

12003

A Model of Renewable Resources and Limitation of Deposit-Feeding Benthic Populations

J.S. Levinton^{1,2} and G.R. Lopez^{2*}

¹ Department of Ecology and Evolution, State University of New York, Stony Brook, New York, NY 11794, USA

² Institute of Ecology and Genetics, University of Århus, Århus, Denmark

Summary. 1. The renewal rate of resources exploited by a population influences carrying capacity and competitive interaction. A model of resource renewal is proposed where P is the fraction of the resource exploited at any given time, p the fraction exploited per day, and a the fraction remaining per day. At equilibrium, $P = p/(1 - a)$, and resource is always available if $p < 1 - a$. A logistic model of recovery is also proposed for living resources that are themselves limited by nutrients or space.

2. The models are used to predict carrying capacities of populations of the mud snail *Hydrobia*. The snail does not reingest its own fecal pellets until they have broken down. Pellet breakdown rate may therefore be a limiting factor to population size. Measured pelletization rates and fecal pellet breakdown rates predict densities within the range of natural *Hydrobia* populations. Pellet breakdown in this case is the renewable resource. As many natural sediments with deposit-feeders are completely pelletized we conclude that pellet breakdown rate is an important limiting factor to deposit-feeder density and that coprophagy may be avoided in deposit-feeding mollusks.

1. Introduction

Many populations exploit resources which are renewable at periodic intervals or are returned at a relatively continuous rate. The rate of renewal in part may determine the pattern of exploitation of the resource, and the favoring of intraspecific territorial defense mechanisms. If the resource must be monopolized for the lifetime of the individual, then interference adaptations may be selected to discourage the usurping of the resource by a neighbor. Thus epifaunal benthic animals have evolved a variety of defense mechanisms to avoid overgrowth of their needed space for attachment to the substratum by conspecifics (e.g. Connell, 1961; Francis, 1973). In some reported cases aggression among individuals alters the

* Present address: Institute of Biology, University of Odense, Odense, Denmark

outcome of interspecific competition (Lang, 1973; Kinzie, 1968). But a case can be made that the evolution of interspecific aggression as a result of interspecific competition for resources should be rare (MacArthur, 1972).

Where resources are renewed frequently relative to the exploiter's lifespan selection for intraspecific interference or territoriality is lessened as the probability of a resource appearing within one's own foraging area is approximately as great as within a neighbor's foraging zone (Levinton, 1972a). In this case we would predict selection for efficiency at exploiting the renewable resource, rather than for discouragement of others from attempts at utilization of the resource.

Mobile deposit-feeding (sediment-ingesting) benthic animals are exploiters of renewable resources. Sediment is ingested and the attendant microorganisms are assimilated with varying degrees of efficiency. Typically, the organic debris upon which many of the microbial organisms live remains undigested, although fragmentation may occur (Hargrave, 1970; Fenchel, 1970; Lopez et al., 1977). After a period of time, the egested material is recolonized by microorganisms, depending upon nutrients derived from interstitial water and organic debris. In the case of bacteria, recolonization may reach preingestion levels in only a few days (Hargrave, 1976). Thus, after a period, the sediment is once again a food source for deposit-feeders.

When a resource is slowly renewed relative to the lifespan of the individual, carrying capacity is merely the total amount of resource divided by the amount required per individual. This calculation is somewhat complicated by density-dependent resource exploitation and changes in resource requirement per individual with age. Neglecting these complications, the carrying capacity of a barnacle population can be ascertained with a knowledge of the available space and the basal attachment area of an average individual. Where resources are renewed at a rapid rate relative to the individual's lifespan, carrying capacity of the exploiter population is differently determined for two reasons. First, rather than dividing the static resource among the population, exploitation must be visualized as a balance of exploitation and renewal. The more rapidly the resource is renewed the greater the exploiter population that can be supported. Second, the exploiter population can enhance the productivity of a renewable resource, and hence the rate of renewal. At low densities epibenthic algal and bacterial production is stimulated by animal grazing, relative to ungrazed sediments (Hargrave, 1970; Fenchel and Kofoed, 1976). Grazing by the amphipod *Orchestia grillus* on *Spartina* litter increases the colonization rate of the microbial community, relative to ungrazed controls (Lopez et al., 1977). Using the grazing fish *Notropis spilopterus*, Cooper (1973) showed that low level grazing enhanced the productivity of autotrophic microorganisms. Reduction of standing crop and increased turnover of the exploited populations was a possible explanation. Selective exploitation, relative digestibility or ability to recover can shift the species composition of the exploited resource populations (e.g. Porter, 1973).

Given these two factors, there must be a population size above which there is no available resource, and below which the regeneration rate of the resource, at least on the short term, always allows some resource to be available. When the resource is food, this availability may be insufficient to maintain the needs of the individual as the species composition of the resource may have shifted to a less valuable part of

the spectrum. But if the renewed resource is sediment available for ingestion, or shelters temporarily used by foragers, then there is always some resource available neglecting the problem of finding the resource when it is rare.

In this study we construct a model showing the limitation of a deposit-feeding population by the renewable resource of ingestible sedimentary particles. The model permits a calculation of the population size that can be maintained by the renewable resource and a prediction of steady state resource levels at different exploitation rates. We employ laboratory microcosms to investigate the balance of sediment ingestion and fecal pellet breakdown when sediment is consumed by the deposit-feeder *Hydrobia*. *Hydrobia* is shown to avoid ingestion of their own fecal pellets until they have been broken down to their constituent particles. The breakdown rate of pellets may therefore limit feeding. We use *Hydrobia* only as a model system and emphasize the laboratory evidence that diatom recovery can limit *Hydrobia* growth (Fenchel and Kofoed, 1976). However, sediments at some Hydrobiid localities and in many shallow subtidal silt-clay sediments are pelletized (this study, Rhoads, 1973) suggesting that the mechanism of pellet breakdown may be important in regulating deposit-feeder population size.

2. Materials and Methods

We have worked upon laboratory populations of *Hydrobia minuta* collected from a high intertidal pool at Flax Pond, Old Field, New York, USA, and *H. ventrosa*, collected from a pond near Kalø Slotsruin (Hylleberg and Lassen, unpublished), and from a lagoon at Lendrup (Fenchel and Kofoed, 1976), both latter localities in Jutland, Denmark. Experiments with *H. minuta* were done at 21°C, whereas those with *H. ventrosa* were kept at room temperature (ca. 21°C).

Sediment finer than 62µ was sieved from sediment collected in the snails' native habitat. Equal fractions were placed in 10 ml beakers or scintillation vials (with 10 ml of seawater), with different numbers of snails. After specified periods of time pellets were collected on an 80µ sieve, transferred to a preweighed glass fibre filter, and weighed on an analytical balance. A negligible number of pellets passed through the sieve. The per cent pelletization was then calculated as the weight of pellets divided by the weight of the sediment that was introduced into the container. To estimate pellet breakdown, we collected freshly egested *H. minuta* pellets and directly counted the number of intact pellets remaining after specified time intervals. For *H. ventrosa*, equal aliquots of pellets less than 12 h old were placed in 5 ml beakers with seawater and samples were sieved at intervals on an 80µ sieve to collect surviving intact pellets.

Recolonization of diatoms and bacteria was followed on fecal material through use of epifluorescence microscopy, after the methods described in Lopez and Levinton (1978); counts are expressed in numbers of cells per mg sediment.

3. The Deposit-Feeding System and the Mud Snail *Hydrobia*

Deposit-feeding marine benthic animals are common in marine bottoms and dominate fine-grained sediments (Sanders, 1958; Levinton, 1972b). They ingest sedimentary particles and organic debris, and egest fecal material consisting of particles bound into elongate pellets, in the case of *Hydrobia*. Pellets of the amphipod *Orchestia grillus* are encased in a chitinous membrane and remain intact for months unless mechanically disaggregated (Lopez et al., 1977). As the ingested material passes through the gut, microalgae, bacteria, protozoa and possibly small

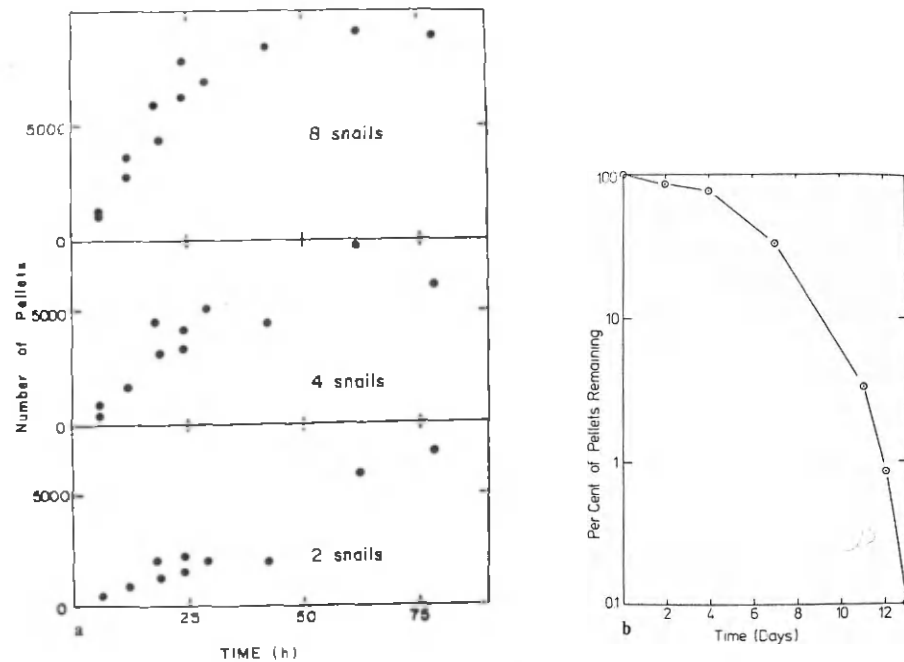


Fig. 1. a Pellet accumulation by *Hydrobia minuta* in chambers ($14 \text{ mg sediment chamber}^{-1}$) with differing snail densities. b Breakdown of pellets over time

meiofauna are digested with varying efficiencies. Egested material is the site of recolonization by the microbial community.

The potential importance of coprophagy among deposit-feeders has been emphasized in several previous studies (Newell, 1965; Frankenburg and Smith, 1967; Johannes and Satomi, 1966). If dense populations of deposit-feeders bind all of the available sedimentary material into fecal pellets, it is possible that no sedimentary material would be available for ingestion. Therefore, trituration of pellets would permit access to this otherwise unavailable resource. However, if fecal pellets were reingested, sedimentary grains might be devoid of digestible microorganisms. When sediment is fed to *Hydrobia ventrosa*, digestion of ingested diatoms may be as high as 70%. However, if fecal material is disaggregated and immediately re-fed to the snails, digestion is negligible (Lopez and Levinton, 1978). Thus there is selective value in avoiding reingestion of recently egested fecal pellets, as they have not yet been fully recolonized by an appropriate food source.

Despite previous observations (Newell, 1965; Frankenburg and Smith, 1967), we have not observed *H. ventrosa* to reingest whole fecal pellets until they have been broken down into component sedimentary particles and organic debris. Figure 1a shows the accumulation of fecal pellets in populations of *H. minuta*. At the highest snail density, ca. 70% of the sediment is pelletized after about 50h and no more pellets accumulate. At this point, snails ceased feeding and either moved about or

withdrew into their shells. If pellets were disaggregated and presented to the snails, feeding resumed immediately. The same experiment was performed on *Hydrobia ventrosa* with similar results. Although we have occasionally observed an individual to tear apart a fecal pellet, cessation of feeding is the rule when most of the sediment is pelletized. The avoidance of reingestion of intact fecal pellets seems adaptive in that it focuses feeding on sedimentary particles that have not recently passed through another individual's gut. Limitation of deposit-feeders, in the context of renewable resources may therefore be due to (1) recolonization of diatoms, bacteria and other microorganisms, and (2) the rate of pelletization as balanced by the rate of fecal pellet breakdown. We concentrate on the latter limiting factor below.

4. A Model of Resource Level with Renewable Resources

A simple model of sediment pelletization and fecal pellet breakdown must take into account the pellet egestion rate per snail, population density, and pellet breakdown rate. A more elaborate model would incorporate density-related feeding rates, and the effect of density upon fecal pellet breakdown. Let P be the fraction of resource that is exploited; $0 \leq P \leq 1$. In the present context, P is the fraction of the sediment that is pelletized at any given time. If p is the fraction of the sediment that is pelletized by a given population density after one day, and a is the fraction of pellets remaining after one day, then after three days:

$$P = p + a \cdot p + a \cdot a \cdot p.$$

The first term of the series is the third day's accumulation, the second term is the 2 day's accumulation, minus the fraction that has broken down in 1 day, while the last term is the 1 day's pellet production, minus 2 days' disintegration. This generalizes to:

$$P = p \sum_{i=0}^n a^i,$$

where n is the number of days. This series converges (as $a < 1$) as:

$$P = p/(1 - a). \quad (1)$$

Thus if pellet breakdown (or any resource return) is a constant fraction per unit time, Equation (1) permits the calculation of the equilibrium fraction pelletized as a balance between pellet production and pellet disintegration. If $p > (1 - a)$, then this equilibrium value is greater than one and the sediment will be completely pelletized. If $p < (1 - a)$, then there is always some available for ingestion. Therefore, a population density corresponding to carrying capacity can be calculated where $p = (1 - a)$. Carrying capacity is b/e , where e is the egestion rate per snail, and $b = (1 - a)$. Figure 2a and b shows the effect of varying a and p , when a population of deposit-feeders are added to an un-pelletized sediment.

If a population is added to an environment with a renewable resource, an

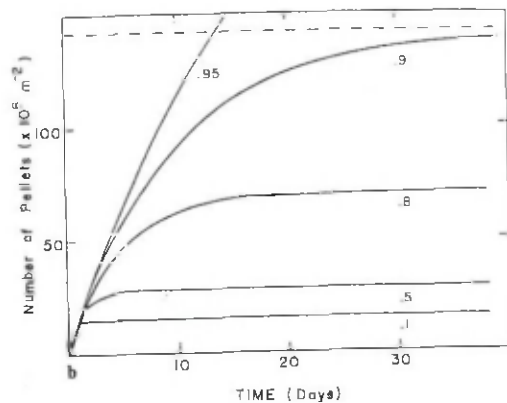
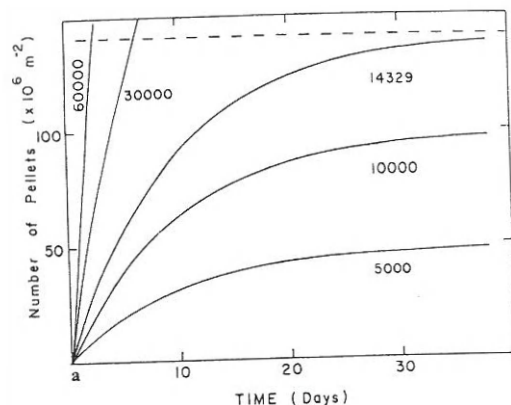


Fig. 2. a Model of pellet accumulation when pellet formation is balanced by pellet breakdown. Dashed line indicates where $P = 1.0$ at a carrying capacity of 14,329 snails m^{-2} ($a = 0.9$). b Steady state pelletization where $p = 0.1$, and a obtains differing values. Dashed line shows $P = 1$

equilibrium value of resource will be reached if $p < (1 - a)$. Such a situation can be visualized when swarms of larvae settle on a mud bottom, a migrating population of crustacea enter a feeding area where shelters are required against predation between feeding periods, or when a population of fish or birds migrate to a feeding ground and commence feeding on a renewable population. However, the time to reach equilibrium is dependent upon a , and not p . If

$$q = p/P = 1 + a + a^2,$$

then

$$q_n = \sum_{i=0}^n a^i,$$

and at equilibrium:

$$q^* = \sum_{i=0}^{\infty} a^i = 1/(1 - a).$$

If we wish to calculate the time to reach 98% of the equilibrium value:

$$(q^* - q_n)/q^* = 0.02$$

$$\begin{aligned} \sum_{i=0}^n a^i - \sum_{i=0}^{\infty} a^i &= a^{n+1} + a^{n+2} + a^{n+3} \\ &= a^{n+1}(1 + a + a^2) \\ &= a^{n+1}(1/(1 - a)). \end{aligned}$$

Thus

$$\frac{a^{n+1}(1/(1 - a))}{(1/(1 - a))} = 0.02$$

$$a^{n+1} = 0.02.$$

Solving for n at 98% of equilibrium:

$$n_{0.98} = \frac{\log 0.02}{\log a} - 1. \tag{2}$$

Because the relationship is logarithmic, as a approaches one, the time to reach equilibrium greatly increases. Thus with a given population density, slow resource renewal results in a disproportionately slow time to reach equilibrium. With a population at carrying capacity, given a small value of a (high renewal), equilibrium will be rapidly attained and the effects of resource shortage immediately felt by the population. However, a population theoretically at carrying capacity when a is near unity (slow renewal) will bring the resource level to equilibrium very slowly (after a cessation of feeding as in a winter slowdown), enhancing the possibility that other factors will control population size. Population size above carrying capacity might decrease by emigration, mortality, or lowered reproduction.

The hyperbolic relation between P and $(1 - a)$ indicates that when a is near unity, small changes in the latter will cause strongly non-linear changes in the steady state value of P . Thus, when a is near unity its value must be accurately determined. By contrast, P is linearly related to p , making small errors in estimating p less important.

In the case of recovery by algae or bacteria, the situation is quite different because of a presumed upper limit to microbial growth. The logistic model of population growth best describes such a situation. In integral form, microbial population size N , after time t , is:

$$N = K/(1 + e^{c - rt}),$$

where K is the upper limit to growth, r is the rate of increase of an unlimited population, and c is a constant of integration defining the position of the curve relative to the origin (Pearl, 1930; Andrawartha and Birch, 1954). This may be arranged to

$$\ln((K - N)/K) = c - rt.$$

The parameters r and c are the slope and intercepts, respectively, of the linear regression of $\ln((K - N)/K)$ on t . Data is fitted to this equation by selecting values of K by trial and error until the best straight line is obtained (Pearl, 1930).

If the minimum ration required by an individual is known, then a particle of sediment must be reingested at a frequency no faster than it takes diatom recovery to reach the minimum level. The deposit-feeder is essentially particle-limited as particles with attached diatoms are ingested (or bacteria). Therefore the minimum ration is best expressed as number of cells per particle, or per unit surface area as ingested particles vary in size.

5. Results

In order to calculate predicted carrying capacity for *Hydrobia* with respect to fecal pellet breakdown, we measured pelletization rate and pellet breakdown rate in *H. minuta* (3–5 mm long). Pellet accumulation was measured at three snail densities: 8, 4 and 2 per beaker. Linear regressions were calculated for pellet accumulation in first 24 h (Fig. 1a). If there is an effect on pellet breakdown due to snail grazing and movement, or a density effect on feeding rate (estimated by egestion rate), then the ratios of the slope of the high and medium density treatments, and the medium and low density treatments should differ from 2.0. They are however 2.1 and 1.9, respectively, so no such effects were noted in the first 24 h.

After about 50 h, pellet accumulation in the high density bowl ceased at about 68% pelletization (Fig. 1a). This may be due to the difficulty of finding particles which at this point were diffusely spread throughout the sediment, adhering to fecal pellets. It is also possible that these remaining particles were close to 62 μ in diameter, and were difficult to ingest (Lopez and Levinton, 1978). In either case, this incomplete utilization was incorporated into our calculations of carrying capacity.

Pellet breakdown is shown in Figure 1b. For the first four days breakdown consists of mechanical fragmentation. However, pellets then began to become indistinct and breakdown greatly increased. This change may be related to disintegration of the mucous binding the pellets. The change of breakdown necessitates a simulation, adjusting the model so that a changes from 0.9 to 0.5 after the 5th day.

In order to estimate carrying capacity we make the following assumptions. If *Hydrobia* exploits the sediment to a depth of 2 mm there are 2000 cc m^{-2} of sediment available for grazing. If the water content of the sediment is 60% (Rhoads and Young, 1970), the specific gravity of the sedimentary grains is 2.7, and a typical sediment consists of about 10% of particles small enough to be ingested by *Hydrobia* (as is approximately the case in Limnfjord localities – Fenchel and Kofoed, 1976), then there are 216 g m^{-2} available for exploitation. We also assume that feeding ceases at 68% pelletization. Figure 3 shows the effect of adding different population densities, using a pelletization rate of 41 $\mu g h^{-1} snail^{-1}$ (Levinton et al., 1977), and the breakdown curve of Figure 1b. These data predict a population density of 27,000 m^{-2} . Table 1 shows *Hydrobia* densities at various localities for comparison.

A similar study was done for *H. ventrosa*, but pelletization was followed for a

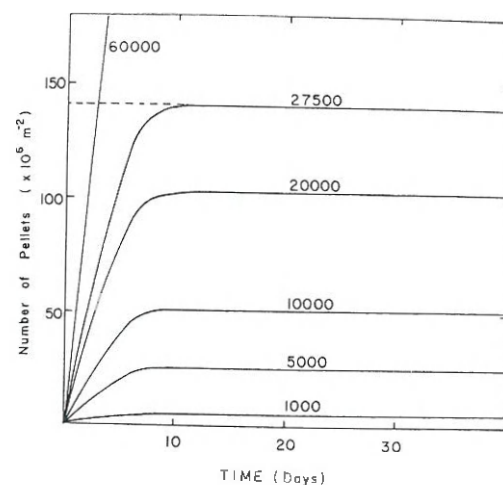


Fig. 3. Modified pellet breakdown model, where $a=0.9$ from day 1–5, the $a=0.5$. Dashed line indicates where $P=1.0$.

Table 1. Typical natural densities of *Hydrobia* populations

Species	Locale	Snails m^{-2}	Source
<i>H. ventrosa</i>	Limnfjord, Denmark	0–37,000	T. Fenchel (unpublished)
<i>H. ulvae</i>	Limnfjord, Denmark	0–44,000	T. Fenchel (unpublished)
<i>H. ventrosa</i>	Kalø Pond, Denmark	500–30,000	J. Hylleberg (unpublished)
<i>H. ulvae</i>	Whitstable, England	400–12,000	Newell (1965)
<i>H. minuta</i>	Barnstable Harbor, Massachusetts, USA	75–24,700	Sanders et al. (1962)

longer period to see if a balance between pellet breakdown and pelletization resulted in a stabilization of the available resource, as predicted by the model. In this case, pelletization rate was estimated to be $38.0 \pm 1.6 \mu g h^{-1} snail^{-1}$ ($n=10$). Figure 4a shows pelletization over time at two densities, corresponding to 8 and 80,000 snails m^{-2} , given the above assumptions. At the low density, pelletization increased to about 15% but did not increase any further. As snails were observed to be actively feeding throughout the whole period of the experiment, we interpret this to be the result of a balance between pelletization and pellet breakdown. At the higher density pelletization increased to about 70%, feeding activity ceasing at this point. This slowdown represents the exhaustion of available resources. Figure 4b shows the measured pellet breakdown, showing a near-linear decay of about 8% per day. We do not know why the breakdown curve was closer to linear in this case as opposed to increasing, as in Figure 1b. In *H. ventrosa*, pellet breakdown seemed exclusively due to fragmentation. It is unlikely that the species difference is important, but in the case of *H. minuta* data was collected in summer, while data was collected in winter for *H. ventrosa*. Feeding, digestive activity and mode of pellet compaction may have differed between seasons. Using the assumptions

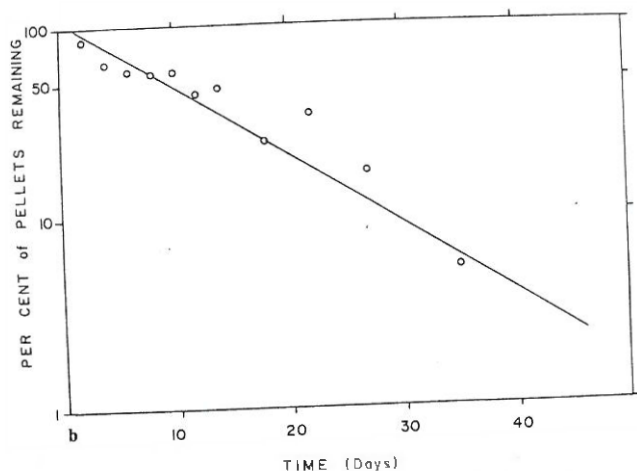
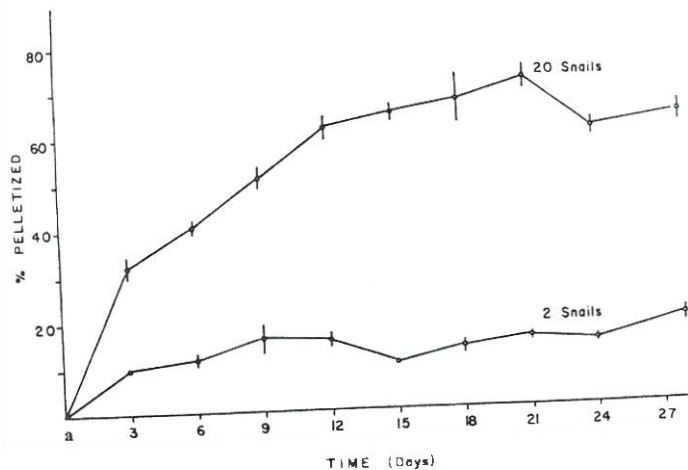


Fig. 4. a Accumulation of pellets in chambers (59 mg sediment chamber⁻¹) with two and 20 snails. Vertical bar is standard error (2 snails: N = 10, 20 snails: N = 5). b Breakdown of pellets over time

discussed above and measured pelletization and breakdown rates, we arrive at a carrying capacity of ca. 13,000 snails m⁻² for *H. ventrosa*.

Given the determined value of *a* at 0.92, and the measured pelletization rate we can predict an expected steady state pelletization for the lower snail density with Equation (1). In this case *p* = 0.033, giving a value of 0.41 for *P*. As the measured value was only about 0.15, pellet breakdown must have been greater than estimated in bowls without snails. Therefore, over several days, snail activity or excretions stimulating microbial attack of fecal pellet mucous may increase breakdown rate,

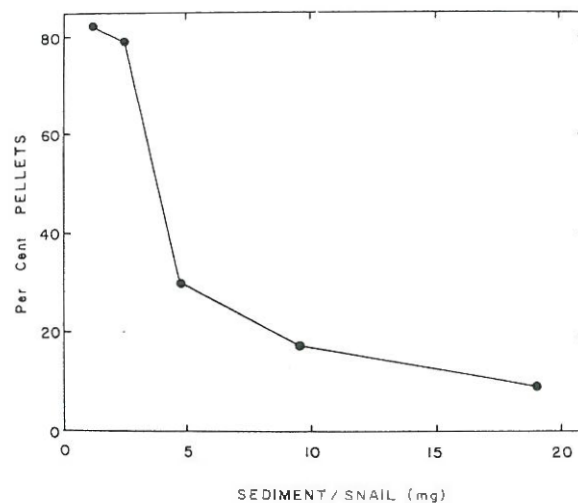


Fig. 5. Per cent pelletization after 40 days with different amounts of sediment per snail

as opposed to our data for the first 24 h in *H. minuta*. It is also possible that conditions in the pellet breakdown experiment did not favor microbial growth but data is lacking. Taking *P* as 0.15 and *p* as 0.033, *a* is calculated to actually be 0.78 in the experiment. With this value of *a*, a carrying capacity of ca. 35,800 snails m⁻² is predicted.

The pellet breakdown model predicts that the steady state per cent pelletization of the sediment will increase with decreasing sediment per snail up to a maximum pelletization rate. Figure 5 shows the per cent pelletization of experimental *H. ventrosa* populations of differing amounts of sediment per snail, kept for 40 days. Pelletization would be 100% even in the lowest density population, were there not a balance between breakdown and pelletization rates. As can be seen, per cent pelletization increases to a maximum of about 80%, somewhat higher than reported above. Pelletization increases below about 5 mg sediment snail⁻¹. Given the assumptions outlined above of sediment availability for a sediment of 10% silt-clay, this corresponds to a density of about 30,000 snails m⁻², a number close to that predicted from the model as revised by the animal-related value of *a* at 0.78.

Figure 6 shows the recovery of diatoms on particles less than 10 μ in size egested as *Hydrobia* pellets. The dashed line indicates the standing stock on naturally collected sediment at Lendrup (May 1977). Recovery under room light to this level occurs in 6 days, and a plateau is reached after about 10 days. As can be seen the logistic model adequately fits the data, with a best fit at *K* = 1.3 × 10⁶ cells mg⁻¹ sediment. Independent evidence shows that the diatoms are not cropped below a density of 5 × 10⁵ cells mg⁻¹ (Lopez and Levinton, 1978). The recovery time to attain the minimum ration might be calculated by measuring *Hydrobia* growth at different densities and calculating the sediment ingested per snail per day above which no growth occurs. Given the independently measured recovery of diatoms,

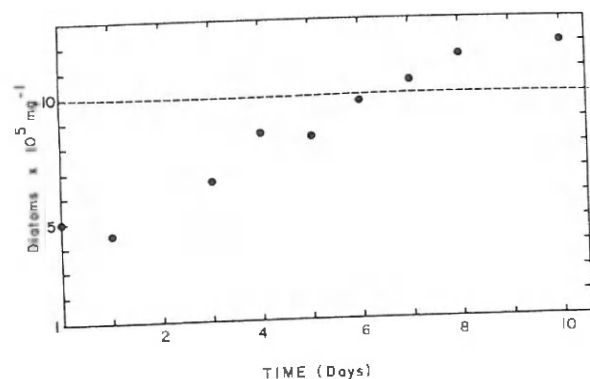


Fig. 6. Recovery of diatoms attached to particles in newly egested *H. ventrosa* feces. Dotted line represents density of diatoms found in the sediment at Lendrup. Starting diatom density is that of newly egested feces

we may infer whether steady state field populations are limited by this particular renewable resource, and predict steady state resource levels in laboratory microcosm experiments. The approach is complicated by the interaction of recovery functions of different resources, and by effects of animal grazing on the recovery function (e.g. Fenchel and Kofoed, 1976).

6. Discussion

Because deposit-feeders exploit a renewable resource, models of the type proposed above predict the grazing level at which no resource is available and the population is thus limited. At population sizes below the carrying capacity, particles are always available, perhaps for consumption by another species. Population densities predicted by the pellet breakdown model are in the general range of *Hydrobia* populations measured in the field (Table 1). At Lendrup, however, the sediment available for ingestion is not pelletized. Abundant species such as the foraminiferan *Elphidium williamsoni* and the amphipod *Corophium volutator* can be shown to break down pellets in the laboratory and probably do so as well in the field. However, other localities have sediments that are completely pelletized. A subtidal locality in the Limnfjord (station 3 of Jørgensen, 1977) was completely pelletized by *Abra* and *Hydrobia*. At a protected flat near Begtrup (Mols, Jutland), the sediment was dominated by populations of *Hydrobia ventrosa* and *H. neglecta*, at densities of $25-30 \times 10^3$ snails m^{-2} . Here, the ingestible sediment was 50-100% pelletized in 5 cores examined (a visual estimate as the preponderance of larger sand grains made sieving impractical). At Sebbersund (locality 10 of Fenchel, 1975) the silt-clay fraction of the sediment was completely pelletized. *H. ulvae* density was $52,000 m^{-2}$. Observations of subtidal sediments dominated by deposit-feeders often show complete or nearly complete pelletization (Rhoads, 1967, 1973).

Our observations are not in conformance with many reports in the literature of coprophagy in deposit-feeding benthic organisms. Although we have observed *Hydrobia* to dismember and ingest its own pellets, the general pattern is fecal pellet

avoidance. As freshly egested pellets are immediately ingested when dismembered by the investigator, we presume that the mechanism is merely cued to the size of the pellet (ca. 100 by 300 μ). Indeed, the production of compact pellets partitions that material recently eaten from particles richer in microorganisms. Before the pellet breaks down and is available for reingestion, recolonization by the microbial community will have occurred. Thus there is adaptive sense to avoidance of coprophagy.

Recent experiments suggest that digestion efficiency with regard to diatoms on particles is influenced by the standing stock and digestibility of the diatoms. This complicates resource renewal models. When sediment of increased diatom standing stock was fed to *Hydrobia ventrosa*, greater digestion efficiencies were measured (Lopez and Levinton, 1978). This can probably be related to a minimum number of diatoms mg^{-1} sediment that could not be digested. When newly egested sediment was re-fed to *Hydrobia*, no digestion was measured. Thus a period of recolonization is essential to renew the resource as fecal material in this case has no nutritive value to the snails. We might, however, imagine cases similar to rabbits (Madsen, 1939) where bacteria-rich and nutritive poor feces are egested, the former being reserved for reingestion. If this can occur among deposit-feeding marine invertebrates then coprophagy should be favored. Our present evidence cannot exclude this possibility for *Hydrobia*.

The rarity of coprophagy in *Hydrobia* does not exclude the possibility that other cooccurring deposit-feeding species can obtain a nutritive reward from freshly egested *Hydrobia* pellets. Fractions of the microbial community not available to *Hydrobia* might be assimilated by other species (see Lopez and Levinton, 1978).

In the case of deposit-feeders where all renewable food resources depend upon particle ingestion, the one with the lowest recovery rate will limit population size. If the minimum diatom ration required by a *Hydrobia* renews less rapidly than pellet breakdown, we must conclude that the latter will not be a limiting renewable resource. But diatoms may not be limiting if fecal pellets break down slowly. Though the models proposed above neglect several factors (e.g. density-dependent egestion), we feel that such a comparative approach to renewable resources is justified and permits an analysis of population control by resources in deposit-feeding benthic populations.

Acknowledgements. S. Kirkpatrick assisted with studies of *H. minuta*. P. Petraitis pointed out to us the calculation for time to reach equilibrium. We also thank T. Fenchel, J. Hylleberg, H. Lassen and D. Schneider for helpful discussion. T. Fenchel read and criticized the manuscript. This is contribution number 239 to the Program in Ecology and Evolution, State University of New York, Stony Brook. This paper is dedicated to the late Professor Ralph Gordon Johnson.

References

- Andrwartha, H.G., Birch, L.C.: The distribution and abundance of animals. Chicago: University of Chicago Press 1954
- Connell, J.H.: The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42, 710-723 (1961)
- Cooper, D.C.: Enhancement of net primary productivity by herbivore grazing in aquatic laboratory microcosms. *Limnol. Oceanogr.* 18, 31-37 (1973)
- Fenchel, T.: Factors determining the distribution patterns of mud snails (Hydrobiidae). *Oecologia (Berl.)* 20, 1-17 (1975)

- Fenchel, T.: Studies on the decomposition of organic detritus derived from the turtle grass *Thalassia testudinum*. *Limnol. Oceanogr.* **15**, 14–20 (1970)
- Fenchel, T., Kofoed, L.H.: Evidence for exploitative interspecific competition in mud snails (Hydrobiidae). *Oikos* **27**, 367–376 (1976)
- Fenchel, T., Kofoed, L.H., Lappalainen, A.: Particle size selection of two deposit feeders: the amphipod *Corophium volutator* and the prosobranch *Hydrobia ulvae*. *Mar. Biol.* **30**, 119–128 (1975)
- Francis, L.: Intraspecific aggression and its effect on the distribution of *Anthopleura elegantissima*. *Biol. Bull. Woods Hole* **144**, 73–92 (1973)
- Frankenburg, D., Smith, K.L.: Coprophagy in marine animals. *Limnol. Oceanogr.* **12**, 443–450 (1967)
- Hargrave, B.T.: The utilization of benthic microflora by *Hyalella azteca*. *J. Anim. Ecol.* **39**, 427–437 (1970)
- Hargrave, B.T.: The central role of invertebrate faeces in sediment decomposition. In: The role of terrestrial and aquatic organisms in decomposition processes (J.M. Anderson, A. MacFadyen, eds.), pp. 301–321. Oxford: Blackwell 1976
- Johannes, R.E., Satomi, M.: Composition and nutritive value of fecal pellets of a marine crustacean. *Limnol. Oceanogr.* **11**, 191–197 (1966)
- Jørgensen, B.B.: Distribution of colorless sulfur bacteria (*Beggiatoa* spp.) in a coastal marine sediment. *Mar. Biol.* **41**, 19–28 (1977)
- Kinzie, R.A.: Replacement of *Pseudosquilla ciliata* by *Gonodactylus falcatus* (Crustacea: Stomatopoda) in Hawaii. *Pacific Sci.* **22**, 465–475 (1968)
- Kofoed, L.H.: The feeding biology of *Hydrobia ventrosa* (Montagu). I. The assimilation of different components of the food. *J. Exp. Mar. Biol. Ecol.* **19**, 233–241 (1975)
- Lang, J.: Interspecific aggression by scleractinian corals. 2. Why the race is not only to the swift. *Bull. Mar. Sci.* **23**, 260–279 (1973)
- Levinton, J.S.: Spatial distribution of *Nucula proxima* (Protobranchia): an experimental approach. *Biol. Bull. Woods Hole* **143**, 175–183 (1972a)
- Levinton, J.S.: Stability and trophic structure in deposit-feeding and suspension-feeding communities. *Am. Nat.* **106**, 472–486 (1972b)
- Levinton, J.S.: The ecology of deposit-feeding communities: Quisset Harbor Massachusetts. In: Ecology of marine benthos (B.C. Coull, ed.), pp. 191–228. Columbia: University of South Carolina Press 1977
- Levinton, J.S., Lopez, G.R., Lassen, H.H., Rahn, U.: Feedback and structure in deposit-feeding marine benthic communities. In: Proc. Eleventh Marine Biology Symposium, Galway, pp. 409–416 (1977)
- Lopez, G.R., Levinton, J.S.: The availability of microorganisms attached to sediment particles as food for *Hydrobia ventrosa*. In preparation (1978)
- Lopez, G.R., Levinton, J.S., Slobodkin, L.B.: The effect of grazing by the detritivore *Orchestia grillus* on *Spartina* litter and its associated microbial community. *Oecologia* (Berl.) **30**, 111–127 (1977)
- MacArthur, R.H.: Geographical ecology. New York: Harper and Row 1972
- Madsen, H.: Does the rabbit chew the cud? *Nature* **143**, 981 (1939)
- Newell, R.: The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*. *Proc. Zool. Soc. London* **144**, 25–45 (1965)
- Pearl, R.: Introduction to medical biometry and statistics. Philadelphia: Saunders 1930
- Porter, K.G.: Selective grazing and differential digestion of algae by zooplankton. *Nature* **244**, 179–180 (1973)
- Rhoads, D.C.: Biogenic reworking of intertidal and subtidal sediments in Barnstable Harbor and Buzzards Bay, Massachusetts. *J. Geol.* **75**, 461–474 (1967)
- Rhoads, D.C.: Organism-sediment relationships on the muddy sea floor. *Oceanogr. Mar. Biol. Ann. Rev.* **12**, 263–300 (1973)
- Rhoads, D.C., Young, D.K.: The influence of deposit-feeding organisms on sediment stability and community trophic structure. *J. Mar. Res.* **28**, 150–178 (1970)
- Sanders, H.L.: Benthic studies in Buzzards Bay. I. Animal-sediment relationships. *Limnol. Oceanogr.* **3**, 245–258 (1958)
- Sanders, H.L., Goudsmit, E.M., Mills, E.L., Hampson, G.E.: A study of the intertidal fauna of Barnstable Harbor, Massachusetts. *Limnol. Oceanogr.* **7**, 63–79 (1962)

Received September 15, 1977

Effects of Salinity and Illumination on Photosynthesis and Water Balance of *Spartina alterniflora* Loisel

D.J. Longstreth and B.R. Strain

Department of Botany, Duke University, Durham, NC 27706, USA

Summary. Plants of the salt marsh grass *Spartina alterniflora* Loisel were collected from North Carolina and grown under controlled nutrient, temperature, and photoperiod conditions. Plants were grown at two different illumination levels; substrate salinity was varied, and leaf photosynthesis, transpiration, total chlorophyll, leaf xylem pressure, and specific leaf weight were measured. Conditions were controlled so that gaseous and liquid phase resistances to CO₂ diffusion could be calculated. Growth at low illumination and high salinity (30 ppt) resulted in a 50% reduction in photosynthesis. The reduction in photosynthesis of plants grown at low illumination was correlated with an increase in gaseous resistance. Photosynthetic rates of plants grown at high salinity and high illumination were reduced only slightly compared to rates of plants grown in 10 ppt and Hoagland's solution. Both high salinity and high illumination were correlated with increases in specific leaf weight. Chlorophyll data indicate that specific leaf weight differences were the result of increases in leaf thickness. It is therefore hypothesized that photosynthetic response can be strongly influenced by salinity-induced changes in leaf structure. Similarities in photosynthetic rate on an area basis at high illumination were apparently the result of increases in leaf thickness at high salinity. Photosynthetic rates were generally quite high, even at salinities close to open ocean water, and it is concluded that salinity rarely limits photosynthesis in *S. alterniflora*.

Introduction

Spartina alterniflora Loisel flourishes in an environment that is characterized by a number of extreme physical factors including high salinity and high irradiance. This plant species dominates the intertidal salt marshes of the Eastern and Gulf Coasts of the United States, often forming a distinct vegetational zone (Adams, 1963; Hinde, 1954).

High salinity has been shown to reduce biomass production of *S. alterniflora* seedlings in laboratory experiments (Mooring et al., 1971) and to be negatively correlated with dry matter production in field studies (Broome et al., 1975;