Measurement of ingestion rate of *Hydrobia ulvae* (Pennant) on intertidal epipelic microalgae: the effect of mud snail density

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**Abstract**

The individual mean ingestion rate of *Hydrobia ulvae* was measured experimentally in controlled microcosms, in the dark to avoid primary production during measurement and at constant temperature. The experimental design was based on the addition of prelabelled epipelic microalgae to microcosms in a constant proportion with unlabelled diatoms, and in such a way that algal food availability was not a limiting factor within the range of tested densities (0.3 to 4.1 snails cm\textsuperscript{-2}). Results show that the individual mean ingestion rate decreased significantly from 26.6±1.1 ng Chl a snail\textsuperscript{-1} h\textsuperscript{-1} to 22.4±1.0 ng Chl a snail\textsuperscript{-1} h\textsuperscript{-1} between 0.7 and 3 snails cm\textsuperscript{-2}. We hypothesize that this sharp decrease (the threshold density was between 1.4 and 2.5 snails cm\textsuperscript{-2}) may account for a density-dependent effect. We have tested this hypothesis by using a simple random walk model including basic behavioural processes such as a break in feeding activity when two individuals contact each other. The model represents quantitatively well the threshold effect, suggesting that behavioural processes have to be taken into account for estimating a global feeding activity of *H. ulvae* populations. © 2000 Elsevier Science B.V. All rights reserved.

*Keywords:* Intertidal mudflat; Feeding ecology; Microphytobenthos; *Hydrobia ulvae*; Ingestion rate; Behavioural processes

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1. Introduction

Microphytobenthalos is the main source of primary production in intertidal mudflats (Admiraal, 1984; Colijn and De Jonge, 1984; De Jonge and Colijn, 1994; Blanchard and Cariou-Le Gall, 1994; Cariou-Le Gall and Blanchard, 1995; Guarini et al., 2000). It directly supplies deposit-feeders, especially gastropods like Hydrobia spp. (Fenchel et al., 1975; Kofoed, 1975; Fenchel and Kofoed, 1976; Lopez and Levinton, 1978; Jensen and Siegismund, 1980; Levinton and Bianchi, 1981; Bianchi and Levinton, 1984; Forbes and Lopez, 1986; Morrisey, 1987), which are often a dominant inhabitant of intertidal mudflats as reported by Barnes (1981) and Reise (1985) for Hydrobia ulvae (Pennant).

In Marennes-Oléron Bay, France, Hydrobia ulvae is the most common deposit-feeder in intertidal mudflats, where it can reach high densities up to 50,000 individuals m$^{-2}$ (Sauriau, 1987; Sauriau et al., 1989). A large fraction of microphytobenthos primary production is thus assumed to flow directly to this deposit-feeding compartment while, in return, the grazing pressure of $H. \text{ulvae}$ is likely to have a strong impact on microphytobenthic biomass dynamics, as suggested by Cariou-Le Gall and Blanchard (1995). To estimate both this flux and this grazing pressure, the relevant variable to measure is the ingestion rate of $H. \text{ulvae}$ on microphytobenthos. However, few data are available on this aspect because the snail feeding activity has generally been assessed indirectly through either its effect on diatom standing stocks (Morrisey, 1988), its production of fecal pellets (Levinton, 1979a) or its oxygen consumption (Jensen and Siegismund, 1980).

The ingestion rate will depend on several controlling factors and, in particular, there are good reasons to believe that the population density of Hydrobia ulvae will decrease its individual mean ingestion rate since it has already been demonstrated that it decreases its mean growth rate (Morrisey, 1987). Similar results were also found by Levinton (1979a) and Levinton and Bianchi (1981) for Hydrobia ventrosa (Montagu) and Hydrobia totteni, respectively.

The objective of this article is therefore twofold: (1) testing an easy-to-use protocol for accurately estimating the individual mean ingestion rate of Hydrobia ulvae on epipelic microalgae in experimentally-controlled microcosms, and (2) assessing the effect of $H. \text{ulvae}$ density on the individual mean ingestion rate. Contrary to field conditions where deposit-feeders in general are assumed to be food-limited (Levinton, 1972; Lopez and Levinton, 1987), rates were estimated under non-limiting food conditions; therefore, our experiment is primarily designed to investigate the competition for space on the basis of behavioural processes (Barnes, 1981; Levinton, 1979a); a simple random walk model is further developed to support the reliability of our assumptions from a quantitative point of view.

2. Materials and methods

2.1. General protocol (see Fig. 1 for a description of the different steps)

The mud containing benthic microalgae and Hydrobia ulvae was sampled on an
Intertidal mudflat located in the Aiguillon Bay, along the Atlantic coast of France (46°15′ N, 1°10′ W). The mean grain size was less than 10 μm. The top 1–2 mm of mud was gently scraped and stored in plastic boxes until further processing in the laboratory; samples were brought back to the laboratory within 1 h (step 1.1).

*Hydrobia ulvae* snails were then separated from the sediment by sieving through a 1-mm mesh (step 1.2); animals were kept in sea water at 20°C and starved overnight before the experiments. The size of the animals was 3–4 mm shell height. Epipelic diatoms — which are motile microalgae exhibiting an endogenous rhythm of vertical migration — were isolated from the mud (step 1.3) using the method described in Riera and Richard (1996): the mud was evenly spread in a tray and covered with a 63-μm net; then a 3-mm layer of silica powder (60 to 210-μm grain size diluted in GF/F filtered seawater) was deposited on top of the net and sprayed with GF/F filtered sea water. After a period of 24–36 h under artificial light in a temperature-controlled culture room, epipelic diatoms had migrated through the net and accumulated in the silica powder. The latter was then collected and filtered through a 63-μm net to separate a suspension of epipelic microalgae from the silica powder. Diatoms were always separated from the sediment early in the morning prior to the experiments. The method does not allow to...
extract all microalgae, and a significant amount of diatoms still remains in the mud after
the separation step (step 1.3).
To label isolated microalgae (step 2.1), NaH\(^{14}\)CO\(_3\) (40–50 mCi mmol\(^{-1}\) stock
solution) was added to 500 ml of the suspension to reach a final concentration of about
0.4 \(\mu\)Ci ml\(^{-1}\). The suspension was then placed at 20°C under saturating light conditions
during 2 h, with continuous mixing using a magnetic stirrer — to homogenize the
suspension and ensure an even labelling of microalgae. After the incubation period, the
microalgal suspension was centrifuged (3500 rev./min during about 3 min) to concen-
trate diatoms (step 2.2); the supernatant containing unused \(^{14}\)C-bicarbonate was
discarded. Filtered sea water was then added to the pellet to rinse diatoms; this step was
repeated twice (step 2.3).
The mud used for the separation of microalgae was further sieved through a 0.5-mm
mesh to remove small macrofauna (step 3.1) and was diluted with GF/F filtered sea
water (1:1 v/v, step 3.2). Labelled and rinsed diatoms were then mixed with this diluted
mud and homogenized (step 4.1). Therefore, as only part of the diatoms are labelled, the
method assumes that labelled diatoms are ingested in the same proportion as unlabelled
diatoms. This allows to convert the ingested radioactivity into ingested Chl \(a\) since the
total amounts of radioactivity and Chl \(a\) contained in each microcosm were known (see
formula hereafter). The Chl \(a\) to radioactivity ratio can be calculated (ng Chl \(a\) dpm\(^{-1}\))
(step 4.2). Chl \(a\) was measured fluorometrically (Lorenzen, 1966).
Experimental microcosms were set up in clear tissue culture flasks. They aim at
reproducing low-tide conditions. Thirty ml of mud containing labelled diatoms were
introduced in these microcosms with \(H.\) \(ulvae\) (step 5). The incubation (feeding
time) was stopped by the addition of formalin (to reach a final concentration of 2.5%),
and the mud contained in microcosms was sieved through a 0.5 mm mesh to retrieve \(H.
ulvae\) snails (step 6). Animals were then carefully rinsed and dried overnight at about
50°C. Snails were placed in scintillation vials with 750 \(\mu\)l of Soluene-350 (Packard) for
72 h at 50°C to solubilize tissues (step 7). Twelve ml of Hionic-fluor (Packard) were
then added for counting radioactivity in a Packard Tri-Carb scintillation counter.
The ingestion rate of \(H.\) \(ulvae\) was determined as the amount of radioactivity
ingested per snail and per hour. To convert radioactivity into Chl \(a\) we used the
conversion ratio (CR) determined at step 4.2: Ingestion rate = \(\frac{\text{ingested radioactivity}}{\text{CR}}\) \times \(\frac{\text{ng Chl } a}{\text{dpm snail } h^{-1}}\) \(\frac{\text{ng Chl } a}{\text{dpm } h^{-1}}\)

2.2. Control experiments

2.2.1. Experiment 1

The method assumes an accumulation of radioactive material into \(H.\) \(ulvae\) proportional to the incubation time. In other words, we assume that labelled microalgae
accumulate in the gut at a constant rate, and that egestion of radioactive material does
not occur during incubation.
The kinetics of radioactive accumulation in the gut of \(H.\) \(ulvae\) was monitored
during 2 h. Eighteen microcosms containing 20 \(H.\) \(ulvae\) each were incubated in the dark
to avoid photosynthesis occurring, at 20°C. Every 20 min, incubation was stopped in three microcosms by adding formalin and the amount of 14C-diatoms accumulated in snails was measured. All measurements were corrected for non-ingestive processes by subtracting radioactivity fixed in formalin-killed controls.

2.2.2. Experiment 2

The method also assumes a conservative behaviour of label in diatoms, i.e. no loss of radioactivity from prelabelled microalgae due to respiration and excretion during incubation with snails.

To check for conservativity of label, a suspension of labelled diatoms was prepared according to step 2 of the protocol presented in Fig. 1. Then, three 1-ml replicates of the rinsed labelled diatoms were filtered on GF/F fiber glass filters every hour until 4 h after the end of labelling. If radioactivity is lost from diatoms through respiration or excretion during the 4-h period following labelling, then the amount of radioactivity on GF/F filters should decrease as a function of time.

2.3. Effect of Hydrobia ulvae density on ingestion rate

It was tested in two experiments.

2.3.1. Experiment 3

Five densities were tested (0.3, 0.7, 1.4, 2.5 and 4.1 snails cm⁻²); we used the same range of densities as in Morrisey (1988), which amounts to 25, 59, 118, 210 and 344 snails per microcosm, respectively. Four replicates and one formalin-killed control were used at each density. The incubation time was 1 h in the dark at 20°C in a temperature-controlled room. At the end of the incubation period, 20 H. ulvae were picked at random and processed according to steps 6 and 7 of the protocol (Fig. 1) to count ingested radioactivity. Ingestion rates were only expressed as dpm snail⁻¹ h⁻¹.

2.3.2. Experiment 4

A second experiment was performed in the same conditions to assess the flux of Chl a from microphytobenthos to gastropods. Only two densities were tested (0.7 and 3 snails cm⁻²). Seven replicates and three formalin-killed controls were used at each density. Mean ingestion rates were expressed as ng Chl a snail⁻¹ h⁻¹ and µg C snail⁻¹ h⁻¹ using a conversion ratio (C/Chl a) of 50 (De Jonge, 1980).

3. Results and discussion

For the sake of clarity (in addition to Figs. 2–6), results and interpretations of the following sequence of experiments are summarized in Table 1.
3.1. Controls

Results of experiment 1 confirm that labelled diatoms accumulated linearly in the gut of Hydrobia ulvae over 2 h (Fig. 2) in agreement with the main assumption of our method. Therefore, there was no evidence of a significant egestion of recently ingested radioactive material. This further indicates that the mean ingestion rate of H. ulvae on epipelic diatoms can be calculated over the same period of time. However, as the amount of ingested labelled diatoms is already high after 1 h (Fig. 2), the incubation time for experiments 3 and 4 was set to 1 h. This is slightly longer than the estimated 30–40 min for the gut residence time by Fenchel (Lopez and Kofoed, 1980).

Results of experiment 2 show that the amount of $^{14}$C accumulated in labelled diatoms did not change during the 4 h following labelling (Fig. 3). The slope of the regression line is not significantly different from zero ($P = 0.55$). We thus conclude that radioactivity was not lost from labelled diatoms during incubation with snails.

3.2. Effect of density on ingestion rate

When density was lower than 1.5 snails cm$^{-2}$ the ingestion rate was ca. 18 dpm snail$^{-1}$ h$^{-1}$, and decreased down to ca. 14 dpm snail$^{-1}$ h$^{-1}$ when density was higher (Fig. 4). Results of a one-way ANOVA indicate that there is at least one difference
among treatments \((P=0.079)\); therefore, the density of *H. ulvae* seems to have a negative effect on individual ingestion rate on epipelic diatoms: there is apparently a threshold effect between 1.4 and 2.5 snails cm\(^{-2}\). However, because of the lack of data between 1.4 and 2.5 snails cm\(^{-2}\), we cannot state whether it is a stepwise decrease or a more smoothed drop in the individual ingestion rate; obviously, further investigations are necessary in this range of densities. Experiment 4 was carried out to provide an estimate of ingestion rate as a Chl \(a\) flux from microphytobenthos to mud snails (since in experiment 3 we only looked at relative ingestion rates and we expressed them as dpm snail\(^{-1}\) h\(^{-1}\)). As expected, the ingestion rate was significantly lower \((t\)-test; \(P=0.02)\) at a density of 3 snails cm\(^{-2}\) \((22.38 \pm 1.04 \text{ ng Chl } a \text{ snail}^{-1} \text{ h}^{-1})\) than at a density of 0.7 snails cm\(^{-2}\) \((26.64 \pm 1.14 \text{ ng Chl } a \text{ snail}^{-1} \text{ h}^{-1})\), that is a 16% decrease (Fig. 5); this amounts to ingestion rates of 1.12 and 1.33 \(\mu\text{g C snail}^{-1} \text{ h}^{-1}\), respectively. These rates are consistent with those previously measured by Forbes and Lopez (1989): they found rates in the range 0.506–1.174 \(\mu\text{g C snail}^{-1} \text{ h}^{-1}\) for *Hydrobia truncata* (Vanatta) fed on microalgae.

The depressed ingestion rates at higher densities in our microcosms are unlikely to be due to food limitation since calculations from experiment 4 show that only 0.4 and 1.2% of total microalgal biomass was ingested during the incubation by all snails at 0.7 and 3 snails cm\(^{-2}\), respectively. The decrease of the individual ingestion rate was rather likely due to a competition for space as the density increased and involved a behavioural response. Lopez-Figueroa and Niell (1987) indeed showed that there is a change in the

**Fig. 3.** Intracellular radioactivity monitoring during 4 h after labelling benthic microalgae. A fixed amount of labelled microalgal suspension is filtered through GF/F filters and radioactive levels are reported as dpm ml\(^{-1}\) suspension.
Fig. 4. Individual mean ingestion rate, with the corresponding standard error, of *H. ulvae* (dpm snail\(^{-1}\) h\(^{-1}\)) as a function of *H. ulvae* density (0.3, 0.7, 1.4, 2.5 and 4.1 snails cm\(^{-2}\)).

Fig. 5. Individual mean ingestion rate, with the corresponding standard error, of *H. ulvae* as ng Chl a snail\(^{-1}\) h\(^{-1}\) at two *H. ulvae* densities (0.7 vs. 3 snails cm\(^{-2}\)).
Fig. 6. (A) Grid used for the simulations and rules used to define successive motions of an individual: $\rightarrow$ motion is possible and realized, $\equiv$ motion is impossible. Shaded cells represent the previous position of the snail, where it cannot crawl back. (B) Example of four computed random walk trajectories (15 steps only). (C) Simulations of the relative individual mean ingestion rate ranging from 1 (corresponding to the ingestion rate of one completely free individual in an unlimited open space) to 0 (corresponding to the absence of activity and ingestion in a space where all cells are occupied by individuals). Thirty trials were performed for each density and standard errors were calculated (vertical bars). The upper line (full diamond-shaped symbols) is the simulation obtained under rules (1) through (4) in the text; the lower line (open diamond-shaped symbols) is the simulation with the same rules plus the fact that snails create mucus tracks which prevent other snails from ingesting algal cells when crossing them.
Table 1
Synoptic table of the different hypotheses, tested by experiments, statistical methods and one model, and their corresponding results. Interpretations constitute important links between experiments. In the modelling case (last row), the hypothesis is formulated as a generic question since concepts are replacing data in testing the hypothesis. Data are thus only compared to simulations

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<tr>
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<td>Linear regression</td>
<td>Linear model fits to the data: $R^2 = 0.90, P &lt; 0.001$</td>
<td>No $^{14}$C egestion during 2 h</td>
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<td>Experiment 2 Control</td>
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<td>Slope does not significantly differ from 0: $P = 0.55$</td>
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feeding behaviour of *Hydrobia ulvae* when its density increases up to 2–3 snails cm$^{-2}$; there is an increase in climbing and emigration. Levinton (1979b) also observed that crawling and feeding rates of *Hydrobia ventrosa* were depressed with increasing density while floating increased. The latter was interpreted as an adaptation to escape crowded conditions.

We propose to develop a model to test whether it is possible to account quantitatively for the decrease in individual ingestion rate (with the threshold effect) when only very simple behaviours are considered. Such a model simply aims at supporting the reliability of our assumptions.

3.3. The behavioural model

There are two basic and related assumptions in our model: (1) *Hydrobia* spp., as mobile deposit-feeders, adjust their crawling rate as a response to changes in food quality and quantity in order to maintain a constant feeding rate (Forbes and Lopez, 1986); therefore, the crawling rate as well as the ingestion rate of *H. ulvae* are likely to be constant in our microcosms where Chl $a$ concentration was homogenously distribut-
ed. (2) Consequently, any physical contacts between snails — as an obstacle to crawling — may inhibit their activity for a short period of time; Levinton (1979a) indeed observed a decrease of the crawling rate of Hydrobia ventrosa as a function of crowding. It is then hypothesized that the increase in snail density will increase the probability of contacts between snails, hence, decrease their crawling rate as well as their individual ingestion rate during a fixed amount of time.

To test these hypotheses we have built an individual-based simulation model, discrete in space and time, where space is divided in cells; one cell can only support one individual, and each individual can move randomly from one cell to any of the adjacent ones with the same probability. It is called a random walk model using cellular automata formalism; such models have been largely used in marine ecology to estimate, e.g. particle dispersion (Okubo, 1975), animal behaviour (Lizon et al., 1998; Rosenberg et al., 1997; Keiyu et al., 1994) or the number of phytoplankton cell contacts in a turbulent flow (Yamazaki et al., 1991).

In the present case, the random walk is justified by the fact that individuals are maintained in a homogenous and unknown environment, of which they have a limited perception. We have derived from these conditions a number of basic rules for the motion of individuals in the two-dimensional space (Fig. 6A): (1) the probability for a snail to move to an adjacent cell is 1/7 since we assume that an individual does not crawl back to the cell it occupied at the previous time-step (actually, each individual keeps in memory the position of the previous two cells); (2) an individual will move only if the randomly chosen cell (random process) is not already occupied by another individual; (3) coprophagy on fecal pellets is not accounted for because duration of the experiment was too short for pellets to be produced, and fresh fecal pellets are not consumed by snails (Lopez-Figueroa and Niell, 1987); (4) boundaries of the simulated area are represented by the microcosm limits (the walls of the incubation flasks); (5) when the random walk of snails directs them towards and against a wall, they stop moving (hence grazing) until the random process brings them back within the simulated area (reflecting boundary conditions). This is consistent with the behavioural capabilities of Hydrobia ulvae as reported by Barnes (1981). Individuals are not allowed to escape definitely from the simulation area. The magnitude of this ‘wall effect’ is ca. 5% in terms of activity decrease (separate simulation not shown) and does not affect the relative change of individual ingestion rate as a function of mud snail density.

Another hypothesis which may be tested is that food accessibility could be limited; therefore, in a separate simulation, we have taken into account the fact that, when crawling, snails may create mucus tracks which prevent other snails from eating algal cells; this assumes to keep individual trajectories into memory where cells cannot be used for grazing any more.

For the simulations we used the following conditions: (1) the maximum flask surface (100 mm×70 mm) was divided in 50×35 cells (Fig. 6B), with a cell dimension being the average individual foot size (2 mm); (2) the number of individuals used in the microcosm experiments (25, 59, 118, 210, 344 per microcosm) were reported for the simulations and the simulation time was equal to the incubation (feeding) time (1 h); (3) the maximum distance (in terms of number of cells) covered by one individual during the incubation time was calculated assuming that the individual speed was constant: the
crawling rate was assumed to be close to 0.2 cm min\(^{-1}\) as found by Forbes and Lopez (1986) on a related species (*Hydrobia truncata*). This value corresponds to an equivalent distance of ca. 60 cells visited during the 1-h simulation time.

Fig. 6C presents simulations of the relative individual ingestion activity of snails as a function of snail density. The relative individual mean activity ranges from 1 (corresponding to the activity of one completely free individual in an unlimited open space) to 0 (corresponding to the absence of activity in a space where all cells are occupied by individuals). Thirty trials are performed for each density.

According to our hypotheses, the simulation (Fig. 6C, curve with full symbols) confirms the observed experimental results, that is a decrease of the individual ingestion rates as a function of mud snail density and, most important, in the same proportions (about 15%). Particularly, there seems to be a threshold effect between 1.4 and 2.5 snails cm\(^{-2}\). This result is important insofar as it points out a non-trivial characteristic of the system already observed in experimentally-controlled conditions. This means that such a simple model, based only on a basic behavioural process, can account for a significant part of the observed phenomenon. So, it may be considered as an interesting tool for investigating the effect of behavioural processes on the feeding activity of *H. ulvae*, by integrating both quantitative and qualitative information. As a result, this model can further test the presumed effect of other processes, such as the limited access to microalgae due to the production of mucus tracks by mud snails (Fig. 6C, curve with open symbols): results clearly show that this hypothesis is unrealistic under our experimental conditions in microcosms since an exponential decrease of the individual ingestion rate is to be expected as a function of mud snail density.

4. Conclusion

Results show that under non-limiting food conditions, *Hydrobia ulvae* reduces its individual ingestion rate as a result of space limitation. Our behavioural hypothesis, as tested in the model, may explain the experimental results in our microcosms characterized by homogenous conditions. However, the extrapolation to field conditions to assess the grazing pressure at the scale of the ecosystem and correlatively the possibility of *H. ulvae* food-limitation — based on the measurement of individual mean ingestion rates — is still difficult because of the heterogeneity of the mudflat at different temporal and spatial scales: additional mechanisms have to be investigated, e.g. interactions between snail feeding behaviour, the problem of pelletization of the sediment, diel rhythm of feeding activity, sediment characteristics and accessibility of food.

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