

Particle Size-Selection of Two Deposit Feeders: the Amphipod *Corophium volutator* and the Prosobranch *Hydrobia ulvae*

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Abstract

The feeding biology of the deposit-feeding amphipod *Corophium volutator* is compared to that of the coexisting, deposit-feeding prosobranch *Hydrobia ulvae*. Regarding ingestion of particles, both forms show size selection which alone can explain their coexistence. Particle size-selection also explains some qualitative differences in the composition of the food of the two forms; thus, diatoms play a relatively larger role in the diet of *H. ulvae* than in the diet of *C. volutator*, whereas bacteria are probably relatively more important for the latter. Results of experiments with feeding of C-14 labelled microorganisms are in accordance with the findings on particle size-distribution of the gut contents, and show that (1) *C. volutator* can only utilize bacteria adsorbed to particles within the size range 4 to 63 μm (this is why the presence of clay and silt particles in the sediment are necessary for efficient feeding of this amphipod); (2) *C. volutator* can utilize bacteria suspended in the water pumped through its burrow for respiration if silt and clay particles are present in the sediment. (3) *H. ulvae* can utilize large particles, and also browses on surfaces, and some evidence is brought forward that it also utilizes mucus for trapping microorganisms. The coexistence of deposit-feeding animals is discussed. It is concluded that the number of coexisting, closely related species is usually small, and that their resource partitioning is probably mainly based on particle-size selectivity. In the case of unrelated forms (e.g. *H. ulvae* and *C. volutator*, a number of behavioural, physiological and morphological differences, and also the widespread ability of deposit feeders to utilize alternative feeding mechanisms may also lead to resource partitioning. Thus, there are often several niche dimensions related to feeding allowing a certain diversity of coexisting deposit feeders.

Introduction

Deposit or detritus feeders, i.e., animals which more or less indiscriminately ingest their substrate, constitute an important and often dominating part of the larger invertebrates living in or on sediments. The ecology and energetics of feeding of these animals have attracted much interest. Evidence has accumulated that they mainly utilize the living components of the ingested sediment - bacteria, fungi, microalgae and the microfauna - whereas the bulk of dead organic material of the sediments, which mainly consists of structural carbohydrates and other difficult decomposable materials, is mainly utilized indirectly through microbial decomposers (Newell, 1965, 1970; Fen-

chel, 1970, 1972; Hylleberg Kristensen, 1972; and papers cited therein).

Less consideration has been given to problems regarding coexistence and competitive interactions. Levinton (1972), from various evidence, concludes that communities of detritus feeders constitute stable, food-limited systems of "K-strategists", in which competition would be important.

Few authors have so far attempted to carry out experimental studies or to analyse the mechanisms allowing coexistence of deposit-feeding animals. Mangum (1964) and Reid and Reid (1969) studied species of maldanids and of the genus *Macoma*, respectively, and could demonstrate several ecological differences between the species within these two groups of related species.

However, most of these differences referred to habitat selection and, where food selectivity was demonstrated, no attempts to analyse whether these differences could explain coexistence were made.

Later papers will deal with the distribution, coexistence, habitat selection, competitive exclusion, and character displacement of the 4 species of hydrobiid snails occurring in Danish waters. The present paper will describe particle size-selection and feeding mechanisms of the amphipod *Corophium volutator* as compared to the prosobranch *Hydrobia ulvae*, with which *C. volutator* coexists in the studied area, as is often the case in shallow water of northern Europe. The distribution, behaviour, and general biology are well described in Meadows and Reid (1966), Muus (1967), and Newell (1970). Both forms are known deposit feeders; their feeding is easily observed in the laboratory and their guts are usually filled with sediment particles, the attached microflora of which is assumed to be utilized. In addition, filter-feeding has been suggested for *C. volutator*, and hydrobiids are often observed browsing on the thallus of *Ulva* spp. and other objects. Finally, it has been suggested that *H. ulvae*, which is often found floating on the water surface, can trap surface-film bacteria with secreted mucus which is then later engulfed. For both forms, diatoms are often stressed as ingested particles of nutritive value, but other micro-organisms which cannot be identified in the gut probably play a similar role, according to their frequency in the sediment ingested.

Materials and Methods

Sampling Locality

The larger part of this study was carried out in January, 1974 at the Aarhus University Marine Biological Laboratory at Rønbjerg Harbour, Limfjorden, northern Jutland; some additional experiments were made at the Department of Ecology in Århus. The material for the study was collected at "Lendrup Strand" about 6 km north of the marine laboratory in a small cove (about 750 x 250 m, average depth 0.5 m) in the opening of an artificial channel. The salinity varies between 9 and 28‰. The sediment consists of fine sand with a median grain size of about 140 µm, and with 5% silt and clay (i.e., particles < 63 µm). The macro-

fauna is dominated by *Corophium volutator* (10800 individuals/m² as based on 20 quantitative core samples taken in February, 1974) and two *Hydrobia* species - *H. ventrosa* (17300/m²) and *H. ulvae* (3060/m²). Also, the polychaetes *Nereis diversicolor* and *Polydora* sp. and the bivalves *Mya arenaria* and *Cardium* sp. are common. The *C. volutator* population fluctuates through the year in accordance with its reproduction in early summer; the other components of the fauna seem relatively constant throughout the year. The size range of *H. ulvae* used in the present study was 4 to 6 mm, and that of *C. volutator* 6 to 12 mm in length. In the present study, only *H. ulvae* was used in experiments for comparison with the particle ingestion of *C. volutator*. However, the general results of this paper regarding comparisons of *C. volutator* with *H. ulvae* are also valid for *H. ventrosa*.

Particle Size-Distribution of Ingested Material

In order to find the particle size-distribution of ingested mineral particles and diatoms, whole animals collected and preserved in the field or animals which had been allowed to establish themselves for at least 24 h in trays with natural sediment in the laboratory were carefully rinsed for adhering particles; in the case of snails, these were removed from their shell which often constitutes a substrate for diatoms. The animals were then placed in centrifuge glasses with 5-ml concentrated HNO₃, and the glasses placed in a water bath at 90°C in the hood for 2 h. The remaining particles, which all derived from the gut contents, were rinsed in distilled water twice and then in ethyl alcohol by successive centrifugations, and finally mounted on microscopic slides in polyvinylalcohol. Very often the gut material, especially of *Corophium volutator*, did not separate during HNO₃-treatment, but had to be spread with a needle on the slide prior to mounting. Observations on intact gut contents showed the volume loss to be small, and that the greatest part of the volume of the gut contents of living animals consists of mineral particles and silica frustules. Under 400 x magnification, the diameter of a number of randomly selected particles were thereafter measured with an ocular micrometer to the closest 2.5 µm. The length of diatom frustules, and in two cases also of the chitin walls of fungal hyphae which apparently are not dissolved in the nitric acid, were

measured in a similar way. The relative volume of particles of different sizes was estimated as the third power of the diameter. This presupposes that particles of different sizes have similar shapes, which is probably not the case. Also, the relatively rare, larger particles constitute an unproportionately large share of the total volume, making the measurement of a large number of particles necessary. It was found that measurement of 200 to 400 particles gave reasonably reproducible results and that grain-size distribution of natural samples of sand measured in this way corresponded fairly well with results obtained by wet-sieving of larger samples and weighing of the size fractions.

Feeding Experiments with Labelled Microorganisms

For tracer studies with labelled microorganisms, a number of bacteria and fungi were isolated from the sediment; of these, two strains of bacteria (Strain *d*, about 4 μm long, mobile vibrios, forming white, convex colonies on agar plates based on sea water enriched with minerals and with suspended chitin as carbon source; and Strain *g*, 1 μm long, mobile rods, forming white, convex colonies on agar-alginate sea water plates on which it was isolated and grown) and a fungus (*fb*, an ascomycete forming green-black spores and grown on agar-alginate sea water plates) were used for the experiments. In order to obtain large numbers of cells for experiments, inoculates of the strains were transferred to 300-ml flasks with an autoclaved nutrient broth (3 g Bacto-beef extract and 5 g Bacto-tryptone/l sea water). These liquid cultures were then used after 1 to 3 days at 25°C. Prior to the experiment, 1-ml 10 μCi C-14 glucose solution was added to the culture. After 10 min shaking at regular intervals, the cultures were centrifuged and rinsed in sterile sea water twice. After a third centrifugation and removal of the supernatant they were ready for use. Each experiment usually lasted only 30 to 40 min; during this period, the loss of activity of the bacteria was less than 10%.

The unidentified pennate diatoms originally isolated from estuarine sediments (A2, length about 40 μm and A30, length about 25 μm) had been grown axenically in stoppered 500-ml flasks with enriched sea water and 4 μCi C-14 HCO_3^- under fluorescent light tubes for several weeks before the experiments. Prior to the experiments, a known vol-

ume was centrifuged and the diatoms were mixed into the sediment with a spatula in the same way as for the labelled bacteria and fungi.

The experiments which should demonstrate the significance of particle size-selection were all carried out in essentially the same way. To small glass dishes (3 cm diameter, 3 cm high) 7 cm^3 sand were added, either natural sand or some specific particle-size fraction. 1-ml suspension of either labelled bacteria, fungi, or diatoms was mixed into the sand. 10-ml sea water were then added. At time zero, 20 *Corophium volutator* and 20 *Hydrobia ulvae* were added to each dish. The animals kept in filtered sea water had been starved for 2 to 3 h prior to the experiments. *C. volutator* usually immediately buried themselves into the sediment of the experimental dishes; sometimes they started to ingest the surface sediment without burrowing, as also described by Meadows and Reid (1966) for starved specimens. The snails normally started to ingest sediment at once; a few snails would usually be found floating in the surface during the experiment, but they were gently poked down on the sediment again with a spatula. Two or 5 min after starting the experiment, and again 4 times during the experimental period of 30 or 40 min (which is approximately the time it takes for both species to fill their guts), 4 specimens of each species were removed for radioactivity counts. Usually several experiments were carried out simultaneously.

In order to study the ability of *Corophium volutator* to use suspensions of bacteria as food, the following experiment was carried out. To 4 containers, 2 of which had a layer of natural sediment on the bottom, 20-ml sea water with 1 ml of a suspension of C-14 labelled Bacterium *d* was added. Ten *C. volutator* were added to one container with, and ten to one container without sediment; the remaining 2 containers, one without, one with sediment, were used as controls. At regular intervals (Fig. 7) 1-ml samples were taken from the containers, membrane-filtered, and the activity measured.

Counting was carried out with a GM-counter. The radioactivity of microbial suspensions was measured by filtering 1 ml through 0.45 μm membrane filters fitting the planchettes of the counter. After rinsing in sea water, whole animals were homogenized in the planchettes in a drop of methanol with a spatula. The "paste" was spread out evenly on the bottom of the planchettes, dried,

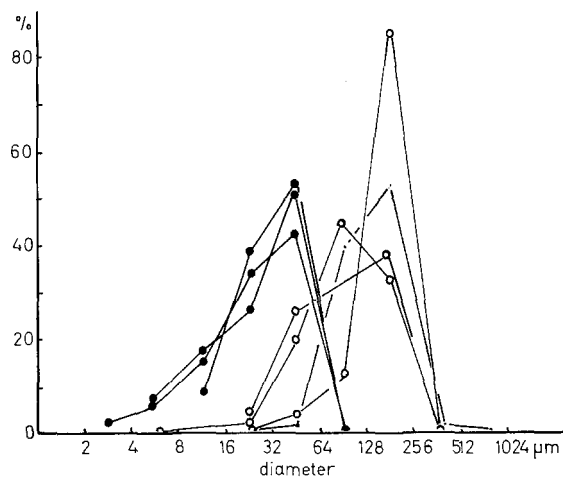


Fig. 1 Particle-size frequency (volume %) of mineral particles ingested by *Corophium volutator* (filled circles) and *Hydrobia ulvae* (open circles) and of natural sediment (dots). Each curve represents gut contents based on pooled gut contents of 10 specimens

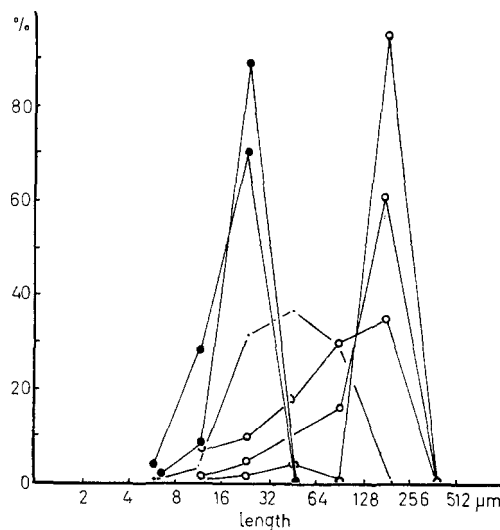


Fig. 2. Particle-size frequency of diatoms ingested by *Corophium volutator* and *Hydrobia ulvae* and of diatoms in sediment. For further explanation see legend to Fig. 1

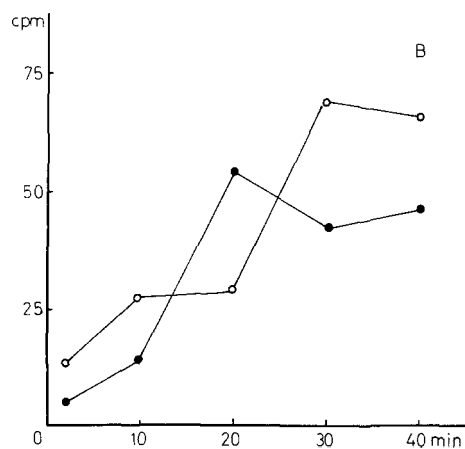
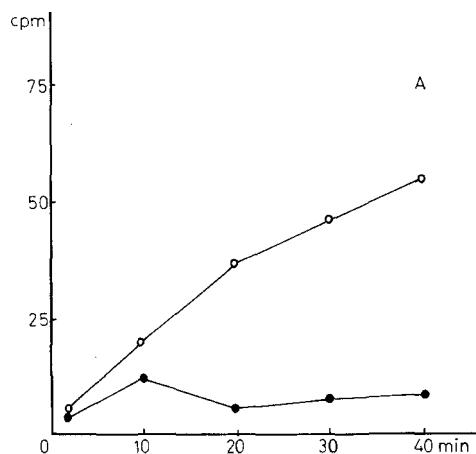


Fig. 3. Uptake of labelled bacteria (Strain g) by *Corophium volutator* (filled circles) and *Hydrobia ulvae* (open circles) in two different sediments: (A) 250 to 500 μm fraction; (B) 250 to 500 μm fraction with addition of 5% silt and clay. cpm: counts/min

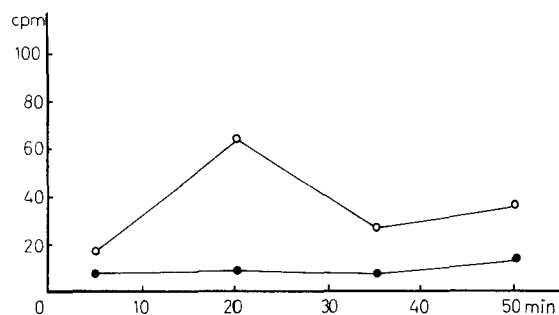


Fig. 4. *Corophium volutator*. Uptake of labelled bacteria (Strain g) in 125 to 250 μm sand fraction with (open circles) and without (filled circles) addition of 5% silt and clay

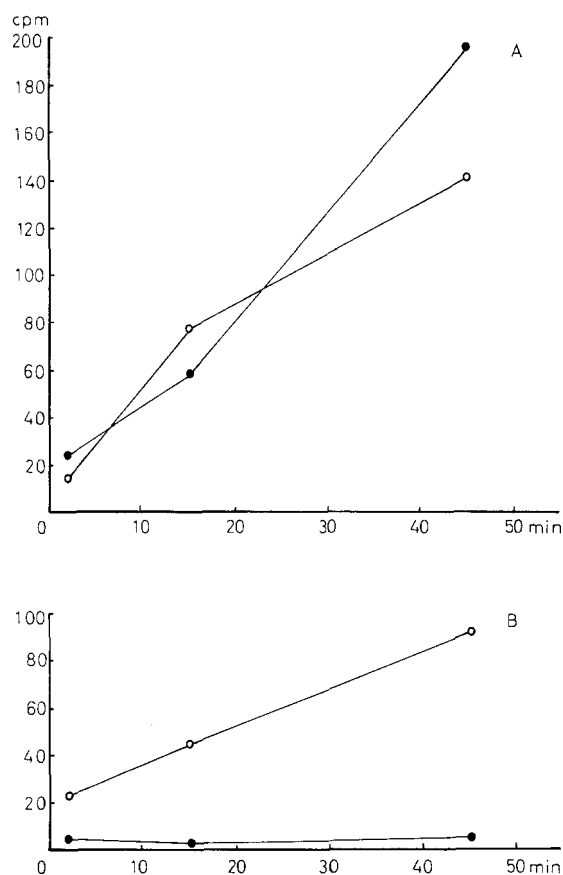


Fig. 5. Uptake of (A) labelled diatoms (A2), and (B) bacteria (Strain d) by *Corophium volutator* (filled circles) and *Hydrobia ulvae* (open circles) in 125 to 250 μm sand fraction without finer particles

and counted. The standard deviation of counts of animals was about $\pm 10\%$. Since this study did not attempt to make quantitative measurements of consumption rates, but only to compare efficiencies of the two forms of deposit feeders as a function of particle size and to describe qualitative aspects of their feeding biology, results are simply given as cpm (counts/min) after subtraction of the background. No correction for self-absorption was made, as this is assumed to vary little from sample to sample since these were of nearly the same thickness, i.e., around $1 \text{ mg} \cdot \text{cm}^{-2}$.

Choice Experiments with *Corophium volutator*

Some simple experiments were carried out in order to study the ability of *Corophium volutator* to discriminate between different qualities of sand. In these experiments, 2 to 6 small dishes ($3 \times 3 \text{ cm}$), with sands of different qualities were placed in crystallization dishes with 300-ml sterile sea water and 15 or 20 *C. volutator* added. After 2 or 3 h, the dishes were removed and the numbers of amphipods in each dish counted. If any attractive sand fraction at all was present (and the amount offered was sufficiently high to prevent competition for space) at most 1 or 2 animals were swimming around in the water at the end of the experimental period.

Results

Particle Size-Distribution of Gut Contents

Particle size-distribution of the mineral particles and diatom frustules from *Corophium volutator* and from *Hydrobia ulvae* were measured on three occasions, as well as the particle size-distributions of the mineral particles and of the diatoms of the sediment in which the animals had lived for several days in a tray (Figs. 1 and 2). Both forms ingest a rather narrow range of particle size, with little overlap; in *C. volutator*, particles between 4 and 60 μm comprise nearly the total volume of the gut content, whereas in *H. ulvae* particles between 20 and 200–300 μm dominate. Fig. 1 would suggest that *H. ulvae* ingests particles in the proportion in which they occur in the substrate. This, however, is not the rule; the particle sizes ingested by hydrobiid snails are mainly a function of individual animal size (Fenchel, in preparation). That *H. ulvae* does not ingest particles in

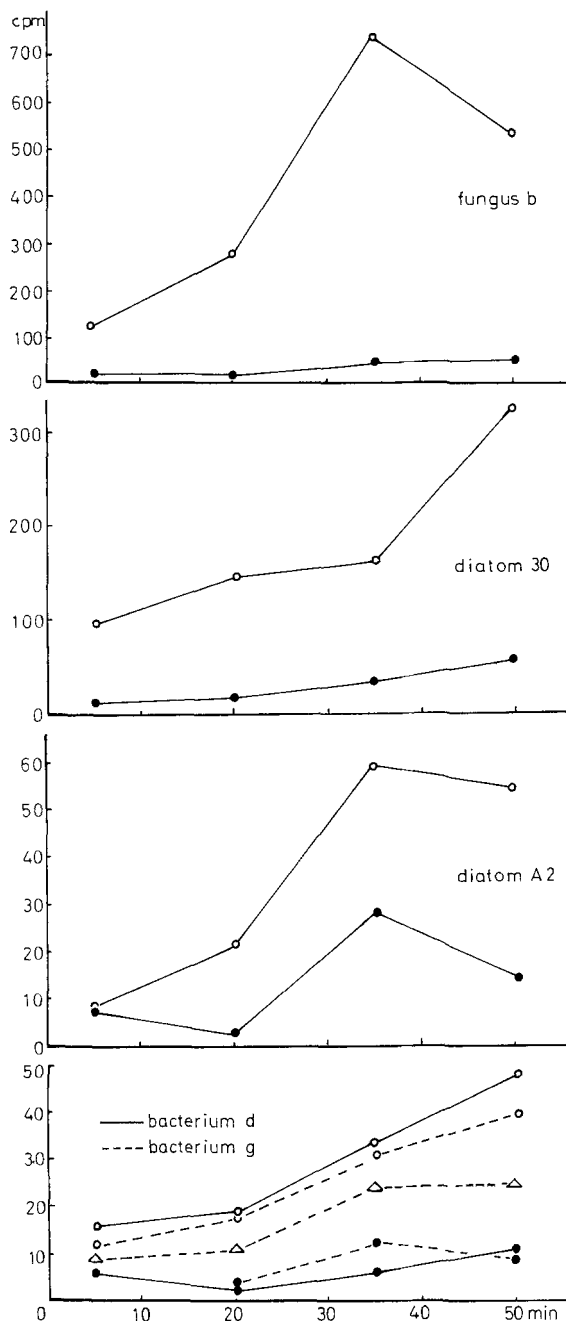


Fig. 6. Uptake of 5 different labelled micro-organisms in natural sand by *Corophium volutator* (filled circles) and *Hydrobia ulvae* (open circles). Triangles represent uptake of bacteria by *H. ulvae* in absence of sediment

proportion to their occurrence is obvious from the ingested diatoms (Fig. 2): the dominating diatoms in the gut contents are larger than the diatoms in the sediment.

Feeding Experiments with Labelled Microorganisms

Figs. 3 and 4 show the ingestion of bacteria by *Corophium volutator* and *Hydrobia*

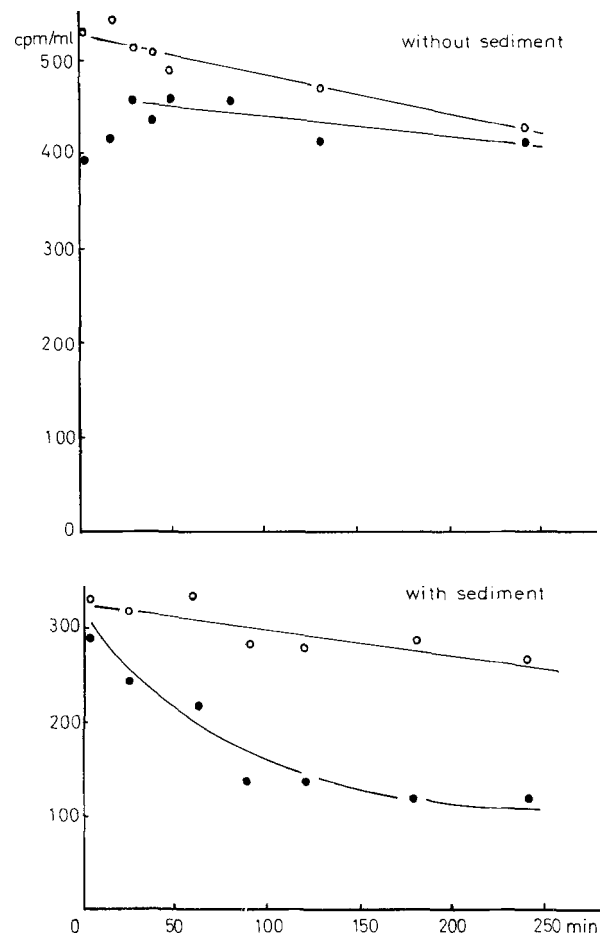


Fig. 7. Decrease of radioactivity of bacterial suspension in presence of *Corophium volutator* (filled circles) and in control experiments (open circles)

ulvae in sands (7 cm^3) with either a particle-size range of 250 to 500 μm or of 125 to 250 μm , and with or without the addition of about 0.3 cm^3 clay and silt (i.e., $< 62 \mu\text{m}$ fraction). These experiments reveal that *C. volutator* is dependent on the presence of fine mineral particles in order to ingest bacteria. The most likely explanation is that bacteria adhere to the particles which *C. volutator* ingest. The bacterial ingestion of *H. ulvae* was not affected by the presence of fine particles.

Fig. 5 shows that, in 125 to 250 μm sand, *Corophium volutator* is able to ingest Diatom A2 (40- μm long) (Fig. 5A), whereas it cannot utilize bacteria in the same sediment (Fig. 5B). This demonstrates that *C. volutator* can feed in the coarser sand fraction if food particles within a suitable size range are available, but in order to utilize bacteria the presence of mineral particles $< 60 \mu\text{m}$ is necessary.

Finally, Fig. 6 illustrates the ingestion of 5 different microorganisms in natural sand from the sampling locality. For reasons not understood, *Corophium volutator* always seemed to ingest less successfully in natural sand than in the size fraction 125 to 250 μm with about 5% clay and silt added. It can be seen that the two diatoms (both within the size range ingested by both animals) and bacteria are ingested with an efficiency ratio of *Hydrobia ulvae* to *C. volutator* of about 4:1. This ratio however, is dependent on the composition of the sand when bacteria constitute the food organisms; furthermore, the bacteria eaten by *C. volutator* are not the same as those consumed by *H. ulvae*, i.e., the bacteria eaten by the former are those adhering to small particles, whereas those eaten by the latter are mainly adhering to larger particles.

With regard to fungal mycelia, only *Hydrobia ulvae* seems able to ingest these; this is understandable, since even small pieces of mycelia are larger than particles which *Corophium volutator* can handle. In some samples of *H. ulvae* and *H. ventrosa* collected and preserved in the field in February, about 1 to 2% of the gut volume was made up of fungal mycelia of the type used for the present experiments.

Filter-feeding in *Corophium volutator*

The result of the experiment for testing the ability of *Corophium volutator* to utilize suspended bacteria is shown in Fig. 7. In the system containing *C. volutator* without sediment no decrease in the suspended bacteria occurred (the somewhat more rapid drop in radioactivity in the control without sediment was probably due to some settlement of bacteria being partially prevented by turbulence created by the amphipods).

In the system with sediment, however, the bacterial concentration of the water in the container with amphipods had fallen to about 40% of that of the control after 4 h. At the end of the experiment, the amphipods in the system without sediment were only slightly radioactive. In the sediment system the tubes were only slightly radioactive, whereas the amphipods themselves were considerably more active. Judging from the counts, the radioactivity of the amphipods could account for about 20% of the loss of activity in the water; however, due to the facts that (1) the amphipods could, during the 4 h, have emptied their guts several times, the assimilation could not have been 100%,

and they would already have respired some of the C-14 assimilated, and that (2) no correction was made for a higher self-absorption of the planchettes with amphipods relative to that of dried filters with bacteria, it is probable that the amphipods did ingest a larger part of the bacteria than indicated by the counts.

Although it can be argued that the specimens in the sediment-free system were unable to filter since they were not established in burrows, the fact that *Corophium volutator* also cannot ingest bacteria in sediments without a clay and silt fraction indicates that also in the case of filtration of suspended bacteria, adsorption to fine mineral particles is necessary prior to ingestion. It is, of course, highly probable that *C. volutator* can directly utilize suspended particles of a somewhat larger size, e.g. small planktonic algae.

According to Meadows and Reid (1966), the sorting of detrital food takes place on the setal basket formed by the 1st and 2nd gnathopods, through which the respiratory water current also flows, whereas the remaining mouth appendages play a role in the transport of food and, to some extent, trituration; according to these authors, very small particles pass through the basket and larger sand grains are discarded.

Photomicrographs taken during the present investigation of the setae of the 2nd gnathopod indicate that the fine bristles form a regular network which will retain particles of $> 4 \mu\text{m}$ or so. It is more difficult to evaluate the filter formed by the 1st gnathopod. The setae of this appendage appear in a thicker, less-ordered layer, with shorter bristles. However, also this filter does not appear to be able to retain bacteria, i.e., particles with the size range 1 to 2 μm .

Ability of *Hydrobia ulvae* to Ingest Bacteria in Absence of Sediment

In contrast to *Corophium volutator*, *Hydrobia ulvae* does attain a certain radioactivity when placed in dishes with a suspension of labelled bacteria in the absence of sediment; in one case, more than 50% of the activity obtained in a parallel experiment with natural sediment was recorded (Fig. 6).

The mechanism responsible for this is probably the ingestion of secreted mucus which has trapped bacteria, a behaviour previously suggested by other authors (see Newell, 1970). As will be

shown by Kofoed (in press, b) *Hydrobia ulvae* willingly browses on bacteria concentrated on membrane-filters, but it seems improbable that browsing on surfaces on which only a thin layer of bacteria is adsorbed (as must have been the case in our experiments) could be sufficient. However, this aspect of the feeding biology of *H. ulvae* was not studied in further detail.

Choice Experiments with *Corophium volutator*

The experiments mainly confirm the findings of Meadows (1964). They all clearly illustrated the ability of *Corophium volutator* to discriminate between different kinds of sand. Experiments with natural sand from the sampling locality, various particle size-fractions of it, and combinations of these size fractions, showed that the presence of particles < 63 μm made the sand attractive and that amphipods will not bury in sands where the < 125 μm fraction has been removed unless no other alternative is offered, and even then a large proportion will always be free-swimming. Furthermore, when the coarser fractions (> 250 μm) were removed from the sand from the sampling locality it became more attractive than untreated sand.

Natural sand was always preferred to sand that had been autoclaved and kept in sterile sea water for some time. The latter would only attract few individuals, even in the absence of alternatives. Mixing with pure strains of bacteria (*d*, *g*, and a few others) rendered the sand attractive again, although in choice experiments with natural sand the majority of amphipods preferred this to sand containing one kind of bacterium. Mixing diatoms into autoclaved sand did not alter its attractiveness significantly, whether tested against sterile sand, sterile sand plus one type of bacterium, or against natural sand, although there was some indications that diatoms plus sterile sand was preferred to sterile sand.

Similar experiments with *Hydrobia ulvae* in Petri dishes partitioned into two halves with different kinds of sand in each compartment failed to reveal any ability of the snails to discriminate between any of the above-mentioned types of sands.

Discussion and Conclusions

The number of species which can coexist in a stable community is, at most, identical to the number of different

limiting resources, provided the species distinguish between them, i.e., utilize the different resources with a differential efficiency or are able to discriminate between them (MacArthur and Levins, 1964). Although detritus feeders do in fact feed on a large diversity of food organisms, it is unlikely that the ability to utilize them in a differential way or to specialize on certain types is widespread, since they ingest them together with the substrate in a seemingly indiscriminate manner. Hargrave (1970) found that the fresh-water amphipod *Hyalella azteca* assimilates representatives of quite different microbial organisms (with the exception of blue-green algae) with about the same efficiency; Kofoed (in press, a) reported that *Hydrobia ventrosa* can utilize different strains of bacteria, blue-greens and diatoms with about the same, high efficiency, and Fenchel (1970) also found this to be the case for the amphipod *Parhyalella whelpleyi*.

The meio- and microfauna, which essentially feed on the same food items as do the detritus-feeding microfauna, are able to specialize on different kinds and size-groups of microorganisms, and the high diversity of the microfauna – a few cm^3 of sand may contain 50 to 100 species – can largely be explained by niche diversification in choice of food (Fenchel, 1969, and references therein). This fauna is thus "coarse grained" in the terminology of MacArthur and Levins (1964) as opposed to the "fine grained" detritus feeders which do not discriminate between different kinds of food particles. Consequently, the diversity of detritus feeders could be expected to be low on any one habitat and, furthermore, their diversity would presumably to a large extent be based on habitat specialization, e.g. according to salinity, type of substrate, depth (Kohn, 1971). Although the number of coexisting detritus feeders usually is low, several species are nevertheless often found together in the same locality without showing any obvious spatial zonation patterns. The present investigation has shown that the two species studied, probably as a result of their respective morphological structures, show particle size-selection. According to empirical findings on coexisting, closely related species as well as theoretical considerations, the stable coexistence based on food size-selection alone requires that the log mean sizes of the ingested particles differ by somewhat more than one standard deviation (as-

suming log normal distribution of the particle sizes eaten by the different species; MacArthur, 1972, and references therein). As seen from Figs. 1 and 2, this requirement is satisfied in the case of *Corophium volutator* and *Hydrobia ulvae*.

Particle size-selection also has more qualitative aspects. In the surface sediment layer (about 0 to 3 mm depth) of the sediments on which the graphs in Figs. 1 and 2 are based, microscopical measurements on two occasions indicated that 8.3 and 11.9%, respectively, of the volume was made up of diatoms. In the gut contents of *Hydrobia ulvae* diatoms made up 29.6, 44.7 and 37.1% of the volume; in *Corophium volutator* gut contents, diatoms constituted 4.0 and 21.5% (in the third case diatoms were not measured). These values constitute an over-estimate of diatoms relative to sand grains, since the third power of the length was used as the measure for diatom volume; however, it is clear that diatoms must play a relatively larger role in feeding of *H. ulvae*. The enrichment of diatoms in the intestinal contents of the snails relative to the sediment can be explained only by particle size-selection, although a tendency to feed in microhabitats where diatoms are more frequent cannot be ruled out. The ability to feed on fungal hyphae in contrast to *C. volutator* has already been mentioned.

Similarly, *Corophium volutator*, by selecting small particles, tends to ingest a relatively larger portion of bacteria. The results also show that attempts to study the ingestion rate and the assimilation efficiency of deposit-feeders by measuring the contents of organic carbon in the substrate and in faecal material may be unrealistic in some cases.

In most cases, investigations on coexisting species are carried out on closely related forms which are fundamentally identical as regards behavioural patterns and physiological and morphological features, all of which change only slowly through evolution; such coexisting species mostly seem to differ along a single niche dimension, often implying size differences, and thus the sizes of food particles or prey and most cases of character displacement documented in the literature involve size differences (Hutchinson, 1959; MacArthur, 1972). Such cases are in one sense more easily analysed. Thus, as will later be shown (Fenchel, in preparation), the two species of *Hydrobia* in the locality studied exhibit differences

in the range of particle sizes ingested which can explain their coexistence.

When dealing with coexisting, unrelated deposit-feeders, we may find, in addition to particle size-selection, that they also differ in a number of other niche dimensions related to food selectivity. Thus, in the case of *Corophium volutator*, we have evidence that this species can utilize suspended food particles, whereas hydrobiids can feed on particles adhering to larger surfaces and perhaps trap particles on the surface film of water with mucus; there are also considerable differences in their behavioural patterns, as exemplified by the choice experiments. Indeed, the ability to use alternative feeding mechanisms seems to be an attribute of many deposit-feeding animals. Thus, evidence shows that the lugworm *Arenicola marina* in addition to swallowing sediment may also function as a suspension feeder. *Nereis diversicolor* filters water with a secreted mucus bag, but is also known to be a predator, and not infrequently mineral particles are found in its gut (for references and other examples see Newell, 1970). Thus, in order to understand the diversity of coexisting deposit-feeders, several niche dimensions besides particle size-selection must be considered. These mechanisms will lead to a partitioning of the total resource spectrum of small food particles available to deposit feeders, although this resource partitioning is not as obvious as prey-specificity of predators.

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