Feeding of the freshwater bryozoan *Plumatella fungosa* (P a l l.). 1. Food composition and particle size selection

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Abstract — The main component of the diet of bryozoan Plumatella fungosa were fine nannoplankton algae and filamentous Cyanophyta and Chlorophyta. Comparing the frequency of various kinds of particles in the seston and in the content of the alimentary canal of P. fungosa, a selective assimilation of algae of various sizes was observed. The finest cells (under 10 μ m or 10-20 μ m) and particles of about 40-170 μ m were filtered most intensively. The mechanism of selection of food particles by bryozoans are discussed.

Key words: Bryozoa, Phylactolaemata, Plumatella, feeding, diet, food selectivity.

1. Introduction

Freshwater bryozoans (Bryozoa) feed on the suspension filtered from the water surrounding their colonies. The literature information about the food composition and also concerning the possibilities of selection by these animals of seston particles is scanty. Jonasson (1963), Ryland (1970), and Bushnell (1974) mention in the diet of bryozoans bacteria, protozoans, various groups of algae, rotifers, microcrustaceans, and particles of organic detritus.

In the existing literature, no information is to be found on the feeding of *Plumatella fungosa* (Pall.), one of the commonest representatives of Phylactolaemata in European waters. It is characterized by large sized individual specimens (zooids) and the forming of massive, compact, and thick colonies (Kluge 1949, Pennak 1953, Lacourt 1968). In some water bodies, this bryozoan achieves a very high biomass, exceeding 1.5 kg fresh weight per m^2 of littoral (Jonasson 1963, Job 1976). In spite of numerous occurrence, its biology is still very little known.

The aim of the present work was to describe the composition of the food of P. fungosa in two eutrophic lakes with a varied composition of seston as well as to investigate the possibilities of selection by these animals of the available food particles.

2. Study area, material, and methods

The investigations were carried out in 1982 on the bryozoan P. fungosa, occurring in eutrophic lakes: Lake Mikołajskie (460 ha, 11.0 m mean depth) and Lake Jorzec (42 ha, 5.5 m depth) both in the Masurian Lake District, northeastern Poland. Additional observations were also made in 1983 and 1984. P. fungosa colonies were found in these lakes on the surface of aquatic plants, mainly on Phragmites australis (C a v.) Trin. ex Steudel and Nuphar lutea Sm.

The investigations were carried out in 1982 on the bryozoan *P. fungosa*, occurring in eutrophic lakes: Lake Mikołajskie (460 ha, 11.0 m (zooids). Samples of colonies were taken at various times, almost throughout the period of occurrence of bryozoans in the two lakes. Fragments of colonies were immediately preserved in 4% formalin. At the same station a 2.5 dm³ sample of lake water was also taken and preserved in formalin, used for the later determination of seston composition. From each colony 10 grown zooids were taken and their gut content was prepared. All particles with a diameter of over 2.5 μ m were identified, counted, and measured under the microscope. The food mass was estimated on the basis of microscopic measurements of particle volume, assuming that the specific gravity of phytoplankton approximates 1 g cm⁻⁸ (S p o d n i e w s k a 1967). In a similar manner the composition of the seston was analysed.

The selectivity of food by bryozoans in comparison with separate groups of particles was estimated on the basis of the coefficient value of food selectivity according to I v l e v (1977), calculated according to the formula:

$$E = (r_1 - p_1) / (r_1 + p_1)$$

where:

 r_i — percentage share of particles in the described kind of food in the alimentary canal,

The coefficient assumes values from +0.1 to -1.0, thus positive ones indicate a positive selection of food particles and negative values a negative one.

3. Results

Analysis of the gut content of zooids of *P. fungosa* showed that they feed on algae, plakton animals, and detritus particles. Particles of mineral suspension and pollen of land plants in the gut content were occasionally found. Although in the investigated lakes the mean food composition of bryozoans for the whole season differed (Table I), in both lakes fine nannoplankton algae (diameter up to 50 μ m) and among net phytoplankton filamentous algae (of various length, maximum 1120 μ m) as well as large cells of dinoflagellates — *Ceratium* sp. (up to 350 μ m) and *Peridinium* sp. (up to 65 μ m), had the greatest share in the food mass.

Kind of food	Share in food mass (%)		Share in particle numbers	
	L. Mikołaj- skie	L. Jorzec	L. Mikołaj- skie	L. Jorzec
Fine nannoplankton algae (various taxons)	33.7	26.7	63.3	61.8
Filamentous Cyanophyta and Chlorophyta	26.2	31.3	14.4	17.8
Peridinium	25.8	0.6	3.7	0.1
Ceratium	12.4	26.9	11.6	7.7
Pennatae	0.7	1.2	5.4	3.9
Dinobryon sp.	0.6	7.8	0.6	4.1
Others	0.6	5.5	1.0	4.6

 Table I. Food composition of Plumatella fungosa in Lakes Mikolajskie and Jorzec, mean values, 1982

The food composition of P. fungosa resembled to a high degree the composition of the seston, though, not all groups of particles were equally assimilated by these animals (fig. 1). From the comparison of phytoplankton composition and the gut content of bryozoans

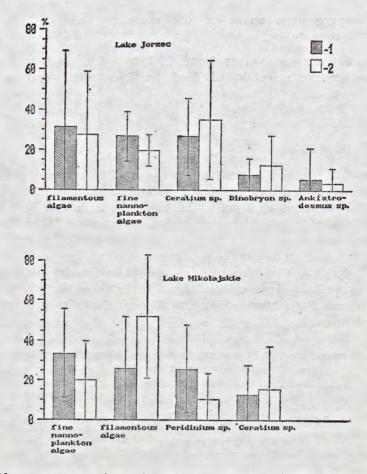


Fig. 1. Mean percentage share of particular groups of phytoplankton in the food mass of P. fungosa (1) and in the seston (2) of investigated lakes in 1982—1984

it can be seen that in Lake Mikołajskie P. fungosa filtered most effectively dinoflagellates of *Peridinium* genus and nannoplankton algae, whereas it rejected a large part of the filamentous algae (Cyanophyta and Chlorophyta). In Lake Jorzec the bryozoans most intensively filtered nannoplakton algae. In smaller quantities than in the seston, coenobia Dinobryon sp. and cells of Ceratium sp. were found in the alimentary canal.

In both lakes nannoplakton algae constituted the largest quantitative share of food particles. Their share changes according to the season from 31 to 84% in Lake Mikołajskie and from 31 to 90% in Lake Jorzec. Nannoplankton algae occurred in the form of single celles or small coenobiae. Cells of 5-10 μ m (29.2) were the most numerous fraction

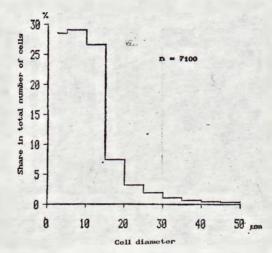


Fig. 2. Mean percentage share of various sized cells of nannoplankton algae, separated from caeca of P. fungosa from both lakes in 1982-1984

of particles, isolated from the gut content. Particles less than 5 μ m in diameter (28.5%) and 10—15 μ m (27.1%) also constitute a high percentage (fig. 2). Amongst the fine algae most frequently found in the guts of *P. fungosa* should be mentioned phytoflagellates, cryptophytes, blue-green algae, and diatoms of the subclass Centriceae. The fraction of nannoplankton algae in the food mass of *P. fungosa* from Lakes Mikołajskie and Jorzec changed during the season (fig. 3) and was distinctly larger in summer than in autumn.

In evaluating food selectivity on the basis of the I v l e v coefficient value it was observed that nannoplankton algae of various size were taken from the suspension with different intensity (fig. 4). In most analyses carried out in the two lakes, it was found that bryozoans positively selected particles under 10 μ m or 10-20 μ m in diameter. Larger cells were generally rejected, but the largest particles (over 40 μ m, sometimes 30 μ m) were usually found in alimentary canals more frequently than would appear from their quantity in the seston.

In the guts of *P. fungosa* filamentous algae were very frequently observed. Their fraction in the mass of food approximated to the mass of nannoplankton algae (Table I). As in the case of the finest fraction of food particles, seasonal changes in the share of these algae were observed in the diet of bryozoans. They approximated to changes of their fraction in the seston mass (fig. 3). Differences in the size of filamentous algae found in the guts of bryozoans and in the seston were observed. In the alimentary canals of *P. fungosa* fragments of filaments shorter than 50 μ m (25.5% of the total number of filamentous algae) (fig. 5) were the most numerous group. The mean length of

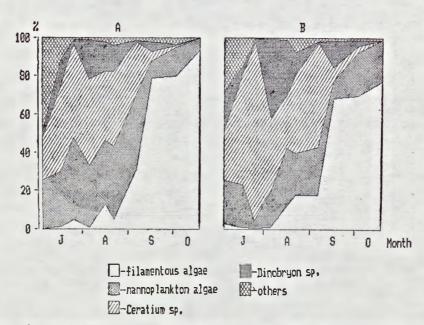


Fig. 3. Seasonal changes of the gut contents of *P. fungosa* (A) and of phytoplankton composition in Lake Jorzec (B), shown by fractions of particular groups of particles in their total mass, 1982

filamentous algae, isolated from the guts of *P. fungosa* was 114 \pm 47 μ m while in the seston it was 246 \pm 123 μ m. These differences probably resulted from the nature of food selectivity of the investigated bryozoans. It is not possible, however, to exclude fragmentation of some of these particles in the guts, as the result of digestion and peristalsis of the alimentary canal.

Cells of large species of dinoflagellates from Ceratium and Peridinium genera (Table I) constituted a considerable percentage of the food of *P. fungosa*, particularly in Lake Mikołajskie. Cells of Ceratium sp. were found in the guts of bryozoans almost exclusively in fragments, whereas *Peridinium* sp. in general occurred in the form of whole cells.

Colonial chrysophyceans of the genus Dinobryon (Table I) were of essential importance in the feeding of *P. fungosa*, particularly in Lake Jorzec. In the seston of both lakes the mean number of cells in coenobia of Dinobryon sp. was 6.9 ± 9.0 . In most cases, in the guts of bryozoans single cells of these algae were found. The few colonies consisted, on the average, of 3.5 ± 2.8 cells. This phenomenon may give evidence both of more intensive filtration of single cells from the seston and the decay of large coenobia of Dinobryon sp. in the course of displacement of food in the gut.

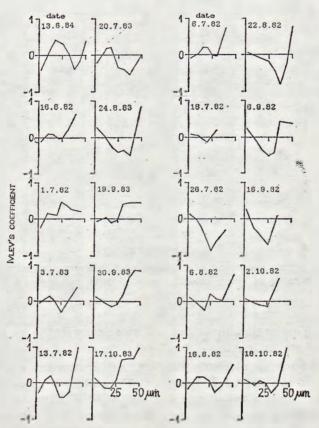


Fig. 4. Intensity of filtration of nannoplankton algae of various diameter indicated by the coefficient of Ivlev's food selectivity in Lakes Mikolajskie and Jorzec in various periods of investigation

Worthy of note is the constant share of elongated and rigid cells of pennate diatoms (Pennatae) in the diet of bryozoans. This ranged from 0.1 to 12.1% of the total numbers of food particles. During filtration the bryozoans most intensively caught cells $85-170 \mu m$ length from the seston (fig. 6). In the guts single diatoms were found more frequently than larger coenobia of these algae. In the guts on average 3.0 ± 2.0 cells per coenobium were observed, while in the seston 7.2 ± 7.3 cells per colony of these algae. The mean length of diatom cells entering into the food composition of *P. fungosa* was in fact less than that of cells of Pennatae in the seston. Many cells extracted from the guts of bryozoans were damaged ($24 \pm 14\%$). Remnants of Pennatae cells were also found in the seston, but they were much smaller in quantity

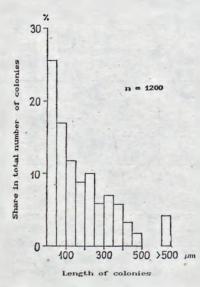


Fig. 5. Mean percentage share of colonies of filamentous algae of various length in the total number of these colonies isolated from the guts of *P. fungosa* from both lakes

(8 \pm 10%). The largest, undamaged diatom cells in the guts of bryozoans reached 350 μm in length.

Animals such as plankton rotifers and protozoans also entered into the food composition of P. fungosa. The method used for preserving the material prevented determination of the number of protozoans consumed. The presence of these animals in the diet of P. fungosa may, however, be inferred on the basis of a few shells of protozoans

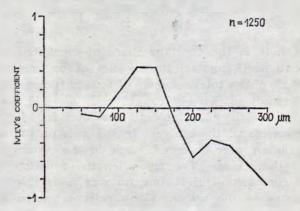


Fig. 6. Intensity of filtration of Pennatae of various cell length indicated by the coefficient of Ivlev food selectivity (mean values for both lakes)

of Tintinnopsis genus retained in the guts. In some of the preparations (35%), the presence of single plankton rotifers was noted. Most often found were rotifers of Keratella and Trichocerca genera. Their share in the food mass of bryozoans was similar in the two lakes and did not exceed 0.6%.

4. Discussion

Raddum and Johnsen (1983) when investigating the feeding of the bryozoans Fredericella sultana (Blum.) observed that it takes from the environment all particles which are able to pass through the mouth opening. They also observed that this species shows food selectivity in relation to some food particles (Bacillariophyceae cells). The food composition of this filter feeder was to a high degree dependent on the composition of the seston. On the basis of investigations carried out on Plumatella repens L., P. fruticosa Allm., and Cristatella mucedo Cuv., Kamiński (1984) found that the diet of bryozoans underwent numerous changes during the season. Particular species differed from each other in the size range of food particles filtered out from the water and in the intensity of assimilation of algal cells of different shapes and sizes from the environment.

The present investigations carried out on *P. fungosa* showed that in spite of a general similarity of the gut content of bryozoans to the composition of the phytoplankton, some differences occurred in the intensity of assimilation of particles of various size. During feeding, *P. fungosa* positively selected the finest particles (under 10 μ m or 10-20 μ m and large particles of about 40 to 170 μ m in size. The explanation of this phenomenon should be sought in the mechanism of food assimilation by Phylactolaemata.

P. fungosa can assimilate food by filtration and sedimentation of suspension. The stretched out tentacles of the lophophore are covered with numerous cilia, whose motion causes rotary water current. With this current fine particles of seston reach the bottom of the lophophore and settle on it. The swallowed food is pushed through the ciliate esophagus to the large caecum. The positive selection of particles, exceeding in size a few μ m, results most likely from ciliary feeding. Particles of smallest size (less than a few μ m) and of lowest weight may for the most part be carried out together with the outlet current beyond the lophophore and reach the esophagus more rarely that would appear from their numbers in the seston.

The effective catching of large-size particles $(40-170 \ \mu m)$ is most likely connected with another mechanism of food assimilation. The feeding of bryozoans on large algae may be accompanied by the motions

of tentacles, this being interpreted in various ways by various authors. Pennak (1953) presumes the motions of the tentacles to be a mechanism of clearing away from the lophophore large and inedible particles which were close to the mouth opening. The changes in positions of the tentacles observed during food assimilation by F. sultana (Raddum, Johnsen 1983) and by some sea bryzoans (Winston 1978, Okamura 1987) were described as motions aimed at enclosing and pushing down food particles into the esophagus (tentacular feeding). Personal observations in vivo of food assimilation by P. fungosa showed that the reaction of zooids, accompanying the swallowing of large particles may be different. Assimilation or rejection of a long particle of seston (Pennatae cells, filamentous colonies of blue-green algae e.g. Aphanizomenon sp.) was dependent on the angle at which it dropped onto the lophophore. Particles settled across the horse - shoe shaped lophophore caused motions of irritated tentacles untill the particle changed its position or was floated off by the water current. Large diatoms or fragments of colonies of filamentous algae directed perpendicularly (from above) to the lophophore immediately reached the mouth opening and were at once swallowed without the tentacles being moved. Thus, by means of the cilia and the suction effect of the esophagus, P. fungosa could assimilate particles of filamentous algae reaching 1120 µm in length. It may be supposed that the motions of the lophophore tentacles contribute to the directing of large particles of seston towards the mouth opening but they do not serve for pushing food into the esophagus. When understood thus, tentacular feeding was the most effective in relation to particles of about 40 to about 170 um in size.

In the caeca of *P. fungosa* it was observed that the share of particles of $20-40 \mu m$ diameter was less than in the seston. The phenomenon of low effectiveness of feeding by bryozoans on that fraction of food had already been observed by Raddum and Johnsen (1983) in investigations on *F. sultana*. One must agree with the interpretation accepted by these authors that such particles are too large for ciliary and too small for tentacular feeding.

5. Polish summary

Odżywianie się słodkowodnego mszywioła Plumatella fungosa (Pall.). 1. Skład pokarmu i selekcja wielkości cząstek pokarmowych

Badania prowadzono w latach 1982—1984 w dwóch jezionach eutroficznych, w Polsce północno-wschodniej. Stwierdzono, że głównym składnikiem pokarmu P. fungosa był fitoplankton. W obydwu jeziorach najwyższy udział w diecie mszywiołów miały drobne glony nannoplanktonowe (różne taksony) o średnicy komó-

rek do 50 μ m oraz nitkowate sinice i zielenice (tabela I) o długości do 1120 um. Skład pokarmu mszywiołów zmieniał się znacznie w ciągu sezonu (ryc. 3). Choć dieta mszywiołów w dużym stopniu przypominała skład fitoplanktonu w wodzie otaczającej kolonie, jednak nie wszystkie frakcje sestonu były równie intensywnie wykorzystywane przez te zwierzęta (ryc. 1). W przewodach pokarmowych mszywiołów najliczniej spotykano cząstki o średnicy poniżej 15 μ m i długości poniżej 50 μ m (ryc. 2, 5). Z porównamia składu fitoplanktonu i zawartości przewodów pokarmowych *P. fungosa* wynika, że mszywioły najintensywniej odżywiają się cząstkami bardzo drobnymi (od kilku do około 20 μ m) oraz cząstkami dużymi, o wielkości od 40 do 170 μ m (ryc. 4, 6). W pracy wyjaśniono zjawisko selekcjonowania cząstek pokarmowych przez *P. fungosa* opisując mechanizm rzęskowego i czułkowego sposobu odżywiania się tych mszywiołów.

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