Crustaceana 44 (3) 1983, E. J. Brill, Leiden

FEEDING BEHAVIOUR OF *GAMMARUS PULEX* (L.) (AMPHIPODA) ON *NITELLA*

BY

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INTRODUCTION

Although *Gammarus pulex* (L.) is a well-known animal, the nature of its preferred detritus food materials, decaying leaves etc., is such that detailed observations on its feeding behaviour have been difficult to accomplish. Preliminary observations made when the alga *Nitella flexilis* (L.) Agardh (Chlorophyceae, Charales) was presented suggested that characteristic feeding postures and activities could be recognised easily; furthermore the food material itself and the faecal pellets produced from it by the animal were very amenable to microscopic analysis. This report summarises the information obtained so far.

When *Nitella* was the sole food of the animal apparent gut passage times, based on length measurements of faecal pellets produced, were extremely variable, ranging from 1.0 to 8.0 h at 15°C. This was in contrast to the situation when decayed elm leaves were the sole food; here gut passage times were more consistent, ranging from 0.5 h to 2.0 h and the animals always had full guts, except immediately prior to moulting (Willoughby & Earnshaw, 1982). The apparently widely variable gut passage times obtained by this method when *Nitella* was the food suggested that feeding was intermittent rather than continuous. Therefore there is the possibility that the actual rate of passage of material which is ingested from *Nitella* may match that following ingestion from decaying elm leaves. Despite this apparent intermittent feeding on *Nitella* suggesting that the material is not a homogeneous food and time is spent in penetrating it rather than eating it, calculated exponential growth rates of the animal are as high with *Nitella* (D. W. Sutcliffe, personal communication) as with decaying elm leaves, where they have been calculated as 4.6% day^{-1} at 15°C (Sutcliffe, Carrick & Willoughby, 1981). This points to the conclusion that *Nitella* must contain constituents of high nutritional value to *G. pulex*.

OBSERVATIONS

Nitella was collected in shallow water in Grasmere (English Lake District) late in the summer season and consisted of main axes and lateral branches.

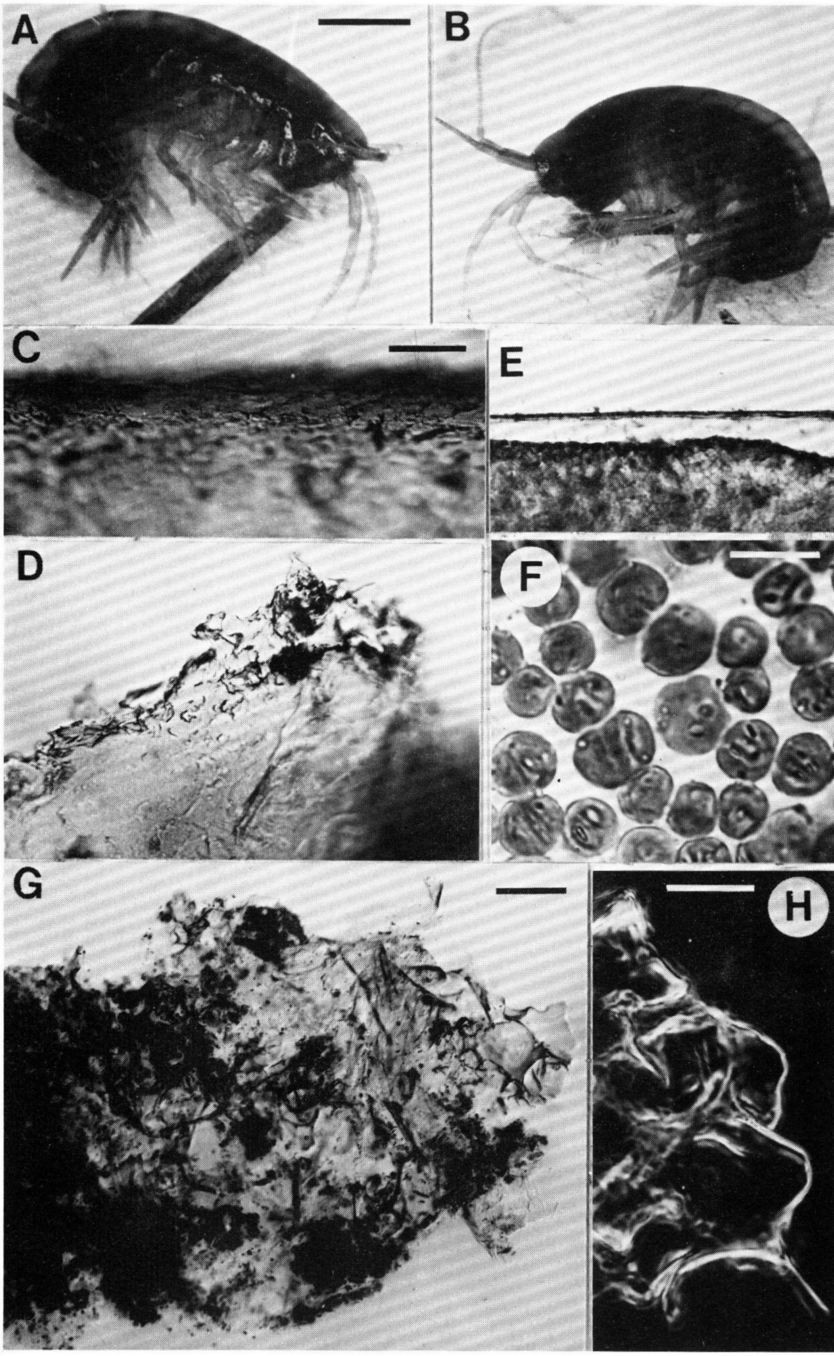

Fig. 1. Food and feeding of *Gammarus pulex* (L.). A, B, feeding positions on *Nitella*; C, surface view of *Nitella* showing wall plate units; D, torn *Nitella* wall following feeding by *G. pulex*; E, chloroplast layer in *Nitella*, withdrawn below cell wall (top); F, healthy chloroplasts of *Nitella*, note starch grain inclusions; G, part of a faecal pellet showing switch from elm leaf food (left) to *Nitella* cell wall food (right); H, part of a faecal pellet showing *Nitella* wall plate material. Scale lines or equivalents: A, B: 4 mm; C, D, E: 300 μm; F: 40 μm; G: 60 μm; H: 30 μm.

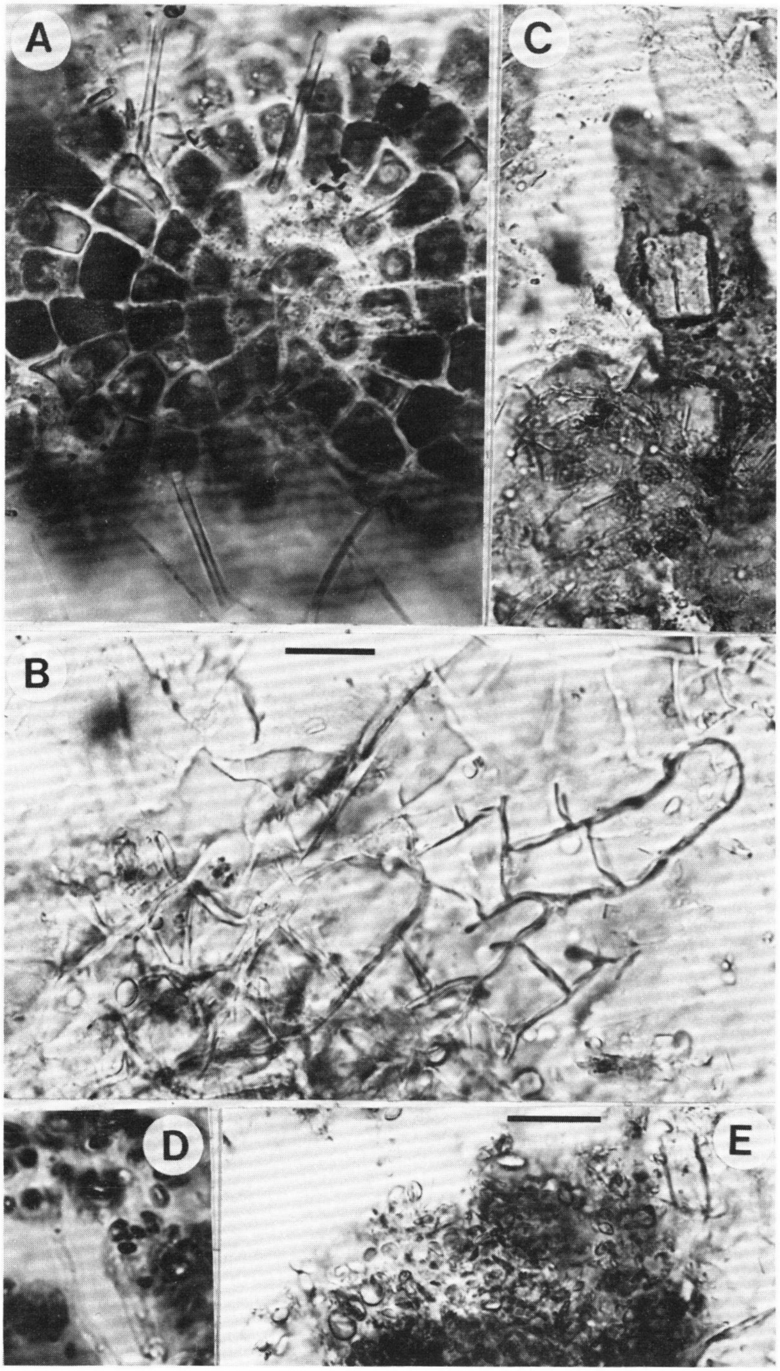

Fig. 2. Food and feeding of *Gammarus pulex* (L.). A, *Coleochaete scutata* colony showing cells with open tubes; B, *Coleochaete scutata* in a faecal pellet showing removal of contents; C, emptied *Eunotia veneris* on *Nitella* wall plates, in a faecal pellet; D, *Pythium* fungus amongst naturally decomposing *Nitella* chloroplasts, starch grains now very conspicuous; E, partially digested *Nitella* chloroplasts, but with starch grains still visible in a faecal pellet. Scale lines or equivalents: A, B, C: 30 μm; D, E: 40 μm.

Cells of the main axes, attached end to end, were 3.0-6.5 cm in length and 1.0 mm in diameter. Most were fully turgid and alive. They showed counter-current streaming in their internal cytoplasm and the continuous lining of chloroplasts (fig. 1F) was pressed tightly against the long walls. These chloroplasts contained large starch grain inclusions, of a characteristic shape, a biconvex disc, staining blue with iodine solution. The walls consisted of characteristic joined 'plates', approximately square in shape and about 40 μm across (fig. 1C). As far as can be ascertained these have not been reported before for *Nitella*; they constituted a valuable morphological marker for consumption of the plant (see below).

Cells of the lateral branches, which originated at the nodes between the main axis cells, were only 0.5 mm diameter and correspondingly shorter. They were vulnerable to mechanical damage and many were flaccid and dead. Both healthy and dead cells of the main axes and lateral branches were liberally clothed with algal epiphytes. The main algal epiphytes were the green algae *Bulbochaete* sp., *Coleochaete scutata* Brébisson (fig. 2A) and *Oedogonium* sp. together with the diatom, *Eunotia veneris* Kützing & O. Müller. *Coleochaete scutata* was most conspicuous on the main axes and the *Eunotia* reached its maximum development on the lateral branches, often covering them entirely. Once the *Nitella* cells were damaged, fungi could enter and grow, initiating the process of decomposition. The main internal fungal colonists were *Diplophlyctis intestina* (Schenk) Schroeter (Phycomycetes, Chytridiales), and *Pythium* sp. (Phycomycetes, Perenosporales) (fig. 2D).

Animals were routinely maintained on decaying elm leaf food and transferred to *Nitella* to make observations. Feeding behaviour on the part of the animal, with *Nitella*, was recognised on the criteria of: (1) firm grasping of the *Nitella* cell with the fore-limbs; (2) close adpression of the projection on the lower side of the head to the *Nitella* cell (fig. 1A, B); (3) strong vibration of the whole body. The frequent predilection of the animals for the lateral branches of the *Nitella*, rather than cells of the main axes was noted. Main axes were of such a diameter that even the largest animals could not ingest them complete.

When single cells of the main axes were trimmed, with scissors, free of all lateral branches, the animals investigated both ends for some time. Eventually one of two feeding strategies was adopted. The first strategy was observed in a large animal (31.6 mg wet weight) which took up a grasping position with the long axis of the *Nitella* cell at right angles to that of its own body. The cell was severed and fell apart in two halves. The open end of one half was then grasped, this time with the long axis of the *Nitella* cell parallel with that of its own body (fig. 1A, B). Examination of faecal pellets from this animal invariably showed *Nitella* cell wall material, usually with its plate structure visible (fig. 1G, H) and epiphytes still attached, but *Nitella* chloroplasts only rarely. Apparently once the large *Nitella* cell was punctured the cytoplasmic turgidity was lost and the chloroplast layer was no longer pressed tightly against the cell wall (fig. 1E). Consequently it was swept into the mouthparts only very occasionally, as the animal consumed that cell wall (fig. 1D). *Nitella* chloroplasts in the faecal pellet material showed changes suggestive of partial digestion, i.e., loss of physical definition and a more yellow to brown colour (denoting degradation from chlorophylls to phaeophytins), although the characteristic starch grains, staining with iodine, were still present (fig. 2E). In fact presence of the latter was regarded as diagnostic. Comparing the appearance of the epiphytes on the unconsumed *Nitella* cell surface and in the faecal pellets, it was clear that the cells of *Coleochaete scutata* were being emptied of their contents in the animal's gut (fig. 2B) whereas those of *Bulbochaete* and *Oedogonium* were not. The second feeding strategy on a large, trimmed, intact *Nitella* cell was observed for a smaller animal (7.5 mg wet weight). This animal clasped the cell in various orientations but did not succeed in puncturing it overnight. However, there were copious faecal pellets, usually showing *Nitella* cell wall material, in association with cells of *Eunotia*, which were often damaged (even crushed) and completely emptied of their contents (fig. 2C). In a few of the faecal pellets the *Nitella* cell wall content was minimal and crushed *Eunotia* cells predominated. This might infer that scraping off the wall rather than its indiscriminate consumption might have occurred.

When a trimmed cell of the main axis was cut into two with scissors, clear cytoplasm (but not chloroplasts) exuded at each cut end. This had not been observed when the cells were severed by the animals themselves. The exuded cytoplasm was visible to the naked eye as a firm hemi-spherical gel which was static for some time. An introduced animal investigated and then ignored the gel at first but eventually firm attachment and body vibration suggested that feeding on it was in progress. In general observations, with individual animals feeding on any part of the plant at their own choice, the lateral branches were often seen to be consumed entire. Sometimes they were broken off by the exertions of the animal and carried away in the manner of a man playing a pipe.

DISCUSSION

In regard to feeding and growth of *G. pulex* there is still uncertainty about the mode of extraction from the various plant cells which are consumed. Observational evidence on fungal food suggests that extraction can occur through submicroscopic pores between adjacent cells of the hyphae (Willoughby & Earnshaw, 1982). In this connection it is likely that the *Pythium* observed inside the decaying cells of *Nitella* would be extracted when this plant material, in a more moribund condition, is consumed. Observational evidence on algal food suggests that diatom cells are particularly vulnerable to extraction because there are exposed cell membranes, uncovered by cell walls, at their external surfaces (Moore, 1975). These current observations confirm the diatom vulnerability for *Eunotia* and add *Coleochaete scutata*, a green alga, to the dietary list. *Coleochaete* *scutata* consists of flat plates of cells, each of which has a protruding tube into which fits a fine bristle. This bristle is frequently lost and the open tube, 2 μm across, is then apparently vulnerable to entry of the digestive enzymes of *G. pulex*. Observations on digestion of the cytoplasm and chloroplasts of *Nitella* itself have been minimal in this present contribution. However, these would obviously be very rewarding if material with healthy rather than senescent lateral branches (as here) could be produced and presented to the animal.

RÉSUMÉ

Lorsque *Gammarus pulex* (L.) (Amphipoda) se nourrit de l'algue *Nitella* (Chlorophyceae, Charales), son comportement se caractérise de la manière suivante: 1) les appendices antérieurs empoignent l'algue; 2) la saillie, à la partie inférieure de la tête, est pressée contre l'algue; 3) le corps entier est soumis à de fortes vibrations. Le paroi cellulaire et les chloroplastes de *Nitella* sont ingurgités et il en est de même de ses épiphytes, c'est à dire *Bulbochaete*, *Coleochaete scutata*, *Eunotia veneris* et *Oedogononium*. L'analyse des excréments prouve cependant que la matière soumise à la digestion provient uniquement des chloroplastes de *Nitella* et des contenus cellulaires de *Coleochaete scutata* et *Eunotia veneris*.

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Received for publication 14 January 1982.