J. Zool., Lond. (1966) **150**, 387–399

The behaviour of *Corophium volutator* (Crustacea: Amphipoda)

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(*Accepted 14 June 1966*)

(With 3 figures in the text)

The behaviour of *Corophium volutator* (Pallas) is outlined. Swimming, crawling, burrowing and feeding activities are described in detail. Animals usually swim on their backs. Every few seconds, swimming alternates with passive sinking. Animals can crawl over surfaces in and out of water. Out of water they do so by a looping motion using their second antennae and telson. When out of water animals crawl away from light and down slopes. In water they swim towards light. Burrowing is initiated by rapid beating of the pleopods; the animal then sinks below the surface by a concerted action of pereiopods, pleopods, telson, uropods and second antennae; within a few minutes, a shallow burrow is formed. The formation of permanent burrows is dependant on particle size, on adhesive properties of detritus and primary films on sand particles, and on a secretion produced by the animal itself. Individuals can turn about in permanent burrows. The species is essentially a detritus feeder. Animals normally feed only when in their burrows, by using their second antennae to scrape material from the substrate surface into the entrance of the burrow. This material is then transported to the mouth by the feeding appendages and respiratory current. The behaviour of small and large animals differs; small animals burrow rapidly and permanently, and do not emerge spontaneously; furthermore, they only swim occasionally. Large animals swim more frequently, spend more time on the substrate surface, and periodically move burrows. It is suggested that new habitats are colonized by large animals which have already bred once.

Contents

Introduction

Amphipods of the genus *Corophium* are frequent inhabitants of intertidal muddy shores. Although restricted in distribution, they may be extremely abundant in mud flats, saltings,

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and estuaries. Eleven British species have been described by Crawford (1937). *Corophium volutator* (Pallas) is the type species and probably the commonest one. It inhabits U-shaped burrows which sometimes extend to a depth of 10 cm in mud around mid-tide level (Hart, 1930; Thamdrup, 1935; Beanland, 1940; Watkin, 1941). The species is present along European coasts from Norway to the Adriatic, including Britain, the Baltic Sea, the Black Sea, and the Azov Sea (Crawford, 1937; Stock, 1952; Segerstråle, 1959; Stock & de Vos, 1960). In North America it is reported from Nova Scotia and the Bay of Fundy (Segerstråle, 1959). In Britain it is distributed between tide marks, but in more northerly parts of its range the species is sometimes found in deeper waters; in Norway, for instance, the species is reported as being dredged from two to five fathoms (Sars, 1895).

Where abundant, it is the dominant animal in a community which frequently contains *Nereis diversicolor* O. F. Müller and *Potamopyrgus jenkinsi* (Smith). In Denmark *Nereis diversicolor* is replaced by *Pygospio elegans* Claparède (Segerstråle, 1959). Densities of 2000 individuals per square metre have been reported for *C. volutator* in Britain (Gee, 1961), while in Denmark 800 animals per square metre is an average density (Segerstråle, 1959).

C. volutator is frequently present in fine grey mud where the black sulphide layer is at least 5 cm below the surface (Gee, 1961); it is not found, however, if decaying organic detritus renders the mud black (Delage, 1881, p. 104). Meadows (1964*a*,*b*,*c*) investigated the substrate preferences of the species, and found that animals prefer fine to coarse sand, and anaerobic to aerobic substrates. The degree of anaerobiosis is probably linked to the amount of organic detritus present, particle size and interstitial water circulation. There is probably an optimum for anaerobiosis and organic content beyond which *C. volutator* does not occur.

The related species *C. arenarium*, which is sometimes confused with *C. volutator* (as in Beanland, 1940), has less distinct substrate preferences. It tends to burrow in coarser sands (Meadows, 1964*c*). Gee (1961) analysed the respective substrates of the two species in Benfleet Creek in the Thames Estuary and found that *C. volutator* substrate contained 37 to 38% silt and clay, in contrast with *C. arenarium* substrate, which contained 14 to 27%; the remaining fraction in both was fine sand. Similar conclusions were reached by Meadows (1964*c*) in a study of populations of the two species on the coasts of Anglesey, North Wales.

Gee (1961) regards physical composition of the substrate as decisive in controlling the presence or absence of *C. volutator*; he does not discuss organic matter. The total amount of organic matter present, however, may be less important in rendering a substrate attractive to the species, than is the nature of the primary film on the surface of particles (Meadows, 1964*a*).

The ecological distribution and habitat preferences of *C. volutator* are, then, fairly well documented, but we still lack a comprehensive account of the species behaviour. The results described in the present paper go some way to remedying this.

Material and methods

C. volutator were collected from fine grey mud on a beach near Greenock in the Firth of Clyde, Scotland. The shore sloped gradually and was covered with small pools at low tide. Other animals commonly present in the mud were *Nereis diversicolor* and *Potamopyrgus jenkinsi*. Many of the *C. volutator* examined bore clumps of a peritrichous ciliate with contractile stalks.

In the laboratory the animals were maintained in circular glass tanks, diameter 33 cm, depth 13 cm, filled with mud to a depth of about 7 cm and topped up with sea water. If aerated continuously the animals survived indefinitely and specimens could be sieved out when required.

In the storage tank all animals burrowed successfully. U-shaped burrows, tubes of cemented particles, could be isolated by removing the surrounding substrate by means of water jets from a pipette. The shape, size and position of the burrow could then be examined.

Crystallizing dishes, 12 cm diameter and 6·5 cm depth, were screened with black paper for use in experiments on burrowing. Sand from the habitat of *C. volutator*, but coarser than the usual substrate, was placed in the dishes to a depth of about 2 cm, covered with sea water, and left to settle overnight. This sand had the advantage of settling much faster than the fine mud and was acceptable to the animals.

In attempts to watch the construction of the burrows several different receptacles were tried without success, including a square-sided tank containing a partition dividing off a compartment 0·5 cm wide. Finally glass tubes bent into a U shape were found to be suitable. Different bores were chosen to accommodate large and small animals; the ones most frequently used were 1·8, 2·0 and 2·2 mm. The animal had to be able to move freely while remaining in contact with the sides of the U-tube. A single animal was introduced into each tube using a pipette. In this way injury to the animal was avoided. The tube was placed upright in sea water for a few minutes, then laid on its side in a crystallizing dish. A small quantity of mud or fine sand was dropped from a pipette near the openings of the U-tube and the behaviour of the animal noted.

Animals were also offered acid cleaned sand (British Drug Houses) which had been soaked overnight in sea water, to burrow in.

The feeding of starved and normal *Corophium* was observed in U-tubes under a dissecting microscope, as was the feeding of animals which were moving about on the surface of mud in crystallizing dishes. The action of the feeding appendages was noted by fixing animals under water on their backs in plasticine (Hart, 1930).

In all the initial observations on swimming and burrowing, small animals between 3·0 and 5·0 mm in length (telson to rostrum) were used. Later, specimens between 5·0 and 8·0 mm were used. *C. volutator* does not attain sexual maturity much below 5·5 mm (Hart, 1930), so specimens below this length can generally be considered immature.

Results

The behaviour of *C. volutator* may be conveniently divided into swimming, crawling, burrowing, and feeding activities. These are considered in turn.

Swimming

There is usually an alternation of brief spurts of swimming, lasting five to ten seconds, with pauses during which the animal lies on its back with pleopods beating, or crawls about, manipulating particles on the bottom. The animal rises from the bottom with a sharp flick of the abdomen, and continues upwards till the antennae come into contact with the surface film. Cessation of pleopod beat and sinking follow immediately. In water more than about 25 cm deep *C. volutator* may pause and sink back before reaching the surface film. The animal always swims on its back during sustained activity. Streamlining is achieved by the pediform second antennae being stretched out parallel to each other; the pereiopods trail behind. Hart (1930) suggests that the broad heavily fringed bases of the fourth and fifth pereiopods help to direct the swimming current backwards. However, their removal appears to have little effect on swimming, and it would seem that the pleopods supply the drive. As they beat they are slightly out of phase, the first pair beginning their backward stroke just before the second pair and so on.

Periodically the animal sinks on its back and then rights itself again in order to leave the bottom or to crawl. It is probable that the animals swim on their backs because of the downward curvature of the second antennae, which would tend to prevent *C. volutator* from swimming upwards if the normal crawling position was maintained. Also, sinking on the back permits a more rapid vertical descent, since less surface area is presented to incur frictional resistance with the water.

Swimming may well be a laborious process, for it is not maintained for more than a few seconds without sinking. If a suitable substrate is present, 80% of immature animals burrow within five minutes and 93% within an hour. Large animals continue swimming longer; the equivalent figures are 40 and 68%. Those animals which do not burrow, alternate swimming with investigation of the substrate for some time. In turbid water very small animals swim for much longer than is usual.

In the absence of any substrate this cycle of activity is repeated continuously for up to three days, when the animals become sluggish and moribund, and swim erratically in circles on their side close to the bottom.

Crawling

Animals crawling on a damp surface out of water push themselves along with the telson and uropods in a looping motion. The second antennae help to pull the animal forward, and the pereiopods assist with a scrambling motion (Hart, 1930).

Under water *C. volutator* can crawl slowly using the fourth and fifth pereiopods, or dart along rapidly in contact with the bottom by strokes of the pleopods. The looping movement does not come into play under water except when the animal alights on an unusually fine and soft substrate.

Corophium is rarely seen swimming after emerging spontaneously from its burrow. Large specimens can be collected on the shore as they emerge and crawl. Small animals do not swim unless no substrate is available or unless the water is highly turbid. Disturbance of mud containing animals causes them to swim very briefly; within seconds they re-alight and burrow.

Burrowing

In burrowing, the animal apparently makes use of a thixotropic effect; agitation of the pleopods creates a furrow into which the body sinks. The pediform second antennae are then inserted into the mud while the gnathopods enlarge the hole thus formed. The pereiopods, telson, and uropods, obtain a purchase and help to push the body forwards and down. When the entire body is submerged the pleopods beat very rapidly, driving the animal further into the mud. A fountain of particles streams out of the newly formed opening. Expulsion of sand and debris continues as the animal excavates a semicircular tunnel. Eventually the head and antennae protrude from the surface 1 to 2 cm away from the point of entry. The entire process usually takes two to three minutes. Expulsion of mud and sand soon ceases, and "scraping" activity follows (Fig. 1): the antennae are protruded from one of the openings of the burrow and they probe the surrounding deposits. They are used like pincers to draw a lump of light flocculent organic detritus into the ɜginning

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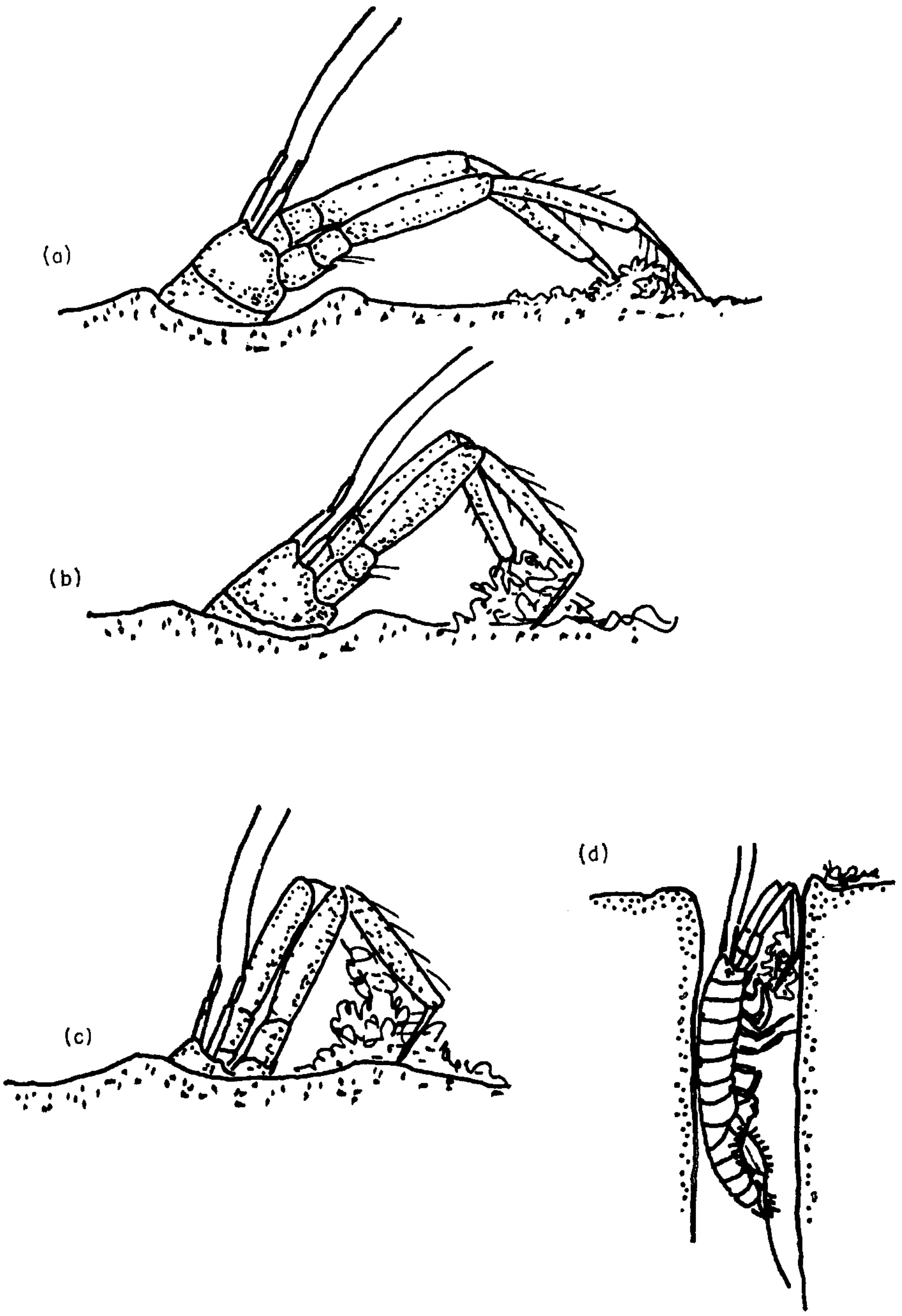

FIG. 1. Diagrams which illustrate how *C. volutator* scrapes detritus from the substrate surface ((a),(b),(c)) and then retreats into its burrow (d). Magnification: (a),(b),(c) ×15; (d) ×7·5.

burrow. Inside the tube the animal curls the antennae round to meet the first gnathopods, and between these two pairs of appendages the detritus is compacted into a ball, and pressed against the side of the burrow, to which it adheres. Some feeding can be seen to take place at this stage. After many repetitions of this process the entire burrow is lined with detritus; this can be seen in a glass U-tube.

When *Corophium* burrows in fine mud, both openings to the tube are built up from the surface to a height of 1 to 1·5 mm. We assume the burrow is lined to ensure that the walls do not collapse. The vigorous respiratory current certainly does not dislodge the lining. Since the openings are raised above the surface, mud is not drawn in; probably only the finest suspended matter enters the tube with the respiratory current. After a burrow has been in existence for a few days, a circle of scrape marks radiates for several millimetres around both openings. When individuals in glass U-tubes are provided with fine mud, the openings are lined and built out with organic debris as in a normal burrow. An animal in a glass tube will move about continually, pausing from time to time to draw a strong current through. The respiratory current serves as a route for the expulsion of faeces and unwanted debris, although it carries little or no food with it as it enters the burrow. Removal of the fifth pereiopods affects the respiratory current. The latter becomes weaker, and eddies form to a much greater extent, therefore these appendages are more likely to be important in assisting efficient ventilation of the burrow than in aiding swimming.

In the confines of the burrow *C. volutator* changes direction by somersaulting; the abdomen is tucked up under the thorax, which then straightens out, so that the animal now lies on its back facing in the opposite direction (Fig. 2). It is probable that the burrow is progressively deepened while the animal inhabits it, since initially the burrow is a shallow semicircular tube, yet well established ones are often up to 5 cm or more deep.

The depth of burrows may also be related to particle size as the following observations show. *C. volutator* burrows readily in fine sand collected from high tide mark on the shore. This sand contains plenty of the flocculent organic debris on which animals can be seen to feed and line their burrows. Burrows in this substrate can be exposed after 24 hours by dislodging the surrounding sand with a jet of water from a pipette. The intact burrows are semicircular and shallow, and seldom lie more than 1 cm below the surface. In mud from the species normal habitat, however, burrows are often up to 5 or 6 cm deep. Perhaps sand is more difficult for animals to burrow in because of its low thixotropy. Experiments conducted by Wautier & Pattée (1955) and by Eriksen (1963*a*,*b*) have demonstrated analogous effects. These authors studied the relationship between oxygen consumption and particle size in nymphs of various *Ephemera* species. Nymphs utilize more oxygen in penetrating unattractive substrates, that is, substrates which they avoid in choice experiments. The ability of nymphs to penetrate substrates also differs between species, and was related to structural adaptions.

Hart (1930) demonstrated that a secretion from the bases of the second perieopods binds together the particles in the walls of the burrow. This cannot be the only cause of cohesion: *C. volutator* is not able to form permanent burrows in purely inorganic substrates or in fine mud from which the primary films have been removed (Table I).

Permanent burrows are formed only in fine mud from the species usual habitat, or in fine sand from the same shore on which the primary films remain undisturbed. However, in fine acid-cleaned sand (B.D.H.) three out of six animals succeeded in forming very short tubes by cementing particles together by means of the secretion from the bases of the second pereiopods. The tubes were no longer than the occupant's body (5 to 6 mm) and lay exposed on the surface of the sand. In coarser sand of this type burrowing did not take place, nor were the animals successful in lining glass U-tubes with any of the sand grains.

Hence it is probable that formation of permanent burrows is dependent on (a) particle size, particles which are above a certain size would be too cumbersome for animals to manipulate, (b) adhesive properties of the primary films on the surfaces of sand grains and of the detritus used to line the walls of the burrow, and (c) the secretion from the base of the second pereiopods.

TABLE 1

Abilities of animals to form permanent burrows in different substrates

	Presence of fine particles in substrate	Presence of flocculent debris in substrate	Ability of animals to form permanent burrows
Untreated mud from normal habitat	+	+	+
* Treated mud from normal habitat	+	—	—
Untreated fine sand from high water on same shore	+	+	+
Fine acid-cleaned sand (B.D.H.)	+	—	—
Coarse acid-cleaned sand (B.D.H.)	—	—	—

* Soaked in distilled water, dried, and then allowed to settle in sea water.

Activity when established in the burrow

We have already described the way in which animals turn about when in their burrows (Fig. 2).

The scraping activity referred to above (Fig. 1) begins 45 seconds to 1·5 minutes after the initial excavation of the burrow. It takes place every few minutes reaching a peak 15 to 20 minutes after burrowing and falling off thereafter. Animals take in detritus every 5 to 10 minutes for several hours. After several days in the burrow scraping occurs at irregular intervals.

The length of time for which large and small animals remain in their burrows was estimated by allowing them to burrow in fine sand in crystallizing dishes and noting the position of the burrows each day. Small animals seem to remain in their burrows indefinitely, but larger ones (above 5·5 mm) emerge and crawl after several days (c.f. Meadows, 1964*b*). In most cases these large animals attempt to occupy a nearby burrow almost immediately. The antennae are inserted and if no resistance is encountered the animal enters. If the original occupant is smaller than the intruder it occasionally leaves to burrow almost instantaneously nearby. Usually, however, the two animals grapple using the second antennae, the intruding animal often being picked up bodily and waved about. In many cases the invading animal frees itself and departs, but is sometimes actually thrown clear. It may repeat this behaviour a number of times; eventually it succeeds in either occupying an empty burrow or in driving an individual from one already occupied. This very characteristic behaviour might be associated with reproduction, for some contact between adult animals is necessary before fertilization can occur. It is rarely seen in immature animals; if disturbed, they will leave the burrow and settle nearby within seconds to burrow again. The length of time a large animal will remain in the same burrow is variable, being one to four days in the present investigation.

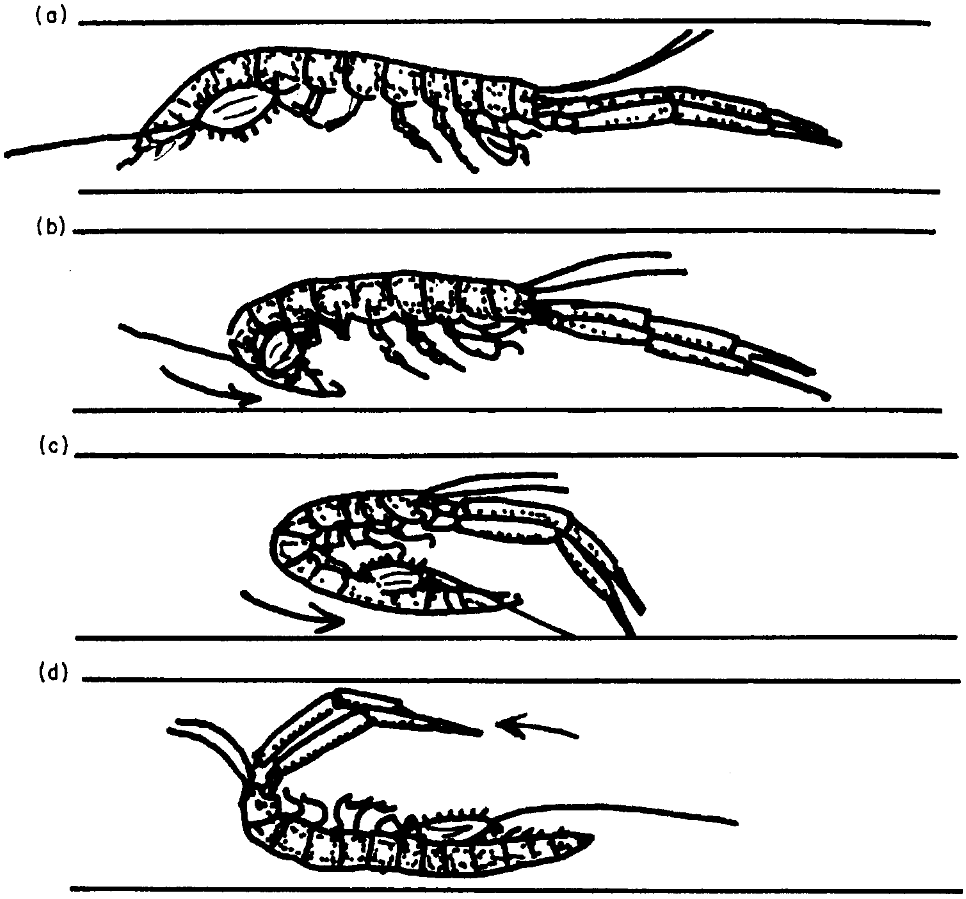

FIG. 2. Diagrams to show how an animal turns about in its burrow. (a), (b), (c) and (d) represent successive stages in this process. Magnification: ×10.

Feeding

Hart (1930) described *C. volutator* as feeding in two ways. The chief method he termed selective deposit feeding, that is, sifting detritus picked up with the gnathopods while moving about on the surface of the substrate. The second method was by filtering fine particles drawn into the burrow by the respiratory current. The first and second gnathopods are adapted for filter feeding of some sort, since both pairs carry long, plumose setae on the meropodite and carpopodite. In the living animal these setae form a basket through which the respiratory current must pass (Fig. 3). Small particles pass through but larger ones are retained. Hart (1930) places most emphasis on selective deposit feeding, suggesting that animals move about on the surface to obtain most of their food. However, small animals do not leave their burrows, and so must be assumed to feed almost entirely on suspended particles. This was not mentioned by Hart. Large animals do not crawl for long; in a tank containing between 400 and 500 burrows, only three or four individuals can be seen crawling at any one time. During the few minutes for which they are on the surface they make repeated attempts to occupy a new burrow. They have not been observed to feed on these occasions, although starved animals transferred to a dish containing mud, after having spent a week in sea water with no substrate, spend several minutes feeding on the surface mud before attempting to burrow.

From these observations it seems likely that *C. volutator* feeds mainly while in the burrow. Specimens can be observed feeding inside glass U-tubes in which they have been established for some hours. When an animal sets up a respiratory current through the tube, suspended particles are drawn in. Since glass tubes are laid on their side there is nothing to prevent this, but as already described, a burrow in the normal muddy substrate has its openings raised 1 to 1·5 mm above the surface; this tends to stop all but the very fine particles being drawn in. Further, most of the particles drawn in pass straight through the setal combs on the gnathopods. Thus it is unlikely that filtering particles from the respiratory current is an important method of feeding.

It is here that the significance of continued scraping activity becomes apparent. An animal will protrude its head and antennae from the burrow, seize a lump of detritus, and withdraw into the burrow with it. The detritus is released just inside the opening, and the animal retreats a short distance inside, trailing a string of particles with it. Material is then drawn into the setal basket on the second gnathopods by the current created by the beating of the pleopods. Small particles pass through, and sand grains drop out of the basket. The retained fragments are brushed forward onto the combs of the first gnathopods. Further sifting takes place as the first gnathopods are rapidly moved up and down against each other. The maxillepedes bear an outer fringe of fine spines, so that when the gnathopods are moved forwards food particles are combed out of the fringe on the carpopodite and passed to the maxillepede. Finally the particles combed from the gnathopod fringe are passed to the first maxillae. The mandibles bear outer incisor and inner molar processes. Some trituration is carried out by the latter.

This process is extremely rapid and the details are difficult to interpret exactly. In starved animals food passes in a continuous stream to the mouth from the first gnathopods. Hart (1930) suggests that suction from the crop is important in swallowing; it appears to be particularly so in starved animals.

Most of the actual selection and rejection of particles is done by the gnathopods. The remaining mouth parts and associated appendages perform the function of transport.

From time to time the animal moves forward to the lump of detritus which has been brought into the burrow and removes portions with the first gnathopods. Sifting and passage to the mouth follow as described above.

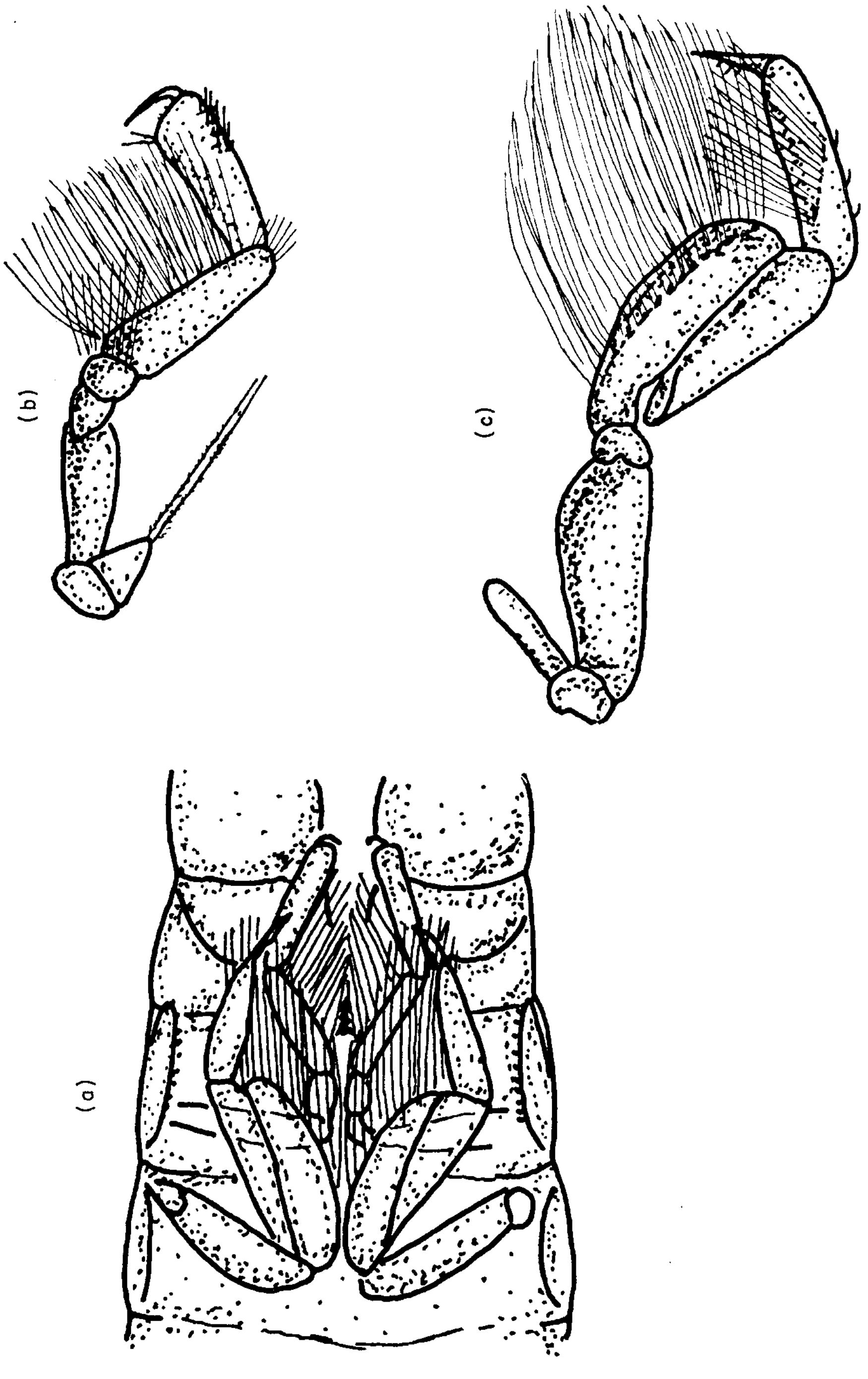

FIG. 3. (a) Diagram of the setal basket seen in ventral view. The animal's second antennae point to the right; (b) and (c) are diagrams of the first and second gnathopods (left side) to show more clearly the long plumose setae. Magnification: (a) ×87·5; (b), (c) ×17·5.

Although not mentioned by Hart, scraping is a very conspicuous part of behaviour. It has been observed in populations from a number of different localities, and so must be considered as an important method of obtaining food.

Discussion

C. volutator placed on a surface out of water crawls away from light (see below). On wet mud without enough superficial water for swimming, animals burrow immediately. This behaviour has the effect of protecting animals from desiccation and predation. Where there is enough water for swimming, an animal which leaves its burrow swims upwards until the antennae contact the surface film. The animal then sinks. On the bottom it manipulates the mud, and either burrows or swims off. Under conditions such as these in the sea, the presence of water currents would allow animals to be carried to other areas which were rich in food. If leaving the burrow is correlated with depletion of food, the presence of suitable deposits may be the stimulus which induces burrowing.

Food is not the only variable which induces animals to burrow or swim. In a previous paper, the importance of particle size was demonstrated by offering animal choice of different grades of sand (Meadows, 1964*c*). Light also controls burrowing behaviour, for strong overhead illumination increases the proportion of animals which burrow. Smaller animals are more affected than larger ones, as they very rarely emerge from their burrows unless the light intensity falls below about 1 lux (unpublished results). This may be associated with sexual maturity, for animals below 5·5 mm are not mature (Hart, 1930); all animals classed as small fell below this length.

Light has another, unexpected, effect on behaviour. While watching animals crawling, we noted that under water they tend to move towards light. This is more evident when they swim, as then they are strongly photopositive to lateral illumination. On the other hand, if placed on a damp surface out of water, animals invariably crawl away from a light source. They also crawl down slopes. All these behaviour patterns are geared to maintaining populations of the species within the intertidal range.

The young of *C. volutator* develop to the first moult within the brood pouch of the female, and are then released (Hart, 1930). They burrow immediately, either on the surface or into the side of the parental burrow. Hence young play no part in the dispersal of the species. Formation of new colonies depends on the behaviour of the adults. Beanland (1940) describes the emergence of large numbers of *C. volutator* to swim "under certain conditions of light and salinity". The subsequent fate of the animals is determined by the strength of the currents and whether or not they are carried to a suitable new area. Beanland (1940) gives no indication of the size of those which are stimulated to emerge and swim. Although workers comment on sudden disappearances of populations (Bate & Westwood, 1863, p. 495; Beanland, 1940), it is probable that very small immature animals remain in the same area, as animals under 2 mm are easily overlooked. From our observations of their behaviour, it seems unlikely that small animals leave their burrows unless there is mechanical disturbance. There is no doubt that small animals, being lighter, would be more likely to be carried passively outwith their normal environment. Furthermore, *C. volutator* is extremely limited in its choice of substrates, and the likelihood of an entire population being swept out to sea seems to outweigh any chances of establishing new colonies if animals behave as Beanland suggests.

FIG. 3. (a) Diagram of the setal basket seen in ventral view. The animal's second antennae point to the right; (b) and (c) are diagrams of the first and second gnathopods (left side) to show more clearly the long plumose setae. Magnification: (a) ×87·5; (b), (c) ×17·5.

Since their normal habitat is a restricted one, the dispersal of large individuals to form new colonies might have more selective advantage than a habit of emerging *en masse* and abandoning favourable habitats. Small and immature animals would remain within the area where they hatched, fed and grew; when they bred, they would do so in a place where the young they produced would be assured of a favourable environment. However, in a model such as this, the large animals which disperse to form new colonies must retain some reproductive potential.

Some doubt has been cast on the importance, first noted by Hart (1930), of a cementing secretion in burrow construction (Gee, 1961). Gee suggested that the main difference in firmness between the burrows of *C. arenarium* and *C. volutator* was due to the relatively coarser substrate chosen by the former species. After the experiments reported above, in which *C. volutator* was given different types of substrate, we conclude that in the formation of permanent burrows, organic content and primary films are important, but that a secretion is certainly involved.

Hart (1930) classed *C. volutator* as a true selective deposit feeder. Our observations substantially bear this out; the method of obtaining food described here, however, differs from that outlined by Hart. Animals do not appear to feed while on the surface, but rake detritus into the burrow with the second antennae, and there sift it and reject inedible matter. Hart (1930) described the filtering of suspended organic matter from the respiratory current while in the burrow, as being a subsidiary mode of feeding. However, the openings of the burrows of *C. volutator* are normally raised slightly above the surface, and so the entry of all but the very finest of particles is prevented. Furthermore, the filter setae on the gnathopods allow most of the fine suspended matter to pass through. They retain only clumps or larger particles of detritus which are not drawn in by the respiratory current at all, but are scraped in by the animal.

Thus it would seem that only a very small part of the species' food could possibly be obtained by filter feeding.

Detritus feeders have to ingest a large bulk of material to obtain sufficient food. It has been generally supposed that detritus feeders digest plant and other material in the debris they ingest. There is little information available on this topic except for the work of Newell (1965). He studied the feeding of the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*. The carbon content of the food of these animals was not decreased significantly during its passage through their guts; the nitrogen content on the other hand was greatly reduced. Incubation of the faeces of *Hydrobia* increased the nitrogen content to its original level. Newell deduced from this, that micro-organisms present utilized carbon compounds as an energy source, while at the same time fixing elemental nitrogen. He was able to conclude that *Hydrobia* digests these micro-organisms. It is interesting to note that many terrestrial soil animals also digest micro-flora and -fauna present in decaying matter.

REFERENCES

Bate, C. S. & Westwood, J. O. (1863). *A history of the British sessile-eyed Crustacea*. **1.** London: Van Voorst.

Beanland, F. L. (1940). Sand and mud communities in the Dovey estuary. *J. mar. biol. Ass. U.K.* **24:** 589–611.

Crawford, G. I. (1937). A review of the amphipod genus *Corophium*, with notes on the British species. *J. mar. biol. Ass. U.K.* **21:** 589–630.

Delage, Y. (1881). Contribution à l'étude de l'appareil circulatoire des Crustacés édriophthalmes marins. *Archs Zool. exp. gén.* **9:** 1–173.

Eriksen, C. H. (1963*a*). The relation of oxygen consumption to substrate particle size in two burrowing mayflies. *J. exp. Biol.* **40**: 447–453.

Eriksen, C. H. (1963*b*). Respiratory regulation in *Ephemera simulans* Walker and *Hexagenia limbata* (Serville) (Ephemeroptera). *J. exp. Biol.* **40**: 455–467.

Gee, J. M. (1961). Ecological studies in South Benfleet Creek with special reference to the amphipod genus *Corophium. Essex Nat.* **30**: 291–309.

Hart, T. J. (1930). Preliminary notes on the bionomics of the amphipod *Corophium volutator* (Pallas). *J. mar. biol. Ass. U.K.* **16**: 761–789.

Meadows, P. S. (1964*a*). Experiments on substrate selection by *Corophium* species: films and bacteria on sand particles. *J. exp. Biol.* **41**: 499–511.

Meadows, P. S. (1964*b*). Experiments on substrate selection by *Corophium volutator* (Pallas): depth selection and population density. *J. exp. Biol.* **41**: 677–687.

Meadows, P. S. (1964*c*). Substrate selection by *Corophium* species: the particle size of substrates. *J. Anim. Ecol.* **33**: 387–394.

Newell, R. (1965). The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica. Proc. zool. Soc. Lond.* **144**: 25–45.

Sars, G. O. (1895). *An account of the Crustacea of Norway.* **1.** *Amphipoda.* Christiania & Copenhagen: Alb. Cammermeyers Forlag.

Segerstråle, S. G. (1959). Synopsis of data on the crustaceans *Gammarus locusta*, *Gammarus oceanicus*, *Pontoporeia affinis*, and *Corophium volutator* (Amphipoda Gammaridea). *Commentat. biol.* **20** (5): 1–23.

Stock, J. H. (1952). Some notes on the taxonomy, the distribution and the ecology of four species of the Amphipod genus *Corophium* (Crustacea, Malacostraca). *Beaufortia* No. 21: 1–10.

Stock, J. H. & de Vos, A. P. C. (1960). Einiger wirbellose Tiergruppen des Dollart-ems-estuarium. *Verh. ned. geol.-mijnb. Genoot.* (*Geol.*) **19**: 203–220.

Thamdrup, H. M. (1935). Beiträge zur Ökologie der Wattenfauna auf Experimenteller Grundlage. *Meddr Kommn Havunders.* (*Fiskeri*) **10** (2): 1–125.

Watkin, E. E. (1941). The yearly life cycle of the amphipod, *Corophium volutator*. *J. Anim. Ecol.* **10**: 77–93.

Wautier, J. & Pattée, E. (1955). Expérience physiologique et expérience écologique. L'influence du substrat sur la consommation d'oxygène chez les larves d'Ephéméroptères. *Bull. mens. Soc. linn. Lyon* **24**: 178–183.