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Life cycle of the freshwater bryozoan *Plumatella fungosa* (P a l l.)

1. Seasonal changes in numbers and biomass

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A b s t r a c t - In the studied eutrophic lakes the freshwater bryozoan *Plumatella fungosa* produced annually at least 3 generations of colonies. The successive generations differed from each other in their biomass and mode of forming colonies (developed from statoblasts or larvae). The biomass and density of *P. fungosa* colonies in the littoral zone changed significantly during the season (May-November) and over a period of many years.

K e y w o r d s: Bryozoa, Phyloctolaemata, *Plumatella fungosa*, biomass, life cycle.

1. Introduction

In the moderate climatic zone the freshwater Bryozoa (Bryozoa, Phylactolaemata) exhibit a typically opportunist growth strategy. The colonies of most species develop from spring till autumn on the surface of substrata available for settlement and perish with the coming of winter. In the summer they may appear in great numbers and are capable of very rapid colonization of new substrata as well as a very rapid increase in biomass (J o n a s s o n 1963, B u s h n e l l 1966, J o b 1976, K a m i ń s k i 1990).

The life cycle of the freshwater bryozoan is as yet little known. The published studies referring to the seasonal dynamics of numbers and biomass of Bryozoa are few and mostly based on the results of short term investigations or chance observations. Only the development of the population of *Plumatella repens* L. in the North American lakes has been described in greater detail (B u s h n e l l 1966). On the basis of the available data it may be assumed that within a single season the freshwater Bryozoa produce from 2 to 4 generations of colonies (R a d d u m 1970, B u s h n e l l 1974) and that the particular generations may differ from each other in the attained biomass and origin (colonies developed from statoblasts or floating larvae).

The aim of the present study was to investigate the seasonal changes in the biomass and density of colonies of one of the most common representatives of Phylactolaemata - *Plumatella fungosa* (P a l l.), considering especially the number of generations developing within one season and the way in which the colonies of these animals were formed.

2. Study area, material, and methods

Investigations of the life cycle of *P. fungosa* were carried out in the periods 1979-1980 and 1982-1983 in the eutrophic lakes Mikołajskie and Jorzec (Masurian Lake District, northeastern Poland). The seasonal changes in the biomass and density of the colonies were investigated at 9 stations established in the littoral zone of the two lakes. Changes in the size of the bryozoan colonies appearing on the leaves of *Nuphar lutea* Sm. were examined only in Lake Jorzec. The colonies were collected from substrata most abundantly inhabited by *P. fungosa*, i.e. the stalks of *Phragmites australis* (C a v.) T r i n. ex S t e u d e l and from the floating leaves of *Nuphar lutea* Sm. (K a m i ń s k i 1990). At each station, many times during the season, there were collected samples comprising 30 fragments of the stalks of *P. australis* (sections from a depth of 0-50 cm) and 10 leaves of *N. lutea*. In the collected samples the density and the (fresh or dry) biomass of the colony of *P. fungosa* as well as the surface area of the examinated plants were determined and these values then recalculated as the mean from the 9 stations. The surface area of the substratum was calculated by measuring the length and diameter (or width) of the particular plant fragments. The origin of the colony was established on the basis of the differences in the structure of young colonies emerging from statoblasts or developed from larvae (K a m i ń s k i 1990). In Lake Mikołajskie also the seasonal changes in the biomass and the distribution of the colonies of *P. fungosa* on artificial substrata were examined. These substrata were 10 cm strips of polythene sheeting suspended vertically in the water (from the surface to a depth of 4 m) and exposed at one station from the beginning of May. Every 15 or 16 days, 2 substrata were collected for investigation until the period of dying off of all colonies (usually until the middle of October).

3. Results

The first colonies of *P. fungosa* appeared in the littoral zone of each lake in May or at the beginning of June, at the water temperature of 12-14°C. Colonies of the first generation of the bryozoans were found on substrata remaining in the lake from the previous vegetation season - dead stalks of *P. australis*, submerged branches of trees, bridge piles, and stones. In that period no development of Bryozoa was observed on living *Nuphar* leaves wintering under the surface of the water or on young germinating shoots of *Phragmites*. Observations of substrata on which the first colonies appeared showed on their surface the presence of sessoblasts and fine, chitinous remnants of *P. fungosa* colonies from the previous year, young colonies of the first generation, numbering at that time from a dozen or so up to some hundreds of zooids, were formed as a result of the development of statoblasts. This was clearly evidenced by the presence of preserved halves of empty capsules of sessoblasts found alongside the oldest zooids, occupying the central part of the colony. At the beginning of June, in Lake Mikołajskie, the biomass of the first generation of *P. fungosa* in the new vegetation season did not exceed 2 mg of fresh weight per 100 cm^2 of the surface of the examined substrata. Towards the end of this month, the colonies of the first generation, developing on the surface of dead stalks of last year's *Phragmites*, reached a biomass of 67.8 ± 14.6 mg of fresh weight per 100 cm^2. In the second decade of July or slightly earlier these colonies died off and fell from the stalks, or were mechanically destroyed by the waves together with the substratum.

Colonization of young shoots of macrophytes by *P. fungosa*, began in Lake Mikołajskie between the first half of June (1979) and the first decade of July (1982). The settling on new substrata occurred in the first place as a result of the settlement of the larvae produced by the first generation of this bryozoan. The presence of a few colonies emerging from floatoblasts was observed in that period mostly on *Nuphar* leaves. Unlike the colonies developing from floating larvae, these colonies were characterized by multi-directional growth and by the presence of chitinous fragments of statoblasts with the oldest zooids. On the surface of the floating leaf blades of *N. lutea* the proportion of colonies emerging from floatoblasts was from 0.7 to 2.0%, while on *P. australis* it did not exceed 0.2% of their total number.

From the moment of appearance of the first young colonies of bryozoan on the macrophytes their numbers increased until after 5-8 weeks they attained their maximum. The maximum density of colonies on *P. australis* was up to 4.3 colonies per 100 cm^2 of the plant surface. Intensive colonization of substrata by the larvae led to an increase in the proportion of macrophytes inhabited by *P. fungosa* (fig. 1). The increase in density of the colonies observed in July was accompanied by an increase in the mean biomass of individual zoaria (Table I). The effect of the rising density of the colonies and the growing numbers of zooids in particular ones approximated to the exponential rate of the biomass increase per unit surface area of substratum (fig. 2).

During the four-year period of investigation it was found that the maximum values of the biomass of *P. fungosa* on *P. australis* appeared between 20th July and 20th August. Considerable fluctuations in the maximum biomass of these animals were observed in particular years - from 130 to 1480 mg of fresh weight

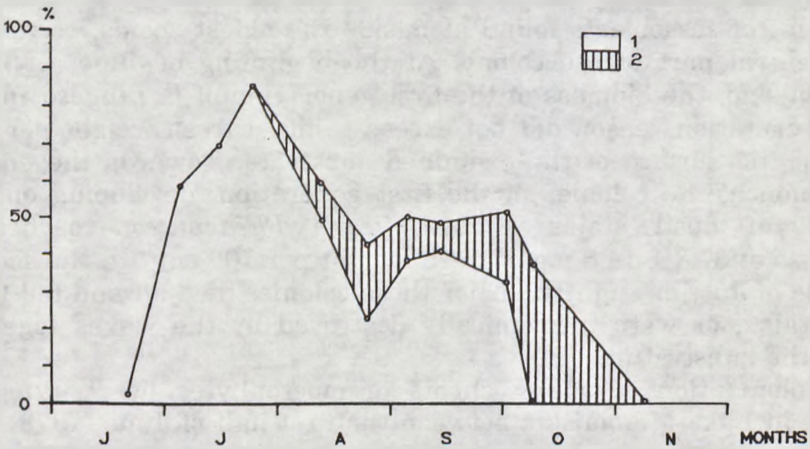

Fig. 1. Proportion (%) of living stalks of *Phragmites australis* inhabited by *P. fungosa* in Lake Mikołajskie in 1983. 1 - living colonies; 2 - dying colonies

Table I. Density and biomass of *Plumatella fungosa* colonies on living stalks of *Phragmites australis* in Lake Mikołajskie in 1983

Date	Number of colonies per 100 cm^2		Biomass of single colony (mg d.w.)	
	living	dead	living	dead
20.06	0.03	0.00	5.8	0.0
4.07	1.98	0.00	5.4	0.0
14.07	3.16	0.00	37.4	0.0
23.07	4.27	0.00	234.6	0.0
11.08	0.34	1.44	834.0	264.7
23.08	0.45	0.52	16.1	14.1
4.09	1.34	0.32	86.2	< 10
13.09	1.24	0.19	178.6	< 10
30.09	0.83	0.30	140.1	< 10
17.10	0.00	1.34	0.0	58.1

per 100 cm^2 in 1980 and 1979 respectively. The greatest biomass of the bryozoan developing on *N. lutea* did not exceed 350 mg of fresh weight per 100 cm^2 of the substratum surface.

After the maximum biomass had been reached, in the course of the following 2-4 weeks a rapid diminution of the density of the colonies and a decrease in their biomass and in the proportion of substrata inhabited by the bryozoans were observed (Table I, figs 1, 2). The colonies began to die away and large fragments or whole colonies fell from the plants.

A renewed increase in the biomass of the studied animals was noted after a further 3-4 weeks. It was observed that new colonies of *P. fungosa* developed both from the floating larvae settling on the substrata and from the sessile statoblasts produced by the second generation of the bryozoan. On the surfaces of *Nuphar* and *Phragmites* the density of colonies was again on the increase. A rise in the proportion of substrata inhabited by the bryozoans was also noted.

The colonies of the third generation of *P. fungosa* developing from the larvae and from the sessoblasts reached a biomass lower than that observed at the end of July and the beginning of August. After the second maximum of density and biomass (less than 180 mg of fresh weight per 100 cm^2) the bryozoans gradually died off (fig. 2). At the end of the vegetation season the remnants of all the colonies fell off the substrata or, especially in the case of colonies developing on *Nuphar*, decayed together with the substratum.

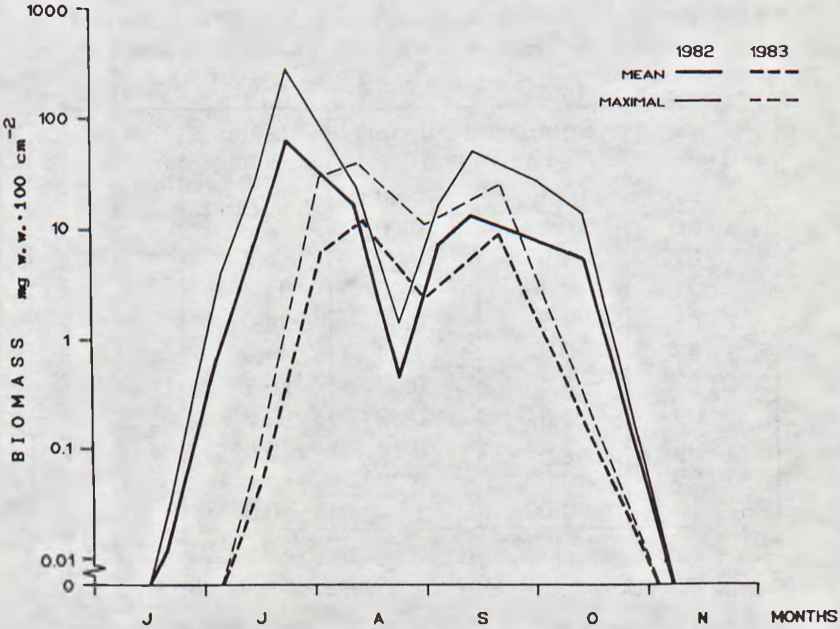

Fig. 2. Mean and maximum biomass of *P. fungosa* on one-year-old stalks of *Phragmites australis* in Lake Mikołajskie

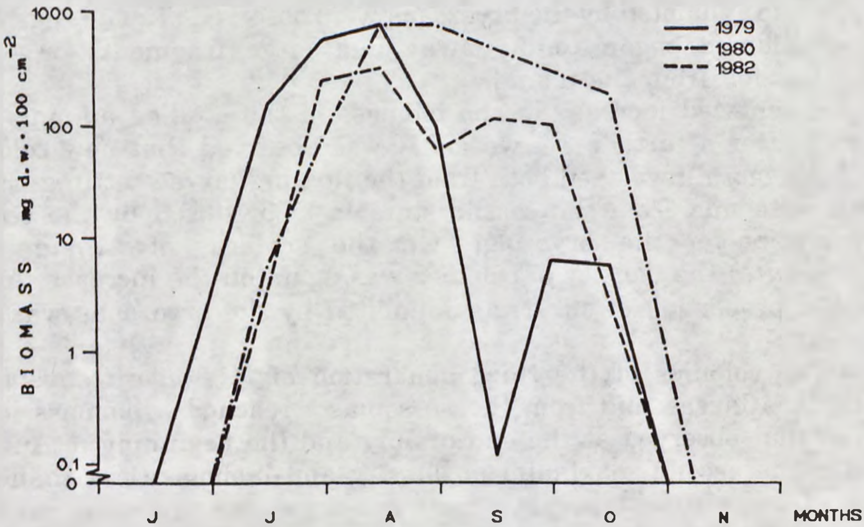

Fig. 3. Biomass of *P. fungosa* on artificial substrata in Lake Mikołajskie. Mean values for depths from 0-3 m

The progress of seasonal changes in the biomass of the second and third generations of the bryozoan developing on artificial substrata was similar (fig. 3). Only in 1980 did the necrosis and disintegration of the colonies of the second generation of the bryozoan and the growth of those of the third generation coincide in such a way that there occurred only one maximum of the biomass of *P. fungosa* (at the turn of August).

During the season not only the total biomass of *P. fungosa* in the littoral zone but also its vertical distribution on the substrata underwent changes (fig. 4). In the first period of the occurrence of the bryozoans (up to middle of August) the maximum values of their biomass were usually recorded at depths from 1 to 3 m. Later on, owing to necrosis and falling off of the colonies from the substrata, the vertical distribution of the biomass of *P. fungosa* underwent considerable changes. Colonies inhabiting substrata at depths from 0 to 0.5 remained on the substratum longer than any others and the biomass they attained was considerable.

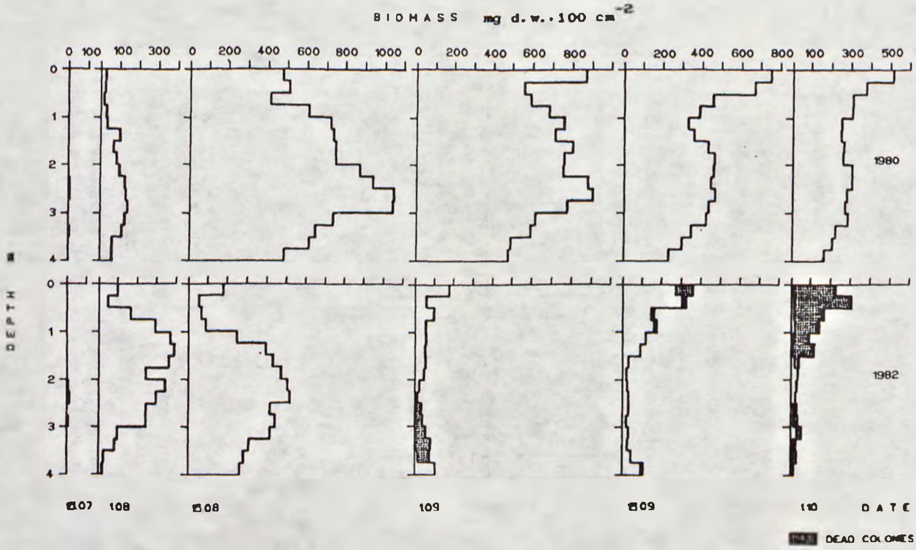

Fig. 4. Vertical distribution of the biomass of *P. fungosa* on artificial substrata in Lake Mikołajskie. The proportion of dead parts of the colonies in their total mass was determined only in 1982

Changes in the density and biomass of the bryozoan were accompanied by structural transformations of the size of their colonies (fig. 5). At the beginning of July the age structure of the population was characterized by a very high proportion of the smallest (youngest) colonies and the absence of zoaria of older age classes. Up to the first ten days of August an increase in the proportion of older colonies was observed, while at the end of that month the structure of the population was "rejuvenated". This was due to mass necrosis of the colonies of the second generation of the bryozoan and gradual recolonization of the *Nuphar* leaves by the young colonies of the third generation of *P. fungosa*. At the beginning of October the age structure acquired the features of a dying population. The youngest age class at that time was very small, forming a narrow base for the age pyramid of the population.

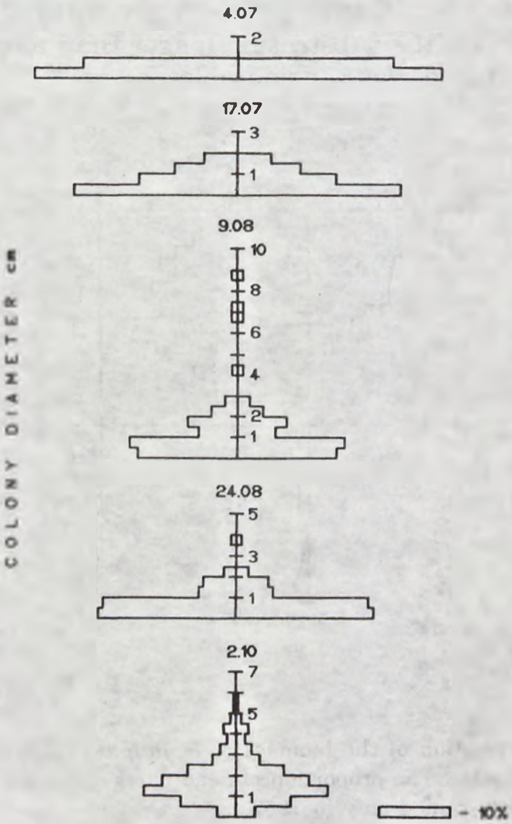

Fig. 5. Size distribution in 1979 of a *P. fungosa* colony on floating leaves of *Nuphar lutea* in Lake Jorzec, expressed as the ratio of colonies having a defined diameter to their total number

4. Discussion

The investigations showed that colonies of *P. fungosa* appear in the lakes from May or June until October or November. Kochańska (unpubl. data), in her investigations carried out in 1965, observed the occurrence of *P. fungosa* in Lake Mikołajskie only from the beginning of August until the end of October, most probably not taking into consideration the presence of the bryozoan on solid substrata on which the colonies of the first generation develop. Job (1976) still found living colonies of *P. fungosa* in a small water body in Belgium at the beginning of December. It may be assumed that on the territory of Poland this species inhabits lakes for 5-6 months in the year, at a time close to the vegetation period of most littoral macrophytes.

The course of changes in the biomass of *P. fungosa* within the whole period of its occurrence, as well as the structural changes in the size of the colonies on living macrophytes, clearly indicate that within one year the studied bryozoan produce at least 3 generations of colonies. The particular generations differed from each other with respect to origin and total biomass of the colony. The maximum biomass was attained by colonies of the second generation of *P. fungosa* between the last ten days of July and the beginning of September.

The general density and biomass of the bryozoan, as well as the course of the seasonal changes in the numbers of these animals may be affected by the trophy of the reservoir, its depth, and the number and kind of substrata available for settlement. Dendy (1963), who conducted research on Bryozoa occurring in ponds, as well as Jonasson (1963) in his investigations of Bryozoa inhabiting lakes, observed that the biomass of the Bryozoa was positively correlated with the trophy of the water body and, accordingly, with the abundance of seston on which these animals feed. The date of occurrence of the biomass maximum was dependent on the mean depth of the water body. In shallow lakes the maximum biomass of Bryozoa was noted earlier than in deep waters (Jonasson 1963). In the eutrophic Lake Esrom in Denmark, with its mean depth close to that of Lake Mikołajskie, the highest values of the biomass of Bryozoa were recorded towards the end of August and in September, thus a little later than in Lake Mikołajskie. Considering the selective character of the settlement of *P. fungosa* on various substrata, the species composition of macrophytes occurring in the lake may be of great importance for the total biomass of these bryozoans (Kamiński 1990). In the studied lakes the greatest biomass and density of the colonies of *P. fungosa* was found on *P. australis* and *N. lutea*, the values for the remaining macrophytes being much lower (K a m i ń s k i 1990). It may be assumed that the optimal conditions for the development of *P. fungosa* are those found in lakes of high trophy, in which the littoral zone is abundantly overgrown by emergent macrophytes and plants with floating leaves.

Worthy of note are the considerable fluctuations of the biomass of Bryozoa in the successive years of investigation. This was earlier noted by J o n a s s o n (1963) and K o c h a ń s k a (unpubl. data). In the successive vegetation seasons the differences in the maximum values of the biomass of these animals may be anything up to even a hundredfold. In Lake Mikołajskie the differences in the maximum biomass of the bryozoans observed in the course of the investigations were some ten- to twentyfold. The reason for such great fluctuations, considering the relatively short period of the present investigations, are difficult to establish. Probably of decisive importance for the development of the population are the spring-summer thermal regime of waters (affecting the development of statoblasts and the effectiveness of the processes of sexual reproduction) and the concentration of seston (determining the rate of biomass increase).

The development of the generations of *P. fungosa* clearly distinguished with respect to origin and time of occurrence has not been described so far. Only R a d d u m (1970) noted that in one of the Norwegian lakes there occur within one season 3-4 generations of *P. fungosa* and that the first of them develops from sessile statoblasts. The origin of colonies forming the successive generations was not explained, probably on account of the then prevailing view concerning the ineffectiveness or limited efficiency of the process of sexual reproduction of Phylactolaemata in a moderate climate. B u s h n e l l (1974) assumed that the successive generations of Bryozoa develop from floatoblasts. On the basis of the results of the present investigations it can be stated that a decided majority of the colonies of the second and some of those of the third generation of *P. fungosa* develop as a result of the settlement of larvae of this species. The numbers of larvae produced as a result of sexual reproduction and their discrimination of the substratum to be occupied have a significant effect on the distribution of the colonies and the biomass of *P. fungosa* in the lake littoral zone (K a m i ń s k i 1990).

5. Polish summary

Cykl życiowy słodkowodnego mszywioła *Plumatella fungosa* (P a l l.)

1. Sezonowe zmiany liczebności i biomasy

Badania nad liczebnością i biomasą kolonii *Plumatella fungosa* prowadzono w latach 1979-1980 oraz 1982-1983 w eutroficznych jeziorach Mikołajskie i Jorzec (Pojezierze Mazurskie, północno-wschodnia Polska). Kolonie mszywiołów pobierano wielokrotnie w ciągu sezonu zarówno z roślin wodnych (*Phragmites australis* (C a v.) T r i n. ex S t e u d e l., *Nuphar lutea* S m.) na 9 stanowiskach w litoralu obydwu jezior, jak i ze sztucznych podłoży eksponowanych na 1 stanowisku w jeziorze Mikołajskim. W zebranych próbkach określano liczebność kolonii, ich masę (świeżą lub suchą) oraz powierzchnię badanych podłoży. Na podstawie różnic w budowie kolonii rozwijających się bądź ze statoblastów, bądź w wyniku metamorfozy larw pływających, określano pochodzenie młodych kolonii *P. fungosa*.

Żywe kolonie mszywiołów spotykano w badanych jeziorach od maja lub czerwca do października lub listopada, przy czym maksymalną liczebność i frekwencję kolonii na podłożach stwierdzano w lipcu, a maksymalną biomasę zazwyczaj w lipcu lub w sierpniu (Tabela I, ryc. 1-3). Maksymalna biomasa *P. fungosa* na podłożach naturalnych wahała się w poszczególnych latach od 130 do 1480 mg św. m. 100 cm^{-2}. Pionowe rozmieszczenie biomasy *P. fungosa* na podłożach oraz struktura wielkości kolonii ulegały dużym zmianom sezonowym (ryc. 4, 5).

Na podstawie zebranych materiałów można twierdzić, iż w ciągu jednego sezonu występowały przynajmniej 3 generacje kolonii *P. fungosa*. Poszczególne pokolenia różniły się między sobą osiąganą biomasą, pochodzeniem (różnym udziałem kolonii powstających ze statoblastów lub larw), a niekiedy także miejscem występowania.

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