Interactions between two species of saltmarsh gastropod, *Hydrobia ulvae* and *Littorina littorea*

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ABSTRACT: On a submergent saltmarsh on the coast of eastern England the gastropods *Hydrobia ulvae* and *Littorina littorea* co-exist. Interactions between these species were investigated using both laboratory and field experiments. Removal of *L. littorea* from patches of intertidal gravel for 3 mo had no effect on *H. ulvae* density, but led to an increase in the density of infaunal oligochaetes and a decrease in *Tetrastemma* spp. and *Capitella* spp. In cleared patches *L. littorea* had returned to original densities by ca 14 d after clearing, indicating a moderate mobility of these populations. Manipulations of field densities of *H. ulvae* suggested that populations in most marsh habitats were limited by density-dependent processes. Examination of the size spectra of particles ingested demonstrated a degree of partitioning of the food resource by particle size. Habitat preference experiments further demonstrated a strong behavioural preference of *L. littorea* for gravel deposits, and of *H. ulvae* for fine mud substrata. Potential interspecific competition between these species is moderated by both resource partitioning and a behavioural mechanism leading to spatial separation.

INTRODUCTION

The extent and significance of interspecific competition in nature has been the subject of much debate (Connor & Simberloff 1979, Strong et al. 1979, Schoener 1982, 1983, Connell 1983, Roughgarden 1983). Many ecological studies have concentrated on mechanisms whereby available resources are partitioned amongst co-existing species (e.g. Cody 1968, Fenchel 1975). In a few cases competition in the field has been inferred from character displacement. The deposit-feeding mudsnails (Hydrobiidae) have been shown to (1) partition the food resource, by means of particle size, with the co-occurring amphipod *Corophium volutator* (Fenchel et al. 1975), and (2) undergo character displacement, to reduce competition, in the presence of congeners (Fenchel 1975, but see also Hylleberg 1986, Cherrill & James 1987).

On the extensive saltmarshes of the North Norfolk coast, in eastern England, 2 species of gastropod commonly co-occur on the submergent saltmarsh. The mudsnail *Hydrobia ulvae* (Pennant) (hereafter *H. ulvae*) is widely distributed over the marsh, feeding predominantly as a surface-deposit feeder but also as an epipsammic grazer on particles too large to be ingested (Levinton & Lopez 1978). *H. ulvae* has been recorded from a wide range of substrata, ranging from fine organically rich mud through sands to deposits of glacial gravel and even bedrock surfaces (Barnes & Greenwood 1978). It commonly colonizes macroalgae such as *Ulva, Enteromorpha* and even fucoids when they are present (Barnes & Greenwood 1978, Barnes 1979). The common edible periwinkle, *Littorina littorea* (L.) (hereafter *L. littorea*), also occurs on the submergent (= lower) saltmarsh. Its distribution is more restricted, generally being associated with glacial gravel deposits or areas of mud adjacent to these deposits (Frid 1988). It is primarily a rocky intertidal species, and it feeds as an epistrate grazer (Watson & Norton 1985). *L. littorea* is also able to feed as a deposit feeder (Graham 1971).

H. ulvae and *L. littorea* are potentially in competition for the same resource (detrital particles and benthic diatoms). Field manipulations of their densities were used to assess the degree of food limitation of surface-deposit feeders and to determine if any competitive release occurs.

If resources are limiting, competition may be lessened through the division of resources, e.g. by particle size or by spatial separation of the competitors. In view of the disparity in size of adults of the 2 species (*H. ulvae* ≈ 5 mm; *L. littorea* ≈ 20 mm) it would seem likely that *L. littorea* would utilize particles above the maximum size ingestible by *H. ulvae* (i.e. 63 µm; Fen-

chel 1975). However the larger the particle the smaller the relative biomass of associated micro-organisms. Hence larger particles should be less attractive as a food source. In this study competition between *H. ulvae* and *L. littorea* was investigated by comparisons of the size distribution of ingested particles.

Moderation of competition in the field by means of spatial separation within the saltmarsh habitat is also possible. Previous studies (Newell 1962, 1965, Fenchel 1975, Barnes & Greenwood 1978, Barnes 1979) have demonstrated a behavioural preference in *H. ulvae* for sediments composed of fine particles. Investigations of the behavioural preferences of *L. littorea* have centered on its food preferences when on a bedrock substrate (e.g. Watson & Norton 1985). We investigate possible lessening of competition by means of behavioural preferences using simple choice chamber experiments, offering a choice of natural mud or natural gravel/pebble substrata.

MATERIALS AND METHODS

Experimental animals were collected from, and the field experiments were carried out on, the submergent saltmarsh at Stiffkey (Ordnance Survey reference TF965449) in eastern England.

Manipulation of *H. ulvae* densities. On 7 and 8 July 1986, 2 pairs of cages were placed in each of the following marsh habitats: Habitat 1: salt pans/pools; Habitat 2: vegetated (mainly *Spartina*) marsh; Habitat 3: mainly unvegetated marsh (some seasonal growth of *Salicornia*); and Habitat 4: areas of glacial gravel deposits. Cages were $1.07 \times 0.85 \times 0.55$ m, and consisted of a wooden frame meshed with 2 mm 'NETLON'. The cages were set into the sediment to a depth of 20 cm.

One of each pair of cages was randomly selected as the control. The control cage was closed containing ambient densities of *H. ulvae*. An area of 4.28×0.85 m was marked out in the habitat adjacent to the cage and the surface 5 mm of sediment was sieved through a 500 μm sieve. The *H. ulvae* retained on the sieve were added to the experimental cage to give an approximate 5-fold increase in *H. ulvae* density. No other organisms were added or removed.

After 3 mo (14 October 1986) the cages were sampled, by taking three 6 cm diameter cores randomly within each cage. These were immediately returned to the laboratory, sieved (500 μm) and the retained gastropods placed into dishes of clean seawater. The number of living individuals of *H. ulvae* and *L. littorea* were counted. Three cores were also drawn from uncaged areas of each habitat at the commencement and termination of the experiment.

***L. littorea* removal and recolonization.** On 8 July 1986 three 1 m × 1 m areas were marked out on an area of glacial gravel on the submergent marsh. Each area was marked by a wooden post driven into the sediment at each corner. Each area was cleared of *L. littorea* by careful searching. The number removed was recorded. The areas were searched and cleared of *L. littorea* on 4 subsequent occasions, the time interval being varied to assess the rate of recolonization.

On 28 August 1986 the experiment was terminated. Each area was searched and the number of *L. littorea* recorded, and three 6 cm diameter cores were drawn randomly from the central 0.5×0.5 m of the area, to avoid any boundary effect. Three cores were taken from adjacent areas of the habitat on 8 July, and 5 and 28 August. Cores were fixed in 70 % alcohol containing 5 % Rose Bengal. Cores were subsequently sieved (500 μm) and the macrofauna enumerated.

Size spectra of particles ingested. *H. ulvae* were collected from sites on the marsh where they occurred allopatrically with respect to *L. littorea*. In addition both species were collected together from sympatric sites. Specimens were maintained on the sediment from which they were collected – allopatric snails allopatrically and sympatric snails sympatrically – in aquaria at 14 °C under a 16 h light : 8 h dark regime.

Crystallizing dishes (12 cm diameter) were filled with natural sediment to a depth of 5 mm, and 31 ‰ natural seawater added to a depth of 5 mm. These were allowed to 'age' for 24 h. Benthic diatoms are highly mobile and very fecund (Gray 1981), so this period allowed natural populations to become established in the upper sediment layers.

The experimental animals were transferred to dishes containing clean seawater (no sediment) and allowed to clear their guts for 4 h. The seawater was changed once during this period. The animals were then transferred to the dishes with sediment. The following experimental treatments were set up: (1) 25 allopatric *H. ulvae* in a dish; (2) 25 sympatric *H. ulvae* in a dish; (3) 5 sympatric *L. littorea* in a dish; (4) 20 sympatric *H. ulvae* and 3 sympatric *L. littorea* together in a dish. Each treatment was replicated a total of 10 times.

The animals were allowed to feed for 2.5 h, at the end of which they were transferred to solid watch glasses containing clean seawater. Individuals of each species from Treatment 4 were kept separately. After 4 h the faecal pellets were removed and the size spectrum of at least 100 particles from at least 2 pellets from each replicate was determined.

Substratum preference. Experiments were carried out using 14 cm diameter crystallizing dishes, which had previously been fitted with internal partitions of 1 cm height, dividing them into 4 quadrants (approximate area 36 cm² each). Sediments were distributed amongst the quadrants according to the scheme

devised by Barnes & Greenwood (1978), and illustrated in their Fig. 1. Quadrants labeled A and B in the figure were gravel filled, and quadrants C and D were mud filled. The characteristics of the sediments are summarized in Table 1. The quadrants were filled to

Table 1. Characteristics of the sediments used

Substrata	Median diameter (phi)	Quartile deviation	% Organics	% Silt/clay
Mud	1.35	0.84	16.26	18.60
Gravel	−0.82	0.34	8.32	8.90

the level of the divisions with sediment and covered with 31 ‰ natural seawater to an approximate depth of 5 mm.

The enclosures were allowed to age for 24 h before the experiments were carried out at 14 °C and under 16 h light : 8 h dark. The experiment of 12 enclosures was repeated twice with each of the following regimes: (1) 3 *L. littorea* only; (2) 20 *H. ulvae* only; (3) 20 *H. ulvae* and 3 *L. littorea*. An experiment was initiated by placing the snails in the centre of the enclosure. Each experiment was run for 48 h after which the number of snails of each species on each substratum were counted. The number of snails climbing the enclosure wall or, in the case of *H. ulvae*, floating at the water surface, were also recorded.

RESULTS

Manipulation of *H. ulvae* densities

With the exception of the gravel habitat, *H. ulvae* numbers were significantly lower in caged than uncaged controls (Table 2). In 3 habitats, with the exception of pools, cage densities of *H. ulvae* were not significantly different whether or not they had been initially increased by 5-fold – the manipulated increase did not persist. Densities and variability in the open areas of all 4 habitats were similar, whereas in the caged areas there was obvious variation in densities.

L. littorea densities on gravel were higher in cages than in the open, especially where *H. ulvae* densities had been initially increased.

L. littorea removal and recolonization

The number of *L. littorea* that recolonized each cleared area increased with time since last clearance up to 10 or 14 d (Fig. 1). In the one set of samples taken after 23 d the density of *L. littorea* had decreased. However at this value does not differ significantly from control values recorded at the time (Mann-Whitney U, p > 0.05), it reflects ambient densities at the sampling date. These results indicate that *L. littorea* is sufficiently mobile within the marsh to recolonize cleared areas within one spring-neap tidal cycle.

Throughout the experiment the relative densities of *L. littorea* in each area were consistent. Area 3 densities

Table 2. Densities of gastropods (individuals per core ± SE) in control areas, caged controls and experimental cages stocked to 5× natural density, after 3 mo enclosure (n = 6). Significance tested (p < 0.05) by Kruskall-Wallis for A, B and C together, denoted KW*, and Mann-Whitney for paired comparisons, denoted A > B etc.

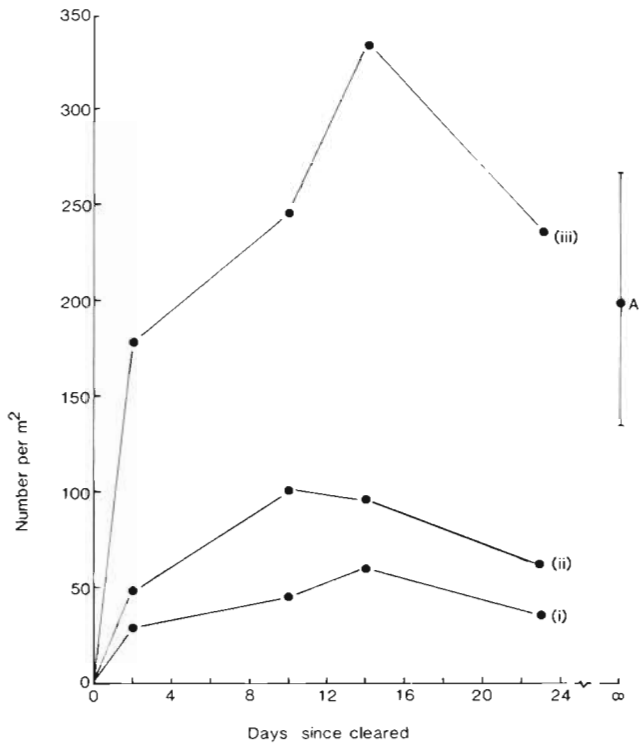| Species & habitat	A Uncaged controls	B Caged natural density	C Experimental cages at 5× natural density	Significance
Hydrobia ulvae				
Mud (Habitat 1)	8.50 ± 2.20	0.17 ± 0.17	0.33 ± 0.21	KW* A > B, A > C
Vegetation (Habitat 2)	6.17 ± 2.06	0.50 ± 0.50	3.83 ± 1.99	KW* A > B, A > C
Pool (Habitat 3)	8.33 ± 2.36	0	20.17 ± 5.9	KW* A > B, C > A, C > B
Gravel (Habitat 4)	5.83 ± 2.04	14.0 ± 6.96	2.83 ± 1.14	NS
Littorina littorea				
Gravel (Habitat 4)	0.17 ± 0.17	2.00 ± 0.86	2.70 ± 0.62	KW* C > A
NS: not significant				

Fig. 1. *Littorina littorea*. Recolonisation of three 1 m square areas [(i) to (iii)] of glacial gravels in a saltmarsh. Point A = mean density in control areas (± SE) (n = 9)

exceeded those in Area 2, which in turn had higher densities than Area 1.

Faunal densities within the areas of lowered mean *L. littorea* density (Table 3) show significant effects of *L. littorea* only on *Capitella capitata* Fabricius, the oligochaetes, and *Tetrastemma* spp. *C. capitata*, the tubificid oligochaetes (mainly *Tubifex costatus* Claparede), and the 'other' oligochaetes (mainly Enchytraeidae) showed a significant increase in the

Table 3. Faunal densities within areas of intertidal gravel from which *Littorina littorea* had been removed, and unmanipulated controls at the end of the experiment (n = 9). Significance assessed at α = 0.05, 2-tailed Mann-Whitney U

| Species | Density (ind. m^{-2} ± SE) | | Significance |
	Removal area	Control area	
Littorina littorea	78 ± 26.0*	197 ± 65.5	Sig.
Hydrobia ulvae	1297 ± 432.3	2437 ± 812.0	NS
Tubifex spp.	472 ± 157.0	39 ± 13.1	Sig.
Other oligochaetes	354 ± 118.0	79 ± 26.2	Sig.
Tetrastemma spp.	39 ± 13.1	432 ± 144.0	Sig.
Capitella capitata	236 ± 78.6	0	Sig.

* Sample consisted of juveniles < 2.0 mm maximum dimension

absence of *L. littorea*, whereas *Tetrastemma* showed a decrease.

Therefore the presence of *L. littorea* had some effect on community structure, but no effect on densities of the surface deposit feeder *H. ulvae*.

Size spectra of particles ingested

Data were analysed using SPSS-x on the Cambridge University Data Network. A multivariate 3-way ANOVA (SPSS-x MANOVA procedure) of particle size class against species, by ecological source, by experimental treatment (i.e. maintained allopatrically or sympatrically during the experiment) showed (1) a significant effect of species on size class utilization (p < 0.05), (2) no significant effect of ecological condition either in the field or during the experiment. The interaction terms were not significant.

From these results (Fig. 2) it can be seen that while *L. littorea* and *H. ulvae* used the same range of particle sizes, *L. littorea* used significantly more of the larger
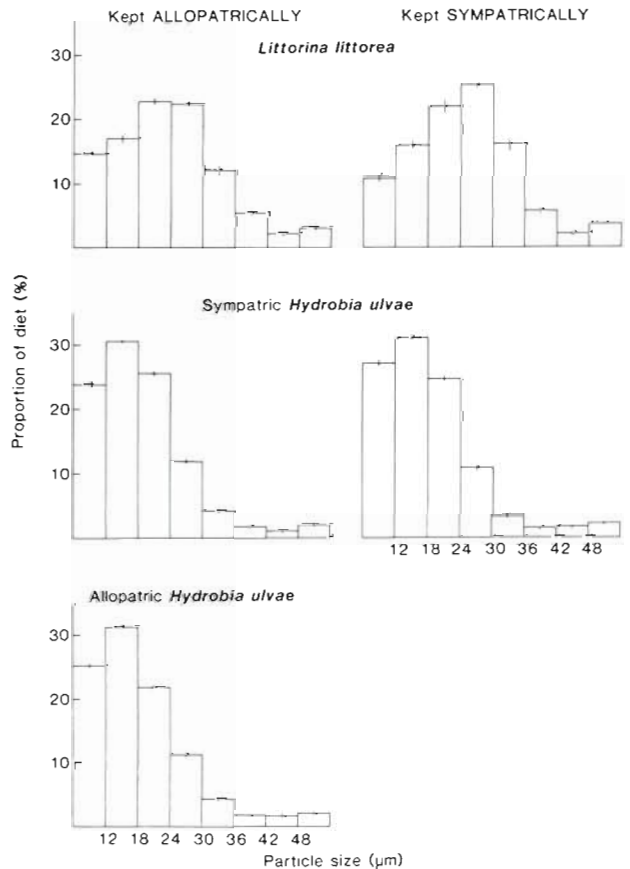

Fig. 2. *Littorina littorea* and *Hydrobia ulvae*. Resource use by snails from different sources maintained sympatrically and allopatrically. (Bars indicate SE)

size classes. There remains, however, considerable overlap in their resource use.

Substratum preference

Results are expressed in terms of the 24 replicates per treatment (Table 4). There was no significant difference between the 2 experiments of 12 replicates each for any given treatment (ANOVA p > 0.05).

Table 4. *Littorina littorea* and *Hydrobia ulvae*. Mean (±SE) number of snails on each substratum after 48 h. (n = 24 replicates)

Species (source)	Mean number of snails (±SE)		
	Gravel	Mud	Sides/floating
L. littorea (allopatric)	2.20 ± 0.15	0	0.79 ± 0.13
H. ulvae (allopatric)	5.33 ± 0.37	10.48 ± 0.43	5.06 ± 0.38
L. littorea (sympatric)	1.33 ± 0.21	0.04 ± 0.04	1.63 ± 0.22
H. ulvae (sympatric)	3.54 ± 0.40	13.04 ± 0.54	3.42 ± 0.32

The number of snails, of each species on each substratum was compared (1-way ANOVA, Student-Newman-Keuls multiple range test), the null hypothesis being that if the distribution of snails were random the numbers on each substratum would be equal. *L. littorea* showed a significant preference for gravel over either mud or the container sides, and selected the sides in preference to the mud. *H. ulvae* showed a significant preference for the mud, but did not distinguish between the sides and the gravel (Tables 4 and 5).

Table 5. *Littorina littorea* and *Hydrobia ulvae*. Significant (Student-Newman-Keuls range test, α = 0.05) differences in substratum preference, denoted·

Species	Gravel vs sides	Gravel vs mud	Mud vs sides
L. littorea	·	·	·
H. ulvae	NS	·	·
NS: not significant			

These behavioural preferences were consistent irrespective of the presence in the enclosure of the other species (Mann-Whitney U, p < 0.005).

DISCUSSION

Hydrobia ulvae is one of the most abundant intertidal organisms on the saltmarshes of the North Norfolk coast, eastern England (Barnes & Greenwood 1978). As such it is likely to play an important role in the dynamics of the intertidal invertebrate community. The work of Fenchel and co-workers (e.g. Fenchel 1975, Fenchel et al. 1975) has emphasized the interactions within the Hydrobiidae (Fenchel 1975) and between *H. ulvae* and a co-occurring amphipod on tidal flats (Fenchel et al. 1975). In both cases it was shown that the species partition food resources on the basis of particle size.

If detrital particles are a limiting resource, then 2 species simultaneously trying to exploit them may enter into interspecific competition. As competitive exclusion is not occurring, the mechanism moderating the effects of competition must be sought. The data presented here reveal some partitioning of food resources on the basis of particle size, but there is considerable overlap in the resources used by the 2 species. The ecological condition, i.e. sympatry vs allopatry, of the organisms either during the experiment or originally in the field had no effect on their subsequent resource use. The maximum degree of similarity in resource use which can still allow co-existence is a matter of debate amongst theoretical ecologists (Sale 1974, Armstrong & McGehee 1976). *H. ulvae* and *L. littorea* do, however, co-exist in the field. Further reduction in the density of *L. littorea* did not lead to an increase in the population of *H. ulvae* (Table 3), and there was no 'competitive release' on the gravel substrata.

The significant increase in *Capitella capitata* and both tubificid and other oligochaetes in the *L. littorea* removal deserves further investigation. A possible cause of this increase is the suppression of *C. capitata* and oligochaetes, at natural densities of *L. littorea*, by periwinkles moving from the preferred large particles on to the mud matrix in response to intraspecific competition. Here they may compete with the infauna. The interactions between *L. littorea* and the infaunal species warrant further investigation.

Caging experiments in soft sediment environments are fraught with difficulties (Virnstein 1978, Peterson 1979, Hulbert & Oliver 1980). The cages used in the increased *H. ulvae* density manipulation introduced a significant caging effect. This could have resulted from a cage-induced environmental change (Hulbert & Oliver 1980), or the cages may also have imposed a direct mortality on the enclosed populations. For example, *H. ulvae* avoids ingesting fecal material, and at high densities the entire sediment surface can become pelletized (Levinton & Lopez 1978). This would increase the amount of intraspecific competition for

food. Additionally, as the cages were in place for 6 sets of neap tides, the mid-marsh areas receive no tidal cover for 3 to 5 d around neaps. The cages may have prevented *H. ulvae* individuals from spending this period in more benign areas and so have increased the mortality due to desiccation. The former process is density dependent while the latter is density independent.

Our results (Table 2) show generally no significant difference in *H. ulvae* densities between cages where initial densities had been increased 5-fold and those at normal densities. In spite of the caging effect noted above, this suggests that density-dependent limitation of *H. ulvae* numbers was probably occurring within the cages in most marsh habitats studied here. Levinton & Lopez (1978) have argued that food is usually limiting for populations of intertidal surface-deposit feeders. We therefore consider it is likely that, over most of the saltmarsh, populations of *H. ulvae* become food limited when their normal mobility is removed.

Partitioning of the habitat into a series of microhabitats by means of temporal or spatial separation of the competitive species can act to alleviate competition. Field data (Frid 1988) show no evidence of temporal partitioning. Both species show an annual minimum in winter, increasing simultaneously in late spring/early summer. However field data did reveal an association of *L. littorea* with gravel deposits. The results of our laboratory experiments to investigate the mechanism, if any, of this association (Tables 4 and 5) indicated a clear preference in *H. ulvae* for natural mud substrata, and in *L. littorea* for natural gravel substrata. Although *H. ulvae* show a clear preference for mud they also occur in low numbers on the gravel of the laboratory enclosures and the field. *L. littorea* occur on mud in the field but avoid it in the trials to the extent that only 1 individual, out of the 144 used, was found on mud after 48 h!

We do not propose that it is the nature of the substratum *per se* that acts to moderate competition, but correlated changes in the nature of the food resource. In the fine organically rich mud there are abundant detrital particles harbouring microbial communities. These microbial communities are the portion utilized by deposit feeders. The gravel deposits are composed of a matrix of fine particles, including detrital particles, and larger (>2 cm) particles, that support on their surface an epiflora of diatoms which are available for grazing.

We conclude therefore that while *L. littorea* and *H. ulvae* may potentially compete for food, in the field this is moderated by (a) some partitioning of the food resource by means of particle size discrimination, and (b) by strong behavioural preferences for different substrata. *H. ulvae* prefers fine organically rich mud deposits, where it feeds predominantly on benthic diatoms and bacteria associated with detrital particles. It also grazes epipsammically on larger particles. In contrast *L. littorea* prefers deposits of large particles, where it feeds predominantly by grazing the covering of algal sporelings and diatoms, in a manner analogous to its feeding behavior on a rocky shore.

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