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Vegetative reproduction of the bryozoan *Plumatella fungosa* (Pallas, 1768) (Phylactolaemata)

by

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Abstract: The development duration is evaluated and five formation stages of *P. fungosa* floatoblasts and sessoblasts are distinguished. It is shown that sessoblasts grow 1.5 times faster than floatoblasts. Dry mass of one sessoblast is 3.6 times larger than that of one floatoblast. The number of floatoblasts in the colony exceeds that of sessoblasts by a factor of 4 in consequence of which the generative increment of the colony is energetically equal for floatoblasts and sessoblasts. The reproductive effort index of the colony due to floatoblasts and sessoblasts is 0.27. The floatoblast and sessoblast production at the level of a zooid and a colony is discussed and the regulation of floatoblast or sessoblast production is considered in respect of their functional role. The colonys choice of its reproduction means, either by vegetative multiplication or by gametogenesis, is being discussed.

Key words: Bryozoa, Phylactolaemata, Belarus, floatoblasts, sessoblasts, cryptobiotic formation, development duration, generative somatic growth index, reproductive effort of the colony, vegetative reproduction, gametogenesis.

Introduction

Reproduction is the main function responsible for multiplication of organisms, conservation in time and space. Asexual reproduction in Phylactolaemata exists as internal bud reproduction which results in statoblasts, homologs of hibernacula in marine Bryozoa and gemmula in sponges. In the present study the freshwater bryozoan *Plumatella fungosa* was used. Vegetative reproduction of *P. fungosa* results in two types of statoblasts: less numerous fixed sessoblasts serving to produce new colonies on the place where the mother colony has grown (the conservative strategy according to Raddum 1981) and a considerable amount of floating floatoblasts, which disseminate in water and air after disintegration of the colony, providing wide dissemination of the species (expansive strategy).

At present bryozoan statoblasts should be considered as specialized structures which were formed during adaptagenesis to extreme environmental conditions. Statoblasts are cryptobiotic formations and have a physiological mechanism of rest similar to cysts of protozoa, sponge gemmulae, arthropod eggs and larvae,

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hibernacula of marine Bryozoa. Statoblasts which are specialized forms of cryptobiotic life occurring in Phylactolaemata have a very wide adaptability to various environmental factors and perform a triple function: reproduction, conservation in time and distribution in space.

The adaptability of statoblasts to various environmental factors has been studied quite well, whereas there are only a few data on the duration of statoblast development (Mukai & Kobayashi 1988). The choice of the reproduction means by a colony has been insufficiently studied so far (Brown 1933, Mukai 1989, Wood 1991, Karlson 1991,1992).

The floatoblast formation process was described histologically (Braem 1890, Oka 1891, Kraepelin 1891, Buddenbrock 1910, Brien 1953, Mukai & Oda 1980, and others), histochemically (Mukai 1973), electron microscopically (Tajima & Mukai 1975, Terakado & Mukai 1978). The sessoblast formation was only described histologically (Mukai 1982). Data on statoblast production at zooidal and colonial levels are not numerous and furthermore contradictory (Bushnell 1966, Mukai & Kobayashi 1988, Karlson 1991, 1992).

Materials and Methods

The material used is represented by *Plumatella fungosa* colonies developing in large masses in a warm channel of the cooling reservoir of the Bereza Electric Power Plant (Belarus). Floatoblasts were isolated from the Bryozoa colonies collected in the warm channel in autumn 1989 and cultivated in April and May of the following year in laboratory conditions with the method developed by the author. Bryozoa colonies were reared at an optimal temperature of 25°C at which mass production of statoblasts was observed in natural conditions. They were fed with *Chlorella*. An 8-hour light / 16-hour dark photoperiod was maintained during the experiment. The development duration of floatoblasts and sessoblasts was determined from the schematic drawings of the colony growth drawn every day. The reproductive effort index Re of the colony was calculated following Khmeleva (1988):

$$Re = \frac{Pg\ floato + Pg\ sesso}{(Pg\ floato + Pg\ sesso) + P\ som}$$

where Pg floato and Pg sesso correspond to the respective production of floatoblasts and sessoblasts in the colony, P som is the production of zooids.

Results

For *P. fungosa* we distinguished 5 stages of floatoblast and sessoblast formation (fig. 1). According to our data the statoblast type can be identified already in stage 1. The sessoblast passes stage 2 three times as fast as the floatoblast and its size is close to the final one. In stage 3 the two types of statoblasts differ therein that the floatoblast's periblast turns dark, whereas the sessoblast although having reached its definitive size still has a white periblast. Thus, a sessoblast starts rapidly increasing in size in the first three stages and in the two final stages it completes chitinization.

A floatoblast increases in size at nearly the same rate in all stages, but starts chitinization earlier.

The floatoblast development stages we have distinguished are consistent with those identified by Mukai & Kobayashi (1988) for *P. emarginata* floatoblasts except for the embryonal stage we do not consider. The previous Japanese researchers have shown that gas filling takes place in a *P. emarginata* floatoblast in stage 5 in only 20 to 30 min., the gas generated in one chamber being transferred through pores to the other chambers.

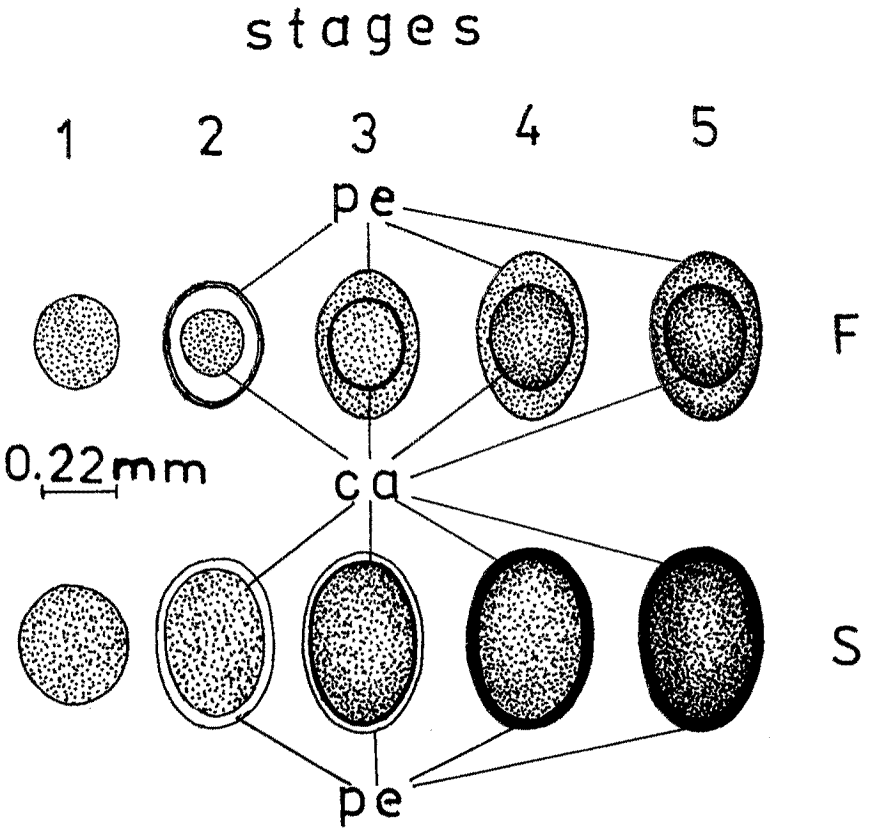


Fig. 1: Schematic diagram of the formation of the floatoblast (F) and the sessoblast (S) of *Plumatella fungosa* (ca = capsule, pe = periblast).

F (dorsal side): 1, milky ripeness of the capsule, no periblast; 2, milky ripeness of the capsule, periblast with a white ferrule; 3, capsule with a brown ferrule, periblast white but denser than the previous; 4, definitive dimensions of F, medium-brown periblast; 5, mature F with dark periblast.

S: 1, milky ripeness of the capsule, no periblast; 2, milky ripeness of the capsule, periblast with a white ferrule; 3, pale-brown ferrule, white periblast, definitive dimensions of S; 4, medium-brown capsule, brown periblast; 5, mature dark-brown S.

Tab. 1: Increase in length and width (L, B, mm) and formation duration (Dq, day) of *P. fungosa* statoblasts in different development stages.

Development stage	Floatoblasts			Sessoblasts		
	L x B, mm	Dq, day	Number of determ.	L x B, mm	Dq, day	Number of determ.
1	0.25 x 0.25	0.07	14	0.33 x 0.33	0.01	2
2	0.30 x 0.25	1.30	13	0.47 x 0.34	0.38	10
3	0.41 x 0.28	2.94	13	0.50 x 0.35	1.11	12
4	0.45 x 0.31	4.18	5	0.50 x 0.35	2.41	10
5	0.45 x 0.31	5.32	10	0.50 x 0.35	3.84	9

Using the statoblast development stages, it was found that the sessoblasts' growth rate was 1.5 times higher than that of the floatoblasts. The sessoblasts reached their definitive size already in stage 3 and maturated 1.48 days sooner than floatoblasts with an average length of 0.5 mm and an average width of 0.35 mm in the final stage. *P. fungosa* floatoblasts had equal rates of development in the different stages, having a maturation rate of 5.3 days with an average length of 0.45 mm and an average width of 0.31 mm in the final stage (tab. 1).

The number of zooids in laboratory culture depends on the experimental data, the volume of the glass containers with the animal cultures and some other conditions. It is, however, evident that statoblast formation is the colony's response to unfavourable conditions. In nature that may be a temperature decrease and a reduction of the light period. In laboratory cultures with equal experimental conditions strictly observed, it is the pressure of the zooid density that probably simulates advent of unfavourable conditions for a bryozoan colony which immediately responds by forming statoblasts.

P. fungosa colonies developed from a statoblast and observed for 35 days formed a small amount of floatoblasts on day 8; sessoblasts were formed only on day 15 and in a slightly smaller number (fig. 2). From that moment on the somatic part of the colony (consisting of the zooids) increased abruptly with a simultaneous augmentation of generative production in the form of floatoblasts. At the zooidal level the floatoblast production amounted to 1:3 (one active zooid producing 3 floatoblasts), that of sessoblasts was 1:1. It is noteworthy that statoblasts were produced by the oldest zooids, whereas the young ones provided for somatic growth of the colony. On day 35 the somatic production was equal to the generative production of floatoblasts.

During the colonies' lifetime the sessoblast production was small. On day 35 the Bryozoa colonies containing an average number of 61 zooids produced on an average 61 floatoblasts with the ratio 1:1 and 15 sessoblasts with the ratio 4:1.

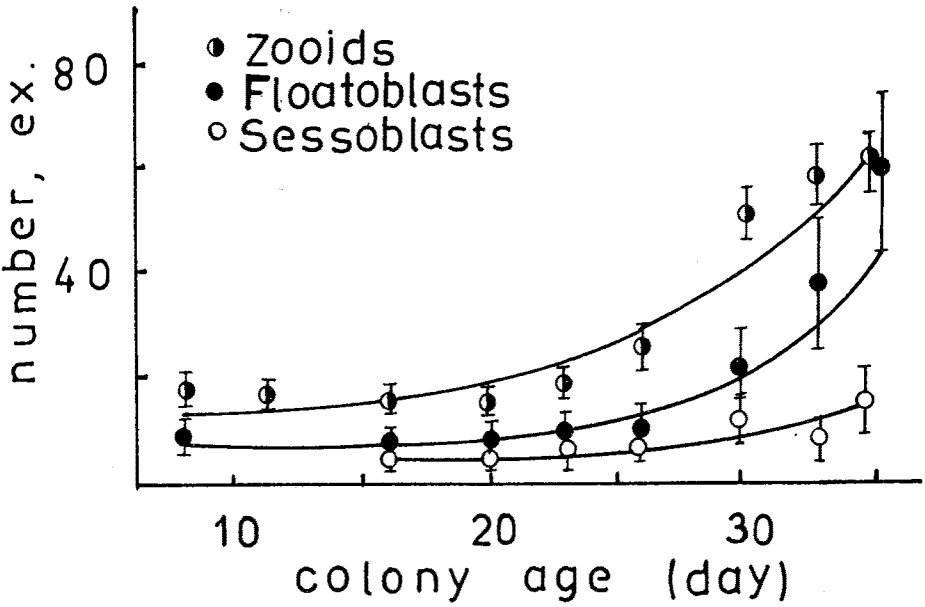


Fig. 2: Increase of the number of zooids (Z), floatoblasts (F) and sessoblasts (S) in *Plumatella fungosa* laboratory cultures.

The generative somatic growth indices calculated in terms of energy following Khmeleva (1988) have a ratio of 1:1 for floatoblasts and sessoblasts. The dry mass of a sessoblast is 3.6 times as large as the floatoblast mass, the energy equivalents are 0.078 and 0.023 cal/ind. respectively, but because the floatoblast number is 4 times as high, the generative increment of the colony is equal in terms of energy in the two statoblast types.

The relative fecundity or the generative somatic growth index of the colony due to the two types of statoblasts was 37% which is within the values found for other invertebrate groups. Combining the increments due to floatoblasts and sessoblasts, the reproductive effort index of the colony was 0.27.

Discussion

Data on the statoblast production at the zooidal level are contradictory. Bushnell (1966) wrote that a *Fredericella sultana* zooid produced 1 to 4 statoblasts. Zooids of some *Plumatella species* can produce more than 20 statoblasts (Bushnell 1968). A *P. repens* zooid produces 15 to 20 statoblasts (Karlson 1992). According to Mukai & Kobayashi (1988) the largest production of statoblasts per zooid is 17, that of sessoblasts is 6. The Japanese authors reported that a colony of 140 *P. emarginata* zooids produced 741 floatoblasts and 34 sessoblasts in the ratio 22:1. They also

wrote that many zooids produced sessoblasts during their whole life, some generating both types of statoblasts. In the latter case the zooids produced a small number of sessoblasts and a lot of floatoblasts. Wood (1973) demonstrated for *P. repens* and *P. casmiana* that production of sessoblasts was usually followed by the death of the zooids. A *P. emarginata* zooid produces 0.27 sessoblasts (Karlson 1991).

In six colonies of *P. fungosa* grown by the author in laboratory culture in spring 1993 at T = 27 °C for 35 to 40 days 210 zooids (Z) produced 300 floatoblasts (F) and 7 sessoblasts (S), 104 Z produced 132 F + 6 S, 370 Z produced 600 F + 38 S, 145 Z produced 205 F, 170 Z produced 398 F and 345 Z produced 1071 F. It can be seen that half of the colonies produced both types of statoblasts in the ratio 16-43 F : 1 S. In the other half of the colonies the zooids produced only floatoblasts: 1-3 F: 1 Z.

Karlson (1992) observed the production of eight sessoblasts and 80 floatoblasts in a *P. repens* colony of 100 zooids (calculated by the present author from the experimental curve).

The regulation of the production of either type of statoblasts and their energy suitability can probably be ascribed to the functionally different roles of the two types of statoblasts. Since the function of floatoblasts is to occupy as large as possible area by the species, they are produced with a lower mass in a larger quantity. The role of sessoblasts is to ensure the development of the colony at the same place were they are fixed. Since sessoblasts are in more stable conditions, they are larger in size and formed in a smaller amount compared to the floating floatoblasts many of which will probably die failing to find a fixing site.

The regulation mechanism of forming two types of statoblasts is not yet known, nor is the mechanism bringing a bryozoan colony to choose either sexual or vegetative reproduction and the factors which induce either reproduction type. Mukai & Kobayashi (1988) stated that in a colony both sessoblast formation and gametogenesis occur rather sporadically. In earlier publications reports on sexual reproduction of freshwater Bryozoa were more frequent (Lampert 1900, Zhadin 1940, 1950, Kluge 1896, 1949, and others). Brown (1933) emphasized that conclusive evidence for a regular alternation of sexual and asexual generations is wanting and that these two methods seem to occur simultaneously even in the same colony. Mukai (1974) reported that in *Pectinatella gelatinosa* vegetative reproduction was preceded by a short-time gametogenesis. Wood (1991) reports that sexual reproduction in Plumatellides occurs for a brief period of time and that relatively few larvae are produced.

In recent years many authors have reported on a rather long vegetative reproduction period (Brown 1933, Mukai 1974; Bushnell 1966, Oda 1959, 1960, Wood 1973). Marcus (1925) wrote that in the tropical zone statoblasts were produced throughout the year. According to Dehdashti & Blinn (1986) *P. repens* produced statoblasts during the whole year in a warm stream of Arizona State. Karlson (1991) shows that nonsexual reproduction by floatoblasts and sessoblasts is essential in the recruitment of *P. emarginata*, whereas he did not notice any evidence of extensive larval production. The present author found that in the warm channel of the cooling reservoir of Bereza Electric Power Plant *P. fungosa* reproduced itself from June to December only by statoblasts (Mikhaevich 1989 a, b). Thus, it is possible that gametogenesis in freshwater Bryozoa is of secondary importance and performs the function of creating heterogeneous genetic material. It

is likely that in warm water Bryozoa use the simpler type of vegetative reproduction in the form of cryptobiotic formations (statoblasts) with a larger amount of offsprings and economically more advantageous.

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