

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

2. Reproduction and general conclusions

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A b s t r a c t - The production of larvae, the formation of statoblasts, and the growth rate of colonies of *Plumatella fungosa* were investigated in two Polish eutrophic lakes. On the basis of the obtained results and data referring to the seasonal changes in the biomass, origin, and distribution of the bryozoan colonies the author gives a schematic presentation of the life cycle of *P. fungosa* in the studied lakes.

Key words: Bryozoa, Phylactolaemata, *Plumatella fungosa*, reproduction, growth rate, life history.

1. Introduction

Similarly, as almost all freshwater Bryozoa (Bryozoa, Phylactolaemata), *Plumatella fungosa* exhibits considerable differentiation in the mode of reproduction. An increase in the number of individuals in the colonies of these sessile animals takes place as a result of germination. Under favourable habitat conditions *P. fungosa* may initiate sexual reproduction, the effect of which is the production of freely floating larvae. Besides reproduction by way of gemmation and sexual reproduction it produces two kinds of statoblast: sessile (sessoblast) attached to the substratum and floating (floatblast) floating naturally on the water

surface. The development of statoblasts may be followed by the settlement of floatblasts on new substrata or by the reconstruction of colonies on a substratum already occupied by the previous generations of these animals (sessoblasts). Under moderate climatic conditions, when the colonies of a decided majority of the Bryozoa species perish with the coming of winter, the statoblasts make possible the permanent occurrence of populations of these animals in water ecosystems.

In the professional literature there have been many controversial opinions concerning the importance of the particular modes of reproduction for the development of a population of Bryozoa. Some authors ascribe the main role to the statoblasts (J o n a s s o n 1963, V i g a n o 1964, R a d d u m 1970). The importance of sexual reproduction is often questioned (P e n n a k 1953, B u s h n e l l 1974, K o n o p a c k a, S z y m a ł k o w s k a 1980, O d a, M a k a m u r a 1980) or, conversely, regarded as the main factor responsible for the density of the Bryozoa colonies in water bodies (K a m i ń s k i 1991). The importance of the particular ways of reproduction may differ in the successive generations of these animals (K a m i ń s k i 1992). The aim of the present work was to study the reproduction strategy of the freshwater bryozoan *Plumatella fungosa* (P a l l.) and to describe its life cycle on the basis of the currently and earlier presented data (K a m i ń s k i 1991, 1992).

2. Study area, material, and methods

The investigations were carried out in 1979, 1980, and 1982 in the eutrophic Lakes Mikołajskie and Jorzec (Masurian Lake District, northeastern Poland). In order to determine the dynamics of the settling of *P. fungosa* on new substrata, the growth rate of the biomass of the colonies, the time of reproduction and numbers of statoblasts, as well as to obtain colonies of known age for laboratory experiments, artificial substrata were employed (K a m i ń s k i 1991, 1992).

The reproduction of floating larvae (fecundity of the zooids) was investigated in laboratory experiments. Fragments of colonies of about 30 g of fresh weight were placed together with the substratum in small (1 dm³) carefully aerated aquaria for 10 or 20 hours. After this period the mass of the colonies and the number of released larvae of *P. fungosa* were determined.

Conclusions as to the dynamics of inhabiting new substrata were drawn on the basis of the rate of occurrence of young colonies on the artificial substrata exposed, for periods of one month, throughout the period of occurrence of *P. fungosa*. The density and the biomass of the colonies were estimated each time on 2 substrata of a total surface of 0.8 m² (1979) or 1.6 m² (1980 and 1982). The growth rate of young colonies was determined on the basis of the changes in the density and biomass of the colonies on the newly inhabited substrata, exposed in Lake Mikołajskie for 1 month. Assuming, on the basis of the data of Bushnell (1966) and of the present author (Kamieński unpubl.) that the growth rate of the density of zooids in young colonies was exponential, the indices of the mean, diel growth rate of the biomass of the colonies -r (mg d.w. mg d.w.⁻¹ 24 h⁻¹) were calculated according to the formula:

$$r = \frac{\ln B_t - \ln B_0}{t}$$

where:

- B_t - the biomass of the colonies (mg d.w.) on the last day of exposure of the substratum,
 B_0 - the mass of the colonies on the first day of exposure,
 t - the duration of the exposure of the substratum (in days).

The growth rate of older colonies of *P. fungosa* was also investigated on the basis of materials collected from substrata exposed in the lake for longer periods (from 1.5 to 3.5 months).

The period of reproduction and the number of prelarval forms produced by *P. fungosa* were investigated in 1980 and 1982 in colonies of known age. During the whole time of occurrence of the bryozoan, samples composed of 5 oldest colonies of *P. fungosa* were collected every 15 days from artificial substrata (exposed from the beginning of the season). The numbers of sessoblasts and floatoblasts in 50 microscopic fields of vision (14.6 cm²) were recorded for each sample.

The numbers of statoblasts floating on the surface of the lakes were calculated on the basis of catches made by means of a sampler, 2.5 cm in diameter and 100 μm mesh. The catch net, half immersed in the water, was pulled along a broken line, for a distance of about 40 m. Floatoblasts were caught above the submersed vegetation, among the emergent macrophytes and in the littoral shallows, at 3-6 stations in each lake. When distinguishing the statoblasts of *P. fungosa* the data from L a c o u r t ' s key (1968) and those of the present author (Kamieński 1984) were used.

In order to determine the density of statoblasts at the bottom of the lakes samples of bottom sediments were collected in the littoral zone. The sediments were brought to the surface by means of a 10 cm² K a j a k apparatus (K a j a k et al. 1965). For investigation the surface layer of sediments (2.5 cm) was sampled and the population of whole, undamaged floatoblasts of *P. fungosa* determined. The density of statoblasts was determined also in the periphyton scraped from the surface of floating leaves of *Nuphar lutea* S m. and from the stalks of *Phragmites australis* (C a v.) T r i n. ex S t e u d e l. In the collected samples the surface area of the plants and the number of statoblasts found in the periphyton were determined.

When statistically elaborating the results the analysis of variance (ANOVA) and Student's t-test were used.

3. Results

3.1. Sexual reproduction

Throughout the period of investigation no occurrence of colonies developing from floatoblasts on the surface of the artificial substrata exposed in Lake Mikołajskie was observed. These substrata were occupied by larvae produced in the colonies of the first (in the new vegetation season) generation of *P. fungosa*. The colonization of new substrata began in the second half of June (1979) or in July (1980 and 1982). The settling lasted till the second half of September (1982) or the first half of October (1979 and 1980). Starting from about 15th October until the end of the period of occurrence of the bryozoan colonies (the first decade of November, at the latest), young colonies no longer developed on those substrata not inhabited earlier. The period of settling on the new substrata was 5-6 weeks shorter than the whole period of occurrence of *P. fungosa* (from May or June to October or November).

On the basis of observations of the settlement of the larvae on new substrata it was possible to establish the period of sexual reproduction in the population of *P. fungosa*. In the particular years it varied from 55 to 75 days and took place at a water temperature above 18°C, with the greatest density of new colonies developing from floating larvae being observed in July and August (fig.1). At the beginning of September, in spite of favourable thermal conditions, the number of settling larvae suddenly diminished.

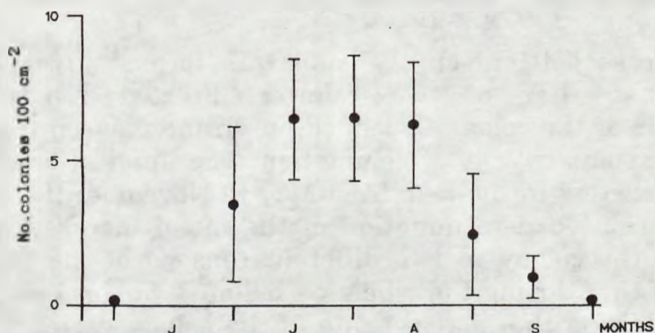


Fig. 1. Dynamics of inhabiting new substrata by the floating larvae of *P. fungosa* expressed as the density of young colonies of Bryozoa appearing on artificial substrata exposed in Lake Mikołajskie during a 1 month period. Mean values and SD for the whole period of investigations

The fecundity of the colonies of the first generation of *P. fungosa*, determined fourteen times in laboratory experiments (at the beginning of July), was greatly differentiated, amounting on the average to 294 ± 435 larvae 100 g^{-1} of f.w. 24 h^{-1} . The colonies of the type of *fungosa* used in the experiments contained a thick layer of decayed zooids, and the proportion of the living surface layer did not exceed 20% of the total mass of the colonies. The diel fecundity of the second generation of *P. fungosa* studied in 3 experiments carried out in the middle of August, was about two times lower and amounted to 143 ± 197 larvae 100 g^{-1} of fresh weight, with the proportion of living individuals in the colonies amounting to about 60%. The mean fecundity of *P. fungosa* was estimated taking into consideration the proportion of living individuals in the total mass of the examined colonies. It amounted to $1.4 \text{ larvae} \cdot 100 \text{ zooids}^{-1} 24 \text{ h}^{-1}$ in the colonies of the first, and $0.34 \text{ larva} 100 \cdot \text{zooids}^{-1} 24 \text{ h}^{-1}$ in those of the second generation of Bryozoa. Assuming that the period of sexual reproduction in the colonies of the first as well as of the second generations of *P. fungosa* lasts for about 3 weeks, and that each zooid participating in the reproduction produces only one larva, it was estimated that in the colonies of the first generation of *P. fungosa* every 3rd or 4th individual multiplies by way of sexual reproduction. In the second generation sexual reproduction was undertaken by every 14th zooid of *P. fungosa*.

3.2. Gemmation and the biomass growth rate

The larvae settling on the substrata formed juvenile colonies consisting at first of two counter directed zooids. Further development of the colony depended on an intensive increase in the number of zooids by way of gemmation. The application of artificial substrata exposed in the lake from May to November (for one month periods) permitted determination of the mean increase rate of the biomass of the colony in two different seasons of the year. It was established that during the whole period of *P. fungosa* occurrence in Lake Mikołajskie the increase rate of the colony varied from 0.0 to 0.26 mg d.w mg d.w.⁻¹ 24 h⁻¹, attaining its highest values (over 0.2 mg d.w.⁻¹ 24 h⁻¹) between the middle of June and the beginning of August (Table I). The differences in the growth rate of the colonies of *P. fungosa* at various depths proved to be statistically non-significant. The time required to double the biomass of the colony varied, depending on the season, from 2.7 to 15.0 days.

The intensity of settlement on the artificial substrata differed in the particular years. The maximum biomass attained by the bryozoan within one month also varied (Table II). The surfaces of the substrata were most rapidly overgrown by the colonies of *P. fungosa* from the middle of June to the middle of July (1979), in July (1982), or from the middle of July to the middle of August (1980).

A fast increase in the number of zooids over a few weeks brought about a change in the shape of the colony from a flat (repens type) form into a mass one (of *fungosa* type). To determine the effect of the age of the colony on the rate of its further growth the gains in biomass of the bryozoan grown on artificial substrata with various periods of exposure (from 1 to a few months) were compared. It was found that the colonies had attained a biomass of some hundreds mg of dry weight, usually after 3-4 weeks, further increase of the colony becoming greatly retarded. Colonies more than 2 month old grew scores and occasionally hundreds of times more slowly than young colonies settling at that time on new substrata (Table III).

3.3 Production and fate of the statoblasts

In the colonies of second generation *P. fungosa* the first statoblasts appeared at the turn of July, after about 3 weeks of development of zooaria (Table IV). The majority of statoblasts (59%) in that period occurred in the form of anlagen of various degrees

Table I. Mean die: rates of biomass increase (r) of young colonies of *P. fungosa* (mg d.w.· $24h^{-1}$) in Lake Mikolajskie

Depth m	Period of substratum exposure													
	1.06-1.07		15.06 - 15.07		1.07 - 1.08		15.07 - 15.08		1.08 - 1.09		15.08 - 15.09		1.09 - 1.10	
	1979	1979	1979	1980	1979	1982	1979	1982	1979	1982	1979	1980	1979	1980
0 - 1	0.19	0.21	0.15	0.19	0.16	0.21	0.12	0.17	0.11	0.16	0.15	0.18	0.15	0.10
1 - 2	0.15	0.21	0.20	0.26	0.18	0.21	0.14		0.11	0.15	0.16	0.15	0.16	0.10
2 - 3			0.23	0.25	0.21	0.21			0.17	0.17	0.14	0.14		0.10
3 - 4			0.21	0.19	0.15	0.15			0.14	0.14	0.14	0.14		0.11

Table II. Biomass (mg d.w. 100 cm^{-2}) of *P. fungosa* on artificial substrata, exposed in Lake Mikolajskie for periods of one month

Depth m	Period of substratum exposure																	
	1.06-1.07		15.06 - 15.07		1.07 - 1.08		15.07 - 15.08		1.08 - 1.09		15.08 - 15.09		1.09 - 1.10					
	1979	1979	1979	1980	1979	1980	1979	1980	1979	1980	1979	1980	1979	1980				
0 - 1	3.9	171	0.4	0.2	23.6	167	149	8.6	307	91.0	9.2	11.4	6.0	4.9	85.8	54.8	<0.1	0.8
1 - 2	2.3	227	3.3	1.9	82.7	180	288	26.6	566	155	7.9	20.2	9.7	12.8	153	37.5	0.1	1.4
2 - 3			7.3	7.1		87.7	255		482	160	23.4	4.1			121	53.6		1.7
3 - 4			4.6	1.2		48.1	44.8		141	54.8	22.6	2.5			107	15.4		2.4

Table III. Relative rate of increase in biomass of a colony of *P. fungosa* of various age on artificial substrata in Lake Mikolajskie. The growth rate of young colonies (less than 1 month old) = 100, mean values for all colonies occurring at depths from 0 to 3 m

Age of the colony months	Year		
	1979	1980	1982
1.0	100.0	100.0	100.0
1.5	82.8	100.0	92.4
2.0	66.2	10.4	33.3
2.5	8.0	2.2	0.0
3.0	0.0	0.0	0.3
3.5	0.0	0.0	0.0

Table IV. Density of floatoblasts ($F \text{ cm}^{-2}$) and sessoblasts ($S \text{ cm}^{-2}$) and proportion of living zooids (%) in colonies of *P. fungosa* on artificial substrata in Lake Mikolajskie in 1982

Date	F	S	Living zooids
15.07	0.0	0.0	100.0
1.08	34.9	8.9	100.0
15.08	39.5	23.2	50.5
1.09	8.8	36.4	33.3
15.09	16.9	38.5	23.1
1.10	118.4	56.1	2.5
15.10	156.5	38.1	0.2
3.11	7.1	37.5	0.0

of development. The earliest statoblasts appeared in the oldest, central part of the colony. Their density depended on the age of the zooids and attained the highest values for the zooids aged 4-5 weeks (in the middle of August). The oldest zooids at that time underwent gradual degeneration, which was accompanied by the maturation of the statoblasts. After the death of the zooids a great part of the floatoblasts left the open cystids. The remainder of the floating statoblasts confined in the cystids, fell off together with the remnants of the colony from the substratum. On the surface occupied so far by the bryozoans there remained the external ring of young zooids which, by gemmation still increased the size of the colony. The loss of its oldest parts was responsible for the decrease in mean density of the floatoblasts in the zoaria of *P. fungosa*. Only at the beginning of October was there

simultaneous necrosis of all zooids preceded by the production of a very large number of floatoblasts. In some parts of the colony as many as 350 statoblasts floating on 1 cm² of the substratum surface were observed. Single floatoblasts, confined in empty cystids of *P. fungosa*, were still found in extinct fragments of the colony at the beginning of November.

Similarly as the floatoblasts, sessoblasts appeared on the substratum inhabited by the bryozoan after about 3 weeks of the colony development. Their numbers increased gradually till the moment of mass mortality of the bryozoans at the beginning of October (table IV). The number of sessoblasts produced during this period was distinctly lower than of floatoblasts. The falling off of dead fragments of the colony from the substratum brought about the loss of about 30% of fully developed sessile statoblasts.

In the multilayer colonies of the *fungosa* type sessoblasts were produced exclusively by the zooids remaining in direct contact with the surface of the substratum. In the upper layers of the colonies only floatoblasts were produced. The number of statoblasts produced by single individuals varied greatly. In the bodies of zooids were found from 0 to 9 floatoblasts or from 0 to 3 sessoblasts. Taking into consideration the mean density of individuals in the colonies (about 300 cm⁻²) and the maximum numbers of statoblasts (up to 440 cm⁻²), it may be assumed that the mean number of the produced statoblasts did not exceed 2 statoblasts for each individual in the colony.

The numbers of floatoblasts drifting on the water surface in both the studied lakes were very high. In Lake Mikołajskie floating above the submersed vegetation, and determined ten times (at various dates), they amounted to 3.4 ± 2.6 floatoblasts m⁻², and in Lake Jorzec to 3.9 ± 2.6 floatoblasts m⁻². The floatoblasts gathered chiefly among the emergent macrophytes and those with floating leaves, as well as close to the lake shore line. In Lake Mikołajskie (in August) the mean density at floatoblasts among the emergent plants was 48.4 ± 84.4 , in the littoral shallow 33.5 ± 46.1 , and in the open water zone only 1.8 ± 1.2 statoblasts m⁻².

A great part of the floatoblasts produced by the bryozoans sank to the bottom sediments. Investigations conducted eight times (at various dates) showed that in the surface layer of the sandy-muddy bottom sediments of the littoral zone of Lake Mikołajskie the mean density of undamaged floatoblasts was $9.2 \pm 2.8 \cdot 10^3$ m⁻². In the muddy sediments of Lake Jorzec these numbers were significantly higher, amounting to $59 \pm 32 \cdot 10^3$ m⁻² of the bottom surface area.

The presence of floating statoblasts was observed also in the periphyton covering the floating leaves of *N. lutea* and the stalks of *P. australis*. While the numbers of undamaged floatoblasts on the blades of floating leaves of *Nuphar* were fairly high (up to 13 per 100 cm²), their numbers on the petioles of this plant were significantly lower (up to 0.6 per 100 cm²). A very small number of statoblasts (less than 0.1 per 100 cm² of the plant surface) were settled on the stalks of *Phragmites*.

4. Discussion

The results of the investigation on the reproduction of *P. fungosa* reported here, as well as the data on the distribution and seasonal changes in the biomass of the Bryozoa (K a m i ń s k i 1991, 1992) make possible the presentation of a complete schematic illustration of the development of the population of this species throughout the season of its occurrence (fig. 2).

The first generation of *P. fungosa*, not very numerous and attaining a rather small biomass (up to 70 mg of fresh weight 100 cm² of the surface area of the substratum), developed almost exclusively from the sessoblasts which survived the winter on more durable substrata occupied in the previous season (mainly stalks of *Phragmites*). The population of this generation was probably determined by the number of surviving sessoblasts, exhibiting high resistance to drought and low temperatures (R a d d u m 1970). The zooids forming the colonies of the first generation of *P. fungosa* began after a few weeks to produce statoblasts as well as starting sexual reproduction.

Worthy of note is the high fecundity of the spring generation of the Bryozoa. The observations made by O d a and N a k a m u r a (1980) of *Pectinatella gelatinosa* O k a seem to confirm the early start of sexual reproduction in Phylactolaemata. Also B u s h n e l l (1974) reported that the greatest population of larvae can be found near the colonies of Bryozoa in late spring or early summer.

The floating larvae, produced in great numbers by the zooids of the first generation, were the beginning of a decisive majority (over 98%) of colonies of the second generation of *P. fungosa*. The number of colonies appearing on the newly occupied substrata no doubt depended both on the fecundity of the previous generation of the bryozoan on factors determining the successful settlement of the larvae (number of habitable substrata, pressure of predators etc.). Larvae, which demonstrate a distinct discrimination with respect to

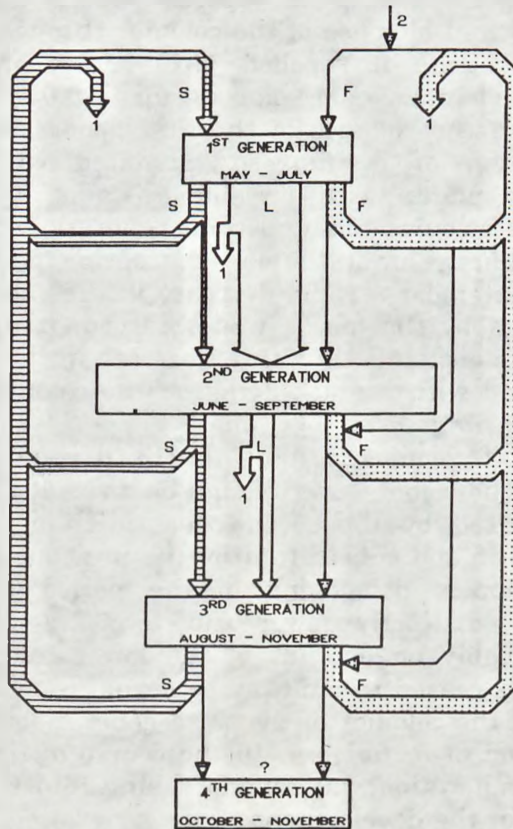


Fig. 2. Schematic illustration of the life cycle of *P. fungosa*. S - sessoblasts; L - larvae; F - floatoblasts; 1 - elimination of larvae and statoblasts (predation, sedimentation, removal beyond the water body, etc.); 2 - inflow from beyond the water body

the substratum to be inhabited, formed colonies mainly on *Phragmites* and *Nuphar* (Kamiński 1991). The settlement of many larvae on new substrata and rapid rise in the number of individuals in the colonies were responsible for the exponential rate of the increased biomass of the Bryozoa in the littoral zone. In the literature can be found examples of extremely rapid colonization of substrata placed in a lake for a short period (e.g. catch nets) and the achievement of impressive biomass by the Bryozoa (Jonasson 1963). This can be ascribed to the high fecundity of zooids of the first generation and to the fast rate of increase in the number of individuals in colonies of the second generation of *P. fungosa*.

The second generation of the bryozoan was characterized by the greatest density and biomass of the colonies throughout the season. On natural substrata it reached up to 1.5g, and on artificial substrata exposed in Lake Mikołajskie up to 9.0 g of fresh weight 100 cm^{-2} . Unlike the colonies of the first generation, those of the second generation of *P. fungosa* inhabited various substrata, including many plants with perishable stalks, dying off in the autumn. In the colonies of the second generation the fecundity of zooids was distinctly lower than in the spring population. At the beginning of September a rapid decrease in the rate of colonization of new substrata by the larvae was observed. It may be assumed that this was connected both with a decrease in the reproduction of the bryozoan and with a quick dying off the colonies of the second generation of *P. fungosa* at this time.

The origin of colonies forming the third generation was more differentiated. The colonies were found as a result of the settlement of larvae produced by the second generation or developed from sessoblasts left on the substratum by the previous generation. The biomass of colonies developing in the period from August to November was distinctly lower (up to 0.2 g of fresh weight 100 cm^{-2}). Probably on account of the lower temperature of the water the zooids ceased to multiply by sexual reproduction.

Dying off of the colonies of the third generation marked the end of the population of *P. fungosa*. In the course of the investigations no successive generation was found. Taking into consideration the time required for the development of one generation (6-7 weeks) and the period of the colony's occurrence (22-26 weeks), it may be assumed that within one season *P. fungosa* might have produced also a fourth generation of colonies. If indeed colonies of this generation occurred at all they were certainly very scarce and perished before producing statoblasts (fig. 2).

In the life cycle of *P. fungosa* worthy of note is the relatively small number of colonies developing from floatoblasts. As revealed in the investigations, the number of statoblasts produced was high, their population on the water surface varying from a few to some scores on 1 m^2 of the lake surface. Under the action of the wind and waves the floatoblasts accumulated in the littoral shallows and could be washed ashore. A great number of the generated floatoblasts did not develop and sank, singly or together with the remnants of the colony, to the bottom sediments. The effect of a numerous occurrence of statoblasts of *Plumatella* sp. in the sediments (up to $800 \cdot 10^3\text{ m}^{-2}$) was earlier described by Ryland (1970). Since not dried out statoblasts of the Bryozoa retain the ability to develop for about 3 years (Mukai 1974), the bottom

sediments may be a reserve source of these pre-larval forms in the lake.

The reasons for the relatively small importance of floatoblasts for the development of the population of *P. fungosa* may be of complex character. The main factors are certainly the small number of substrata in contact with the surface film and unfavourable conditions for the development of colonies in the near-surface layer of the water (undulation, periodical drying up of the substratum, etc.). In spite of the fact that in the studied lakes most of the colonies developed from sessoblasts or larvae, the floatoblasts may play an important role in the propagation of the population. Floatoblasts may be carried out over long distances by water or on the feathers of birds and thus contribute to the occupation of new habitats by the Bryozoa.

5. Polish summary

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

2. Rozmnażanie się oraz wnioski ogólne

W latach 1979, 1980 i 1982 prowadzono w eutroficznych jeziorach Mikołajskie i Jorzec (Pojezierze Mazurskie, północno-wschodnia Polska) badania nad rozmnażaniem się *P. fungosa*, produkcją larw, wytwarzaniem statoblastów oraz tempem przyrostu biomasy kolonii. Stwierdzono, że w ciągu jednego sezonu okres rozmnażania płciowego w populacjach *P. fungosa* trwał od 55 do 75 dni i przebiegał przy temperaturze wody powyżej 18°C. Najwyższą liczebność larw kolonizujących nowe podłoża stwierdzono w lipcu i sierpniu (ryc. 1). Płodność kolonii pierwszego pokolenia *P. fungosa* (około 1.4 larw 100 zooidów⁻¹ 24 h⁻¹) była czterokrotnie wyższa niż w koloniach drugiej generacji tych zwierząt.

Młode kolonie drugiego pokolenia *P. fungosa* charakteryzowały się szybkim tempem przyrostu biomasy (do 0.26 mg s.m. mg s.m.⁻¹ 24 h⁻¹) (tabela I). W ciągu jednego miesiąca mszywioly osiągały biomasę dochodzącą do 570 mg s.m. 100 cm⁻² powierzchni podłoża (tabela II). W starszych koloniach tempo przyrostu biomasy było zdecydowanie niższe (tabela III).

Liczba floatoblastów, wytwarzanych przez poszczególne osobniki (od 0 do 9), była zdecydowanie wyższa od liczby produkowanych sessoblastów (od 0 do 3). Najwyższą liczebność form przetrwałych w koloniach *P. fungosa* stwierdzano w październiku (tabela IV). Pomimo liczego występowania floatoblastów w litoralu jeziornym inicjowały one rozwój stosunkowo małej liczby kolonii (poniżej 2%).

W ciągu jednego sezonu występowały w badanych jeziorach co najmniej 3 generacje kolonii, różniące się między sobą pochodzeniem i sposobami rozmnażania się (ryc. 2).

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