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The habitat and feeding preferences of *Littorina obtusata* (L.) and *L. mariae* Sacchi et Rastelli

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Abstract: The vertical zonation of the flat periwinkles *Littorina obtusata* (L.) and *L. mariae* Sacchi et Rastelli is different, but overlaps. At a sheltered location on the Isle of Cumbrae, Scotland, *L. obtusata*, although most abundant on *Fucus vesiculosus* L. and *Ascophyllum nodosum* (L.) Le Jol. on the midshore, ranged over the entire shore from the *Pelvetia* zone down to the upper limits of *Laminaria*. *Littorina mariae* exhibited a much more restricted distribution being associated predominantly with *Fucus serratus* L. on the lower shore. In laboratory trials with adult plants, flat periwinkles found fucoid algae both more attractive and more palatable than other seaweeds. *Littorina obtusata* also preferred the reproductive receptacles of fucoid algae to their vegetative tissue. Tiny germlings of a diversity of seaweeds were readily consumed by *L. obtusata*. In choice experiments germling *Ulva lactuca* L. was preferred to adult *U. lactuca*, whereas adult *Fucus serratus* was preferred to germling *F. serratus*. Contrasting foraging behaviours between different species of flat periwinkle are discussed in relation to differences in their radular dentition.

Key words: *Littorina obtusata*; *Littorina mariae*; Flat periwinkle; Selective grazing

INTRODUCTION

Detailed investigations of polymorphism in *Littorina obtusata* revealed morphological, physiological, and ecological differences which prompted Sacchi & Rastelli (1966) to separate the species into two sympatric units describing the dwarf form as a new species *L. mariae*. Interspecific differences have since been elaborated further by Sacchi (1967, 1969a,b, 1972), Reimchen (1974), and Goodwin & Fish (1977).

Although the feeding preferences of *L. obtusata* were studied prior to the subdivision of the species (Barkman, 1955; Van Dongen, 1956; Bakker, 1959), the value of these studies is now open to question. Many of the distinctive features of the sibling species hint at a degree of divergence in feeding behaviour. Reimchen (1974), for example, recorded differences in radular morphology and it has been shown that relatively small differences in the structure and functioning of the feeding apparatus (Steneck & Watling, 1982; Watson & Norton, unpubl.) can impose dietary restrictions and promote the partitioning of food resources between coexisting species.

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The present paper examines differences in the radular morphology and field distribution of the flat periwinkles *L. obtusata* (L.) and *L. mariaae* Sacchi et Rastelli from the Firth of Clyde, Scotland. The feeding preferences of the two species are also compared by means of choice experiments in the laboratory.

METHODS

All material was collected from Butter Lump on the Isle of Cumbrae, Scotland (Grid Ref. NS182556), a relatively sheltered east-facing location.

Two major anatomical features were employed to separate the flat periwinkles *L. obtusata* and *L. mariaae* in vivo: the morphology of the shell and the structure of the male reproductive organs. When the authors became familiar with the precise shell form of mature animals from the collecting site, it proved possible to separate the two species, both in the laboratory and in the field, on this basis alone.

ZONATION AND HABITAT

The vertical zonation of the sibling species in relation to the dominant canopy and understorey algae was examined at Butter Lump in order to define the potentially available macroalgal foods. The abundance of algae and adult snails was recorded in adjacent 0.5×0.5 -m quadrats along a 16-m transect line stretching down the shore from the upper limit of furoid distribution, 3.2 m above Lowest Astronomical Tide (LAT). The quadrats were divided into 10×10 -cm grids to facilitate visual assessment of percent cover for each algal species. Distribution along the transect was examined initially during September 1982 and was later re-assessed in April 1983 to reveal any seasonal changes in the distribution patterns.

The habitat of flat periwinkles on two contrasting parts of the shore was also investigated. Samples were collected from a *Fucus serratus* stand with an understorey of *Ulva lactuca* and from a mixed stand of *Ascophyllum nodosum*, *Fucus serratus*, and *F. vesiculosus*. Algal nomenclature follows Parke & Dixon (1976).

To coincide with a period of high littorinid activity, all samples were collected on a rising tide, 10–15 min after submersion. Two quadrats (0.5×0.5 m) were placed on the substratum and each plant attached within the quadrats was carefully excised at the holdfast and placed in a polythene bag for subsequent examination in the laboratory. Care was taken not to dislodge snails from the algae during removal. In the laboratory the snails were identified and counted and the total surface area of each plant was determined using a portable surface area meter (LAMBDA Instruments Corporation Model L1–3000). A correction factor was calculated to allow for the extra surface area of *Ascophyllum* bladders. The distribution of juvenile flat periwinkles (immature specimens, shell length generally <0.7 cm) was also recorded.

RADULA STRUCTURE

Radulae were extracted from adult snails and prepared by rinsing in a dilute solution of sodium hypochlorite and drying in a graded acetone series (30, 50, 70, and 90%). Specimens were then mounted on stubs and examined under a scanning electron microscope.

CHOICE EXPERIMENTS

The techniques used to determine the edibility of macroalgae and their attractiveness are detailed in a separate paper (Watson & Norton, 1985) and will be described only briefly here. The edibility of the major canopy and understorey species was assessed for both species of flat periwinkle in a series of two-way choice experiments in which the consumption (wet weight) of each test alga was gauged against consumption of a standard reference material (*Ulva lactuca*). Ten replicates, each containing 10–15 snails, were run for each test alga. Any replicate in which total consumption after 5 days failed to exceed 20 mg, was discarded and subsequently repeated. Consumption was corrected for weight changes by subtracting changes in 10 ungrazed controls.

The ratio of test alga to reference material consumed was calculated, giving a palatability index (PI) similar to that used by Carefoot (1967) and Grime *et al.* (1970), such that:

$$\text{PI} = \frac{\text{mg fresh weight test alga consumed}}{\text{mg fresh weight reference material consumed.}}$$

Although this is a measure of edibility, not palatability, the term Palatability Index has been retained as it is in common use.

For all species with a calculated PI < 0.1, two-way choice experiments were repeated (three replicates), using unblemished fragments of test alga. Where no evidence of grazing (macroscopic or microscopic) was apparent after 4 days, the PI was amended to 0.

Algal attractiveness was assessed for both species of snail in a separate series of experiments. Pairs of test algae were placed in an aquarium containing 60 adult snails and the position of the snails relative to the algae was recorded after 60 min. Both snails and plants were completely submerged. The experiment was repeated with every possible combination of test algae, using a fresh batch of periwinkles in each trial.

In order to examine possible changes in food preferences induced by seasonal changes in the food plants the consumption of fertile female receptacles of *Fucus serratus* and of *Ascophyllum nodosum* by *Littorina obtusata* was compared with that of vegetative tissue after 5 days (10 replicates). Ten further replicates without snails allowed adjustments to be made for the growth of the algae.

A series of experiments was done in which *L. obtusata* was offered a choice between germlings of different species of algae, and between germlings and adult tissue of the same species. Lawns of algal germlings were cultured on glass microscope slides (see

Watson & Norton, 1985) and consumption of tissue was assessed in terms of dry weight. When tested the lawns were 21–28 days old depending on species, and the plants were 0.8–1 mm tall. The initial density of each lawn was estimated using a portable area meter and linear regression equations were calculated to relate germling density to dry weight. Following 1–3 days of grazing (depending on voracity), surviving germlings were oven dried and weighed. In choice experiments (involving adult plants) wet weight against dry weight regression equations were calculated to estimate the initial dry weight of adult tissue.

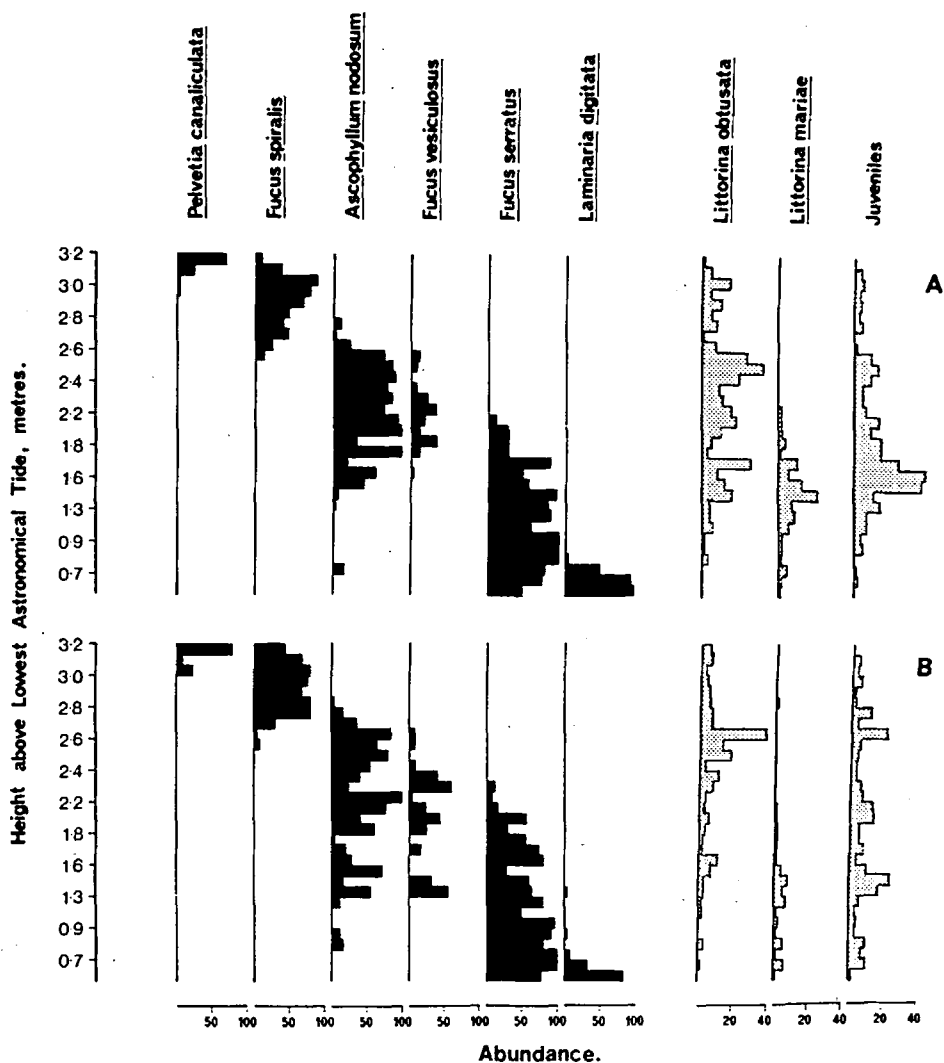


Fig. 1. Vertical distribution of flat periwinkles and the dominant seaweeds at Butter Lump, Isle of Cumbrae in September 1982 (A) and in April 1983 (B). Dark bars indicate canopy-forming algae and stippled bars indicate snails. Animal abundance is given as numbers per m^2 , plant abundance as percent cover.

Feeding on germlings of the perennial fucoid *Ascophyllum* and the ephemeral green alga *Enteromorpha intestinalis* (L.) Link was compared in 10 replicates (10 snails per replicate). Experiments offering a choice between adult and juvenile *Fucus serratus* and *Ulva lactuca* were also replicated 10 times.

In all experiments in which each replicate compared consumption of two test species, the Wilcoxon signed rank test for paired comparisons was used as a statistical test of preference.

RESULTS

HABITAT AND INTERTIDAL ZONATION

Fig. 1 illustrates the vertical zonation of flat periwinkles relative to the available seaweed cover. Only algae with an estimated maximum cover > 10% were recorded.

Littorina obtusata was locally abundant from the *Pelvetia* zone, 3.2 m above LAT, to the upper limits of *Laminaria* at the bottom of the shore. Maximum abundance occurred on the midshore canopy of *Fucus vesiculosus* and *Ascophyllum*, especially in the spring. *Littorina mariae* was virtually confined to the *Fucus serratus* zone. Juvenile flat periwinkles were abundant along the entire length of the transect. Overall densities were markedly higher in the autumn, reaching a distinct peak at 1.6–1.8 m above LAT.

In the *Fucus serratus* zone, foraging adult snails of both species were confined almost exclusively to the fronds of the canopy species (Table I). Juvenile animals, however,

TABLE I
Distribution of foraging periwinkles on various substrata in the *Fucus serratus* zone.

Substratum	Total surface area sampled (cm ²)	Abundance (no. · m ⁻² + range)		Juveniles
		<i>L. obtusata</i>	<i>L. mariae</i>	
<i>Fucus serratus</i>	28 350	3.5 (2.6–7.2)	6.0 (4.4–12.7)	37.0 (31.1–61.6)
<i>Ulva lactuca</i>	8 158	0	1.2 (0–1.6)	73.5 (68.1–90.5)
Rock	5 000	0	0	14.0 (8–20)

TABLE II
Distribution of foraging periwinkles on various algal substrata in a stand of mixed fucoids.

Substratum	Total surface area sampled (cm ²)	Abundance (no. · m ⁻² of algal thallus + range)		Juveniles
		<i>L. obtusata</i>	<i>L. mariae</i>	
<i>Ascophyllum nodosum</i>	14 277	7.9 (7.7–8.3)	7.7 (6.6–10.4)	20.3 (17.7–27.0)
<i>Fucus serratus</i>	31 301	5.4 (4.8–6.3)	6.1 (4.7–7.0)	11.8 (7.1–15.0)
<i>Fucus vesiculosus</i>	22 571	12.9 (11.0–20.4)	3.1 (2.8–4.5)	13.7 (10.5–27.3)

occurred at high densities in the "wrinkles" of *Ulva lactuca* fronds and in rock crevices. Amongst stands of mixed fucoids (Table II) *Littorina obtusata* was most abundant on *Fucus vesiculosus* and to a lesser extent on *Ascophyllum*. *Littorina mariae* was most common on *Fucus serratus*, and notably rare on *Ascophyllum*. Juvenile animals occurred on all fucoids but achieved their maximum densities on *A. nodosum* where damaged bladders provided a suitable microhabitat.

RADULA STRUCTURE

Radulae of both species were studied because they are likely to influence the feeding capabilities of the animals. Over 100 radulae were examined and those illustrated in Fig. 2 are typical. The major variation between individuals of the same species seem to result from the degree of wear on the teeth. In *Littorina obtusata* the outer marginal tooth possesses numerous rather indistinct, angular cusps (Fig. 2A). In *L. mariae* these are replaced by very distinct lobate cusps (Fig. 2B). The intermediate teeth also differ markedly. In *L. obtusata* the dominant has three large cusps, flanked on either side by a small, more pointed cusp. In contrast *L. mariae* has only two large cusps in the centre of the tooth.

CHOICE EXPERIMENTS WITH MACROALGAE

The results of edibility trials with young adult plants are presented in Table III. Preference rankings are almost identical for the two species of snail. The fucoid algae are preferred to other types. For both snails the upper shore species *Fucus spiralis* headed the rankings and was consumed in significantly ($P < 0.01$) greater quantities than *Ascophyllum nodosum* the lowest ranked fucoid. For the other fucoids the ranking was not significant, but the order of preference was the same for both species of snail (Table III).

TABLE III

Macroalgal food preferences of *Littorina obtusata* and *L. mariae* - edibility. Asterisks denote significance of difference between consumption of test and reference material (Wilcoxon signed rank test); ns = not significant; * $0.01 < P < 0.05$; ** $0.001 < P < 0.01$.

Species	PI (\pm SE)	
	<i>L. obtusata</i>	<i>L. mariae</i>
<i>Fucus spiralis</i>	9.67 \pm 1.43**	5.36 \pm 1.27**
<i>Fucus vesiculosus</i>	3.72 \pm 0.67**	4.04 \pm 1.59 ns
<i>Fucus serratus</i>	3.63 \pm 1.02*	3.10 \pm 0.53**
<i>Pelvetia canaliculata</i>	3.51 \pm 0.99**	2.51 \pm 0.36*
<i>Ascophyllum nodosum</i>	2.05 \pm 0.80 ns	0.94 \pm 0.17 ns
<i>Ulva lactuca</i>	1	1
<i>Cladophora rupestris</i>	0	0
<i>Polysiphonia lanosa</i>	0	0

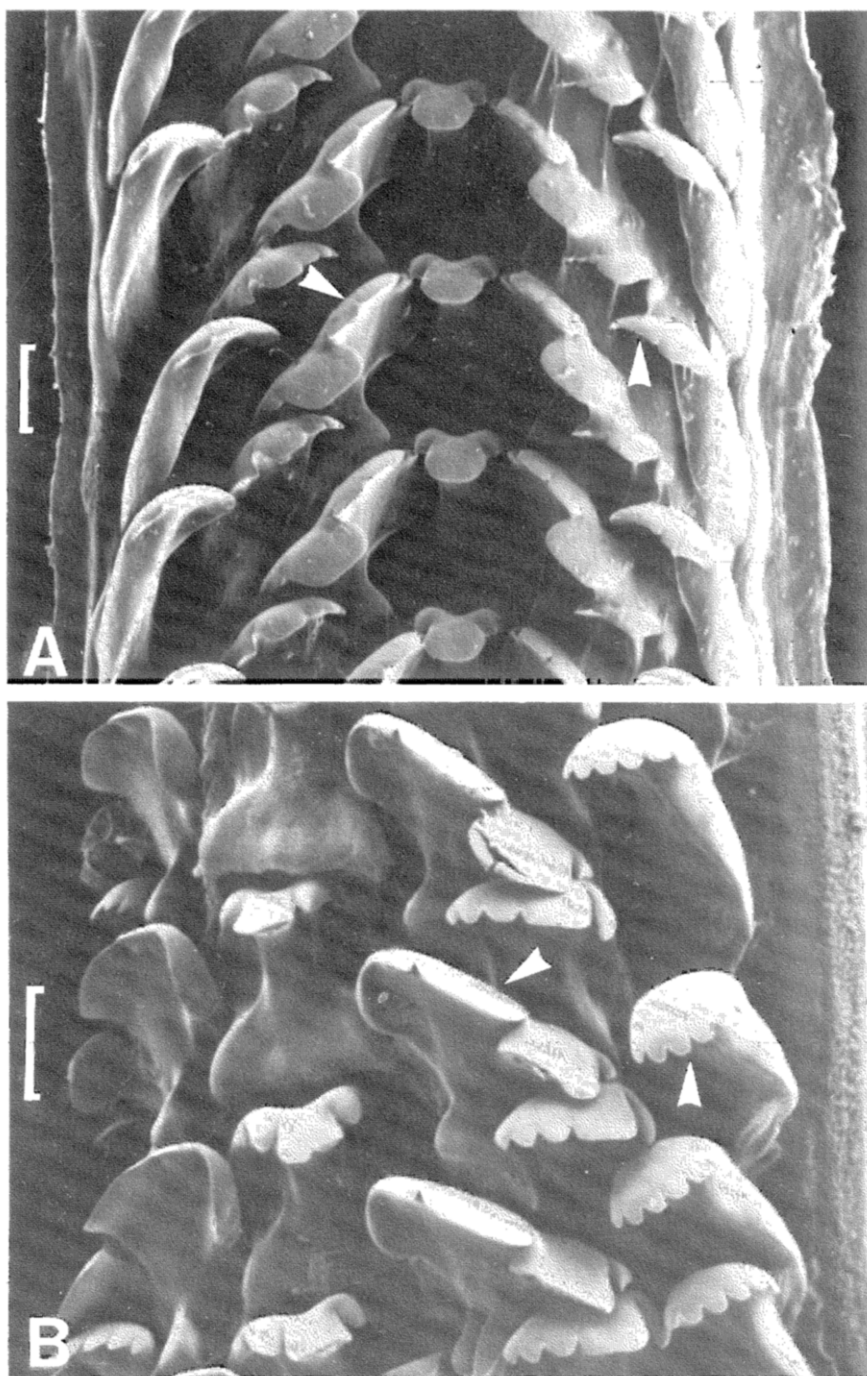


Fig. 2. Differences between the radulae of *Littorina obtusata* (A) and *Littorina mariae* (B). Pointers indicate differences between the cusps on the intermediate and the outer marginal teeth. Scale bars = 50 μ m.

To test the reliability of the Palatability Index as a means of comparing edibility, a series of trials was carried out in which consumption of several test species was compared directly, using *Littorina obtusata* (Table IV). Ten replicates were used each with 10–15 snails. Preference rankings derived from these trials were as follows: *Fucus*

TABLE IV

The amount of algal tissue consumed ($\text{mg} \cdot \text{replicate}^{-1} \cdot \text{day}^{-1}$, means \pm SE) by *Littorina obtusata* in choice experiments: ns = not significant; *0.01 < P < 0.05; **0.001 < P < 0.01; Wilcoxon signed rank test.

Comparisons			
<i>Fucus spiralis</i>	20.4 \pm 0.97	<i>Fucus vesiculosus</i>	5.8 \pm 0.47**
<i>Fucus serratus</i>	6.6 \pm 0.39	<i>Fucus vesiculosus</i>	5.6 \pm 0.39 ns
<i>Fucus serratus</i>	4.6 \pm 0.23	<i>Ascophyllum</i>	2.0 \pm 0.17*
<i>Fucus vesiculosus</i>	6.4 \pm 0.37	<i>Ascophyllum</i>	2.8 \pm 0.20*

spiralis > *F. serratus* and *F. vesiculosus* > *Ascophyllum*. This corresponds closely to rankings determined on the basis of PI values (Table III).

In feeding trials with *Littorina obtusata* the consumption of reproductive receptacles in terms of weight exceeded that of vegetative tissue for both *Ascophyllum nodosum* and *Fucus serratus* (Table V).

TABLE V

The amount of algal tissue consumed ($\text{mg} \cdot \text{replicate}^{-1} \cdot \text{day}^{-1}$, means \pm SE) by *Littorina obtusata* offered both reproductive and vegetative tissue: *0.01 < P < 0.05; Wilcoxon signed rank test.

Algae	Reproductive	Vegetative
<i>Ascophyllum</i>	41.8 \pm 1.38	20.6 \pm 4.72*
<i>Fucus serratus</i>	46.8 \pm 1.26	35.4 \pm 1.34*

In an additional choice experiment using the flattened receptacles of *F. serratus* consumption was assessed in terms of surface area consumed rather than weight. This again demonstrated that *Littorina obtusata* consumed more reproductive tissue ($0.12 \text{ cm}^2 \cdot \text{replicate}^{-1} \cdot \text{day}^{-1} \pm 0.008 \text{ SE}$) than vegetative thallus ($0.03 \text{ cm}^2 \pm 0.008$, P < 0.05, Wilcoxon signed rank test).

The results of attractiveness trials are summarized in Tables VI and VII. There is a significant difference between rankings, but not between species given the same ranking. Both species of snail were attracted to furoid algae. *Ascophyllum* with *Polysiphonia lanosa* as an epiphyte, was consistently ranked lower than "clean" *Ascophyllum*, while *Fucus serratus* was more attractive to *Littorina mariae* than to *L. obtusata*. The coarse-textured, branched, filamentous alga *Cladophora rupestris* was avoided by both species.

CHOICE EXPERIMENTS WITH GERMLINGS

Littorina obtusata showed no significant preference (Wilcoxon signed rank test) when offered juvenile *Ascophyllum* or *Enteromorpha intestinalis* simultaneously, both were grazed voraciously (Table VIII). In comparisons between adult and juvenile plants of

TABLE VI
Attractiveness of macroalgae to *Littorina obtusata*.

Preference ranking (χ^2 analysis)	Algae	Percentage of snails choosing each alga (in all comparisons)
I	<i>Fucus vesiculosus</i>	67
	<i>Fucus spiralis</i>	64
II	<i>Ascophyllum nodosum</i>	61
	<i>Fucus serratus</i>	50
	<i>Pelvetia canaliculata</i>	49
III	<i>Ascophyllum</i> + <i>Polysiphonia lanosa</i>	45
	<i>Ulva lactuca</i>	36
IV	<i>Cladophora rupestris</i>	24

TABLE VII
Attractiveness of macroalgae to *Littorina mariae*.

Preference ranking (χ^2 analysis)	Algae	Percentage of snails choosing each alga (in all comparisons)
I	<i>Fucus spiralis</i>	60
	<i>Fucus serratus</i>	57
	<i>Fucus vesiculosus</i>	53
	<i>Ascophyllum nodosum</i>	52
II	<i>Pelvetia canaliculata</i>	50
III	<i>Ascophyllum</i> + <i>Polysiphonia lanosa</i>	45
IV	<i>Ulva lactuca</i>	43
V	<i>Cladophora rupestris</i>	33

TABLE VIII

The amount of algal tissue consumed ($\text{mg} \cdot \text{replicate}^{-1} \cdot \text{day}^{-1}$, means \pm SE) by *Littorina obtusata* in choice experiments: ns = not significant; $*0.01 < P < 0.05$; Wilcoxon signed rank test.

Comparisons			
Germling <i>Enteromorpha</i>	2.4 ± 0.23	Germling <i>Ascophyllum</i>	2.2 ± 0.09 ns
Germling <i>Fucus</i>	0.4 ± 0.04	Adult <i>Fucus</i>	$4.4 \pm 0.43^*$
Germling <i>Ulva</i>	0.4 ± 0.03	Adult <i>Ulva</i>	$0.2 \pm 0.02^*$

the same species, no consistent preference was shown for either growth stage. *Fucus serratus* was preferred at the adult stage, while germling *Ulva lactuca* was preferred to the adult thallus of *Ulva*.

DISCUSSION

Reimchen (1974) claimed that the sibling flat periwinkles occur at essentially different levels on the shore, but with a zone of overlap. The present study indicates that the distribution of *Littorina mariae* is simply more restricted than that of *L. obtusata*. In the early part of the year the latter species occurred everywhere that *L. mariae* was found, extending well below the lowest levels recorded for different sites by Sacchi (1969a) and Reimchen (1974). At Butter Lump, even though there was little wave splash to raise distribution limits, *L. obtusata* extended up the shore to the top of the *Pelvetia* zone – well beyond MHWN, which was formerly considered to be the upper limit of the species (Colman, 1939; Bakker, 1959; Reimchen, 1974). The distribution of *L. mariae* agrees with that recorded by Reimchen (1974) and Watson & Norton (unpubl.) for sheltered shores on the Isle of Man.

The snails are not merely found within the zones dominated by particular algae, but actually inhabit the canopy plants themselves. It is therefore not surprising that in laboratory trials the snails were attracted to the canopy algae rather than to the species characteristic of the understorey. On the shore, although *Littorina obtusata* is sufficiently widely distributed to encounter all the intertidal fucoids, it is most abundant on *Fucus vesiculosus*, the species that also proved most attractive in the laboratory. Similarly, adult *Littorina mariae* are largely confined to *Fucus serratus* in the field and this species also ranks very high in laboratory tests of attractiveness.

In edibility trials the canopy-forming fucoids again outranked other algae, suggesting that these species provide not only a habitat for the snails, but also a source of food. The blunt shovel-like cusps of the radula teeth of flat periwinkles are quite unlike the pointed teeth of rock-dwelling littorines (Steneck & Watling, 1982), and are ideal for excavating fucoid thalli. They are, however, unable to cope effectively with a foliose thallus and this is reflected in the low ranking of adult *Ulva* in edibility trials. This is in marked contrast to the rock-dweller *Littorina littorea* which greatly prefers ephemeral algae such as *Ulva* to fucoids (Watson & Norton, 1985). By consuming tiny germlings both *Littorina littorea* and *L. obtusata* can, however, prevent colonization of the shore by *Fucus* (Lubchenco, 1983).

Specific parts of the thallus of an alga may be consumed preferentially. Both *Littorina obtusata* and *L. mariae* were seldom observed grazing on the apical portion of *Ascophyllum*, probably because this region of the thallus is usually too narrow to accommodate the entire foot of the snail and thus provide a secure perch. In addition, different parts of the thallus may be differentially edible. Fertile receptacles, for example, were grazed in preference to vegetative tissue, as they are by *Littorina littorea* (Watson & Norton, 1985). In nature, preferential destruction of receptacles might jeopardize the

production of the new generation of plants. On the Isle of Cumbrac, *Fucus serratus*, however, reproduces mostly in winter at a time when flat periwinkles abandon the canopy, migrate to the rock surface and feed little, if at all (pers. obs.). *Ascophyllum*, on the other hand, reproduces in the spring when flat periwinkles are at their most active and, therefore, appears to be more vulnerable. Such preferential grazing may contribute to the notorious inability of *Ascophyllum* to colonize the shore (e.g., Knight & Parke, 1950; Printz, 1956).

If, as has been claimed by Geiselman & McConnell (1981), *Ascophyllum* is rendered distasteful to grazers by virtue of the polyphenols it contains, it is surprising that the polyphenol content is reduced during the fertile period of the plants (Ragan & Jensen, 1978) leaving the vulnerable reproductive receptacles undefended. Moreover, the polyphenols are clearly ineffective against *Littorina obtusata*. The rôle of polyphenols as grazer repellents will be examined in a future paper.

Some authors (e.g., Reimchen, 1974; Lubchenco, 1982) have assumed that the main source of food of flat periwinkles is the epiphytic microflora inhabiting the surface of fucoids, and that the ingestion of tissue from the macroalgal "host" is inadvertant. This seems highly unlikely in view of the depth to which the seaweed thalli are excavated by adult *L. obtusata*, and the great quantity of tissue ingested. None the less, our results confirm that flat periwinkles can graze microalgae. The epiphytic microflora probably constitutes a major component of the diet of juvenile specimens, and of the relatively small adult *L. mariae*. In both cases the less powerful buccal musculature is probably insufficient to permit efficient excavation of tough fucoid thalli, but the radula can be used to brush microalgae from the surface of the seaweed into the buccal cavity. Differences in the shape of the radular teeth of *L. obtusata* and *L. mariae* may be associated with these differences in grazing behaviour. The differences in the marginal teeth are particularly significant, for it is these teeth that splay widest and move furthest across the substratum during the grazing stroke (Watson & Norton, unpubl.) and therefore perform the major rôle in the brushing and collecting action associated with grazing the microalgae.

It appears that differing sensitivities to chemical cues allied with slightly different feeding abilities enables closely related species and even large and small specimens of the same species to inhabit the same level on the shore by utilizing different trophic resources.

To date, much research on the diet of littorinid snails has concentrated on the selection and consumption of adult seaweeds. Belatedly it has been recognized that much of their ecological impact is exerted by consuming the tiny juvenile stages of seaweeds (Lubchenco, 1983; Watson & Norton, 1985). An even newer notion is that different parts of the thallus of an adult seaweed may be grazed differentially and that reproductive organs may be more vulnerable than vegetative tissue (Watson & Norton, 1985). It seems, therefore, that until recently most of the research on the effects of grazing by littorinid snails may have been concentrating on the least significant aspects of their activities.

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