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Cyclical contributions of the digestive epithelium to faecal pellet formation by the copepod *Calanus helgolandicus*

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Abstract

Faecal pellet formation within the gut of Stage V and adult females of the copepod *Calanus helgolandicus* Claus involves (1) cyclical processes of digestion and (2) the contribution of parts of the gut epithelium to the pellets. During an experimental regime in which dim lighting was restricted to day-time and feeding to night-time (17.00 to 09.00 hrs), the copepods responded with cyclical changes in both the quantity of pellets they produced and the fine structure of the contents. During the feeding period, the contents showed changes in the relative amounts of materials originating from disintegrated cells of the digestive epithelium and those derived directly from the ingested food. The vacuolar B-cells of the gut contribute to the content of the pellets and the distal, necrotic N-cells appear to be involved in forming the peritrophic membrane which encloses each pellet. Cells of the gut epithelium which are broken down during feeding are all replaced during the non-feeding period. Other individuals were taken directly from the sea and in these, also, the cells of the gut broke down during feeding and contributed to the faecal pellets. The supply of epithelial cells may limit the duration of the feeding period.

Introduction

In the open ocean, a substantial fraction of the downward flux of particulate organic carbon is contributed by faecal pellets, either intact or incorporated in aggregates (see for example Honjo, 1976; Bishop *et al.*, 1978; Turner and Ferrante, 1979). This material represents an important input to sediments and provides the principal food supply for the benthic fauna (Bishop *et al.*, 1978). The faecal pellets are released mainly by the zooplankton which, in many sea areas, is dominated by copepods.

The importance of these faecal pellets in the vertical transport of organic compounds has led to studies of their chemical composition (Volkman *et al.*, 1980; Prahl *et al.*, 1984a, b), such studies being mainly concerned with the effects of the digestive processes of copepods on the chemical characteristics of their faecal products.

Marshall and Orr (1955) concluded that the rate of feeding by *Calanus helgolandicus,* as measured by faecal pellet production, can remain "fairly constant" for a period of 24 h, and this assumption has been accepted in later experimental work (see review by Marshall, 1973). However, there are reasons to believe that under natural conditions the copepod feeds periodically rather than continuously. For example, it is apparent that during the summer the later-stage copepodites and adults in the Celtic Sea show daily vertical migrations and feed in the euphotic zone at night (Williams and Conway, 1984). Likewise, during late summer in the arctic, *C. hyperboreus* and *C. glacialis,* although they show no daily migration, restrict their feeding activity to night-time (Head *et al.*, in press). It seems probable that faecal material will be produced only during the feeding and digestion period of the diel cycle. This conclusion is also consistent with field observation by Staresinic *et al.* (1978), who found that sediment traps deployed in the Peru Upwelling region collected more particulate material, including faecal pellets, by night than by day.

In addition, investigations of the digestive processes of decapods (Hopkin and Nott, 1980; Al-Mohanna *et al.*, in press) and amphipods (Icely and Nott, 1984) show that these animals have a 24 h cycle which causes regular changes in the nature of the material packed in the faecal pellets. This cycle, which cannot be measured by the rate at which food passes through the gut, includes the processes of ingestion, extracellular digestion, uptake into the cells of the gut, intracellular digestion, assimilation of nutrients into the haemolymph and disposal of the residual material in the faeces. During the first part of the cycle, indigestible food debris which cannot be taken up

by the gut epithelium forms the major constituent of the faecal pellets. Later, when intracellular digestion is complete, much of the epithelium breaks down into the lumen and the cell remnants are egested in the faecal pellets. The digestive epithelium of copepods (Ong and Lake, 1969; Raymont *et al.*, 1974; Briggs, 1977; Arnaud *et al.*, 1978, 1980; Hallberg and Hirche, 1980) contains cells which are similar to those in decapods (see review by Gibson and Barker, 1979) and amphipods (Icely and Nott, 1984). Furthermore, there is differentiated development of the fine structure and enzyme activity of the digestive epithelium, with respect to development stage, sex and season (Hallberg and Hirche, 1980). It seems, therefore, from considerations of both the daily behaviour patterns and the various studies of gut cytology of copepods, that in *Calanus helgolandicus* the processes of digestion are cyclical and could be reflected in changes in the nature of the contents of the faecal pellets.

Already there is structural and biochemical evidence that *Calanus helgolandicus* contributes some of its own tissue components to the faecal pellets. Thus, it has been established that vacuolar cells in the gut epithelium are released into the lumen (Arnaud *et al.*, 1978, 1980) and that the epithelium of the posterior region of the gut can break down completely. Also, *C. helgolandicus* contributes its own lipid "signature" to faecal pellets produced from various diets (Neal, 1984; Prahl *et al.*, 1984b) in that samples collected over an 18 h feeding period contained sterols, fatty alcohols and fatty acids characteristic of this copepod. These observations, however, did not take into account the possibility of daily cycles in the digestive processes.

In the present work, the cells of the digestive epithelium and the contents of the gut have been examined during an experimental regime designed to simulate, broadly, the natural daily feeding cycle. In addition, similar observations have been made using "wild" copepods sampled directly from the sea. Particular attention has been paid to the breakdown of gut epithelial cells which contribute to the faecal pellet as it forms in the gut. It has been shown how changes in the cytology of the gut occur during feeding, and how and when breakdown of the epithelium contributes to the faecal pellets.

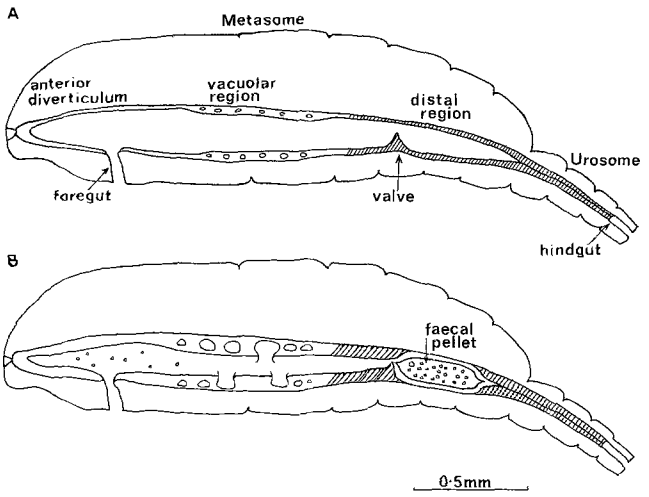


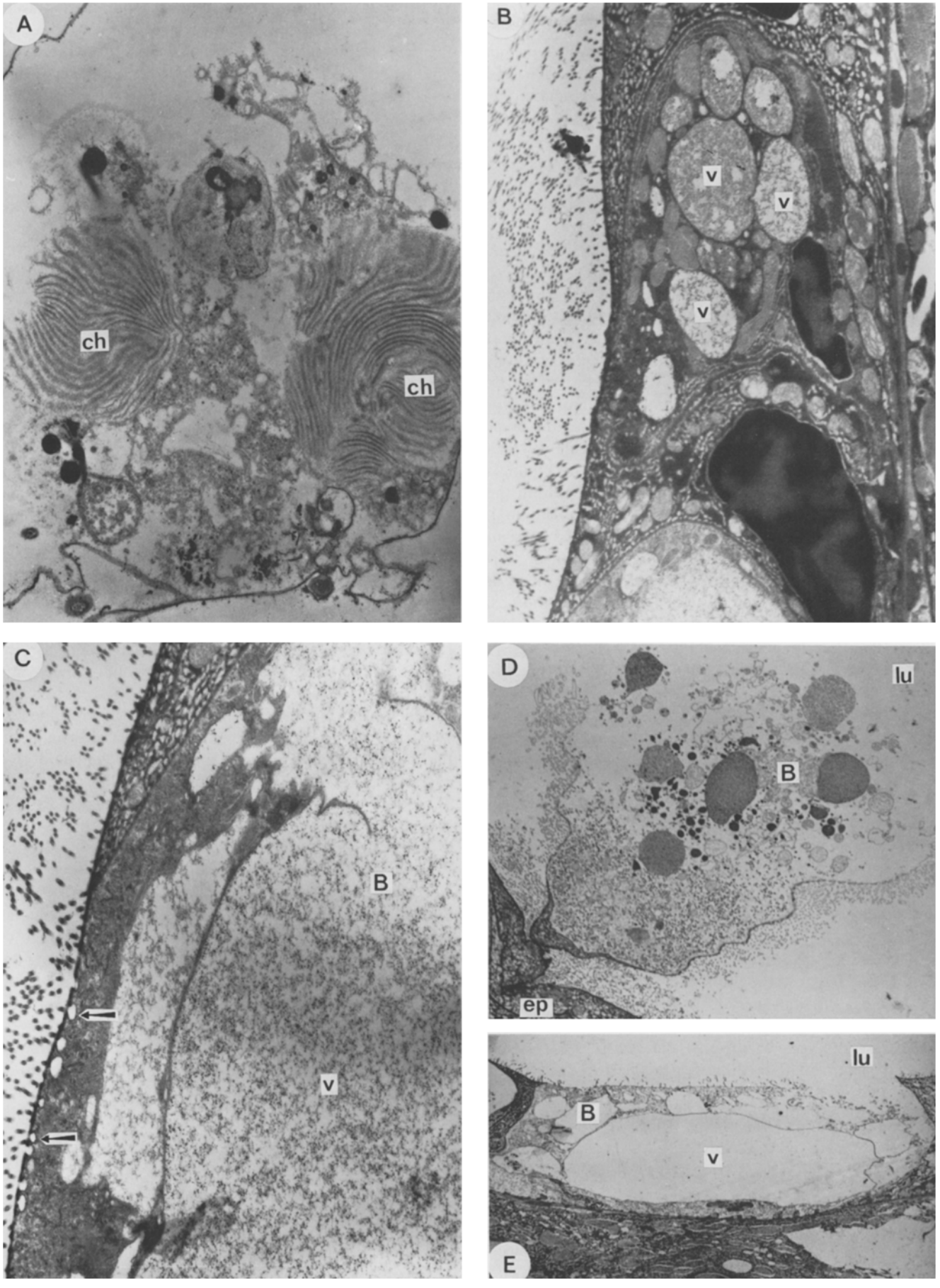
Fig. 1. *Calanus helgolandicus.* (A) Non-feeding individual during the daytime; epithelium of anterior diverticulum and vacuolar region is thin and the B-cells are restricted and not bursting; epithelium of distal region is entire. (B) Feeding individual during the night; anteriorly, epithelium is thicker and vacuolar region is extended; the B-cells are bursting into the lumen; epithelium of distal region shows some breakdown; anteriorly, in the lumen, food is dispersed but posterior to the valve it is packaged in a faecal pellet

Materials and methods

Fine structure

Seventy five Stage V and adult female *Calanus helgolandicus* Claus, separated from zooplankton freshly caught by tow-net at Station L3 (entrance to Plymouth Sound, England) were maintained on a diel cycle at 10 °C. During the daytime they were kept in dim light and given no food. During the night they were kept in the dark and fed (17.00 to 09.00 hrs) with the thecate dinoflagellate *Scrippsiella trochoidea* obtained from the Plymouth Culture Collection and grown in *f*/2 medium (Guillard, 1975) under a 10 h light:14 h dark cycle. Sampling commenced on the third day, when five copepods were taken at each of the following times: 09.00, 11.00, 15.00, 17.00, 17.30, 18.00, 21.00 and 24.00 hrs. They were fixed whole in 3% glutaraldehyde in sodium cacodylate buffer (1 200 mOsmol) at 7.4 pH for 30 min, then post-fixed in 2% osmium cacodylate buffer for 1 h. They were rinsed in the cacodylate buffer and 2% ascorbic acid in distilled water. The specimens were rotated in this de-calcifying mixture for 12 h before being rinsed in distilled water, dehydrated in ethanol and embedded in epoxy resin. Sections were stained sequentially in uranyl acetate and lead citrate and viewed in a Jeol 200 CX electron microscope using both the TEM and STEM images. Concurrently, copepods were taken directly from the sea in mid-October at 17.00 hrs, when they were feeding. They were processed immediately on the boat by the same fixation and embedding procedure.

Fig. 2. *Calanus helgolandicus.* Transmission electron micrographs (TEM) of gut longitudinal sections (LS). (A) Partially digested thecate dinoflagellate, *Scrippsiella trochoidea,* in anterior diverticulum with remains of peripheral chloroplasts (ch) [XF, ×9 000]; (B) epithelial cell at anterior end of vacuolar region, where intracellular vacuoles (v) form without any pinocytosis [XNF, ×6 900]; (C) vacuolar B-cell (B) showing apical pinocytosis (arrows) [XNF, ×9 600]; (D) B-cell bursting into gut lumen (lu) from epithelium (ep) [WF, ×4 000]; (E) another disintegrating B-cell [XF, ×3 200]. [XF: experimental copepod, feeding; XNF: experimental copepod, non-feeding; WF: wild copepod, feeding]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Aryl-sulphatase measurements

The method used was that described by Hopsu-Havu *et al.* (1967). p-nitrocatechol sulphate was the substrate and barium sulphate the insoluble product of the reaction. The initial fixation was the same as for "Fine structure" (see above).

Results

Morphology

The gut of calanoid copepods is divided into the foregut, midgut and hindgut (Fig. 1). Both the foregut and hindgut are short and lined with cuticle. The midgut is the most important region of the digestive tract, and recent accounts of its morphology and cytology have been given by Arnaud *et al.* (1978, 1980). Within the head of *Calanus helgolandicus*, the midgut extends forwards from the oesophagus to form a thin-walled anterior diverticulum which has been described by Ong and Lake (1969). This region is continuous with the vacuolar region which lies within the back of the head and the first thoracic segment. The final, thin-walled distal region changes from a dilated tube in the thorax to a constricted tube in the abdomen or urosome. Within the fourth thoracic segment it has a valve or constriction with associated muscles. In feeding individuals, ingested material remains free, dispersed and mobile within the anterior diverticulum and vacuolar region. However, within the distal region, all the material is tightly packed within a faecal pellet which is lined with a peritrophic membrane. The valve or constriction in this region of the gut sets the anterior limit of the pellet. Movement of the food and the formation and egestion of the pellet has been described by Gauld (1957).

When experimental individuals, and those taken directly from the sea, are not feeding, the gut is completely empty of all material, including faecal pellets.

Fine structure

In the anterior diverticulum, the cells of the epithelium show some change throughout the 24 h cycle. During the non-feeding daytime period they become increasingly flattened at the extreme anterior end of the gut, but remain more columnar towards the mid-region (Fig. 1). They all have long, medium-dense microvilli, flattened nuclei and dense cytoplasm which contains extensive cisternae of smooth endoplasmic reticulum and large mitochondria. The mitochondria form a dominant feature and, in some cells, they are associated with infoldings of the basal cell membrane. This configuration resembles the "mitochondrial pump" described by Ong and Lake (1969).

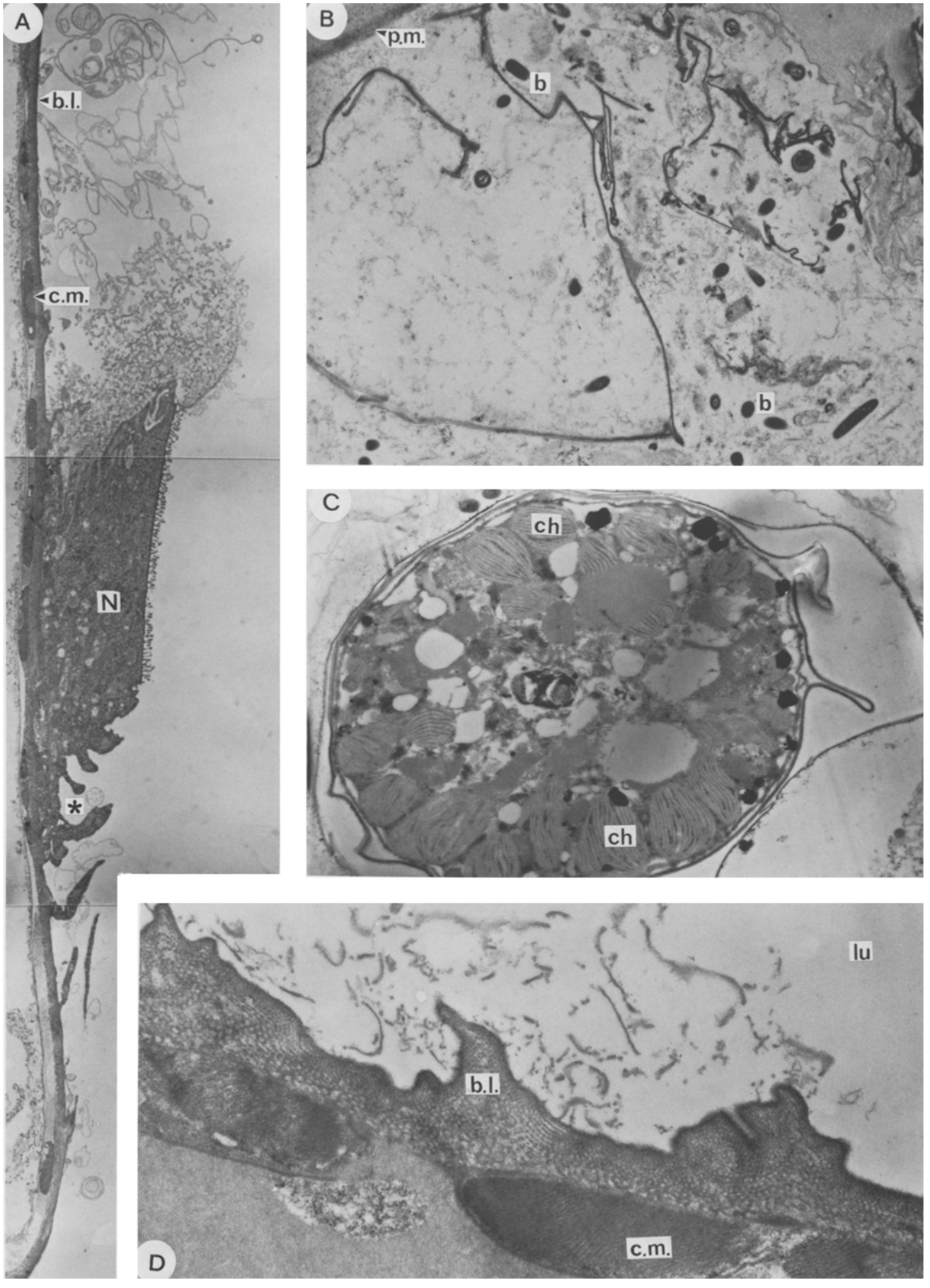
During the feeding period, when the copepods had *Scrippsiella trochoidea* as the diet, the epithelium remained entire and retained the cytological characteristics of the non-feeding stages, except that the cells became less flattened. They showed no aryl-sulphatase activity. *S. trochoidea* cells were accumulated in the anterior diverticulum, and extracellular digestion commenced (Fig. 2 A).

Towards the posterior region of the diverticulum, at the junction with the vacuolar region, the cisternae of the endoplasmic reticulum enlarge or fuse together to form vacuoles, and the cells look like B-cells but without any apical pinocytosis (Fig. 2 B). B-cells occur generally in the digestive epithelia of Crustacea and they have been described for copepods by Arnaud *et al.* (1978). They are characterised by a large vacuole which is formed by the addition of material pinocytosed from the lumen. Intracellular digestion occurs in the vacuoles (Arnaud *et al.*, 1983, 1984 a, b), and when this process is complete the whole cell bursts into the lumen of the gut.

In *Calanus helgolandicus*, the vacuolar region of the midgut is characterised by B-cells (Fig. 2 C) and, in the present work, these showed variations in frequency and activity which were associated with changes in the experimental conditions. From 09.00 hrs, when the copepods were in a dim light and deprived of food, the vacuolar region became progressively less extensive and the remaining cells were less active. Pinocytotic activity was reduced, the vacuoles were smaller and the cells did not burst into the lumen (Fig. 1 A). Feeding was resumed at 17.00 hrs, and by 18.00 hrs there was a marked change in the vacuolar region. It had increased in length at the expense of the cells of the anterior diverticulum, and many of the cells were bursting into the lumen (Figs. 1 B, 2 E). In individuals which had been feeding for 2 to 3 h there was extensive breakdown of the B-cells, and the contents of the vacuoles in all the cells showed aryl-sulphatase activity. Also, in the feeding individuals, cells of *Scrippsiella trochoidea* were dispersed throughout the lumen of the vacuolar region and some of these were at an advanced stage of digestion. "Wild" copepods which were feeding during the evening showed the epithelium of the vacuolar region to be in a similar condition, with many B-cells disintegrating into the lumen (Fig. 2 D).

Posterior to the B-cells is a distal region of squamous, cuboidal epithelium, with microvilli which can be short, stubby and spaced out on some cells (Fig. 3 A), but much longer and densely packed on others (Fig. 4 B). The cells

Fig. 3. *Calanus helgolandicus.* TEM of gut sections (LS) from distal region in metasome (Fig. 1). (A) Lone N-cell (N) with lateral pseudopodial extensions (*); there are membranous and vesicular remains of a neighbouring cell (top); basal lamina (b.l.) and circular muscles (c.m.) are well developed [WF, ×3 800]. (B) Low-density contents of faecal pellet in copepod feeding for only 30 min; note bacteria (b) and peritrophic membrane (p.m.) [XF, ×6 500]. (C) Partially digested *Scrippsiella trochoidea* with peripheral chloroplasts (ch) in faecal pellet of copepod feeding for 7 h [XF, ×7 400]. (D) Detail of basal lamina (b.l.) and circular muscles (c.m.) after disintegration of an N-cell into the lumen (lu) [WF, ×16 500]. [XF: experimental copepod feeding; WF: wild copepod, feeding]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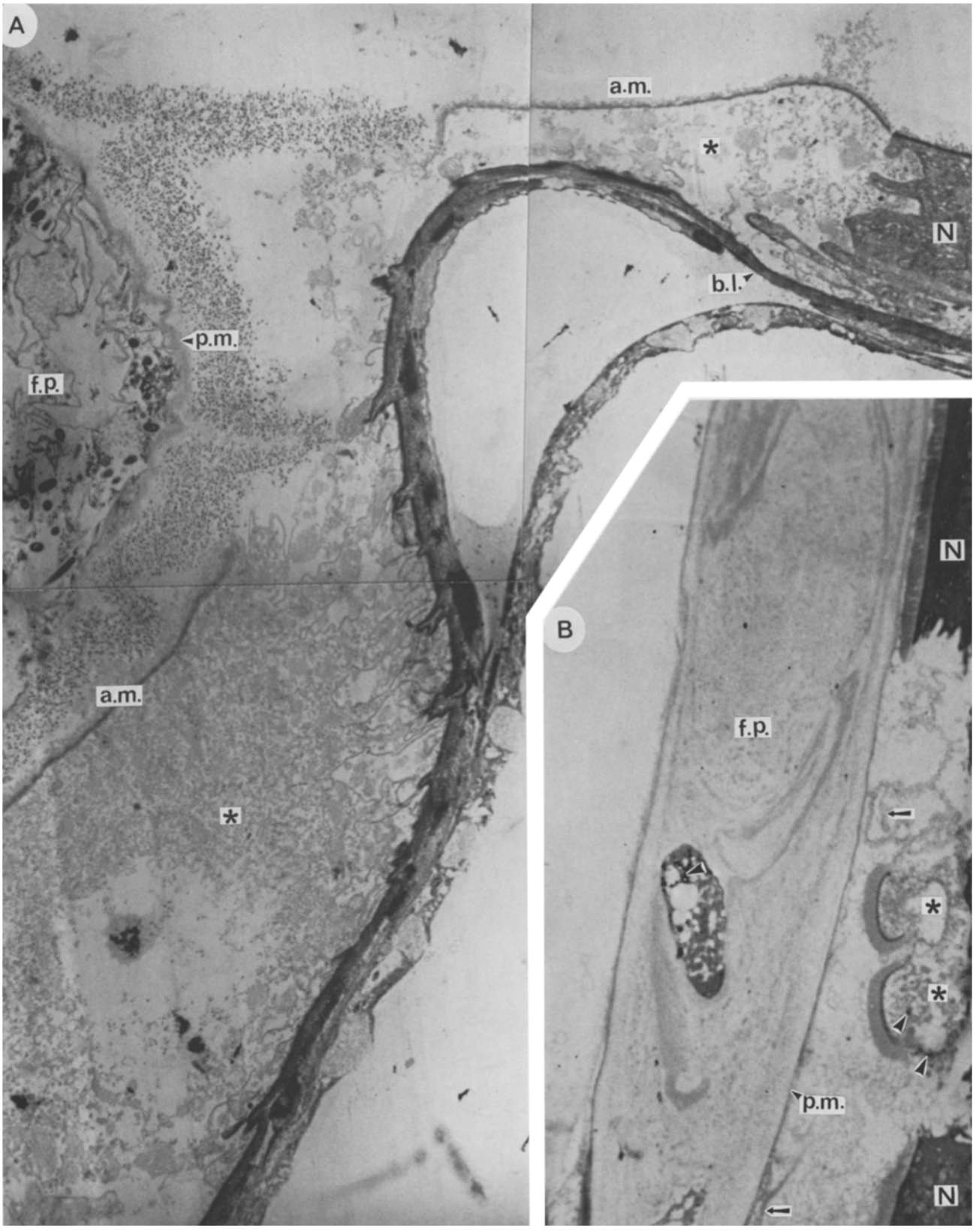

Fig. 4. *Calanus helgolandicus.* TEM of gut sections (LS) with faecal pellets. (A) Posterior end of a faecal pellet (f.p.); two N-cells are disintegrating and contents (*) and apical membranes (a.m.) are associated with peritrophic membrane (p.m.) of the pellet; remaining N-cell (N) appears to have separated from basal lamina (b.l.); experimental individual after feeding for 1 h [×7 900]. (B) N-cells disintegrating (*); some fragments of apical membrane are closely associated (arrows) with peritrophic membrane (p.m.) of the faecal pellet (f.p.). barium-sulphate precipitate (arrowheads) marks sites of aryl-sulphatase activity in pellet and epithelium [XF, ×2 800]. [XF: experimental copepod, feeding]

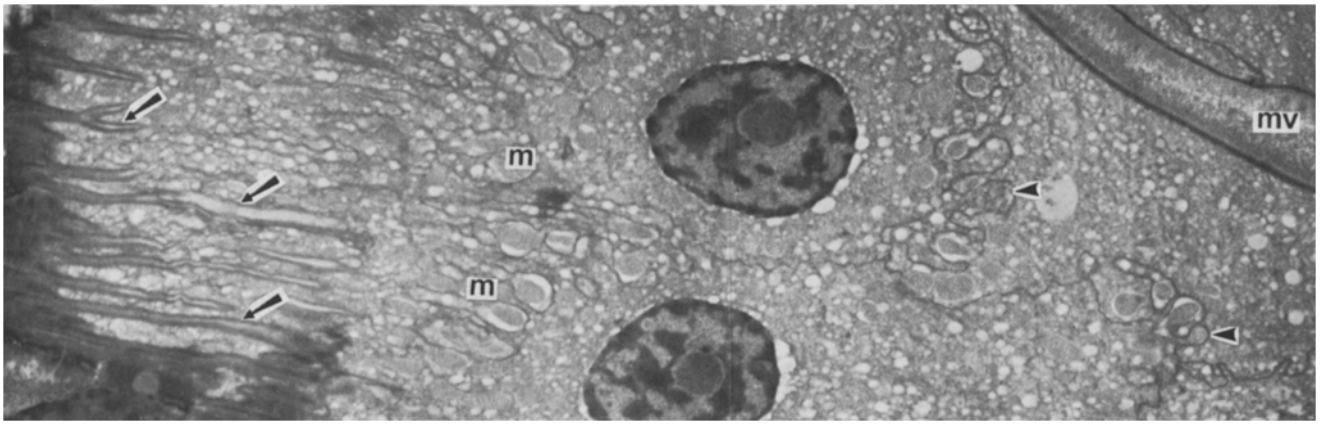

Fig. 5. *Calanus helgolandicus.* TEM of gut sections (LS) from distal region in urosome (Fig. 1). Epithelium is organised as a "pump". Basally, cells have infoldings (arrows) which are associated with mitochondria (m). Laterally, cell membranes interdigitate in association with mitochondria (arrowheads). Apical microvilli (mv) are long and dense [XNF, 3 500]. [XNF: experimental copepod, non-feeding]

are described as necrotic, N-cells by Arnaud *et al.* (1978), the cytoplasm being particularly featureless and undifferentiated. The only organelles, apart from the nucleus, are mitochondria, within which the cristae are less dense than the matrix. Some of the mitochondria appear to be breaking down. Endoplasmic reticulum and vacuoles are absent. These cells line the gut posterior to the valve or constriction and within the posterior third of the metasome. When the copepod is not feeding they form a continuous lining to the epithelium (Fig. 1). However, when the experimental and wild copepods start to feed, individual cells in this region disintegrate into the lumen of the gut, leaving neighbouring cells with lateral pseudopodial extensions exposed (Figs. 3 A, 4 A, B). This situation can produce a much-extended lateral membrane compared with the length of the apical membrane. The apical membranes of the disintegrated cells form a dominant feature, which can be closely associated with the peritrophic membrane of the faecal pellets (Fig. 4 A, B). After the copepods have been feeding for less than 3 h, the epithelium in this region can be practically devoid of cells and all that remains is the basal lamina and its associated musculature (Fig. 3 D). The basal lamina has numerous folds which protrude into the lumen and could allow distension of the lumen when a faecal pellet is being formed.

The faecal pellets contained *Scrippsiella trochoidea* in various stages of digestion, groups of bacteria and membranes: other material was also present but could not be identified. Characteristically, the pellets were of low density when the copepods commenced feeding (Fig. 3 B), but increased in density after 7 h, at which time they contained cells of *S. trochoidea* showing little sign of digestion (Fig. 3 C). A test for aryl sulphatase on an individual which had been feeding for 1 h showed some activity within the remains of a cell in the faecal pellet and some indication of activity within the necrotic cells of the epithelium (Fig. 4 B).

In the terminal segment of the metasome and the first three abdominal somites, the structure of the gut epithelium changes. The cells have the characteristics of a "pump" (Fig. 5). Apically the microvilli are long and dense and basally the cell membrane and basal lamina have numerous and extensive infoldings. Many large mitochondria are closely associated with the folded membrane. There is a lack of endoplasmic reticulum and ribosomes. Laterally the cells interdigitate with each other and mitochondria are closely associated with these folded membranes.

Discussion

During the 24 h cycle of the experiment with *Calanus helgolandicus,* there were cytological changes in all the regions of the midgut and the production of faecal pellets was affected.

The B-cells of the vacuolar region, in particular, reflected the feeding/non-feeding situations and could change the material packaged in the pellets. However, breakdown was complete and cell organelles from the epithelium did not retain a recognisable structure in the pellets. The vacuoles of the intact cells showed arylsulphatase activity, which indicates that when they burst they released hydrolytic enzymes into the lumen. This could account for the extracellular digestion of *Scrippsiella trochoidea* in the anterior diverticulum and vacuolar region. In the crab *Carcinus maenas* (Hopkin and Nott, 1980) and the shrimp *Penaeus semisulcatus* (Al-Mohanna, 1983) the cells are voided intact into the faecal pellet, but the enzymes needed for extracellular digestion are secreted by other cells in the form of zymogen-like granules (Al-Mohanna *et al.*, in press).

In *Calanus helgolandicus,* breakdown of the B-cells is so extensive after a few hours feeding that it could exhaust the supply of replacements and limit the duration of the

digestive cycle. According to Arnaud *et al.* (1978), mitotic figures occur in the epithelium where the vacuolar region changes to the distal region. However, the B-cells are numerous and massive by the time they burst, and it seems unlikely that they can be replaced continuously at the rate at which they are lost. In the experimental copepods at 24.00 hrs, gaps appeared in the active epithelium, which suggests that a rebuilding period is required.

During feeding, the supply of *Scrippsiella trochoidea* cells in the anterior diverticulum and vacuolar region is continuous. This loading must show a variable balance with the disintegrating vacuolar B-cells. When feeding commences the B-cells are small, reduced in number, and show little sign of bursting into the lumen; after the copepods have fed for 1 h, some B-cells disintegrate and this process is almost complete at the end of 7 h. It seems likely, therefore, that the proportion of the contents of the pellets which originates from the B-cells increases markedly after feeding has been in progress for some hours. The situation appears to change again when the B-cells are exhausted. Under these conditions, the pellet contains mostly undigested cells of *S. trochoidea.* These observations indicate that sterols, fatty alcohols and fatty acids in the pellets, which derive from the copepod (Neal, 1984; Prahl *et al.,* 1984 b), could vary markedly as a proportion of those originating from the diet, depending upon the time of feeding and hence the number of epithelial cells which have disintegrated. The B-cells also break down in "wild" copepods, and if these individuals have daily patterns of feeding, the contents of the pellets could change regularly over a 24 h cycle.

The state of the distal epithelium of the gut is also linked directly with the feeding/non-feeding states of experimental and "wild" copepods. Structures released by the breakdown of the N-cells, particularly the membranes, appear to contribute to the formation of the peritrophic membrane which encloses the faecal pellet. The material voided as faeces is always packaged in such a membrane and it seems probable, therefore, that exhaustion of the supply of epithelial N-cells, together with the B-cells, may limit the period of feeding.

The test for aryl-sulphatase activity showed that extracellular digestion continues within the faecal pellet. If the products of hydrolysis are to benefit the copepod, however, they will have to diffuse rapidly out through the peritrophic membrane because, when food is plentiful, as many as 3 to 5 pellets can be voided each hour (Marshall and Orr, 1955). It is possible that the soluble products of hydrolysis are transferred from the gut lumen to the blood space by the epithelial "pump" (Fig. 5) situated posterior to the N-cells.

The bacteria in the pellets occur in groups, which suggests that they are actively dividing (Fig. 3 B). They take the form of short rods or cocci with a diameter of 0.3 to 0.4 μm. So far, no bacteria have been found within the empty guts of non-feeding copepods, which suggests that those packaged in the pellets are taken in with food and are not derived from any population resident in the gut.

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