Interference competition in the intertidal mud snail *Hydrobia ulvae*: egestion rates revisited

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Egestion in the intertidal mud snail *Hydrobia ulvae* was investigated under conditions in which coprophagy did not occur, both in laboratory populations (comprising 11 experimental densities from 1000 to 120,000 ind m^{-2}) and in a field population with an average density of 50,000 ind m^{-2} (24 test densities spanning the local range of $<$5000–$>$120,000 ind m^{-2}). In contrast to an earlier study that suggested marked reduction in egestion rate in *H. ventrosa* as a consequence of interference competition, no such effect occurred in the natural population of *H. ulvae*, or in the experimental populations except at densities of at least 100,000 ind m^{-2}. Neither did any significant increase in inactivity or movement off the experimental substrata occur with increasing density. These results are discussed in relation to resource limitation in natural densities of mud snails.

INTRODUCTION

Hydrobiid mud snails, especially *Hydrobia ulvae* (Pennant), are dominant members of finely particulate coastal habitats in the northern North Atlantic (Smidt, 1951; Asmus & Asmus, 1985) where they provide the food of many invertebrates, fish and birds (Fish et al., 2000). Being such a key species, it is not surprising that the factors responsible for controlling the populations of *H. ulvae* have attracted considerable attention. The contrasting importance of predation (Reise, 1978; Frid & James, 1988) and environmentally induced mortality (Planas & Mora, 1987; Hall, 1994) in keeping populations below carrying capacity, and conversely of competition for resources, including food (Morrisey, 1987; López-Figueroa & Niell, 1987; Lopez & Levinton, 1987), in maintaining it at carrying capacity have all been argued. The major food source of mud snails is living microalgae, especially diatoms (Jensen & Siegismund, 1980; Levinton & Bianchi, 1981; Levinton & DeWitt, 1989), non-living detritus being unimportant (López-Figueroa & Niell, 1987).

Work in Denmark on the related *H. ventrosa* (Montagu) (Levinton, 1979), using faecal production as a measure of feeding activity (Hargrave, 1972), has shown that egestion rates fell by 50% with increase in density from 5,000 to 80,000 ind m^{-2}. Levinton suggested that this was a result of interference competition, frequent encounters with other conspecific individuals causing snails to 'crawl over each other, roll off and take approximately a half minute to resume movement' and feeding. The same effect, although here caused by interaction with the larger gastropod *Ilyanassa*, was later also noted in American *H. truncata* (Vanatta) (as *H. totteni* Morrison) (Levinton, 1985; Levinton et al., 1985). Levinton (1979) assessed egestion rates in *H. ventrosa* by establishing artificial populations at different densities in beakers containing sediment, and by then counting the numbers of faecal pellets present in subsamples of the sediments after 12 h. López-Figueroa & Niell (1987), however, later showed

that, contrary to the then generally prevailing view (e.g. Levinton & Lopez, 1977; Lopez & Levinton, 1978), *Hydrobia* (in this case *H. ulvae*) would not only consume its own faecal pellets from within a sediment but that coprophagy became the most important feeding mode at densities of $>$16,000 ind m^{-2}. Thus it is possible that the apparent decrease in egestion with increase in mud snail density observed by Levinton (1979) was due to coprophagy rather than to interference competition.

Levinton's (1979) apparent demonstration of intraspecific interference competition for food in *Hydrobia* being widely cited as evidence of resource limitation in natural densities of mud snails, the work described below was carried out to ascertain whether egestion rates in *H. ulvae* do decrease with increase in density in laboratory and/or field populations, and to assess whether egestion rate is affected by competition.

MATERIALS AND METHODS

Sediment (passing a 500 μm sieve) and *Hydrobia ulvae* (retained by that sieve) were collected from the muddy sand bed of Hut Gap Marsh Creek, Scolt Head Island National Nature Reserve, Norfolk, UK (52°59′10″N 00°41′3″E) during September 2000 and were maintained under field conditions on site in The Watcher's Hut, less than 150 m from the collection area. Hut Gap Marsh approximates 'a low' *sensu* Chapman (1960; Steers, 1960): a partially dune-enclosed basin into which undiluted seawater flows during high water of high spring tides and within which this water is partly retained during low tide by virtue of a sill across its mouth (where the creek flows across the shingle base of a dune). The creek therefore contains some 0.3 m depth of ponded-back water at all times except for the effects of evaporation during series of neap tides. Collection of mud snails from such a system (a) ensured that they had had continual opportunity to feed for many days prior to assessment; and (b) also had

the advantage of avoiding the problem of rapidly changing local population densities consequent on the involuntary transport effected by tides flooding across mudflats (Barnes, 1998). Seawater salinity (>33 psu) and high summer temperatures are also optimal for egestion in *H. ulvae* (Hylleberg, 1975).

Gut passage time was assessed by placing 15 snails fresh from the field each in a separate seawater-containing 45 mm diameter Petri dish (without sediment) and by counting the number of faecal pellets produced every ten minutes until no further pellets had been produced for an hour. Like most deposit-feeders (Kofoed et al., 1989), gut residence time was very short, some 75% of the total pellets voided being produced in the first 30 min. No new faeces were egested by any snail after 60 min. The number of pellets produced in 60 min was then adopted as the measure of egestion in all experiments. Snails were observed using a binocular microscope during this process and, as expected from the results of López-Figueroa & Niell (1987), none was ever seen to ingest any of its fresh faecal pellets.

Forbes & Lopez (1986, 1989a) have shown that egestion rate is constant in *H. truncata* and does not vary with the concentration of potential food materials in the sediment. That this was also the case in *H. ulvae* was checked by placing 12 snails for 24 h in 85-mm diameter Petri dishes containing a thin layer of seawater over (a) their natural sediment, (b) natural sediment diluted 1:1 with clean dune sand, and (c) natural sediment diluted 1:3 with that sand. No differences in the number of faecal pellets produced after exposure to these substrata were found (ANOVA: $F=1.63$; $P=0.22$), the mean number egested being 39.3 (SE ±2.76).

Snails were then collected from the field and similar sized individuals (some 3–4 mm shell height) were placed for 24 h in 85-mm diameter Petri dishes containing natural sediment from the collection site covered by a thin layer of seawater in such numbers as to give experimental densities of 1, 2, 5, 10, 20, 40, 70, 80, 90, 100 and 120×10³ *H. ulvae* m⁻². Only at densities of >80,000 ind m⁻² were any snails or crawling trails present on the lids of the dishes on harvesting, and any snails not on the sediment surface—which represented <0.007% of any contained population—were discarded. At least ten randomly selected snails from each density were then placed individually in 45-mm diameter Petri

dishes containing only seawater, and the number of faecal pellets produced after 1 h was assessed. Any zero total was discounted on the basis that it represented an inactive, non-feeding snail (López-Figueroa & Niell, 1987).

Egestion rates in these experimental populations were compared with those in the natural population by taking samples from the creek bed by means of a 60-mm diameter core tube to a depth of some 100 mm. Each sediment sample covered by its overlying water was rapidly and carefully conveyed within the core tube to The Watcher's Hut (a journey taking 3 min) so as to cause minimum disturbance to the contained mud snails. On arrival the sample was immediately sieved through 500 μm mesh in rainwater (to ensure that the snails remained withdrawn into their shells so that they would not void faeces prior to assessment), and then 12 randomly selected 3–4 mm high snails were quickly transferred each to an individual 45-mm diameter Petri dish as described above. The total number of all living *H. ulvae* in each core sample from which the experimental animals were obtained was also assessed. Twenty-four such core samples were taken to cover the field density range of <5000– >120,000 ind m⁻². Mean density in the region of the creek sampled was some 50,000 ind m⁻².

RESULTS

Over the whole range of experimental density (1000– 120,000 ind m⁻²) there was a significant relationship between egestion rate and density (analysis of variance (ANOVA), Table 1). Fisher's protected least significant difference procedure (Table 2) shows that this effect is caused mainly by significant differences between the

Table 1. *Effect of experimental population density on egestion rate (one way ANOVA).*

	df	sum of squares	mean square	F	P
Experimental densities of 1000–120,000 ind m⁻²					
density	10	1363	136	2.17	0.03
residual	91	5728	63		
Experimental densities of 1000–90,000 ind m⁻²					
density	8	617	77	1.21	0.30
residual	78	4962	64		

Table 2. *Matrix of Fisher's protected least significant difference probabilities between mean numbers of faecal pellets produced at the different experimental population densities (in 10³ m⁻²).*

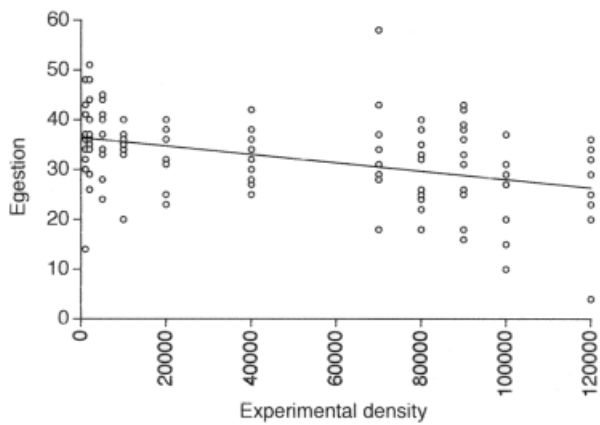| 1	-										
2	*	-									
5	*	*	-								
10	*	*	*	-							
20	*	*	*	*	-						
40	*	*	*	*	*	-					
70	*	*	*	*	*	*	-				
80	*	0.016	0.031	*	*	*	*	-			
90	*	0.045	*	*	*	*	*	*	-		
100	0.008	0.0005	0.001	0.024	0.026	0.044	0.014	*	*	-	
120	*	0.016	0.029	*	*	*	*	*	*	*	-
	1	2	5	10	20	40	70	80	90	100	120

*, $P>0.05$.

Figure 1. The relationship in experimental laboratory populations of *Hydrobia ulvae* between the number of faecal pellets produced by individual mud snails in 60 min after removal from their food source and the number of such snails m^{-2}. The fitted simple regression equation significantly describes the data (regression $r^2=0.135$; regression ANOVA $F=15.65$; $P=0.0001$).

Table 3. *Effect of field population densities of 4720–121,340 ind m^{-2} on egestion rate (one-way ANOVA).*

	df	sum of squares	mean square	F	P
density	23	2649	115	1.43	0.10
residual	213	17189	81		

100,000 ind m^{-2} density and the lower ones. Faecal production then decreased according to the simple regression (Figure 1):

$$\text{N faeces voided} = 36.163 - 0.0000746 \text{ density (N m}^2) \quad (1)$$

Nevertheless over the wide range of 1000–90,000 *H. ulvae* ind m^{-2}, there was no significant variation in the numbers of pellets egested (ANOVA, Table 1), an overall mean ($\pm$SE) number of 33.67 ($\pm$0.86) pellets being produced.

There was no correlation between the numbers of non-feeding snails and snail density (Spearman $\rho=0.28$; $\mathcal{Z}=1.03$; $P=0.30$). Individual snails were clearly variable (Figure 1) in terms of the number of faeces produced at any population density, standard errors being 5.2–12.8% of the mean values, but the degree of variation (as estimated by SE/mean) was unrelated to population density (Spearman $\rho=0.36$; $\mathcal{Z}=1.14$; $P=0.26$).

No relationship between faeces egested and natural field density was present (ANOVA, Table 3). Nevertheless, if the numerical value of the population density is taken into consideration as in regression, the faeces produced do significantly, albeit slightly, increase with that of density by the simple equation (Figure 2):

$$\text{N faeces voided} = 31.121 + 0.0000615 \text{ density (N m}^2) \quad (2)$$

The overall mean number of faeces produced in the 1 h, 33.96 ($\pm$0.61) (Figure 2), is the same as that produced in the experimental populations (unpaired *t*-test, $t=-1.30$; $P=0.19$).
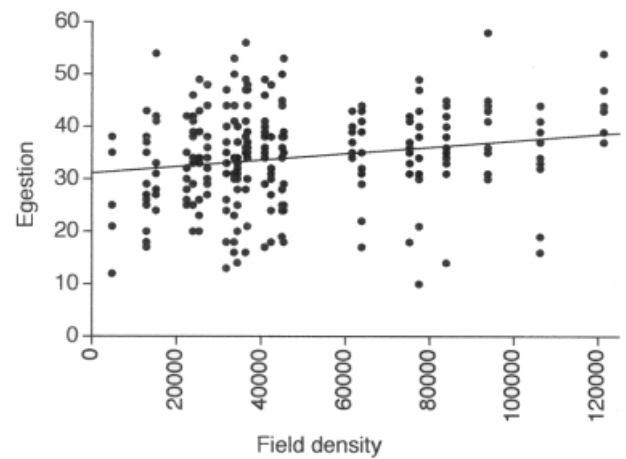
Figure 2. The relationship in a field population of *Hydrobia ulvae* between the number of faecal pellets produced by individual mud snails in 60 min after removal from their natural habitat and the number of snails m^{-2} in the immediate area from which they were taken. The fitted simple regression equation significantly describes the data (regression $r^2=0.038$, regression ANOVA $F=9.21$; $P=0.003$).

There was no correlation between the numbers of non-feeding snails and snail density (Spearman $\rho=0.14$; $\mathcal{Z}=0.82$; $P=0.41$). As in the experimental populations, individual snails were clearly variable (Figure 2) in the number of faeces produced at any population density, standard errors being 3.0–13.3% of the means, but the SE/mean was unrelated to population density (Spearman $\rho=-0.18$; $\mathcal{Z}=-0.85$; $P=0.39$).

DISCUSSION

Regardless of whether the decreased egestion found in *Hydrobia ventrosa* by Levinton (1979) is an artefact of coprophagy, no such effect appeared to occur in *H. ulvae* except at the highest of densities and then only under laboratory conditions. It would appear that whatever effects competition might cause in these *H. ulvae*, at field density it did not seem to decrease feeding rate, as measured by egestion rate, either exploitatively or via interference. Neither, in the same habitat, could Barnes & de Villiers (2000) find any effect of dense populations of these mud snails on sedimentary chlorophyll. It is perhaps significant here that Forbes & Lopez (1986) in *H. truncata*, and this study in *H. ulvae*, found egestion rate not to vary with amount of food present in the sediment [although Cammen (1989) found that it did vary—inversely—with chlorophyll-*a* content in Danish '*Hydrobia* sp.' supplied only with the <67 µm sediment fraction—this could reflect a change in feeding mode from epipsammic browsing (Lopez & Kofoed, 1980) to simple ingestion of the substratum]. The ingestion rate of chlorophyll-*a* by *H. truncata* has also been found to be a direct function of the chlorophyll-*a* content of the sediment, suggesting an inflexible sediment processing rate (Kofoed et al., 1989, as *H. totteni*). Any reduced food availability consequent on exploitative competition might therefore not be immediately detectable by the snail. The effect of food shortage could manifest itself only in the longer term, via for example decreased growth (Morrisey, 1987) and/or reproductive output (Barnes & Gandolfi, 1998). Increasing

speed of movement has been found in food-poor areas (Forbes & Lopez, 1986) and this will tend to carry snails away from such regions.

One possible confounding variable that is difficult to account for objectively is activity level. Egestion is a general measure of activity (Hargrave, 1972; Hylleberg, 1975), and, as also found by López-Figueroa & Niell (1987), some *H. ulvae* although clearly alive did not appear to have been feeding prior to experimentation. There is no reason, however, why feeding activity should be an all-or-none reaction. General activity levels may be stimulated by increasing density in the wild (Levinton, 1979), or be depressed at low densities, and this may be reflected in feeding rate. Nevertheless, under experimental conditions López-Figueroa & Niell (1987) found that more mud snails became inactive as density increased, although such (in the form of non-feeding) was not apparent in the present study. Egestion rate is also very variable between individuals in *Hydrobia* (Forbes & Lopez, 1986; this study) and this may represent physiological differences within a population (Taghon & Jumars, 1984). It is therefore possible that selection may act on semi-isolated populations such as the one under study to adapt responses in some as yet unknown manner to local conditions.

The literature contains conflicting data on the carrying capacities of coastal habitats for *H. ulvae*. Sand-dwelling populations of *H. truncata* at densities of $<4500 \, \mathrm{ind \, m^{-2}}$ have been shown to be below carrying capacity by Forbes & Lopez (1989a,b). López-Figueroa & Niell (1987), working in the productive Palmones Estuary in southern Spain, recorded natural population densities of *H. ulvae* of $5000–10,000 \, \mathrm{ind \, m^{-2}}$, and they found marked effects of competition at experimental densities of only $16,000 \, \mathrm{ind \, m^{-2}}$. This density was not achieved in the estuary and indeed they concluded that 'the persistence of such a dense population in the field may be impossible'. Included in the effects of competition was climbing of the walls of the experimental containers away from the sediment, affecting up to 40% of the population. Forbes & Lopez (1986) also found that crawling rate increased when in food-poor areas. Yet in the present study, no more than 0.007% of any experimental population climbed off the sediment notwithstanding that being small the containers had a large edge in relation to their surface area, and this only happened at densities of $>80,000 \, \mathrm{ind \, m^{-2}}$. Morrisey (1987)—also working on Scolt Head Island—found growth rate in *H. ulvae* to decrease rapidly between 3000 and 6000 mud snails $\mathrm{m^{-2}}$, and considered that the carrying capacity of the Cocklebight habitat was only $20,000 \, \mathrm{ind \, m^{-2}}$. In some trials, but not in others, he found significant density dependent mortality between 3000 and 50,000 mudsnails $\mathrm{m^{-2}}$. These carrying capacities are very much lower than the routine densities of *H. ulvae* that do indeed persist in the Gironde Estuary (Bachelet & Yacine-Kassab, 1987), the Wadden Sea (e.g. Smidt, 1951) and Scolt Head Island and adjacent areas of Norfolk (Barnes, 1990, 1999). Yet the growth rates of individuals from the dense Norfolk population studied by Barnes (1990) were far from slow, neither were levels of sedimentary chlorophyll-*a* there particularly unusual (Barnes & de Villiers, 2000). *Hydrobia ulvae* may be much studied but the explanation of these contrasts is still far from evident.

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