

Feeding preferences of periwinkles among four species of *Fucus*

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Abstract. A widely accepted view of intertidal community organization in the NW Atlantic proposes that fucoid vegetation is maintained by the actions of predators which remove species competitively superior to *Fucus* species. Herbivory is an important component of these predatory interactions, but has been studied largely with reference to the interaction between *F. vesiculosus* and *Littorina littorea*. There are many species of fucoids and herbivorous invertebrates on the shores of the NW Atlantic and this paper reports field and laboratory experiments performed in 1987 (in or near Halifax, Canada) on the effects of grazing by three species of *Littorina* on adults and juveniles of four species of *Fucus*. In laboratory experiments, portions of *Fucus* species were presented singly (no choice) or together (multiple choice) to single species of *Littorina*. Adult *F. distichus* was grazed to only a small extent. *F. evanescens* and *F. vesiculosus* adult tissues were heavily grazed in most laboratory experiments. *F. spiralis* adults were heavily grazed in no choice experiments, but were grazed only slightly in multiple choice tests. When adult fucoid tissues were exposed to a mixed suite of grazers in the field, only *F. vesiculosus* was grazed heavily. Tests done on adult tissues showed clearly that *Fucus* species are highly variable in their vulnerability to grazers. Moreover, we found variability among periwinkle species in grazing rates on adult *Fucus*. We also found a great disparity in the feeding rates of different periwinkle species on juveniles of *Fucus*. Therefore, it is not possible to extrapolate from a single periwinkle species/single fucoid species interaction when attempting to identify vegetation structuring processes.

Introduction

Apart from polluted areas, rocky shores of Atlantic Nova Scotia, Canada, are vegetated through much of the eulittoral zone by luxuriant stands of fucoid seaweeds (Mann 1972, Chapman and Johnson 1990). Both exposed and sheltered shores are dominated by fucoids, but there is

some variation in species composition along the wave exposure gradient. At sheltered sites, the dominant species in the intertidal are *Ascophyllum nodosum*, *Fucus spiralis* and *F. vesiculosus*. At more exposed sites, *F. distichus*, *F. evanescens*, *F. spiralis* and *F. vesiculosus* are predominant. A fifth fucoid species, *F. serratus* has a restricted geographical distribution in the Canadian Maritime provinces.

Within the fucoid zone, the most obvious grazers are gastropod molluscs and gammarid amphipods. The impact of mollusc grazing has been the subject of intense investigation in New England, USA (Lubchenco and Menge 1978, Lubchenco 1982, 1983, Lubchenco 1986, Petraitis 1987). Some interesting conclusions have been drawn from this work. Although fucoids are common on many shores of New England, they are poor competitors for space. Ephemeral algae e.g. *Scytosiphon lomentario* and *Ulva lactuca* are able to competitively exclude fucoids in the absence of grazers (Lubchenco 1986). However, grazers preferentially consume ephemeral algae, allowing competitively inferior fucoid vegetation to develop. Similarly, the hold on space exerted by mussels and barnacles is thought to be broken by carnivores (Menge 1976). Hence, the establishment of fucoids is dependent on the actions of predators which remove competitively superior forms.

Although fucoid algae seem to depend on grazers for successful establishment, the gastropod species found in New England also eat the fucoids themselves (Lubchenco 1982, 1983, Petraitis 1987). According to Lubchenco (1983), juvenile fucoids are especially susceptible to grazing. How then can a fucoid vegetation develop? It is Lubchenco's (1983) thesis that juvenile fucoids may escape grazing by settlement in crevices or among barnacle shells where grazers cannot find them. Alternatively, patchiness in grazer distribution may allow survival of fucoids to a larger, invulnerable size. A third proposal is that the herbivores are swamped by heavy algal recruitment.

Of key importance to Lubchenco's (1983) view of the maintenance of fucoid vegetation is size dependent susceptibility to grazing in *Fucus* species. Her experiments

showed that plants of *F. vesiculosus* of more than 3 cm length are relatively invulnerable to grazing and so there is an "escape" in size.

Petraitis (1987) found that, in sheltered bays of New England, fucoids rarely escape to invulnerable size before they are found by grazing snails. Nearly all germlings are eaten and fucoid vegetation is sparse.

Chapman (1989) has found quite different relationships between the size of *Fucus spiralis* plants and their susceptibility to grazing in the wild. Abundance of *F. spiralis* juveniles was unaffected by the presence of grazers. In contrast, the canopy of adult plants was grazed heavily. Because of apparently contradictory results, it is important to determine the effects of grazing on both adults and juveniles of all *Fucus* species. This paper reports such a study with species of *Littorina*. Parallel work with grazing amphipods is also being done and will be reported separately.

Materials and methods

Natural densities of *Littorina* species at Cranberry Cove

The abundances of three *Littorina* species in each of the fucoid zones were measured at Cranberry Cove (a wave-exposed site, close to Halifax, Nova Scotia, Canada). The structure of the fucoid vegetation on exposed Atlantic shores of Nova Scotia is described by Chapman and Johnson (1990). Our objective was to relate the palatabilities of *Fucus* species to the intensities of grazing pressure at each shore level. A stratified random sampling procedure was used. In each month (May 1987 to January 1988) a line transect was laid down parallel to the water line in each *Fucus* zone. Periwinkle densities were counted in ten 15 × 15 cm quadrats placed at random along each transect line.

No choice laboratory experiments: adult fucoids

The following species of *Fucus* were presented individually to grazing littorinids: *F. distichus*, *F. evanescens*, *F. spiralis*, *F. vesiculosus*. Three species of periwinkle were tested: *Littorina littorea*, *L. obtusata*, *L. rudis*.

All *Fucus* species were collected from an exposed site at Cranberry Cove, Nova Scotia. *Fucus* species at the site are differentially distributed: *F. distichus* occurs only in pools in the littoral fringe; in the eulittoral zone, *F. spiralis* forms a conspicuous belt on the high shore; lower on the shore, there are contiguous belts of *F. evanescens* and *F. vesiculosus*. Specimens for each experiment were collected from the various shore levels at the same low tide interval and returned to the laboratory in an insulated container.

Six days before gathering *Fucus* species specimens, we collected periwinkles from Cranberry Cove, or from another nearby exposed site, Polly Cove. After collection, periwinkles were maintained without food for 6 d in 225 l tanks of fresh seawater.

Feeding preferences by periwinkles were determined as follows: Vegetative portions of fucoid thalli were cut into 2.5 g segments (blotted wet wt) and placed in 4 l glass dishes of aerated, filtered seawater maintained at either 15°C (summer temperature) or 5°C (spring temperature) in a constant temperature room with a natural light/dark cycle. Snails of each species were added at a density of 40 dish⁻¹ and a mass of 20.00 g dish⁻¹ ± 0.05 g. Each species of *Fucus* was thus presented to each species of periwinkle. There were four replicates of each treatment (treatment variable was species of *Fucus* presented to each species of periwinkle). In addition, four controls were set up for each *Fucus* species (without the addition of periwinkles).

Experiments were run for 5 d during which time the water in each dish was changed twice. At the end of an experiment, we weighed all plant portions. This allowed us to calculate increases in mass due to growth and losses due to grazing (difference in mass between control and treatment was used to estimate gross loss to grazing). After drying for 3 d at 60°C, the organic dry weights of *Fucus* species specimens were calculated following combustion in a muffle furnace for 12 h at 450°C. Similarly, organic dry weight of periwinkles was estimated after combustion for 24 h at 450°C. Hence, periwinkle feeding preferences were measured as mg organic dry mass of *Fucus* species eaten per g organic dry mass of periwinkle per d.

Multiple choice laboratory experiment: adult fucoids

The protocol above was repeated with 2.5 g of all four *Fucus* species in each of four treatment and four control dishes. Only *Littorina littorea* and *L. obtusata* were tested in this experiment which was run at 15°C.

No choice laboratory experiment: juvenile fucoids

Our field observations showed that *Littorina littorea* and *L. obtusata* have different distributions in the presence of a fucoid canopy. Most *L. littorea* specimens grazed epilithically, while *L. obtusata* grazed ephytically. To test the hypothesis that juveniles of each *Fucus* species are equally susceptible to grazing by each of two periwinkle with different feeding habits, we cultured microscopic juveniles for presentation to the grazers.

Receptacles of *Fucus* species were collected from Cranberry Cove, blotted dry and kept in the dark at 5° or 15°C for 3 to 4 d. Gametes were released over grooved ceramic tiles by placing treated receptacles in fresh seawater above the tiles in the presence of strong light. After gamete release, receptacles were removed and zygotes left in static water for 3 to 5 d to allow attachment to tiles. The water was changed once or twice during this period. Subsequently, tiles bearing attached germlings were placed under high pressure sprays of seawater for 7 d under high light. This treatment encouraged firm attachment of germlings.

After removal from the sprays, the juvenile plants were censused (at × 100) on marked portions of each tile. Juveniles were then exposed to grazing by placing tiles in 4 l dishes of fresh static seawater at 15°C with 40 periwinkles weighing 20.00 g (± 0.10 g). Each treatment and control (dish without periwinkles) was replicated four times and water was changed daily. After 72 h juveniles were censused again. The impact of grazers was measured as proportional survivorship of juvenile plants.

Multiple choice field experiment: adult fucoids

Adult specimens of all four *Fucus* species were exposed to natural grazing pressure in a littoral fringe tide pool at Berry Point, an exposed shore near Halifax, Nova Scotia. Portions of seaweed weighing 2.5 g were threaded onto lines attached to the bottom of the pool. Four replicate portions of each *Fucus* species were arranged in random order on the lines. Controls (no grazers) were set up within cages which excluded grazers. The cages were 15 × 15 × 10 cm with 1 mm mesh stainless steel sides and 1 mm mesh nylon monofilament roofs. Cages were bolted to the rock floor of the pool with wedge anchor bolts. Foam gaskets provided a good seal to the pool floor.

Use of cages carries a risk of introducing procedural artifacts. We therefore set up procedural controls. These controls were partially meshed cages which allowed free access to grazers. Three full mesh and three partially meshed cages were set up. Four replicate portions of each *Fucus* species were suspended on lines in random order within the cages.

After 5 d (July 29 to August 3, 1987) all plants specimens were returned to the laboratory and weighed. Weight losses of plants exposed to grazers (specimens uncaged or within partially meshed cages) represent grazing rates and are expressed as mg organic dry weight of fucoid eaten per day. Weight gains in specimens within cages represent growth.

Data analysis

Single factor analyses of variance (ANOVA), with or without, repeated measures were used to test for significant effects. We checked for homoscedasticity (Bartlett's test) and normality (visual inspection of frequency distribution data). When transformations were required to make data fit the assumptions of the analysis, this is indicated in the Results section.

Results

Natural densities of *Littorina* species at Cranberry cove

Total densities of littorines varied significantly among the zones occupied by different *Fucus* species (one way ANOVA with repeated measure, $F=37.33$, $df=3$, $p=0.001$) and were clearly higher in the *F. distichus* pools than in any other zone studied (Fig. 1). *Littorina littorea* was the major species responsible for elevated snail densities in the *F. distichus* pools (Fig. 1). *L. obtusata* was more common in the low shore zones. *L. rudis* was infrequent at all shore levels examined (but was common on emergent rock in the littoral fringe, a habitat not included within this study since fucoids are absent).

No choice laboratory experiments: adult fucoids

Periwinkle consumption rates of adult fucoids with no choice among species are shown in Fig. 2. The only valid statistical comparisons are among *Fucus* species within periwinkle species. Snail species were tested at different times, so time is a confounding influence.

Littorina littorea: There were significant differences in consumption rates among *Fucus* species at 15°C (ANOVA, $F=13.171$, $df=3$, $p=0.004$) and at 5°C (ANOVA, $F=5.838$, $df=3$, $p=0.0107$). *F. distichus* clearly was eaten to a lesser extent than the other species (Fig. 2). An a posteriori multiple comparison test (Dunnett's t , Howell 1987) showed significant differences in consumption rates by *L. littorea* at 15°C among the following *Fucus* species: *F. distichus* vs *F. evanescens* ($p<0.01$); *F. vesiculosus* vs *F. evanescens* ($p<0.01$); *F. spiralis* vs *F. evanescens* ($p<0.01$). Other pairwise comparisons were not significant ($p>0.05$). In this test, it is clear that *F. evanescens* was more palatable than other species tested (Fig. 2).

At 5°C (Fig. 2) the only significant ($p<0.05$) pairwise differences in consumption rates among *Fucus* species were: *F. distichus* vs *F. evanescens*, and *F. vesiculosus* vs *F. evanescens*. Consumption rates at 5°C were about one half of rates at 15°C, but *Fucus* species retained the same rank order at each temperature (Fig. 2).

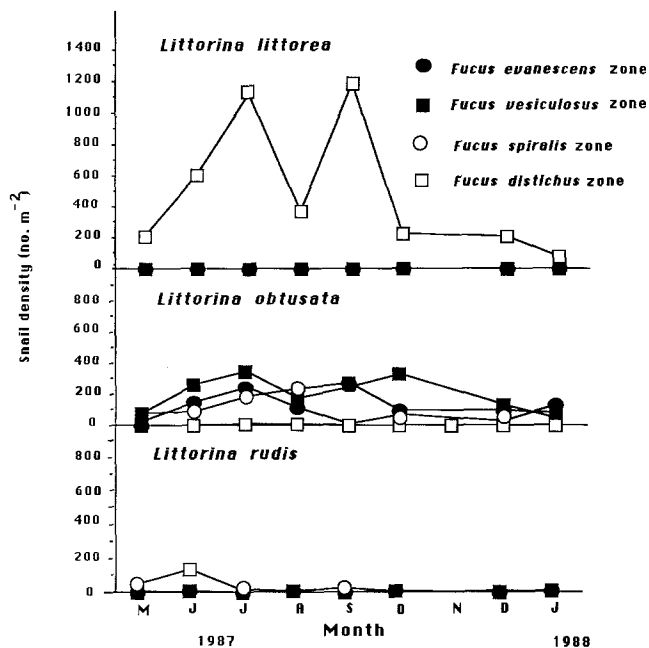


Fig. 1. *Littorina* species. Densities of three of *Littorina* species in four *Fucus* species zones at Cranberry Cove, Nova Scotia. Data are means for 10 samples at each shore level

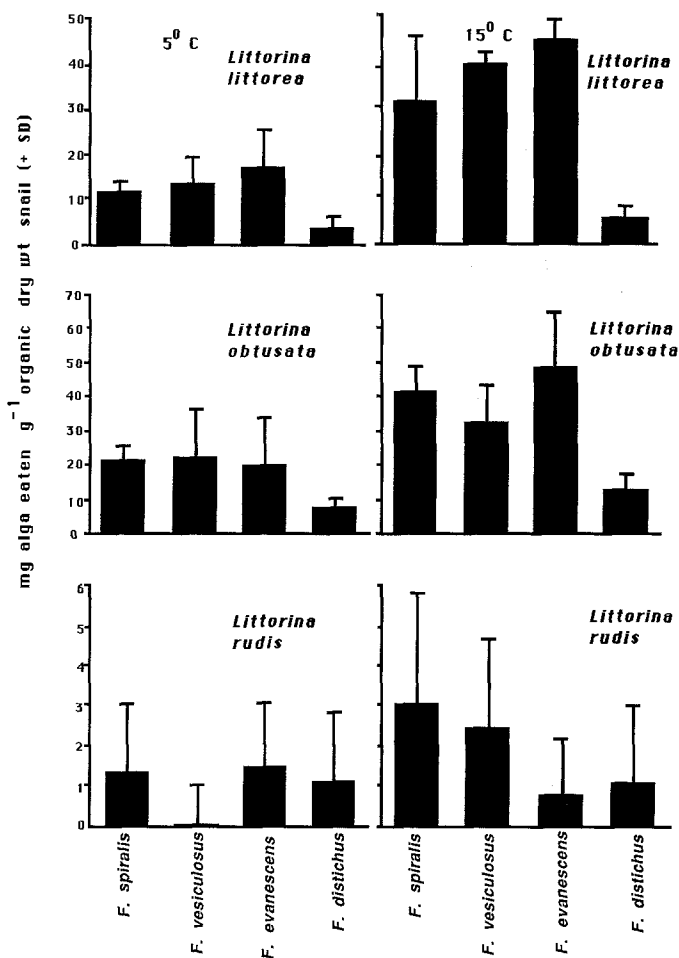


Fig. 2. *Fucus* species. Laboratory consumption rates of adult specimens of four species of *Fucus* by three species of *Littorina* at two temperatures. Periwinkles were given no choice among *Fucus* species. Data are means + SD of four replicates

Littorina obtusata: At 15°C there were significant differences in consumption rates among *Fucus* species (ANOVA, $F=17.225$, $df=3$, $p=0.0001$). At 5°C there were no significant differences (ANOVA, $F=3.36$, $df=3$, $p=0.0551$). At 15°C, *F. distichus* was again the least preferred species (Fig. 2). Dunnett's *t*-test among means showed significant ($p<0.05$) differences among all *Fucus* species pairs except *F. spiralis* and *F. vesiculosus*. Consumption rates were broadly similar for *Littorina littorea* and *L. obtusata* at both temperatures tested.

Littorina rudis: This species consumed adult fucoids an order of magnitude more slowly than the other two periwinkle species (Fig. 2). At 15°C there were no significant differences in consumption rates among *Fucus* species tested (ANOVA, $F=3.307$, $df=3$, $p=0.0574$). However, there were significant differences at 5°C (Fig. 2, ANOVA, $F=7.364$, $df=3$, $p=0.047$). Pairwise multiple comparisons (Dunnett's *t*) showed significant differences in the consumption rates of *F. evanescens* and *F. vesiculosus* ($p<0.05$) and between *F. evanescens* and *F. distichus* ($p<0.01$). Other pairwise comparisons were not significant ($p>0.05$).

Food preferences of *Littorina rudis* among *Fucus* species were either weak (5°C) or absent (15°C). This snail species was uncommon in the *Fucus* species zones examined (Fig. 1) and, for these reasons, *L. rudis* was not included in other laboratory tests.

Multiple choice laboratory experiment: adult fucoids

The results of this experiment are shown in Fig. 3. Because of the lack of independence among treatments, the experimental design does not allow tests for significant differences in consumption rates among *Fucus* species. That is, increased consumption of one *Fucus* species results in reduced consumption of another. Nevertheless, it has biological relevance because herbivores in the wild have multiple choices among food species.

It is quite clear that *Fucus vesiculosus* is much preferred over other species for both *Littorina littorea* and *L. obtusata* (Fig. 3). The species rankings below *F. vesiculosus* were *F. evanescens* > *F. distichus* > *F. spiralis*. Negative values in Fig. 3 indicate that plants in the treatment dishes (with periwinkles) increased in weight to a greater extent than plants in the control dishes (without periwinkles).

For the periwinkles species tested, the rank order was different in no choice and multiple choice experiments (Fig. 2 vs Fig. 3).

No choice laboratory experiment: juvenile fucoids

The mortality of various species of *Fucus* juveniles exposed to *Littorina littorea* grazing varied from 70 to 100%. *L. obtusata* consumed only 20 to 50%. Losses of juveniles in controls were very low (Fig. 4). These differences among periwinkle species were highly significant ($p<0.05$) for feeding rates on juveniles of all four *Fucus* species (Dunnett's *t*-test on angular transformed data).

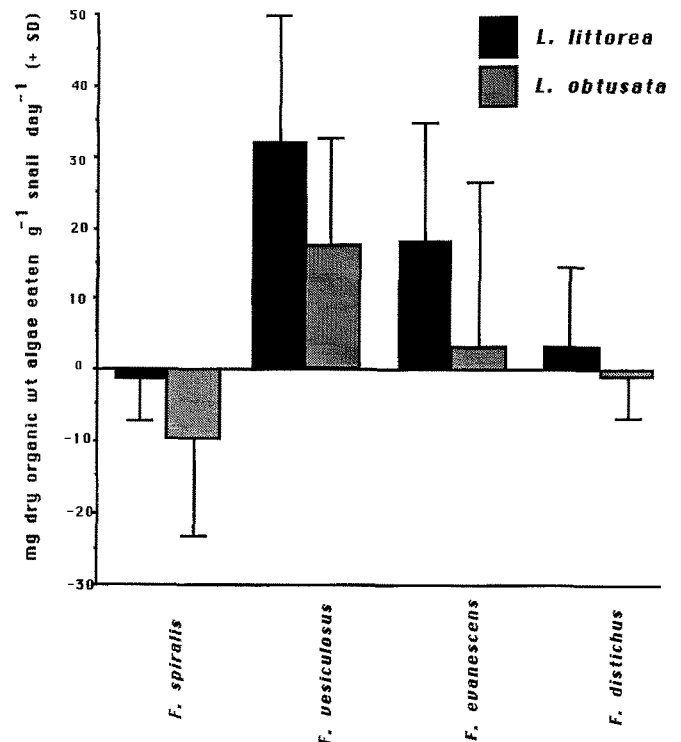


Fig. 3. *Fucus* species. Laboratory consumption rates of adult specimens of four species of *Fucus* by two species of *Littorina*. Periwinkles were presented with a choice among *Fucus* species (multiple choice design). Data are means + SD of four replicates. Consumption rates are shown as negative when mass increases of plant portions were greater in treatments (with periwinkles) than in controls (without periwinkles)

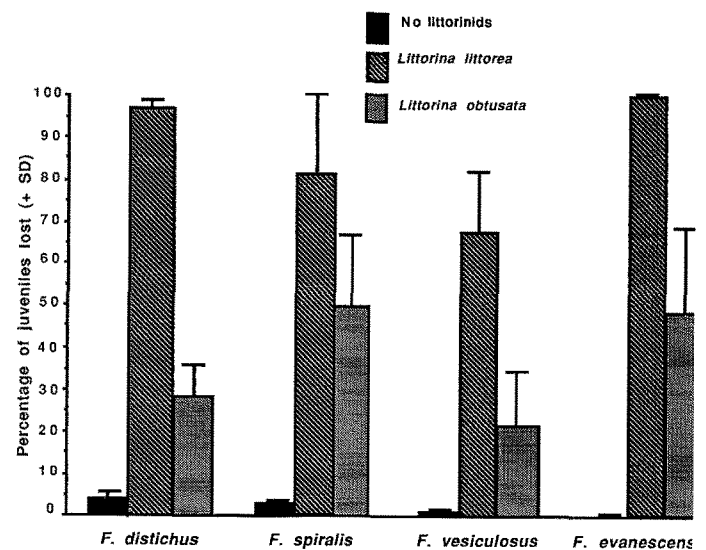


Fig. 4. *Fucus* species. Survivorship of juveniles of four species of *Fucus* when exposed to grazing by two species of *Littorina* in the laboratory. Data are means + SD of four replicates

Multiple choice field experiment: adult fucoids

We found no significant ($p>0.05$) differences in changes in plant mass in partially caged and uncaged plots. Thus procedural artifacts were insignificant.

When we tested preferences among *Fucus* species presented to a mixed guild of herbivores (snails, amphipods,

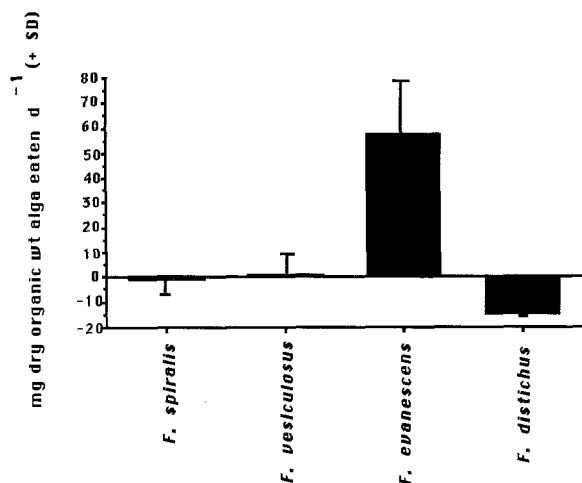


Fig. 5. *Fucus* species. Consumption rates of four species of *Fucus* by a mixed herbivore guild within a tide pool at Ketch Harbour, Nova Scotia. Data are means +SD of four replicates. Consumption rates are shown as negative when mass increases of plant portions were greater in treatments (with periwinkles) than in controls (without periwinkles)

isopods) the results were not concordant with our laboratory multiple choice test (Fig. 5). *F. evanescens* was the most palatable and *F. distichus* the least. The preference rankings in the field experiment matched those from our no choice laboratory experiments (Fig. 3).

Discussion

Our results show that periwinkle densities are much higher in tide pools dominated by *Fucus distichus* than on the lower shore where other *Fucus* species grow (Fig. 1). *Littorina littorea* densities are entirely responsible for this differential (Fig. 1). High shore pools are therefore habitats with heavy grazing pressure because they have the highest periwinkle densities, grazers are permanently submerged and thus able to forage at all times and they contain large populations of *L. littorea* which is a voracious consumer of *Fucus* juveniles (Fig. 4). In contrast, there was little difference in periwinkle densities among the zones occupied by *F. evanescens*, *F. spiralis* and *F. vesiculosus*.

In two of three palatability tests, we found that *Fucus distichus* was the least preferred species among those offered to *Littorina littorea* and *L. obtusata*. In no-choice laboratory tests, the remaining *Fucus* species were found to be similar in palatability and this is concordant with the observation that periwinkle densities were about equally abundant on emergent rock surfaces occupied by *F. evanescens*, *F. spiralis* and *F. vesiculosus*. Hence, for some of the palatability tests done on adult *Fucus* species, we find that there is a negative correlation between each plant species' susceptibility to grazing and density of periwinkle herbivores in its habitat.

Separate work (Denton and Chapman unpublished) has shown that the levels of polyphenols (anti-herbivore metabolites, Hay and Fennical 1988) are about four times higher in *Fucus distichus* than in other species studied at our site. On this evidence, we hypothesise that in areas of

high grazer pressure, *Fucus* species channel resources into anti-herbivore chemicals. In low herbivore habitats these resources may be channeled elsewhere.

Rank order palatabilities varied among the three experiments we performed on adult *Fucus* species. We do not know why this is so, but it should be pointed out that the plants in our field experiment were subjected to many more kinds of grazers than those in the laboratory, so it is hardly surprising that disparate results were obtained. In all cases, *F. distichus* had a low palatability ranking, but in the multiple choice experiment done in the laboratory, *F. spiralis* was less preferred *F. distichus* plant showed no evidence of grazing damage at the termination of this experiment, but specimens of *F. spiralis* were clearly grazed (portions of fronds missing). This apparent contradiction may be accounted for by differences in growth rates between the two species. *F. distichus* grew very slowly and was little grazed, whereas *F. spiralis* was grazed, but grew much faster. In consequence, net changes in weight (positive, in the presence of grazers) were greater for *F. spiralis*. Mineral fertilization may account for the faster growth of *F. spiralis* in the presence of grazers feeding on other species of fucoids. Grazers feeding rapidly on *F. vesiculosus* in multiple choice experiments must have released inorganic waste products (probably ammonium) which can enhance the growth of other fucoid species in the same medium. In a sense, the snails might have acted as the vectors converting organic nitrogen in their plant food into inorganic nitrogen which is thus made available as a mineral nutrient.

The results from our experiments on juvenile fucoids are clear cut. *Littorina littorea* grazing had a devastating effect on juvenile fucoid survivorship. Miller and Vadas (1984) also found that this epilithically grazing littorine greatly reduced the survivorship of the fucoid *Ascophyllum nodosum*. We found that *L. obtusata* had much less of an effect on juveniles of *Fucus* species. These findings are concordant with our natural history observations which showed that *L. obtusata* feeds mainly in the canopy of fucoid vegetation (Chapman 1989).

The findings presented here and elsewhere (Parker 1987, Chapman 1989) suggest that among the complex suite of amphipod and littorine grazers in the NW Atlantic, only *Littorina littorea* has a controlling effect on the abundance of juvenile fucoids. Since *L. littorea* is uncommon on emergent rock of exposed rocky shores in Nova Scotia, whereas other grazers are common, we suggest that the role of littorines as determinants of juvenile fucoid abundance may have been overestimated by extrapolation from New England shores.

Littorina littorea was introduced to the NW Atlantic in historical times (Brenchley and Carlton 1983). It seems reasonable to propose, therefore, that generalizations about the relationships between vegetation and grazers (Lubchenco 1982, 1983, 1986) derive from this artifact. It may well be that before European influence, intertidal epilithic grazing was unimportant in the NW Atlantic.

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