson & Mann, 1986; Chavanich & Harris, 2002) or on *Nereocystis* palatability with grazers other than *L. vincta* (Steinberg, 1985; Morris & Campbell,

1996; Van Alstyne et al., 1999; Van Alstyne et al., 2001; Pelletreau & Muller-Parker, 2002), but little is known about interactions between *L. vincta* and *Nereocystis*.

Young and old macroalgal tissues often have different palatability or antigrazing characteristics and may suffer different grazing pressures (Watson & Norton, 1985a; Van Alstyne et al., 1999; Van Alstyne et al., 2001; Taylor et al., 2002; Heaven & Scrosati, 2004). Unlike many other canopy forming kelps, *Nereocystis* is an annual. However, individuals that mature late can overwinter, resulting in juvenile, first year, and second year individuals coexisting in a single bed (Maxell & Miller, 1996). Since various age classes of *Nereocystis* can be potential food for grazers in a kelp bed, we investigated age preference using a common mesograzer. As such, the objectives of this study were to (1) determine food preference and the extent of grazing damage of *L. vincta* on juvenile, first-year adult, and second-year adult *Nereocystis* blades in the laboratory, (2) determine substrate (blades of different ages) preference of *L. vincta* in the laboratory, and (3) estimate in-situ herbivore abundances and densities on juvenile and adult *Nereocystis* thalli.

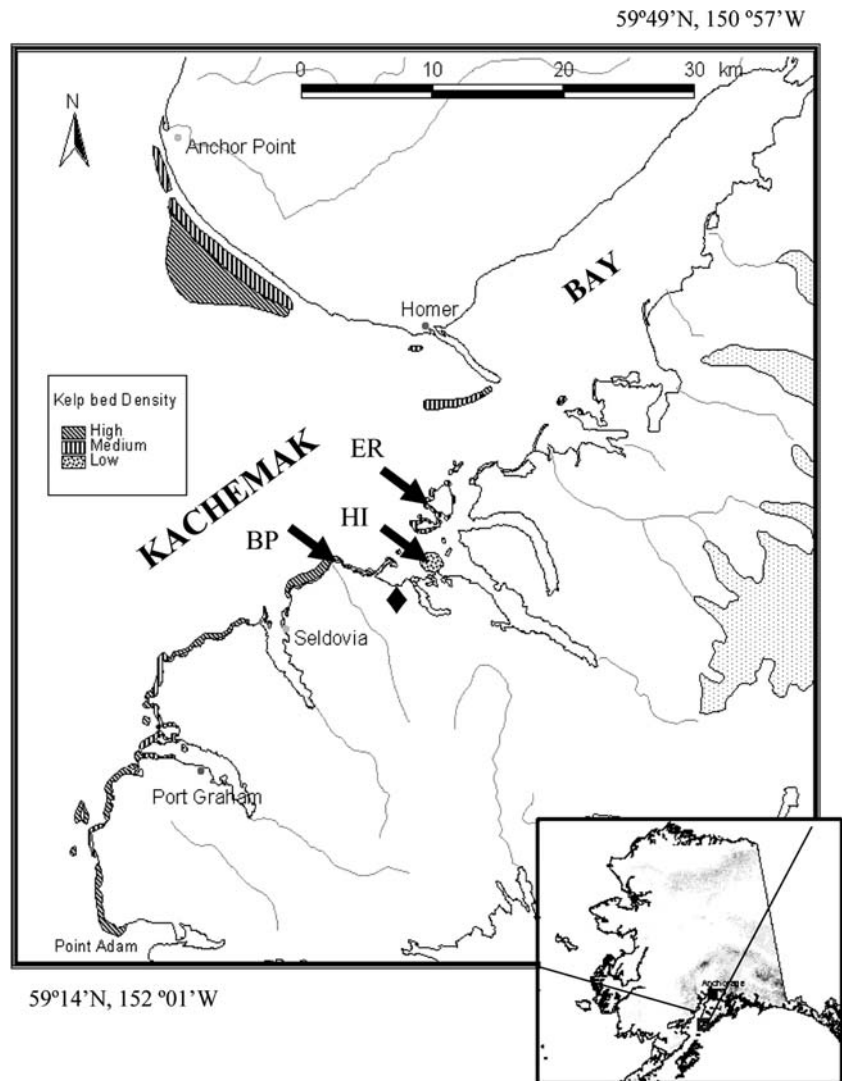
## Materials and methods

### Laboratory experiments

The experiments were conducted in September 2003 at the Kasitsna Bay Laboratory in Kachemak Bay, Alaska using an outdoor flow-through seawater system. *Nereocystis* blades of different age classes and *L. vincta* snails were collected at sites close to the laboratory (Barabara Point (BP), Herring Islands (HI), or Elephant Rock (ER); Fig. 1) within 24 h of each experiment. Only vegetative blades were used. All blades were gently brushed to remove epiphytes and were cut in pieces of 50 cm<sup>2</sup> (2.5 × 20 cm), blotted dry and weighed.

Ten replicate chambers (27 × 30 × 12 cm), each containing twenty snails and one *Nereocystis* blade of each age-class were tested. Once introduced to the containers, the snails were gently stirred to randomize their settlement. To assess

**Fig. 1** Map of the study sites (Barabara Point (PB), Herring Islands (HI), and Elephant Rock (ER)) and the Kasitsna Bay Marine Laboratory (♦)(from Chenelot, 2003). The location and size of the kelp beds were estimated from an aerial survey conducted by the Kachemak Bay Research Reserve in August 2000



autogenic changes during the experiment, three control containers with all blade types but no snails were weighed and monitored. Two experiments were performed on different days, using separate snail and blade batches. The experiments were run long enough to allow sufficient grazing to be detected. Experiment 1 was run for 24 h and Experiment 2 was run for 48 h.

To determine feeding preference of *L. vincta*, the weight change of each blade type was compared between the start and termination of the experiment. To account for any weight change not due to herbivory, the termination weight of each individual blade was adjusted by subtracting the average weight change of the control blades

of the corresponding age class. Weight loss for all blades was also calculated as a percent of their original weight because juveniles were thinner and weighed less than adults.

To determine the extent of grazing damage on different age class blades, the percentage of each blade's total surface area damaged by grazing was estimated. The difference between grazed and intact tissue was obvious as the exposed translucent medulla contrasted against the darker cortex layer of grazed blades while intact blades showed no contrast. A  $2.5 \times 20\text{-cm}^2$  grid was used and all squares, each  $0.65 \times 0.65\text{ cm}$  and representing 0.83% of the blade's total surface area ( $50\text{ cm}^2$ ), were scored for grazing marks.

To determine whether *L. vincta* preferentially resided on one type of blade (juvenile, first-year or second-year adult blades), the location of the snails was recorded for each chamber 24 h after the start of the experiment. The number of snails on each blade type was expressed as percentage of the total number of snails per container (20 snails).

Nonparametric Kruskal-Wallis tests were performed to determine if blade type had a significant effect on absolute weight loss, percentage weight loss, surface area grazed, and location (StatView, 1999). Because non-parametric analyses do not provide pairwise mean comparison Post Hoc tests to statistically determine preference between individual blade types, when  $P < 0.05$ , basic unpaired mean comparisons were performed for all pairs of blade types based on 95% confidence intervals (Pelletreau & Muller-Parker, 2002; Heaven & Scrosati, 2004).

#### In-situ herbivore abundance

Herbivore abundance at each kelp bed (BP, HI, and ER) was estimated by counting the number of grazers (*L. vincta*) found on juvenile and first-year adult *Nereocystis* plants. For this study, juvenile arbitrarily refers to individuals whose stipe was less than 1.5 m in length and adult refers to individuals with a stipe longer than 3.5 m. Second-year adults were not surveyed as preliminary counts showed very few grazers on those plants. Additionally, second-year adults were heavily covered by epiphytes and were patchily distributed. Grazers were counted separately on the stipe (including the pneumatocyst region) and on the blades of individual plants. Scuba was used to survey the stipe and blades of juveniles and the stipe of adults. Adult blades were examined from a skiff at the surface because of the great number of grazers encountered and the difficulty of thoroughly surveying the long (~3 m) and numerous (~50–60) blades of tall adult plants underwater without dislodging the snails. Consequently, the blade and stipe counts of adult thalli could not be paired for each individual. Approximately 25 stipes and clusters of blades were surveyed on juvenile and adult plants at each site, however, some variation in sample size did occur.

In the field, the stipe and blades of juvenile *Nereocystis* ( $96.3 \pm 4.0$  cm,  $n = 79$  and  $31.2 \pm 3.5$  cm,  $n = 69$ , respectively; mean  $\pm 1$  SE) were significantly ( $P < 0.001$ ) shorter than that of adults ( $473.0 \pm 19.3$  cm,  $n = 70$  and  $241.2 \pm 8.9$  cm,  $n = 90$ , respectively). In consequence, adult thalli provided substantially more surface area to the grazers than juvenile thalli. To take this factor into consideration, *L. vincta* counts were normalized into densities. Snail densities were estimated for each individual by dividing the number of snails counted on the stipe or the blades by the length of the corresponding thallus section. Because of the extreme tides and currents in Kachemak Bay, we had only a limited amount of time available at each site to safely perform the surveys; as a consequence blade widths and blade numbers were not recorded.

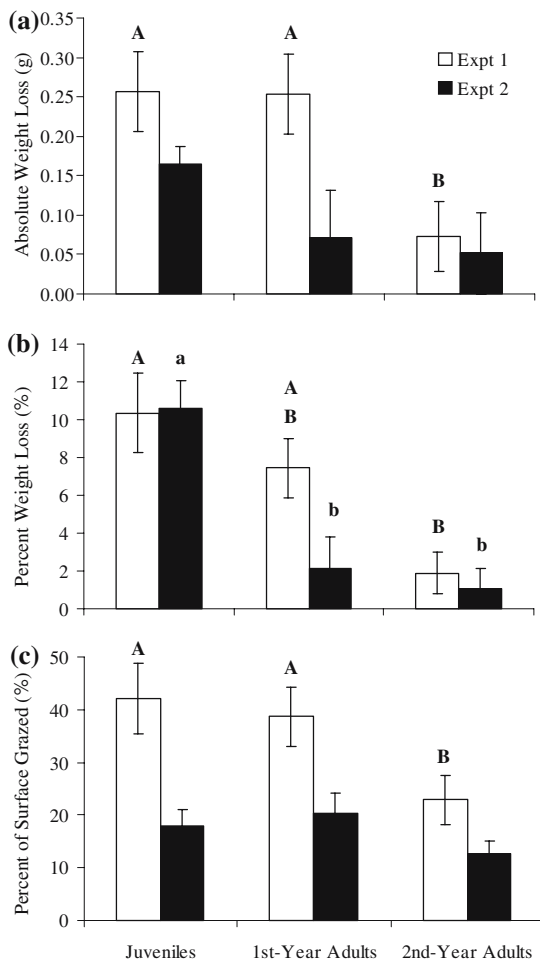
*Lacuna vincta* abundance and densities on stipes and blades were compared for the different age class plants amongst and between sites using a 3-way ANOVA followed by a pairwise Tukey test (SAS Institute Inc., 1999).

## Results

### Laboratory experiments

Average weight for the various age classes was significantly different with means  $\pm 1$  SE of  $2.0 \pm 0.1$  g,  $3.7 \pm 0.1$  g, and  $4.8 \pm 0.1$  g for juvenile, first-year and second-year adult blades, respectively ( $P < 0.0001$ ;  $n = 20$ ). The difference in weight was due to blades of different age classes having significantly different thicknesses ( $0.19 \pm 0.03$  mm,  $0.54 \pm 0.03$  mm, and  $0.82 \pm 0.03$  mm, respectively;  $P < 0.0001$ ;  $n = 20$ ).

*Lacuna vincta* preferentially fed on juvenile blades while older blades were least favored (Fig. 2). The adjusted amount of blade eaten by the snails was significantly greater for juvenile and first-year adult than second-year adult blades ( $P = 0.0304$  and  $0.2350$ ;  $n = 10$ , for Experiment 1 and 2, respectively; Fig. 2a). Snails grazed an average (mean  $\pm 1$  SE) of  $0.256 \pm 0.51$  g and  $0.164 \pm 0.23$  g of juvenile blades,  $0.253 \pm 0.51$  g and  $0.071 \pm 0.61$  g of first-year adult blades, and  $0.073 \pm 0.44$  g and  $0.0052 \pm 0.0052$  g of second-



**Fig. 2** Grazing impact by *Lacuna vincta* on juvenile, 1st-year, and 2nd-year adult *Nereocystis* blades. Experiment 1 and 2 were conducted for 24 and 48 h respectively. Grazing impact was measured as mean ( $\pm$  SE) (a) absolute weight loss in mg (b) percent of weight loss and (c) percent of blade surface grazed ( $n = 10$ ). Significant differences, based on unpaired mean comparisons, between age classes are marked with different letters (A or B for experiment 1, a or b for experiment 2)

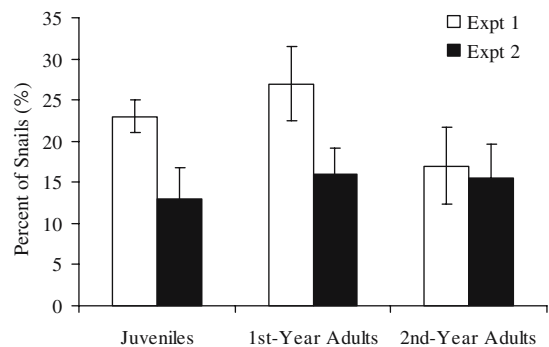
year adult blades (during Experiment 1 and 2, respectively).

Juvenile blades lost a significantly greater proportion of their original weight to herbivory than second-year adult blades ( $P = 0.0066$  and  $0.0004$ ;  $n = 10$ , for Experiment 1 and 2, respectively; Fig. 2b). Juvenile blades lost  $10.360 \pm 2.101\%$  and  $10.570 \pm 1.473\%$  of their original weight whereas first-year adult lost  $7.440 \pm 1.574\%$  and  $2.120 \pm 1.648\%$  and second-year

adults lost  $1.900 \pm 1.101\%$  and  $1.080 \pm 1.029\%$  (for Experiment 1 and 2, respectively; mean  $\pm$  1 SE).

Herbivory also was examined by comparing surface areas with radula marks between the different blade age classes. Although the proportions of surface area grazed by *L. vincta* for blades of different age classes were not significantly different at  $\alpha = 0.05$  ( $P = 0.0554$  and  $0.2814$ ;  $n = 10$ , for Experiment 1 and 2, respectively), the trend was similar to the one observed in absolute and percent weight loss, with juvenile blades being more impacted than first- and second-year adult blades (Fig. 2c). *Lacuna vincta* grazed  $42.1 \pm 6.6\%$  and  $17.9 \pm 3.2\%$  of the surface area of juvenile blades,  $38.7 \pm 5.6\%$  and  $20.3 \pm 3.9\%$  of the surface area of first-year adult blades, and  $22.8 \pm 4.5\%$  and  $12.7 \pm 2.4\%$  of the surface area of second-year adult blades (during Experiment 1 and 2, respectively; mean  $\pm$  1 SE). The less obvious grazing preference displayed in surface area grazed may be attributed to the irregular depth of the grazing marks (personal observation). This observation may be supported by the relatively weak correlation between percent of original weight loss and surface area grazed ( $R^2 = 0.536$ ;  $P < 0.0001$ ;  $n = 60$ ).

Substrate preference data, recorded 24 h after incubation, showed no substrate preference ( $P = 0.1277$  and  $0.7125$ ;  $n = 10$ , for Experiment 1 and 2, respectively; Fig. 3). Although snails grazed more intensively on juvenile tissue, they



**Fig. 3** Percent of snails located on each blade type after 24 h of incubation. Twenty snails were added to each of ten replicate containers. The values represent means  $\pm$  1 SE. No significant differences were observed in the percentage of snails between the different blade types

did not preferentially reside on juvenile blades ( $4.6 \pm 0.4$  and  $2.6 \pm 0.8$  snails for Experiment 1 and 2, respectively; mean  $\pm 1$  SE) versus first-year ( $5.4 \pm 0.9$  and  $3.2 \pm 0.6$  snails) and second-year ( $3.4 \pm 0.9$  and  $3.1 \pm 0.8$  snails) adults. Some snails were located on the walls of the plastic container rather than kelp blades. In Experiment 1, the majority of the snails (77.0%) were found on blades ( $23.0 \pm 2.0\%$  were one juvenile blades,  $27.0 \pm 4.5\%$  on first-year adult blades, and  $17.0 \pm 4.7\%$  on second-year adult blades). In Experiment 2, a greater proportion of snails (55.5%) were located on the containers' walls ( $13.0 \pm 3.8\%$  were one juvenile blades,  $16.0 \pm 3.1\%$  on first-year adult blades, and  $15.5 \pm 4.1\%$  on second-year adult blades). The results recorded after 48 h of incubation for Experiment 2 were comparable to those obtained after 24 h of incubation.

### In-situ Surveys

Overall snail abundance on juvenile versus adult thalli was not significantly different, although there was a trend for more snails to occur on juvenile plants compared to adults (Fig. 4; Table 1). Snail abundance was not significantly different ( $P = 0.4676$ ) between juvenile versus adult blades ( $31.2 \pm 3.5$  versus  $37.5 \pm 8.9$  snails;  $n = 69$  and  $90$  for juvenile and adult blades respectively). This is most likely due to the extensively larger surface area available on adult blades; juveniles rarely had more than 20 blades, most of which were shorter than 50 cm long. In contrast, adults had up to 65 blades, most of which were longer than 250 cm in length. Highest

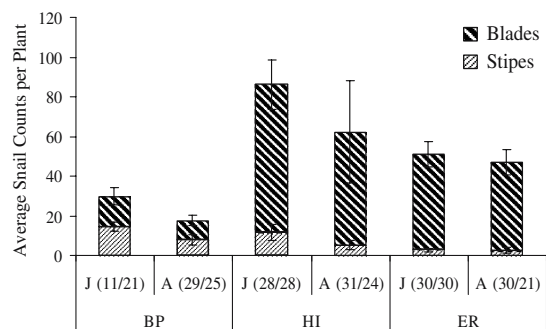
snail abundance on juvenile blades (with a blade length of 60 cm) was 271 at Barabara Point versus 340 for an adult (with a blade length of 250 cm) at the Herring Islands.

Snail abundance was consistently lower on *Nereocystis* stipes ( $7.2 \pm 1.1$  snails;  $n = 149$ ) than blade clusters ( $44.5 \pm 5.9$  snails;  $n = 159$ ; Fig. 4; Table 1). Despite the great difference in stipe length ( $96.3 \pm 4.0$  versus  $473.0 \pm 19.3$  cm, for juveniles and adults, respectively), significantly more snails ( $P = 0.0468$ ) were counted on juvenile than adult stipes ( $9.0 \pm 1.7$  versus  $5.4 \pm 1.3$  snails;  $n = 79$  and  $70$  for juvenile and adult stipes, respectively). The highest number of snails counted on the stipe of a juvenile (on a 120-cm long stipe) was 95 at the Herring Islands versus 61 for an adult (on a 350-cm long stipe) at Barabara Point. Snail abundance was significantly ( $P = 0.0066$ ) different among sites with the mean  $\pm 1$  SE number of snails per plant section being highest at the Herring Island ( $38.7 \pm 8.3$  snails;  $n = 111$ ), intermediate at Elephant Rock ( $26.2 \pm 3.2$  snails;  $n = 111$ ), and lowest at Barabara Point ( $11.1 \pm 1.4$  snails;  $n = 85$ ). Snail abundance also displayed a significant interaction between sites and thallus section ( $P = 0.0019$ ).

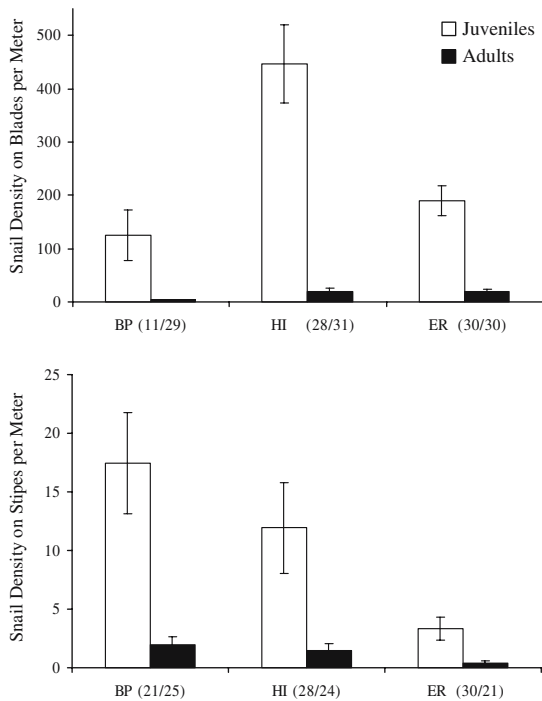
When the difference in size, and thus in surface area available to grazers, between juvenile and

**Table 1** Results of analyses of variance on the effects of age (juvenile or adult), site (BarabaraPoint, Herring Islands, Elephant Rock), and section (stipes or blades) on the number of snails counted on *Nereocystis* kelp ( $n = 357$ )

Source	df	MS	F Value	Pr > F
Age	1	3176.400	1.12	0.2910
Site	2	14475.535	5.10	0.0066
Section	1	82430.094	29.04	<0.0001
Age $\times$ Site	2	677.823	0.24	0.7878
Age $\times$ Section	1	395.601	0.14	0.7092
Site $\times$ Section	2	18197.988	6.41	0.0019
Age $\times$ Site $\times$ Section	2	222.384	0.08	0.9247



**Fig. 4** *Lacuna vincta* abundance on the stipe and blades of *Nereocystis* plants at three sites in Kachemak Bay, Alaska; Barabara Point (BP), Herring Islands (HI), and Elephant Rock (ER). The bar values represent mean ( $\pm 1$  SE) numbers of snails counted on juvenile (J) and adult (A) blades and stipes at each site. The bars representing the mean numbers of snails counted on blades are positioned on top of the bars representing the mean numbers of snails counted on stipes. The numbers in parentheses refer to the number of stipes and blades surveyed, respectively



**Fig. 5** *Lacuna vincta* density on the blades (Top) and stipes (Bottom) of juvenile (J) and adult (A) *Nereocystis* plants at three sites in Kachemak Bay, Alaska; Barabara Point (BP), Herring Islands (HI), and Elephant Rock (ER). The bar values represent the mean ( $\pm 1$  SE) numbers of snails counted per meter of stipe or blade. The number of juveniles and adults surveyed at each site is indicated in parentheses. All densities between juvenile and adult stipes or blades are significantly different ( $P < 0.05$ ) at all sites

adult thalli was accounted for by normalizing snail abundances into densities, the greater affinity by grazers for juvenile *Nereocystis* became highly significant (Fig. 5; Table 2). Snails were

**Table 2** Results of analyses of variance on the effects of age (juvenile or adult), site (BP, HI, ER), and section (stipes or blades) on the density of snails on the stipes of *Nereocystis* kelp. Density, expressed as snail number/m, is calculated by dividing the number of snails counted by the length of the stipe or blades surveyed ( $n = 357$ )

Source	df	MS	F Value	Pr > F
Age	1	1103075.731	63.90	<0.0001
Site	2	189948.227	11.00	<0.0001
Section	1	1170473.674	67.80	<0.0001
Age $\times$ Site	2	169603.556	9.82	<0.0001
Age $\times$ Section	1	938824.209	54.39	<0.0001
Site $\times$ Section	2	188916.725	10.94	<0.0001
Age $\times$ Site $\times$ Section	2	167314.443	9.69	<0.0001

observed at significantly greater densities on the blades of juveniles ( $284.0 \pm 36.7$  snails/m of blade;  $n = 69$ ) versus that of adults ( $14.8 \pm 2.5$  snails/m of blade;  $n = 90$ ;  $P < 0.0001$ ; Fig. 5, (top)). Greater snail densities were observed also on the stipes of juveniles ( $10.1 \pm 1.9$  snails/m of stipe;  $n = 79$ ) versus adults ( $1.3 \pm 0.3$  snails/m of stipe;  $n = 69$ ;  $P < 0.0001$ ; Fig. 5 (bottom)). Overall, snail densities were consistently lower on stipes than blades ( $131.6 \pm 19.1$  snails/m of blade versus  $6.0 \pm 1.1$  snails/m of stipe). The highest snail density on a juvenile stipe was 79.2 snails/m in the Herring Islands versus 17.4 snails/m on an adult stipe at Barabara Point. The highest snail density on juvenile blades was 1540.0 snails/m versus 136.0 snails/m on adult blades in the Herring Islands. Snail densities, as observed with snail abundances, were significantly different among study sites ( $P < 0.0001$ ). In addition, all variance interactions among kelp age, site, and thallus section were highly significant ( $P < 0.0001$  for all).

## Discussion

Grazing plays an important role in structuring algal communities. The negative impact of *L. vincta* on the fitness and possible survivorship of kelp has been reported in several studies. Despite its small size (ca. 5 mm), *L. vincta* can consume large amounts of algal biomass (Fralick et al., 1974; Johnson & Mann, 1986; Padilla, 1993; Toth & Pavia, 2002a) and can puncture through the stipe and pneumatocyst of *Nereocystis* (Duggins et al., 2001; Chenelot, 2003; Carney et al., 2005). In the present study, *L. vincta*, grazed significantly more on juvenile than adult tissues of *Nereocystis*. The intensity and role of several algal chemical and structural attributes that could influence grazers in their food choice can vary within individuals of the same species and be age-specific. Young and old macroalgal tissues often have different palatability or antigrazing characteristics and may suffer different grazing pressures (Watson & Norton, 1985a; Van Alstyne et al., 1999; Van Alstyne et al., 2001; Taylor et al., 2002; Heaven and Scrosati, 2004).

It is unclear how much nutritional quality influences food preference. In some cases nutri-

tional quality has been found to play a substantial role in grazing selection (Steinberg, 1985; Johnson & Mann, 1986; Van Alstyne et al., 2001; Chavanich & Harris, 2002). However, Pelletreau & Muller-Parker (2002) found no correlation between algal nutritional content (percent nitrogen and C:N ratio) and food preference in feeding experiments where *Strongylocentrotus droebachiensis* preferred *Nereocystis*, *Laminaria saccharina* and *Costaria costata* (C. Agardh) Saunders to *Alaria marginata* Postels & Ruprecht and *Desmarestia munda* Setchell & N.L. Gardner. Although *Nereocystis* had the highest nitrogen content (ca. 3.5% of dry mass (DM), versus less than 3% DM for the other algal species) and lowest C:N ratio (ca. 11 versus greater than 12 for the other algal species), it was concluded that grazer preference was influenced more by the amount of anti-herbivory compounds in the alga. In addition, because nutritional values are similar in juvenile and adult *Nereocystis* (with nitrogen content around 2.5% DM and carbon to nitrogen ratios around 12; Steinberg, 1985; Van Alstyne et al., 2001), nutritional quality is not thought to be a factor in *L. vincta* preference for juvenile *Nereocystis* thalli.

Like most brown algae, *Nereocystis* produces polyphenolic compounds, which often act as an antigrazing mechanism. The low level of polyphenolic compounds in this species has been reported to be associated with higher feeding selection during palatability assays (Winter & Estes, 1992). The preference for juveniles observed in this study may be due to age-specific differences in secondary metabolites since, in contrast to *Alaria marginata* Postels & Ruprecht, *Fucus gardneri* P.C. Silva, and *Hedophyllum sessile* (C. Agardh) Setchell, *Nereocystis* juvenile tissues contain 43% less phlorotannin than adult tissues (Van Alstyne et al., 2001). However, the levels found in *Nereocystis* juveniles and adults are relatively low (ca. 0.5% DM) and probably do not effectively deter grazers (Steinberg, 1984, 1985; Johnson & Mann, 1986). Instead, it appears that *Nereocystis* might use rapid growth to reach a size refuge rather than chemical defenses to deter grazers as larger/older tissues tend to be tougher and harder for grazers to puncture (Steinberg, 1985; Van Alstyne et al., 2001).

Thallus morphology (Steneck & Watling, 1982; Johnson & Mann, 1986; Chavanich & Harris, 2002) and tissue toughness (Padilla, 1985; Steinberg, 1985; Johnson & Mann, 1986; Van Alstyne et al., 2001; Chavanich & Harris, 2002) are other anti-herbivory plant characteristics. Thallus toughness may be especially important in algal species that lack strong chemical defenses (Steinberg, 1985). Algal palatability is most likely determined by a combination of structural and chemical algal features in association with the feeding apparatus of the considered grazer species (Padilla, 1985; Watson & Norton, 1985b). Littorinids possess a versatile taenioglossan radula that is efficient at scraping and excavating a variety of soft tissues (Watson & Norton, 1985a; Norton et al., 1990) but some species such as *L. vincta* may not be efficient at chewing through tougher, leathery tissues (Steneck & Watling, 1982). Juvenile tissues may be thinner and easier to puncture than tissues of older individuals (Van Alstyne et al., 1999; Van Alstyne et al., 2001; Taylor et al., 2002). The present study showed that grazing by *L. vincta* caused a greater loss of juvenile blade weight compared to older blades. In the laboratory, some juvenile blades were completely punctured and became almost translucent due to extensive grazing damage, whereas only the superficial outer medulla layer of older blades was grazed. Juvenile plants in the field also were more damaged by grazing than older plants and exhibited damage consistent with what was observed in the laboratory (personal observation). Many of the young kelps had lost their blades and most of the meristoderm layer of their thalli to grazing. Some young pneumatocysts had lost their flotation due to grazing holes, which will often result in plant death (Foreman, 1970; personal observation).

Some small grazers mainly consume epiphytic algae, bryozoans, hydroids, diatoms, bacteria or detritus by browsing on kelp surfaces but usually have minimal impacts on host kelp survival (Leighton, 1971; Norton & Benson, 1983; Williams, 1990). In contrast, many other mesograzers such as the gastropods *Lacuna variegata* Carpenter, *Littorina littorea* (Linnaeus), and *Laevilacunaria antarctica* (Martens) and amphipods are known to consume macroalgal tissues (Norton &

Benson, 1983; Watson & Norton, 1985a; Taylor, 1998; Iken, 1999; Taylor et al., 2002). *Lacuna vincta* has previously been observed to feed on algal epidermal tissue as well as on diatoms and detritus (Fretter & Manly, 1977) and we suspect that they did ingest epiphytes in our study as well. However, the obvious deep radula scars on the algal tissue, observed both in the laboratory and in the field, suggest that feeding marks are not only a consequence of grazing epiphytes but that *L. vincta* undeniably feeds on *Nereocystis* tissue. The tougher meristoderm of old blades seemed to be an effective ‘barrier’ against grazing making them more difficult to consume than younger blades. Despite its marginal effectiveness at chewing through leathery tissues, if *L. vincta* successfully abrades or punctures the tough outer layer of older tissues, it may still critically weaken the thalli (Koehl & Wainwright, 1977; Denny et al., 1997; Duggins et al., 2001).

In addition to the direct impact of tissue removal, holes in stipes and blades produced by the mesograzers may become centers of infection or breaking points, thus producing secondary tissue loss and indirectly jeopardizing plant health and survival (Jones, 1971). *Nereocystis* stipes are adapted to survive strong currents, however if the stipe is damaged, it loses its tensile strength and easily breaks (Koehl & Wainwright, 1977; Denny et al., 1997). It has been shown that *L. vincta* grazing makes kelp more vulnerable to physical forces such as currents (Duggins et al., 2001). In Kachemak Bay, tidal cycles are extreme (with a mean range of 4.7 m and a maximum of 8.5 m) and produce strong cyclic tidal currents. The current regimes at the study sites may fit into the “lethal” category described by Duggins et al. (2001) and may enhance the destructive ability of mesograzers. In summer 2001, high *Nereocystis* mortality coincided with sites of high *L. vincta* grazing pressure in Kachemak Bay (Chenelot, 2003). One study reported extensive damage and mortality of *Laminaria saccharina* (Linnaeus) J.V. Lamouroux and *L. digitata* (Hudson) J.V. Lamouroux as a result of intense *L. vincta* grazing (Fralick et al., 1974). Even when grazing pressure is low, *L. vincta* can influence *Nereocystis* population structure. As example, in one study while only 0.05% of the total annual blade biomass

(fresh weight) of *Laminaria longicuris* Bachelot de la Pylaie was directly consumed by *L. vincta*, the actual impact of herbivory on the kelp canopy was significant as grazing was concentrated on blades that were easily shredded and torn away (Johnson & Mann, 1986). This reduction of blades can influence future *Nereocystis* populations by reducing spore production or photosynthetic capacity.

Although *L. vincta* preferred to graze on juvenile *Nereocystis* compared to adults, the laboratory experiment showed no significant preference for snail location between juveniles, first-year or second-year adults. *Lacuna vincta*’s lack of preference for substrate type in the laboratory is unclear. We analyzed snail location only after 24 h of incubation, but snail movements were observed every 12 h for 48 h during Experiment 2. Throughout that period, snails moved from one substrate to another showing substantial mobility (personal observation). In the field, *L. vincta* densities were significantly higher on juvenile than adult *Nereocystis*. In a different study, *L. vincta* showed no significant preference in its distribution amongst *L. hyperborea* (Gennarus) Foslie fronds of different ages in the field, although it showed a significant preference for younger tissue in the laboratory (Toth & Pavia, 2002a). *Lacuna vincta* has considerable dispersal ability during its post-metamorphic stage (Smith, 1973; Fretter & Manly, 1977; Martel & Chia, 1991a, b), which gives this gastropod a high capacity for colonization (Johnson & Mann, 1986). Juvenile and adult *L. vincta* have the ability to “sail” through the water column with the current by extending their foot and antenna and producing mucus threads that allow them to travel easily between plants and to be transported long distances through the water column (Johnson & Mann, 1986; Martel & Chia, 1991a, b; Martel & Diefenbach, 1993). *Lacuna vincta* may use its drifting behavior to haphazardly land on juvenile versus adult *Nereocystis* thalli. In addition, *L. vincta* can also easily and quickly migrate up and down kelp thalli (Duggins et al. 2001).

The field surveys showed that *L. vincta* was more abundant on *Nereocystis* blades over stipes. This observation may be explained by *Nereocystis* thalli having up to 65 blades (but only 1 stipe) and

blade number was not accounted for in our estimation of snail densities. It is also possible that there are ecological reasons (protection from water movements or predation, or palatability differences between the different thallus sections) for *L. vincta* to prefer residing and feeding on *Nereocystis* blades versus stipes. The significant interactions observed in *L. vincta* densities between sites and kelp age or thallus sections, may possibly result from different hydrographic characteristics or predatory pressures at the different sites. Kachemak Bay is an extremely dynamic estuary with complex current and tidal regimes, *L. vincta* may find better protection against severe water motion by hiding in the blades. Predators are known to influence the habitat choice of mesograzers (Duffy & Hay, 1994), but very little is known about *L. vincta* predators. We can only speculate that in Kachemak Bay some fish (such as greenlings) and crustaceans prey upon *L. vincta*. The higher structural complexity of blades may provide better protection from predators than exposed stipes.

## Conclusions

*Lacuna vincta* can successfully graze on macroscopic sporophytes and as such can be an important factor in structuring subtidal communities (this study; Fralick et al., 1974; Johnson & Mann, 1986). Results from this study suggest that *L. vincta* has the potential to have dramatic impacts on *Nereocystis* populations because of its grazing ability and potential high densities. *Lacuna vincta* can be associated with a variety of algal species, but densities on *Nereocystis* can reach up to 1,540 snails/m on juvenile blades. The combination of greater grazer densities (grazing pressure) and grazing impact (probably due to reduced tissue strength) makes juvenile *Nereocystis* more susceptible than adult *Nereocystis* to *L. vincta* herbivory. This discriminatory damage to the new generation could minimize the number of individuals reaching maturity and consequently jeopardize the maintenance of healthy kelp beds. Since juvenile kelps are more susceptible to grazing than older plants, the synchrony in

recruitment timing of grazers and algae seems critical and worthy of further investigation. Abundance and grazing activity of *L. vincta* are patchy through out Kachemak Bay (Chenelot, unpublished data) and therefore may not be a major factor in the large-scale distribution of *Nereocystis* kelp beds. However, at a local scale, grazing activities can possibly eliminate individual populations. More detailed studies are needed to further elucidate the ecological impact of *L. vincta* on *Nereocystis* kelp forests and to understand the biological, chemical, and physical factors that shape their association.

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