

---

The Feeding Mechanism of *Yoldia* (= *Aequiyoldia*) *eightsi* (Courthouy)

Author(s): J. Davenport

Source: *Proceedings of the Royal Society of London. Series B, Biological Sciences*, Vol. 232, No. 1269 (Jan. 22, 1988), pp. 431-442

Published by: [The Royal Society](#)

Stable URL: <http://www.jstor.org/stable/36327>

Accessed: 19/08/2013 10:24

---

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at  
<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The Royal Society is collaborating with JSTOR to digitize, preserve and extend access to *Proceedings of the Royal Society of London. Series B, Biological Sciences*.

<http://www.jstor.org>

## The feeding mechanism of *Yoldia* (= *Aequiyoldia*) *eightsi* (Courthouy)

BY J. DAVENPORT

*Animal Biology Group, Marine Science Laboratories,  
University College of North Wales, Menai Bridge,  
Gwynedd LL59 5EH, North Wales, U.K.*

(Communicated by G. E. Fogg, F.R.S. – Received 24 June 1987)

The protobranch bivalve mollusc *Yoldia eightsi* Courthouy is both a deposit feeder (on mud) and a suspension feeder (on diatoms in the ventilatory streams, which are trapped on the ctenidia). The species has a similar anatomy to other *Yoldia* species, but is a more shallow burrower which adopts a more horizontal shell orientation than the vertically burrowing *Yoldia limatula* and *Yoldia ensifera*. Although capable of feeding on the surface layers of mud by extending its palp proboscides outside the partly buried shell, *Yoldia eightsi* spends most of its time feeding while totally buried. To do this, sediment is taken into the mantle cavity by opening the shell valves, or by foot movements. The sediment is moved by ciliary action to the posterior part of the mantle cavity where it forms a compact, mucus-coated sediment slug. The slug is repeatedly sorted largely by the palp proboscides, fine material being transferred to the mouth via the palps. Sorting appears to be done on a simple size–density basis, with large, dense particles being rejected. After sorting, the inorganic fraction of the slug is expelled through the inhalant siphon ('pseudofaecal plume'). Expulsions occur every 6–35 min. True faeces ('faecal plume') are expelled much more frequently in the expiratory bursts of water from the exhalant siphon. Pseudofaecal output is about 170 times the faecal output (on a dry mass basis), suggesting that *Yoldia eightsi* ingests 0.6% of processed material.

### INTRODUCTION

The protobranch bivalve mollusc *Yoldia eightsi* Courthouy has a circumpolar distribution in Antarctic and Subantarctic waters (Dell 1964). It is a dominant member of the macrofauna of muddy seabeds over an unusually wide range of depths (from about 5 m at Signy Island to at least 728 m near South Georgia). Despite its importance to soft-bottom benthic ecology in the Southern Ocean, the species has been essentially unstudied. The present paper arose from an investigation of the growth and metabolism of *Yoldia eightsi* (which will be reported upon elsewhere), when it became clear that the species' feeding habits and mechanisms departed significantly from the descriptions of feeding recorded for the equivalent northern species, the Atlantic *Yoldia limatula* (Drew 1899; Kellogg 1915; Yonge 1939; Rhoads 1963; Bender & Davis 1984) and the Pacific *Yoldia ensifera* (Stasek 1965).

## MATERIALS AND METHODS

*Collection and maintenance*

Specimens of *Yoldia eightsi* were collected by SCUBA diving in Borge Bay, Signy Island, South Orkneys (60° 43' S, 45° 38' W) at a depth of 10–15 m. The animals were rapidly transferred to an aquarium containing natural sediment (collected from the *Yoldia* beds at the same time as the animals) and supplied with running seawater (33‰; –0.5 to +0.5 °C). Fresh animals and sediment were collected every 2–5 d to ensure that animals were in as normal and vigorous a state as possible. Unused animals were returned to the environment. All experiments were done during December 1986 and January 1987 when the seawater contained considerable quantities of natural phytoplankton (mainly diatoms).

*Observation*

Whole animals were observed in glass-sided aquaria and also in a narrow, Perspex 'ant farm' tank of variable width (5–12 mm), which allowed specimens of *Yoldia eightsi* of different sizes to be studied with a minimum of sediment around them. Some animals were observed in clean seawater without sediment. Direct vision, a hand lens and a binocular microscope (up to 25 times magnification) were all used.

To observe the workings of structures within the shell of *Yoldia eightsi*, several preparations of animals were made in which one of the shell valves was removed. To do this, the periostracum at the growing edge of the shell valve was slit along its whole length with a fine scalpel blade. The blade was then carefully inserted between mantle and shell so that the adductor muscles were cut. The valve was slowly peeled away from the mantle, all tissue connections being served, until only the shell ligament held the two valves together. The ligament was broken by levering the freed valve off, so that the whole animal lay within the other shell valve. The preparation was transferred to clean seawater and observed beneath a binocular microscope. Experience showed that such preparations survived for several days (displaying foot movements, ciliary activity and heartbeat), but were always studied between 2 and 6 h after surgery. In some cases, parts of the mantle on the operated side of the animal were also removed to reveal structures; natural sediments were used to visualize ciliary tracts. All observations were made upon animals or preparations held either in running seawater at –0.5 to +0.5 °C, or in a constant environment room at +1 to +2 °C.

## RESULTS

*Anatomy*

Figure 1 shows the gross anatomy of the parts of *Yoldia eightsi* that are relevant to a consideration of feeding. As in other *Yoldia* species, the mantle cavity is dominated by the enormous labial palps which are cream-yellow in live specimens. From the apex of the posterior edge of each palp-pair springs a palp proboscis. Each palp proboscis is very muscular and extensible and its edges are curled ventrally so that the structure effectively has a cylindrical cross section, but with

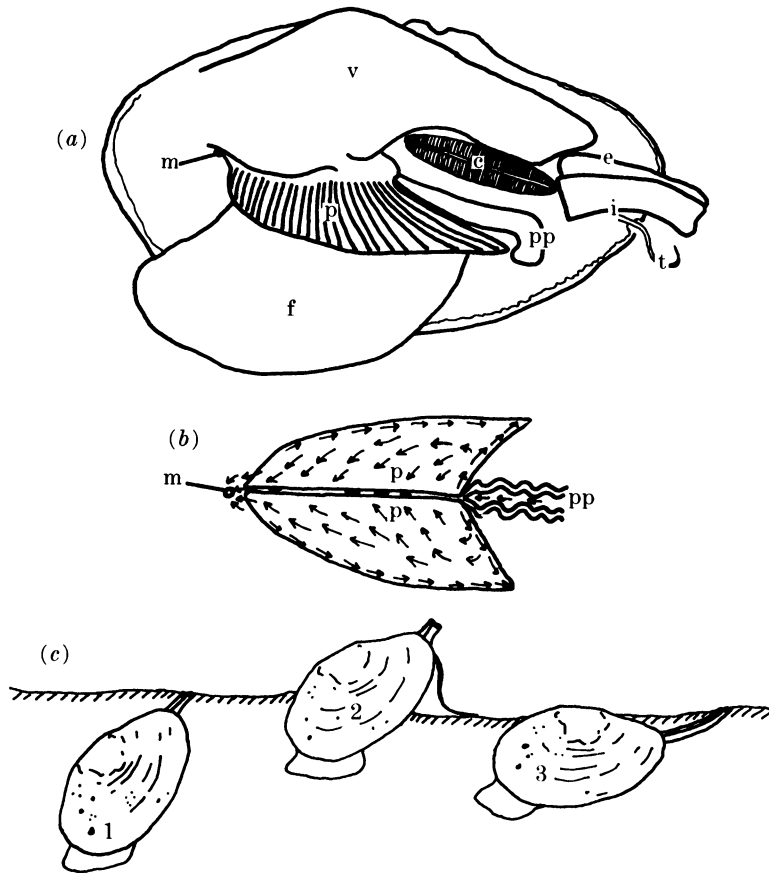


FIGURE 1. (a) Gross anatomy of *Yoldia eightsi* (shell length 35 mm). c, ctenidium; e, exhalant siphon; f, foot; i, inhalant siphon; m, mouth; p, palp; pp, palp proboscis; t, sensory tentacle; v, visceral mass. (b) View of parted apposed palp surfaces (p) and palp proboscis (pp) from ventral aspect. m, Mouth; arrows indicate ciliary tracts. (c) Burrowing habits of *Yoldia eightsi*. (1) Most common posture: subsurface feeding; (2) partly buried, feeding on surface with palp proboscides extended; (3) common posture in large animals; subsurface feeding with horizontal shell axis.

an open slit directed ventrally. When the proboscis is fully extended the walls of the slit are straight, but when it is contracted they are thrown into folds (figure 1), particularly at the thicker proximal end of the proboscis. The proboscides can be extended within the mantle cavity, but may also be protruded into the external environment. In the latter case they are always passed through the feeding aperture formed between the mantle edges immediately ventral to the inhalant siphon. The proboscides can project beyond the feeding aperture by as much as two thirds of the shell length, but appear to be rather less extensible than those of *Yoldia limatula*.

The large and extremely mobile foot is bilobed, as described for *Yoldia limatula* by Drew (1899) and Yonge (1939).

The mouth is situated slightly anterior to the foot, its lips being continuous with

the pairs of labial palps. The rectum opens into the suprabranchial chamber above the red-brown ctenidia.

#### *Observations on intact animals*

##### *Burrowing behaviour*

In aquaria *Yoldia eightsi* spend most of their time burrowed in the sediment so that only the siphonal openings are visible at the mud surface; the inhalant siphon is of substantially greater diameter than the exhalant siphon. A small proportion of the animals project their siphons beyond the mud surface; an even smaller number remain at the mud surface with only  $\frac{1}{3}$  to  $\frac{2}{3}$  of the shell buried. Unlike *Yoldia limatula*, which adopts a vertical position when burrowed and may be as much as 8 cm below the mud surface (Bender & Davis 1984), *Yoldia eightsi* is rarely found below 2–3 cm depth (even in the case of large animals of about 35 mm shell length) and normally adopts a position in which the shell axis is some 40–60° to the horizontal (see figure 1). Large animals tend to adopt an even more horizontal position, often with the shell umbones at the mud surface. During burrowing, sediment often enters the mantle cavity, either directly between the shell valves when the mantle edges are parted, or adhering to the sides of the foot when the foot is contracted during the digging cycle.

##### *Horizontal locomotion*

*Yoldia eightsi* is surprisingly mobile horizontally, often moving 5–10 cm in a few seconds by ploughing through the surface layers of the mud. To accomplish this, the animal first partly emerges from the substratum and the shell axis becomes nearly horizontal. The foot is repeatedly pushed forwards and slightly downwards, the foot tip 'anchor' deployed and the shell drawn towards the foot tip, presumably by contraction of longitudinal muscles within the foot. Usually the animals burrow again after travelling a few centimetres, but occasionally specimens travel as much as 20 cm before re-entering the substratum.

##### *Expulsion of material*

Burrowed *Yoldia eightsi* regularly expel large quantities of sediment from the mantle cavity, usually through the inhalant siphon, but occasionally (if the siphons are retracted and the posterior end of the shell is above the mud surface) through the feeding aperture. During these expulsions the exhalant siphon is invariably closed. Expulsion of material occurs every 6–35 min (mean = 18 min;  $n = 8$ ) with the interval between expulsions being apparently unconnected with the size of the animal. With some difficulty it proved possible to collect complete expulsion plumes (by placing a glass beaker on the mud surface immediately downstream of the inhalant siphon opening), and dry masses of plume material and animal tissue were obtained on 9 occasions (see figure 2). On average, dry plume material corresponds to about 16% of dry tissue mass, suggesting that (given a plume expulsion every 18 min) a specimen of *Yoldia eightsi* would expel material corresponding to about 13 times its dry tissue mass in 24 h. The expelled material consists almost entirely of particles of quartz and other inorganic material (the neighbouring island of Signy is composed largely of quartz–mica–schist and

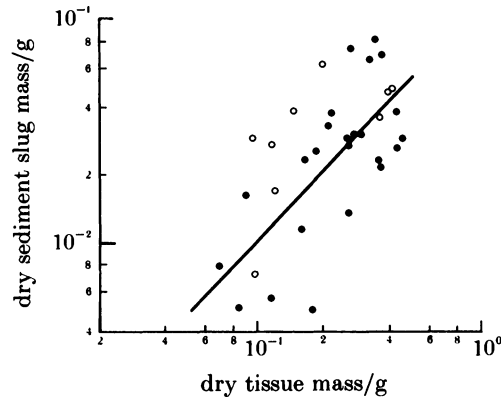


FIGURE 2. Relation between dry tissue mass and individual sediment slug mass in *Yoldia eightsi*. Filled circles, individual sediment slug masses ( $n = 25$ ). The straight line indicates the regression of sediment slug mass on dry tissue mass ( $\log_{10} y = -0.941 + 1.053 \log_{10} x$ ). Open circles, pseudofaecal plume masses ( $n = 9$ ).

this appears to be reflected in the near-shore sediments). Because of its inorganic composition and issue from the inhalant siphon, this material will be referred to as the 'pseudofaecal plume'. The size of the particles is identical with that of the large and medium-sized particles of the surrounding sediment. The expelled material is heavy and rises no more than 2–3 cm into the water column, so forming fan-shaped deposits immediately downstream of the inhalant siphon. Observations in the 'ant farm' clearly demonstrated that the expulsion is produced by a sharp adduction of the shell valves, and that the exhalant siphon tip closes just before expulsion of the pseudofaecal plume through the inhalant siphon. Pseudofaecal plumes are never produced by partly buried animals feeding on the surface with their proboscides.

Closer examination with a hand lens and binocular microscope showed that plumes of material also issue from the exhalant siphon of all specimens of *Yoldia eightsi*, whether they are buried in mud, feeding at the mud surface or held in clean seawater. These plumes are far smaller and produced much more frequently, though in an irregular fashion. There is often an expulsion every 12–15 s coinciding with ventilatory pulses (see below), but sometimes as many as 160 s pass between expulsions; an expulsion every 60 s would be representative. These plumes clearly consist of far lighter material than the pseudofaecal plumes, because they travel much further into the water column (by as much as 5–8 cm) and drift away from the animal for several seconds before falling back to the mud surface. Examination of this plume material showed that it consists mainly of a soft, dark, green-brown substance identical with faeces present in the rectum of dissected animals. The faeces are accompanied by a small amount of very fine inorganic material (apparently quartz), but this probably makes up no more than 5% of the total of the 'faecal plumes'. It is not clear whether the inorganic fraction passes through the gut or consists of material that has passed through the ctenidia to the suprabranchial chamber. Faecal plumes could not be collected individually because of their rapid dispersal. Instead, 25 specimens of *Yoldia eightsi* were held in



clean seawater for 1 h to 'cleanse' the mantle cavity, then each was transferred to a Petri dish of clean seawater and left for 8 h. Faecal material was collected, dried and weighed, as were the soft tissues of the animal producing it. On average the animals expels faecal plumes corresponding to 7.7% body mass (on a dry mass basis) in 24 h. Approximately speaking, therefore, the pseudofaecal output is some 170 times the faecal output, suggesting that buried animals ingest about 0.6% of the sediment material that they process.

#### *Sediment in the mantle cavity*

Feeding animals, whether wholly buried, or partly buried at the mud surface, always protrude the foot. With practice, it was found possible to grasp an animal suddenly between finger and thumb, so that the shell valves were tightly closed, but the foot, siphons and palp processes (if extended) still partly protruded. While keeping the valves tightly closed, the exterior of the animal could be washed off thoroughly in running seawater. The animal could then be opened to allow examination of the mantle cavity.

Animals feeding on the surface with their palp proboscides extended onto the mud surface always have very small quantities of fine material on the palp surfaces and (to a lesser extent) on the tentacles; the mantle, foot and visceral mass are quite clean. Burrowed animals captured immediately after expelling pseudofaeces also have virtually empty mantle cavities as far as sediment is concerned. However, in the case of burrowed animals that have expelled pseudofaeces at least 5 min beforehand, there is always a compact 'slug' of sediment in the posterior part of the mantle cavity. The slug contains mucus and is always in contact with the posterior limit of the ventral margin of each labial palp, so lies on the main rejection tract of the mantle (see figure 3); the palp proboscides are always contracted within the shell and in touch with the sediment slug. The remainder of the mantle cavity is quite clean, although mucus strings and fine material can be seen on the labial palps. In the case of 25 animals, sediment slugs were individually collected, dried and weighed (as were the soft tissues of the animals themselves). It may be seen from figure 2 that the sediment slug masses are very similar to the pseudofaecal plume masses already mentioned, supporting the hypothesis that the slug is expelled as a single pseudofaecal plume when sorting is completed.

#### *Ventilation and filter feeding*

By using a binocular microscope (12 times magnification) it was possible to study the siphons of intact animals very closely. At the tip of the siphons the wall dividing the exhalant and inhalant siphons is often (though not invariably), turned up to form a small flexible flap which partly obstructs the exhalant siphon opening (see figure 3). The siphons themselves are transparent and the animals were held in water that contained natural particulate material. It was therefore easy to see the direction of water flows, and also to gain qualitative information about their velocities. Undisturbed animals have a regular ventilatory rhythm, expressed in slight pulsations of the siphons accompanied by strong outflows of water from the exhalant siphon. Three estimates of ventilatory frequency were made upon each of six animals at a temperature of 0 °C. A mean ventilatory pulse

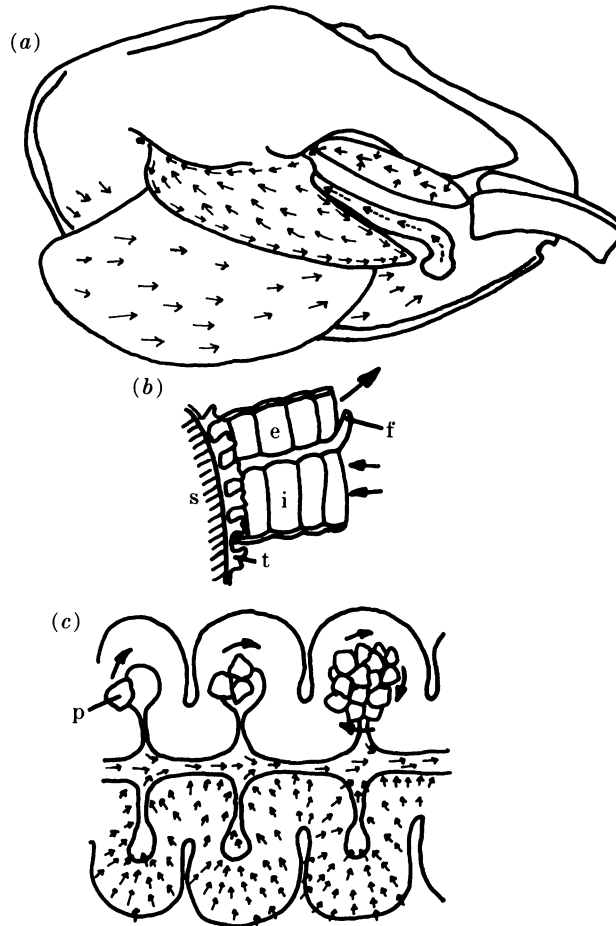


FIGURE 3. Food collection and sorting in *Yoldia eightsi*. (a) Ciliary tracts. Arrows indicate the direction of particle transport. Dashed arrows represent ciliary tracts within the central channel of the palp proboscis. (b) Siphons of *Yoldia eightsi*. e, exhalant siphon; f, flap; i, inhalant siphon; s, shell; t, tentacle of mantle edge. Arrows indicate directions of water flow. (c) Close up of folded edges of the ventral slit of palp proboscis. Small arrows indicate ciliary tracts. Large arrows indicate spin of large, dense particles (p) which aggregate before falling from the proboscis.

rate of 4.39 pulses per minute (standard deviation = 0.60) was recorded. By concentrating upon the tip flap of the exhalant siphon and the particulate material in the water, it could be seen that the strong, narrow outflow from the exhalant siphon is accompanied by a broader, slower inflow into the inhalant siphon. The tip flap of the exhalant siphon tends to separate the flows (figure 3). At the end of the exhalant pulse, there is a marked inflow of water into the exhalant siphon as the pumping ctenidia rebound. This backflushing of water clears all of the exhalant siphon and presumably does much to fill the suprabranchial chamber. Both the inflow into the inhalant siphon, and the backflushing water entering the suprabranchial chamber, contain quantities of diatoms (either single organisms or



in chains). These diatoms never emerged during the next exhalant pulse and it is clear that all of the phytoplankton carried in the incoming ventilatory streams is trapped and presumably eaten.

#### *Use of palp proboscides*

The palp proboscides are only extended outside the shell under two circumstances. Most animals living at the surface of the substratum project their palp proboscides through the feeding aperture and down onto the surface of the mud. Sometimes only one proboscis is protruded, but usually both proboscides are employed. The proboscides remain on the surface, with the ciliated ventral surfaces facing downwards, and material can be seen moving along the proboscides towards the feeding aperture. Commonly, large particles fall off the proboscides when they reached the aperture. The palp proboscides are not extended very far from the animal, and are simply moved around on the surface for quite long periods, before the animal moves through the surface sediments to another location. No noticeable marks are left on the surface of the substratum by the palp action, nor are the proboscides pushed into the mud. On one occasion, a newly burrowed specimen of *Yoldia eightsi* in the 'ant farm' was seen to have a water-filled cavity between the shell and the Perspex of the ant farm. One end of the cavity included the posterior portion of the shell and the palp aperture. A palp proboscis was protruded into the cavity and was observed to pick up particles from its lower surface. However, within a few minutes the walls of the cavity collapsed and the proboscis was withdrawn. At no other time was a palp proboscis seen outside the shell in a burrowed animal. Although cavities do sometimes appear momentarily during digging activity, they normally collapse within seconds, because of the soft, thixotropic nature of the sediments. It seems probable, therefore, that the ant farm observation was an artefact caused by rigid Perspex and rigid shell being close enough for a cavity to be sustained in a manner unlikely in the real environment.

At no time was a burrowed *Yoldia eightsi* seen to project palp proboscides alongside the siphons to reach the surface in the manner described for *Yoldia limatula* by Bender & Davis (1984).

#### *Observations on preparations*

##### *Ciliary tracts and mucus*

Ciliary tracts on the foot and mantle (see figure 3) direct all particulate material to the posterior part of the mantle cavity where sediment slugs are found in intact animals. The foot and mantle secrete clear mucus that binds particles together. Natural sediment placed on the foot and mantle of washed preparations is transformed within 1–2 min into a mucus-coated 'slug' indistinguishable from those seen in intact animals. The palp proboscides invariably sort the material of the slugs. Much of the palp proboscis was found to be ciliated, only a narrow strip on the dorsal surface appearing to be incapable of transporting particles. The ciliary tracts tend to transport material into the channel of the proboscis, but the width of the slit is so narrow, particularly in the folded proximal portion of the proboscis, that larger particles cannot enter. The smaller particles that do enter the slit are

rapidly transported to the palps. Minute organic particles travel from one end of the palp proboscis to the other in less than 10 s. The larger particles adhering to the edges of the slit are also carried (albeit much more slowly) towards the palps. However, when they reached the heavily folded parts of the proboscis they tend to spin slowly within the fold (see figure 3). When a second particle arrives in the same fold, it adheres to the first particle by mucus and spins with it. More particles arrive and adhere, until the mass of particles falls off the proboscis and back into the 'slug'. The relatively slow movement of large particles along the palp proboscides makes it quite impossible that the sediment slug (composed predominantly of large particles) is collected by the proboscides, because the slug appears within about 5 min of the expulsion of a pseudofaecal plume. It must be collected in bulk fashion, either by parting of the ventral mantle edges, or by foot movements.

Two types of material arrive at the proximal end of the palp proboscis; fine material contained in discoloured mucus strings travelling along the channel of the proboscis, and masses of large particles, bound together, which have accumulated along the folded edges of the proboscis slit, but not fallen back into the slug of sediment. The former material moves straight into the dorsal ciliated groove between the palps and thence to the mouth. The masses of larger particles are moved to a downwardly directed ciliary tract at the posterior, backwardly directed edge of the palp which rejects the particles back into the sediment slug. Some fine material moves out of the rejectory tract onto the palp faces where it is carried mouthwards. The palps themselves have ciliary tracts, both on the apposed inner surfaces and on the outer surfaces. Most tracts carry material dorsally and mouthwards, but the free edge of each palp has a tract that directs material backwards (at a rate of about  $5 \times 10^{-2} \text{ mm s}^{-1}$ ) where it is rejected into the sediment slug. Sorting of a given slug proceeds for up to 30 min with the mass of large particles being repeatedly handled by the proboscides as fine material is extracted from the slug before the latter is ejected as an essentially inorganic pseudofaecal plume.

Throughout the period of sorting, fine material in mucus strings can be seen moving along the palp proboscis channels, the dorsal ciliary grooves of the palps, and across the surface of the palps. The mucus strings are slightly discoloured (brown), suggesting that the initially clear mucus secreted by foot and mantle becomes coloured, in the sorting and mixing process, by material too fine to be seen under the binocular microscope. Occasional large inorganic particles getting on to the palp surface are transported anteriorly at first, but progressively fall down the palp to the rejection tract where they are transported rearwards to the sediment slug. After about 30 min the whole process of sorting and transport of material ceases, leaving a slug of large- and medium-sized particles in the posterior part of the mantle cavity. Sorting starts immediately if fresh sediment is added; a motionless palp proboscis is restored to activity as soon as a few particles are dropped onto it.

Material reaching the mouth area is invariably very fine, and simply moved straight into the mouth. There is no sign of any rejection of material after it enters the mouth in the manner described for *Yoldia limatula* by Kellogg (1915).

Fine material is also transported by the ctenidia. Newly opened animals usually

have fine material on the gills, and added fresh sediment was readily transported by the ctenidia of preparations. The tracts are arranged in such a manner (figure 3) that material is moved from the ctenidia to the palps, and fine material may be observed moving all the way from the ctenidia to the mouth. Taken with the observations of diatom intake described above, it is therefore clear that the gills have a filter-feeding function. Large particles placed on the ctenidia are transported to the rejection ciliary tract on the palps along clear mucus strings running from ctenidia to palps.

#### DISCUSSION

*Yoldia eightsi* is a successful species, being much the most common bivalve mollusc over large areas of the Antarctic and Subantarctic seabed. Dominant, common species tend to be generalists. It is evident that the animal can feed on the surface layers of mud, which tend to be rich in newly deposited detritus, but they are also able to exploit the organic content of subsurface layers, as well as being able to trap suspended material in the ventilatory water stream on their ctenidia. The relative importance of these different feeding methods is difficult to assess. Presumably, filter feeding occurs at all times, but will tend to be effective only during the summer periods of diatom bloom, because the winter period is characterized by water of unusual clarity (especially in areas where sea-ice forms). Surface feeding appears to be uncommon (probably because it exposes the animals to the risk of predation), so feeding on subsurface mud layers must be the main source of organic material for much of the year.

It is in the mechanism of subsurface feeding that *Yoldia eightsi* departs most from the published descriptions for other *Yoldia* species. *Yoldia eightsi* reworks considerable quantities of sediment; an animal of 30 mm length, with a dry tissue mass of some 0.35 g will expel about 4.55 g dry sediment per day, or around 1700 g per year, if feeding occurred at a constant rate throughout the year (which it probably does not, though relevant data are as yet unavailable). These values are comparable with the 440 g per year calculated for a 14.7 mm *Yoldia limatula* by Bender & Davis (1984). However, whereas *Yoldia limatula* apparently collects all material from outside the shell by the palp proboscides, and expels relatively small quantities of combined faeces and pseudofaeces at frequent intervals through the exhalant siphon (with some rejection of larger particles between the valves (Yonge 1939), *Yoldia eightsi* appears to take much material into the mantle cavity either by opening of the shell valves (after the sharp adduction which produces the pseudofaecal plume), or (probably less often) by foot movements. The material is then brought to the posterior part of the mantle cavity by foot and mantle ciliary tracts (being mixed with mucus in the process), where it is repeatedly sorted, primarily by the palp proboscides. When all fine material has been transferred to the mouth via the palps, the remaining mass of larger, essentially inorganic particles is expelled through the inhalant siphon. *Yoldia eightsi* expels fine material (mainly faeces) through the exhalant siphon very frequently, but expels the large pseudofaecal plumes infrequently.

Why is there such variation in behaviour between species of considerable mor-

phological similarity? The different orientation of *Yoldia eightsi* when buried (i.e. often more nearly horizontal than vertical), coupled with its shallow burrowing habit, may provide the answer. Because the ventral surface of *Yoldia eightsi* tends to face downwards instead of laterally, rejected large and dense particles will always fall into the posterior part of the mantle cavity, rather than towards the palps and mouth as would be the case if the animals burrowed vertically like *Yoldia limatula*. Any large particles which do get onto the palps also tend to fall downwards onto the rejecting ciliary tracts at the ventral palp margins. The horizontal orientation will also allow the animal to take in bulk sediment quickly by parting the shell valves and the ventral mantle edges, with minimum risk of clogging the ctenidia. It also seems likely that the more horizontal orientation and much shallower burrowing of *Yoldia eightsi* allows the regular expulsion of large quantities of dense material, in a manner that would be difficult, and perhaps energetically expensive, in a species living at greater depth and needing to project the material vertically upwards. It is not clear why *Yoldia eightsi* is a much shallower burrower than its northern relatives. Lack of competition from other burrowers in the low diversity, low stress Antarctic habitat may be relevant, but equally it might be suggested that predation pressures are lower.

The dual faecal and pseudofaecal plume output of *Yoldia eightsi* has implications for the effect that populations of the animals have on surrounding sediments, and upon the turbidity of the water columns. Bender & Davis (1984) demonstrated that the combined faecal and pseudofaecal plume of *Yoldia limatula* consisted of fine material, so that the species played a large part in resuspending the fine component of deposited sediments. They also showed that the species caused a progressive increase in particle size at the burrowing depth. The situation for *Yoldia eightsi* is different. Although the species does separate large and fine particles (ingesting the latter), it expels both types of particle at the surface. The fine material projects further into the water column than the pseudofaecal plume (though less than in *Yoldia limatula* which apparently delivers a vertical plume 10 cm high), so some resuspended material will presumably be carried away from the beds of *Yoldia eightsi*. Certainly the species is a powerful agent for the aeration, winnowing and turnover of the top layers of sediments, not only when feeding, but also during its frequent horizontal locomotion when the shell acts like a plough.

From the data presented here it would appear that *Yoldia eightsi* ingests about 0.6% of the material that it processes when feeding on subsurface mud (calculated on a dry mass basis). Crude analysis of fresh sediment (achieved by measuring dry masses and ash-free dry masses on several mud samples) indicates that organic material makes up  $1.35 \pm 0.08\%$  of the dry sediment. Given the imprecision of measurement of masses of faecal and pseudofaecal plumes, this suggests that the sorting process of the palps and palp proboscides is extremely efficient, removing a high proportion of the available organic material. Taken with the observation that the species traps all of the diatoms carried in ventilatory streams, and can feed from the mud surface on occasion, it would seem that *Yoldia eightsi* exploits all energy sources available to it.

The author thanks the divers of the British Antarctic Survey, Signy Base, for their invaluable help; particular thanks are due to the Diving Officer, Mr G. Wilkinson. The study was done with the aid of N.E.R.C. Grant (Antarctic Special Topic) GST/02/96.

## REFERENCES

- Bender, K. & Davis, W. R. 1984 The effect of feeding by *Yoldia limatula* on bioturbation. *Ophelia* **23**, 91–100.
- Dell, R. K. 1964 Antarctic and subantarctic Mollusca: Amphineura, Scaphopoda and Bivalvia. 'Discovery' Rep. **33**, 93–250.
- Drew, G. A. 1899 The anatomy, habits and embryology of *Yoldia limatula* Say. *Mem. biol. Lab. Johns Hopkins Univ.* no. 4. (37 pages.)
- Kellogg, J. L. 1915 Ciliary mechanisms of lamellibranchs with descriptions of anatomy. *J. Morph.* **26**, 625–701.
- Rhoads, D. C. 1963 Rates of sediment reworking by *Yoldia limatula* in Buzzards Bay, Massachusetts and Long Island Sound. *J. sedim. Petrol.* **33**, 723–727.
- Stasek, C. R. 1965 Feeding and particle-sorting in *Yoldia ensifera* (Bivalvia: Protobranchia) with notes on other nuculanids. *Malacologia* **2**, 349–366.
- Yonge, C. M. 1939 The protobranchiate Mollusca: a functional interpretation of their structure and evolution. *Phil. Trans. R. Soc. Lond.* B **230**, 79–147.