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Selective Feeding and Epipsammic Browsing by the Deposit-Feeding Amphipod *Corophium volutator*

Marianne V. Nielsen and Lars H. Kofoed

Institute of Biology, Odense University, DK 5230 Odense M, Denmark

ABSTRACT: Feeding behavior of the amphipod *Corophium volutator* (Pallas), related to particle size was studied by comparing carbon content in ingested food and faeces with carbon content in the food offered. Assimilation efficiency is independent of particle size. In addition to swallowing particles, *C. volutator* browses upon particles (epipsammic browsing) of both smaller and larger size than the maximum that can be swallowed. Epipsammic browsing is responsible for about 90 % of total carbon ingestion under the experimental conditions. Scanning electron microscopy of gnathopods reveals structures accounting for this feeding mechanism. Epipsammic browsing was not previously described for *C. volutator,* which may be a highly selective deposit feeder

INTRODUCTION

Reports on selective feeding by deposit feeders are numerous (Odum, 1968; Hughes, 1970; Brinkhurst, 1972; Fenchel, 1972; Whitlatch, 1974; Fenchel et al., 1975; Hylleberg, 1975; Hylleberg and Galucci, 1975; Lopez and Kofoed, 1980). Selecting organic matter can occur in 3 basic ways: (1) Selecting fine particles with a favorable surface-to-volume ratio and thus a high organic content (Odum, 1968; Whitlatch, 1974; Fenchel et al., 1975; Hylleberg, 1975; Hylleberg and Galucci, 1975). (2) Browsing upon particle surfaces and scraping off attached micro-organisms, thereby enriching food with organic matter (Wieser, 1956; Lopez and Kofoed, 1980). (3) Selecting non-surface-bound organic matter or particles especially rich in attached organics (Whitlatch, 1974; Hylleberg, 1975). In a deposit-feeding animal more than one of these strategies can be used for selecting organic matter (Fenchel, 1972; Whitlatch, 1974; Hylleberg, 1975; Hylleberg and Galucci, 1975; Lopez and Kofoed, 1980).

The deposit-feeding amphipod *Corophium volutator* is a common inhabitant of fine silty habitats (Meadows, 1964) and selects fine particles when feeding (Fenchel, 1972). All protozoans, 98 % of the bacteria and more than 80 % of the diatoms ingested are removed during passage through the gut (Fenchel, 1972). At present, there is little information on the feeding mechanism underlying particle selection or on the assimilation efficiency of different components of the diet. The present study was therefore undertaken to clarify the feeding mechanism of *C. volutator* and to establish whether the ingestion of organic matter can be enhanced by a combination of the mechanisms outlined above.

MATERIALS AND METHODS

Corophium volutator (Pallas) were collected at Langø, Funen, Denmark. They were stored in sediment and seawater (18 ‰ S) from the sampling locality under 12 h light-dark cycle at experimental temperature (20 °C in Experiment I, 15 °C in Experiment II). Females about 6 mm from rostrum to telson were used for experiments. Seawater for experiments was filtered (Whatmann GF-filter). Two types of experiments were carried out. In the first, representing near-natural conditions, animals established in burrows were fed with size-fractionated sediment. In the other, animals were placed in artificial burrows and fed with size fractionated glass spheres colonised with the sessile diatom *Amphora perpusilla*. We call the material offered to animals the 'food complex', which illustrates that this material is composed partly of food particles and partly of inorganic particles with no food value.

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Ingestion Rate and Assimilation Efficiency with Fractionated, Labelled Sediment

Preparation of food complex. Sediment fractions (<20 µm, 25 to 32 µm, 32 to 40 µm, 40 to 63 µm, 63 to 80 µm, 80 to 125 µm, 125 to 250 µm, 250 to 500 µm) were prepared by wet sieving of freshly collected surface sediment. Each fraction was washed thoroughly to eliminate smaller particles.

Glass flasks with 10 % sediment suspension in seawater were added 400 µCi $H^{14}CO_3\ l^{-1}$, and incubated in a rotating wheel in light for 3 d. Immediately before use the food complex was washed 3 times with seawater by sedimentation and decantation. In this way both excess ^{14}C and less dense organic material not bound to particle surfaces were eliminated. The 2 finest fractions were centrifuged between washings. The food complex was resuspended in seawater.

Experimental procedure. One day prior to the feeding experiments, the amphipods were allowed to acclimate in plastic beakers (38 mm diameter) containing 15 mm roughly sorted sediment (125 to 250 µm) covered with seawater. Three females were pipetted into each beaker giving a population density within the normal range of 1000 to 4000 m^{-2} (Muus, 1967). Most amphipods burrowed immediately. Only beakers with all test individuals established in burrows were used in the experiment.

Experiments started by removing the water from beakers taking care not to disturb established amphipods. The sediment surface was then covered with a 3 to 5 mm layer of the food complex. During this operation food complex and underlying sediment were separated with a plastic sheet to minimize mixing. When the plastic sheet was withdrawn, amphipods immediately elongated the mounds of their burrows through the food complex. Feeding then took place at the surface of the ^{14}C-labelled sediment within a few minutes. The procedure induced a few test individuals to start swimming, these were removed and only the remaining individuals considered. After 20 min amphipods were separated from food, washed thoroughly with seawater and placed in a vial with 5 ml seawater to clear their guts. This defaecation period lasted 60 min. Preliminary experiments with dye particles showed a gut-passage time not shorter than 20 min and microscopic examinations revealed that the gut was emptied within the defaecation period.

The experiment was designed to obtain data according to the energy equation: $C = P + F + U + R$. Consumption (C) was estimated by summation, assimilation efficiency (a) by insertion in $a = (C-F)/C$. Particulate and dissolved organic carbon were assumed to express defaecated (F) and excreted (U) carbon respectively. Acitivity after defaecation (P) was obtained by transferring amphipods to another vial with 3 ml tissue solubilizer and scintillation liquid (Lumasolve : Lipoluma : water, 1 : 10 : 0.2). Faeces (F) were collected on a 0.45 µm Millipore filter separating the content in the first-mentioned vial into particulate and dissolved material. The vial was washed with 3 ml distilled water. The dissolved fractions, containing respired carbon dioxide (R) and excreted organic carbon (U), were acidified with 1 ml 0.5 M H_2SO_4. For 10 min, CO_2 was washed out of the liquid phase by aeration; it was then collected by 5 ml CO_2 absorber (ethanolamin: ethyleneglycolmonomethylether, 1 : 7 (v : v)) in a vial on a vigeraux funnel. The vigeraux funnel was washed with 5 ml CO_2 absorber. During separation, a suction pump was in continous operation, and all operations were made without opening the system (and vials were used directly for collection). To each vial 10 ml Lumagel was added. The 0.45 µm Millipore filter with adhering material was placed in a vial and 5 ml Lumagel added. A small amount of the food complex was placed on another 0.45 µm Millipore filter. After washings with distilled water to eliminate salts and determination of dry weight, the filter was placed in a vial and 5 ml lumagel added. Samples were counted to 10 000 counts or 10 min and corrected to dpm by the external standard method in a liquid scintillation counter (Searle, Mark III).

Egestion Rate and Carbon Content in Food and Faeces with Fractionated, Colonized Glass Spheres

Description of artificial burrow. Burrows were drilled in Plexi-glass blocks (4 x 4 x 6 cm). The hole had the form of a Y with upper branches prolonged by upturned vertical holes. The diameter of the lower branch was only 1 mm, and too narrow for amphipods to enter. This functioned as a faeces trap. The upper branch had a diameter of 2 mm and formed the main burrow. The vertical dimension of the main burrow was 3 cm. Feeding activity could be watched and faeces collected without disturbing the amphipods. These were placed singly in the burrows with a pipette.

Preparation of food complex. The sessile diatom *Amphora perpusilla* (20 to 25 µm in length) was isolated from the sampling locality and grown in axenic culture. The diatoms were grown on sterilized, size-fractionated glass spheres (<20 µm, 20 to 30 µm, 40 to 80 µm, 63 to 80 µm, 80 to 160 µm, 250 to 500 µm) for 2 to 4 wk depending on degree of colonisation desired. Cultures were grown in light in 100 ml Erlenmeyer flasks with stirring in an enriched seawater medium for marine diatoms (ESW) (Fenchel and Hem-

mingsen, 1974). Before use, the food complex was shaken on a Whirlymixer for 30 s to detach flocculent material and washed three times in sterile seawater by decantation. Microscopic examination revealed that the majority of the diatoms were attached to the surface of glass spheres. Glass beads were used since their surface area is easily calculated.

Feeding experiments. The food complex was placed near the upper mounds of the artificial burrow, where amphipods had acclimated for at least 3 d. Normal feeding behavior, i.e. scraping food into the burrow, was observed. Only rarely was it necessary to pipette food directly into the burrow. Faecal pellets were collected every hour and were carefully separated with a micropipette from material scraped into the burrow but not ingested by the amphipod. Pellets were immidiately rinsed twice in distilled water to eliminate salt, placed in pre-weighed aluminium boats and frozen. Samples were freeze-dried and dry weight determined on a microbalance (Mettler ME 22). Samples of the food complex were handled similarly. Carbon content was measured using a C-H-N analyzer (Hewlett Packard, 185 B) connected to an integrator (Hewlett Packard, 3380 A). Numbers of glass spheres in samples were counted under an inverted microscope (Diavert) at 100 x or 320 x magnification.

Calculations. The enrichment ratio for ingestion is defined as ratio of carbon content in the material ingested to carbon content in the food complex offered. The carbon content in ingested material is calculated from carbon content in faecal pellets; applying correction for assimilation of the organic fraction, the following arguments are used:

X mg carbon mg^{-1} faecal pellets amount to $(k \cdot X)$ mg organic matter mg^{-1} faecal pellets. Assuming the difference $1-(k \cdot X)$ mg mg^{-1} faecal pellets stands for non-assimilable inorganic material, the carbon content per mg ingested material is calculated as $I = [X / (1-a)] / [(k \cdot X / (1-a)) + 1-(k \cdot X)] = [((1-a)/X) + a \cdot k]^{-1}$, where a = assimilation efficiency for organic matter; k = conversion factor for weight of organic carbon and weight of organic matter; $a = 0.85$ and k = 1.9 (Winberg, 1971).

Rate of assimilated carbon is calculated from [(mg faeces individual^{-1} h^{-1})·(µg carbon mg^{-1} faeces)·a]/[$1-a$]. Assimilated carbon per mg food complex handled is calculated from [rate of assimilated carbon]/[rate of handling]; rate of handling is obtained from [(mg faeces ind.$^{-1}$ h^{-1})·(µg carbon mg^{-1} faeces)]/[(µg carbon mg^{-1} food complex)·$(1-a)$]. Carbon egestion due to deposit feeding is calculated from [$(1-a)$·(µg carbon mg^{-1} food complex)·(no. of glass spheres mg^{-1} faeces)]/[no. of glass spheres mg^{-1} food complex]. The ratio between deposit feeding and total feeding is obtained from [µg carbon mg^{-1} faeces by deposit feeding]/[µg carbon mg^{-1} faeces]. Rate of surface browsing is calculated from [((µg carbon mg^{-1} faeces)·(mg faeces ind.$^{-1}$ h^{-1}))/((µg carbon mg^{-1} food complex)·$(1-a)$)]·[(no. of glass spheres mg^{-1} food complex) (µm^2 glass sphere^{-1})]. The surface area of spheres is given as geometric mean values with upper and lower particle sizes of fractions as limits. Assimilation efficiency a is 0.85.

Standard deviations (SD) of calculated values are estimated as $\sigma_{A \cdot B} = A \cdot B \cdot ((\sigma_A/A)^2 + (\sigma_B/B)^2)^{1/2}$ and $\sigma_{A/B} = A/B \cdot ((\sigma_A/A)^2 + (\sigma_B/B)^2)^{1/2}$. Numbers of experiments are given in parentheses.

Ivlev's (1961) selectivity index is used as a measure for the degree of selective feeding. The index is defined as $E_i = (r_i - p_i)/(r_i + p_i)$; values between -1 and $+1$, r_i and p_i represent the fraction of any ingredient in the ingested food and the offered food, respectively. Positive values indicate selective feeding in favour of the examined ingredient.

Structure of the Feeding Apparatus

Gnathopods were gently extracted by pulling with a pair of forceps. Adhering muscles were cut away with a scalpel and the dissected appendages washed in distilled water to eliminate salt and freeze-dried. Appendages were fixed to stubs with silverglue, coated with a 200-Å layer of gold and observed under a scanning electron microscope (SEM).

RESULTS

Rate of handling expresses the amount of food complex processed per individual per hour. This is identical to rate of consumption if feeding is non-selective; in case of selective feeding it exceeds consumption rate. Rate of handling comprises the minimum amount of food complex handled, assuming 100 % efficiency while browsing food off particle surfaces.

Different formulas are used for calculating rates of handling in Experiments I and II. In Experiment I, rate of handling is based on ingested material and obtained as ratio between rate of ^{14}C ingestion (dpm ind.$^{-1}$ h^{-1}) and activity of the food complex (dpm mg^{-1}). In Experiment II rate of handling is based on egested material and calculated as ratio between rate of carbon egestion (mgC ind.$^{-1}$ h^{-1}) and carbon content in the food complex (mg C mg^{-1}). Correction for assimilated material, i.e. multiplication of the latter with $(1-a)^{-1}$ renders the rates comparable.

Ingestion Rate and Assimilation Efficiency with Fractionated, Labelled Sediment

Table 1 shows that rate of handling does not vary significantly for particle sizes below 63 µm but at 63 to

Table 1. *Corophium volutator*. Rate of handling of food complex related to particle size. Rate of handling is calculated as ratio between ^{14}C ingestion (dpm ind.$^{-1}$ h^{-1}) and acitivity of food complex (dpm mg^{-1}). Dry weight of test individuals and diameter of faecal pellets are indicated

Particle size (µm)	Rate of consumptions ± SD (dpm ind.$^{-1}$ h^{-1})	Rate of handling ± SD (mg ind.$^{-1}$ h^{-1})
< 20	791 ± 469 (4)	0.2 ± 0.1
25– 32	7139 ± 410 (2)	0.3 ± 0.1
32– 40	1066 ± 456 (3)	0.2 ± 0.1
40– 63	542 ± 87 (5)	0.4 ± 0.1
63– 80	8986 ± 1568 (3)	4.0 ± 0.9
80–125	4700 ± 540 (4)	5.8 ± 0.9
125–250	3688 ± 1977 (4)	3.0 ± 1.7
250–500	5689 ± 1596 (5)	9.5 ± 2.7

Dry weight ind.$^{-1}$ = ca 1.5 mg
Diameter of faecal pellets = ca 150 µm

80 µm the rate increases from 0.4 mg ind.$^{-1}$ h^{-1} to 4.0 mg ind.$^{-1}$ h^{-1}. At particle fractions from 80 µm to 500 µm the rate of handling increases from 4.0 to 9.5 mg ind.$^{-1}$ h^{-1}, dropping to 3.0 mg ind.$^{-1}$ h^{-1} at particle sizes of 125 to 250 µm.

Assimilation efficiency (Table 2) shows no change with particle size (Students T-test, $P<0.05$), yielding a mean value of 0.87 ± 0.04. In percent of assimilated carbon, mean values for DOC (U), CO_2 (R) and P were 8, 24 and 69 respectively.

Table 2. *Corophium volutator*. Assimilation efficiency of fractionated ^{14}C-labelled surface sediment

Particle size (µm)	Assimilation efficiency (%)	SD	No. of experiments
< 20	85	5	4
25– 32	83	2	2
32– 40	82	7	3
40– 63	83	6	5
63– 80	90	2	3
80–125	89	4	4
125–250	90	3	4
250–500	92	4	5

Egestion Rate and Carbon Content in Food and Faeces With Fractionated, Colonized Glass Spheres

Rate of egestion increases significantly for the 3 lowest particle sizes, from 11 µg ind.$^{-1}$ h^{-1} at particle sizes below 20 µm to a maximum of 74 µg ind.$^{-1}$ h^{-1} at 40 to 80 µm. Above that particle size there is a slight and not significant decrease in egestion rate to 40 µg ind.$^{-1}$ h^{-1} at 250 to 500 µm (Fig. 1).

Rate of handling (Fig. 1) is not corrected for assimilated material. It increases significantly at all particle sizes from 25 µg ind.$^{-1}$ h^{-1} at particle sizes below 20 µm to 182 µg ind.$^{-1}$ h^{-1} at 40 to 80 µm. Above 63 µm the increase is more pronounced: from 332 µg ind.$^{-1}$ h^{-1} at 63 to 80 µm to 2.5 mg ind.$^{-1}$ h^{-1} at 250 to 500 µm.

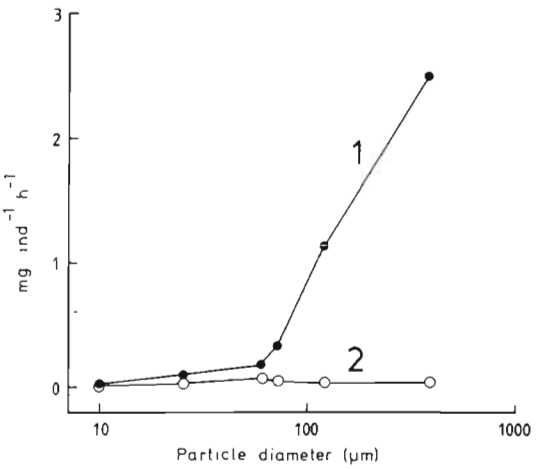

Fig. 1. *Corophium volutator*. Rates of handling of food complex (1) and egestion (2) related to particle size. Rate of handling is calculated as ratio between carbon egestion rate and carbon content in food complex; it is not corrected for assimilated material

Table 3 shows that carbon content in the faeces exceeds carbon content in the food complex at all particle sizes. The enrichment of organic carbon in the ingested material relative to the food complex offered increases from a factor of 9 at particle sizes less than 20 µm to a factor of 16 at 20 to 30 µm. At 40 to 80 µm the enrichment factor drops to 12; it increases to a factor of 30 at particle sizes of 63 to 80 µm; a factor of 116, at 80 to 160 µm; and a factor of 240, at 250 to 500 µm.

Ivlev's (1961) selectivity index, based on data in Table 3, yields E_i values from 0.81 to 0.99.

The carbon content per glass sphere gives a reference standard which is more reliable than weight for the carbon content in food complex and faeces. Fig. 2 illustrates a double log plot of ng carbon per glass sphere in food complex and faeces. The slopes of the regression lines are 1.8 and 1.6 respectively. Carbon content per glass sphere in faeces always exceeds the corresponding value for the food complex. The particle fraction < 20 µm was omitted when calculating the regression line because particles in this fraction are smaller than the diatoms, hence it is uncertain whether diatoms are bound to particle surfaces or to each other.

From data in Fig. 2 the carbon enrichment ratio is

Table 3. *Corophium volutator*. Carbon content in food complex and faecal pellets, and enrichment ratio for ingested material

Particle size (μm)	Carbon content in food complex ± SD (μg mg^{-1})	Carbon content in faecal pellets ± SD (μg mg^{-1})	Carbon enrichment ratio for ingested material ± SD
< 20	24.3 ± 0.9 (3)	53.5 ± 13.5 (4)	9 ± 2
20– 30	12.0 ± 1.6 (3)	43.5 ± 6.5 (2)	16 ± 3
40– 80	12.9 ± 1.6 (7)	32.2 ± 9.4 (6)	12 ± 1
63– 80	6.7 ± 1.2 (6)	46.1 ± 13.3 (12)	30 ± 11
80–160	2.6 ± 1.0 (12)	89.1 ± 33.8 (10)	116 ± 62
250–500	1.0 ± 0.0 (6)	61.6 ± 22.6 (4)	240 ± 88

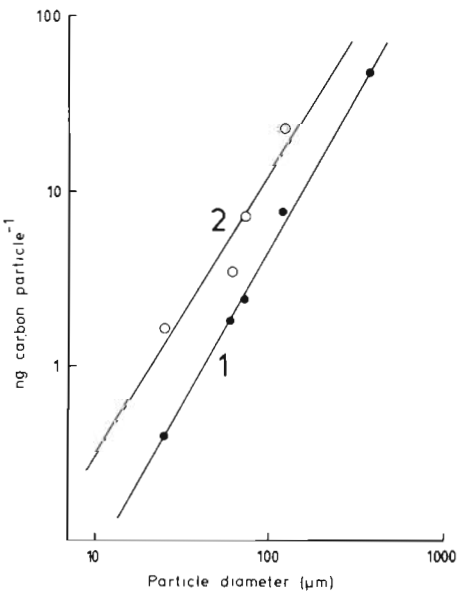

Fig. 2. *Corophium volutator*. Particle surface relation of carbon content in food complex (1) and faecal pellets (2). Regressions: log Y = 1.8 log X − 2.9 (r^2 = 0.99, N = 5) (food complex), log Y = 1.6 log X − 2.2 (r^2 = 0.91, N = 4) (faecal pellets), where Y = ng carbon/no. of particles; X = particle diameter (μm). Carbon content in fractions <20 μm not included in regressions (see text)

obtained as ratio of carbon content per glass sphere ingested to that offered. Carbon content per glass sphere ingested is calculated from the carbon content per glass sphere in faecal pellets corrected for assimilated material, i.e. multiplicated with $(1-a)^{-1}$. The enrichment ratio does not change significantly with particle size and the mean value ± SD is 20 ± 14.

The rate of assimilated carbon (Table 4) increases from 3.4 μg ind.$^{-1}$ h^{-1} at a particle size less than 20 μm to 6.7 μg ind.$^{-1}$ h^{-1} at 20 to 30 μm; it increases further to a mean level of 15.2 μg ind.$^{-1}$ h^{-1} above that particle size.

Assimilated carbon per mg food complex handled decreases from 20.7 μg mg^{-1} at a particle size less than 20 μm to 0.9 μg mg^{-1} at particle sizes of 250 to 500 μm.

Table 5 shows, that deposit feeding relative to total

Table 4. *Corophium volutator*. Assimilation rate of carbon and assimilated carbon per mg food complex handled, as a function of particle size

Particle size (μm)	Assimilationrate of carbon (μg ind.$^{-1}$ h^{-1})	Assimilated carbon per mg food complex handled (μg mg^{-1})
< 20	3.4 ± 2.3	20.7 ± 0.8
20– 30	6.7 ± 1.6	10.2 ± 1.4
40– 80	13.5 ± 7.0	11.0 ± 1.4
63– 80	14.1 ± 9.8	5.7 ± 1.0
80–160	19.2 ± 10.9	2.2 ± 0.9
250–500	14.0 ± 10.4	0.9 ± 0.0

Table 5. *Corophium volutator*. Ratio of deposit feeding to total feeding (deposit feeding + browsing) as a function of particle size

Particle size (μm)	Carbon egestion due to deposit feeding ± SD (μg mg^{-1})	Ratio of deposit feeding ± SD × 10^{-3}
< 20	2.5 ± 0.5	47 ± 15
20– 30	1.6 ± 0.3	37 ± 8
40– 80	2.5 ± 0.4	78 ± 26
63– 80	2.3 ± 0.7	49 ± 21
80–160	4.5 ± 2.5	50 ± 34
250–500	–	0

feeding never exceeds 10 %. The ratio shows a minimum value of 3.7 % for particle sizes of 20 to 30 μm; this is significantly lower than the 7.8 % for particle sizes of 40 to 80 μm. Differences at other particle sizes are statistically not significant.

Table 6 lists surface browsing rates at various particle sizes. Rates increase from 11.3 mm^2 ind.$^{-1}$ h^{-1} at particle sizes less than 20 μm to a mean level of 134.5 mm^2 ind.$^{-1}$ h^{-1} above 40 μm.

Structure of Feeding Apparatus

Dense toothlike structures are found along the setae on the carpopodite of the first gnathopod (Fig. 3). Prox-

Table 6. *Corophium volutator*. Rate of surface browsing as a function of particle size

Particle size (μm)	Sphere surface (μm^2)	Surface browsing rate ± SD (mm^2 $ind.^{-1}$ h^{-1})
< 20	628	11.3 ± 8.3
20– 30	2042	39.8 ± 10.6
40– 80	12566	109.2 ± 59.4
63– 80	16487	113.0 ± 80.7
80–160	50265	145.1 ± 102.7
250–500	490874	170.7 ± 95.7

imal to the setae the teeth are arranged in 2 rows; they fuse into 1 row in the distal setae parts. The teeth in 1 row are placed 2 to 3 μm apart and the length of 1 tooth is 10 μm. Setae on the second gnathopods bear fine bristles; these form a regular network with mesh size of about 4 μm.

DISCUSSION

Microorganisms are considered to be an important food source for deposit feeders (e.g. Newell, 1965; Fenchel, 1970, 1972; Lopez et al., 1977). At incubation periods of only 3 d, ^{14}C-labelled material in food is believed to consist mainly of diatoms and bacteria. Assimilation efficiencies found in this study are slightly higher, but comparable with data from literature on these food items. Hargrave (1970) reports that the amphipod *Hyalella azteca* assimilates diatoms and bacteria with efficiencies of 75 % and 60 to 83 %, respectively. The corresponding values for the prosobranch *Hydrobia ventrosa* are 60 to 71 % and 75 % (Kofoed, 1975); they are 47 % and 43 % for the holothurian *Parastichopus parvimensis* (Yingst, 1976). Later experiments under similar conditions revealed some defaecation following the defaecation period of 60 min. While this could cause an overestimation of assimilation efficiency, calculations showed that the mean assimilation efficiency would maximally be lowered from 87 % to 83 %.

In long-term experiments Hargrave (1971) determined that the amphipod *Hyalella azteca* lost 36 % of the assimilated energy as soluble excretory products. The present study documents a dissolved fraction of 8 % of the assimilated material even in experiments of short duration (60 min).

When corrected for assimilated material, rates of handling recorded in Experiments I and II (Table 1, Fig. 1) are alike in spite of very different experimental designs, thus indicating that the constrained conditions in Experiment II did not modify feeding behavior.

According to Fig. 1, rate of egestion is smaller than even the uncorrected rate of handling at all particle

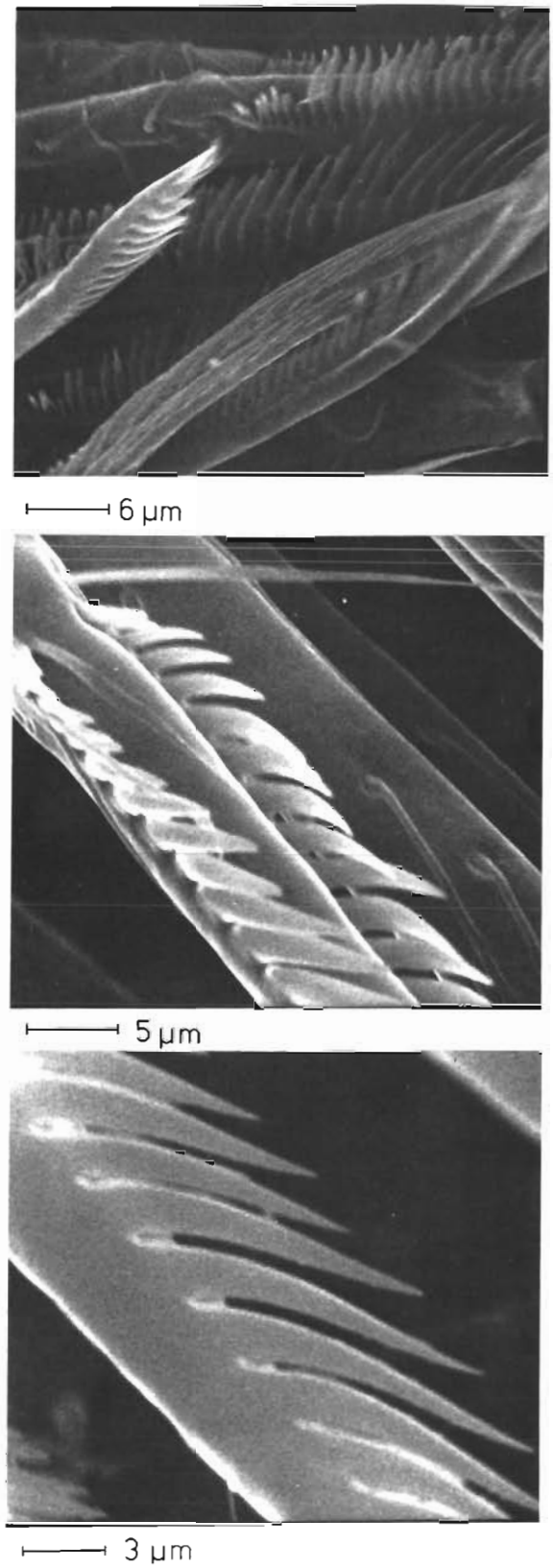

Fig. 3. *Corophium volutator*. Toothlike structures on setae of carpopodite of second gnathopod

sizes studied. This indicates that only a fraction of the material handled is consumed. The consumed material is richer in organic content than the food complex offered, i.e. selection for organic matter occurs. The experiments are designed so that the carbon source is attached to particle surfaces. The exponent for the regression for carbon content per glass sphere in the food complex (Fig. 2) is close to 2, supporting microscopic observations which revealed that diatoms in food were associated with particle surfaces. Food selection must thus occur in terms of epipsammic browsing.

Selection for organic carbon is shown when using Ivlev's (1961) selectivity index as well as by enrichment ratios for ingested material. Ivlev's selectivity index (E_i) produces values close to the upper limit (+1); this documents a high degree of selectivity for carbon at all particle sizes. The 2 enrichment ratios for ingested material based on carbon content per mg sample (dry wt) and carbon content per glass sphere, respectively, are within the same range – except at particle sizes of 80 to 160 µm where the former ratio increases. This difference can be explained as a selection for fine particles; it results in lower values for carbon content per glass sphere ingested, thus causing underestimation in the enrichment ratio. The enrichment ratio for ingestion, based on carbon content per mg sample (dry wt), indicates that enrichment increases with particle size.

The rate of assimilated carbon shows that *Corophium volutator* obtains more carbon per hour when browsing large particles relative to small particles (Table 4). Compared to the rate of assimilated carbon calculated from data by Hargrave (1971) on *Hyalella azteca* (1.1 µg carbon ind.$^{-1}$ h^{-1}, dry wt 700 µg ind.$^{-1}$), rates of assimilation in the present study account for the carbon needs of *C. volutator* (3.4 to 14.0 µg carbon ind.$^{-1}$ h^{-1}, dry wt 1500 µg ind.$^{-1}$).

Epipsammic browsing has not been described previously for *Corophium volutator*. Hart (1930) and Meadows and Reid (1966) report that *C. volutator* selects food with the sieves formed by setae on its first and second gnathopods. Active sifting takes place by moving the gnathopods up and down against each other. Fenchel et al. (1975) used photo-micrographs to study the structure of the feeding apparatus. They report that bristles on the setae of the second gnathopods form a regular network with a mesh size of about 4 µm. The setae on the first gnathopods appear in a thicker, less-ordered layer and the filter is more difficult to evaluate. This supports observations in the present study. Moreover, scanning electron microscopy reveals toothlike structures along the setae of the first gnathopod. These teeth probably scrape assimilable food off sediment particles collected on the filter formed by the second gnathopods.

Only a few deposit feeders have been described previously as being able to browse on particles in addition to swallowing particles. Wieser (1956) found that in sand predominantly finer than 150 µm and in mud, *Cumella vulgaris* (Crustacea, Cumacea) feeds as a deposit feeder, while in sand predominantly coarser than 150 µm it feeds as an epistrate feeder, i.e. taking individual sand grains between its maxillipeds and maxillae, and scraping food off the grain surface using maxillulae and mandibles. Lopez and Kofoed (1980) showed, that 3 species of *Hydrobia* and *Potamopyrgus jenkinsi* are capable of epipsammic browsing by taking particles into their buccal cavity, scraping off attached microorganisms with the radula and then spitting out of the particles.

Amphipods other than *Corophium volutator* are able to clean sand grains. Nicolaisen and Kanneworff (1969) reported that the diets of *Bathyporeia pilosa* and *B. sarsi* consist of matter adhering to sand grains. The sand grains are handled one by one and cleaned with the mouthparts by biting and scraping. No sand grains were found in the guts of *B. pilosa* and *B. sarsi*.

For *Hydrobia ulvae* the ratio of deposit feeding to total feeding is estimated to be about 15 % for particles smaller than 160 µm (Lopez and Kofoed, 1980). In the present study, the ratio is somewhat lower but within the same range (Table 5). Both studies indicate a high degree of selection even at small particle sizes. Surface feeding rate is also within the same range in the 2 studies. *H. ulvae* is most efficient in surface exploitation at small particle sizes, while *Corophium volutator* is most efficient at large particle sizes. This is probably due to different feeding mechanisms used by the 2 species. Above a particle size of 40 µm the rate of surface browsing by *C. volutator* shows no significant variation. At particle sizes below 40 µm rate of surface browsing drops to very low values, indicating inefficient browsing. In nature, *C. volutator* might change to a more favorable feeding mechanism at small particle sizes, e.g. a specific selection for organic material not bound to sediment particles. This hypothesis is supported by selection for organic carbon at particle sizes of 20 to 30 µm, where diatoms and inorganic particles are of equal size and the selection not due to size differences. At particle sizes below 20 µm, inorganic particles tend to be smaller than diatoms and the selection for organic carbon cannot be explained as selection for fine particles. The possible feeding strategies at this particle-size range would be negative selection for small (inorganic) particles or specific selection for non-surface bound organic matter.

It may be argued that the results in this study can be explained by selection for fine particles as well as by browsing. A selection for fine material within each particle fraction cannot be excluded, but selection for

fine particles alone cannot account for the differences in carbon content found in food and faeces.

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