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Encrusting bryozoan colonies on stones and algae: variability of zooidal size and its possible causes

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This study compared the sizes of zooids in colonies of the cheilostome bryozoan Cribrilina annulata *collected from two differing substrata (stones and algae) in three regions of the White and Barents Seas. Zooids of the colonies growing on stones were larger than those in the colonies growing on the thalli of the red alga* Odontalia dentata. *Size differences of the zooids in the colonies growing on the same substratum in different regions were minor. Three possible explanations for these dimensional differences of zooids are discussed: (1) larvae of different sizes settle on different substrata; (2) ancestrulae of different sizes survive on different substrata; and (3) substrata influence the ancestrulae's size.*

Keywords: encrusting, bryozoan colonies, stones, algae, variable zooidal size, possible causes

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INTRODUCTION

Bryozoans are sessile colonial organisms, whose colonies grow by consecutive budding of zooids. Variability of zooidal sizes within a colony can be high. The size of newly forming zooids increases during early stages of astogeny (colony development). This part of the colony is referred to as the zone of astogenetic change (Boardman & Cheetham, 1969). Then the zone of astogenetic repetition is formed where zooidal size can vary, but there are no regular changes in connection with the generation number (Pachut *et al.*, 1991). The sizes of bryozoan zooids in the zone of astogenetic repetition can be affected by ambient temperatures (Harmelin, 1997; O'Dea & Okamura, 1999; O'Dea & Jackson, 2002; Lombardi *et al.*, 2006), abundance of feeding (Jebram, 1973, 1978; Jebram & Rummert, 1978; Sebens, 1979; Okamura, 1987; O'Dea & Okamura, 1999), water salinity (O'Dea & Okamura, 1999), and hydrodynamic conditions (Partridge & Okamura, 1999).

In the case of sessile colonial organisms the local conditions of their habitat strongly reflect the characteristics of the substratum on which they grow. The substratum shape and its rigidness generally define local hydrodynamics, which is significant for attachment of larva (Abelson, 1997; Lapointe & Bourget, 1999), and feeding of adult zooids (Grunbaum, 1995). Its suitability for settling larvae and successful growth of the colony is defined by physical and chemical properties of the surface (Buss, 1979). Metabolites excreted by living substrata can affect the growth of colony as well (Manriquez & Cancino, 1996).

Many bryozoan species live on the substrata of a certain type (Seed & O'Connor, 1981; Barnes & Clarke, 1995; Manriquez & Cancino, 1996; Kuklinski *et al.*, 2006) and size (Håkansson & Winston, 1985; Bishop, 1989), and even take a certain position on it (Stebbing, 1972; Boaden *et al.*, 1975; O'Connor *et al.*, 1979; Bishop, 1988; Cadman & Ryland, 1996). The choice of substratum and the position on it occurs during larval settlement (Abelson, 1997; Mariani, 2003). Differences in density of larvae settling on different parts of a substratum can depend on hydrodynamic conditions (Harvey & Bourget, 1997) or chemical factors (Seed & O'Connor, 1981; Harvey & Bourget, 1997). Larvae survival is influenced by their sizes. Size of a larva also defines the size of ancestrula, as well as size of the colony, its fertility and ultimately sizes of the next generation of larvae eventually formed by it (Marshall & Keough, 2004a, b). Experiments with two bryozoan species showed that the size of settling larvae was higher at higher densities (Marshall & Keough, 2003). This may be due to large larvae being able to swim longer and have greater probabilities of finding optimal attachment substrata (Bennett & Marshall, 2005).

Thus, substratum properties are important both during settlement, metamorphosis and life of a bryozoan colony. Therefore, it is reasonable to suggest that zooidal size in colonies of the same species living in different biotopes (e.g. on different substrata) can differ. The purpose of the current study was to determine the components of variation in zooidal size connected with colony habitat in common boreal cheilostome bryozoan *Cribrilina annulata* (Fabricius, 1780).

MATERIALS AND METHODS

Zone of astogenetic repetition is traditionally used to study the variability of zooidal sizes caused by external factors. Variations in zooidal size in this zone caused by astogeny,

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are considered to be casual (Boardman & Cheetham, 1969; Pachut *et al.,* 1991; O'Dea & Okamura, 2000). We intentionally worked with zooids from the ancestral zone (the zone of astogenetic change). It provides an opportunity to compare individual zooids forming during certain moments of astogeny and occupying definite positions in the colony. Thus the variability caused by astogenetic and environmental factors can be separately examined (Taylor & Furness, 1978). We used the encrusting species *Cribrilina annulata* because its early astogeny is well established. *Cribrilina annulata* lives on different substrata and has a wide geographical (coastal) distribution.

The early astogeny of *C. annulata* has been well studied (Powell, 1967; Ostrovsky, 1998; Nikulina, 1999, 2001; Yagunova, 2002, 2005). The first generation of zooids is an ancestrula, the second—one zooid, the third—two, and the fourth generation—four zooids (Figure 1). Deviations from such sequence of budding are rare.

Colonies of *C. annulata* were collected during summer 2002 in three areas: Chupa Inlet (Kandalaksha Bay, White Sea), Solovetski archipelago (Onega Gulf, White Sea) and Dalnezelentskaya Inlet (East Murman Region, Barents Sea). These sites are denoted as Ch, Sol, DZ in Figure 2. Colonies growing on thalli of the red alga *Odontalia dentata* and on stones were collected at each of the three sites. Samples of this alga were collected from 5–15 m depth using grapnel and SCUBA-diving. Stones bound to rhizoids of red algae were collected in the White Sea area. In the Barents Sea stones were collected at extreme low water spring tide level. *Cribrilina annulata* was abundant on thalli of *O. dentata* in all three regions, and in the Barents Sea—on stones too. Colonies of this species were rare on stones in the White Sea area.

Only colonies of *C. annulata* without visible obstacles in their early development were considered. The length and width of completely formed zooids (with calcified distal walls) budded during early astogeny were measured in each colony using an ocular micrometer.

Collecting was repeated in 2006 in the Dalnezelenetskaya Inlet (Barents Sea). Young colonies of *C. annulata* on stones and algae *O. dentata* were digitally photographed. Photographs of colonies were cropped to obtain separate images of each zooid. These photographs of zooids were transformed into black-and-white binary format and examined with image analysis software. The program used defined the area of each image as the number of black pixels in each photograph. The boundary line of image was defined, then, after a smoothing procedure, the boundary of each zooid was plotted as a graph in polar coordinates. This allowed calculation of the zooidal length and width (maximal size in two perpendicular directions), and its perimeter. Representation of the zooids' contours in graphic form enabled to plot an image of an 'average' zooid by calculation of average sizes in all directions and to estimate averaging error.

Analysis of variance (ANOVA) was used to compare the influence of the generation number, the collecting site and the substratum (colonies of year 2002) on the zooidal length and width, as well as to determine the astogenetic, geographical and habitat components of variability. To compare the extent of influence of the factors the portions of dispersion resulting from each factor were calculated. Comparison of ancestrula sizes from the two study substrata were repeated with specimens collected in 2006.

The sample size (total number of zooids investigated from colonies collected in each region for each substratum) is listed in Table 1. Data are presented as means with confidence intervals corresponding to the significance level $P = 0.05$.

RESULTS

The zooidal length in colonies on stones was much higher than in colonies on algae *Odontalia*. This was the case in all three geographical regions (Figure 3). The zooidal width in colonies collected on stones in the Barents Sea was significantly greater than the width of zooids collected on the alga *O. dentata*. In the White Sea the average width of the ancestrula in colonies from the two study substrata appeared to be identical, however zooids of 3rd and 4th generations had greater widths on stones than on algae. The influence of substratum on zooidal size was significant and substantial (Table 2). The habitat component of variability of zooids' length and width was 5% and 8%, correspondingly, and its value was close to the astogenetic component of variability.

The sampling region also had significant influence on zooidal size (see Table 2): average size (length and width) of zooids in colonies from the Barents Sea was higher than in colonies from the White Sea (Figure 4). It should be noted that the geographical component was less substantial than habitat and astogenetic components of variability (Table 2). Moreover, the geographical differences of zooidal size are irregular: for different generations of zooids and different substrata larger zooids were in different localities (Figure 5 A, B).

Comparison of the ancestrulae on stones and *Odontalia* in the Barents Sea to the 2006 sample yielded similar results. The length of ancestrulae was consistently higher when collected on stones compared with those on algae (ANOVA, $F = 13.04$, $P < 0.05$). No consistent differences in ancestrular widths were established between different substrata (Figure 6). Additionally, the ancestrulae on stones had a greater average perimeter (ANOVA, $F = 4.84$, $P < 0.05$). However, there was no consistent difference in their average area. The

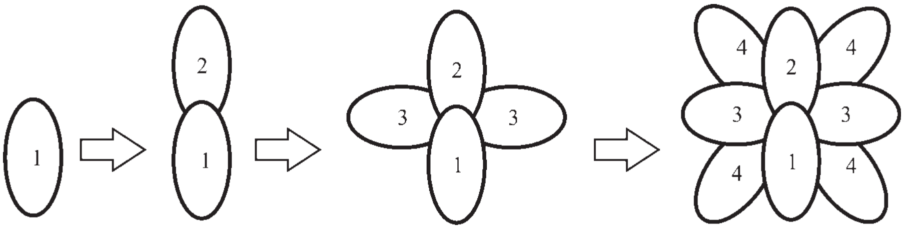

Fig. 1. The scheme showing a sequence of zooidal budding in the early asthogeny of *Cribrilina annulata*. 1, ancestrula; 2–4 sequential generations of zooids (from Yagunova, 2005).

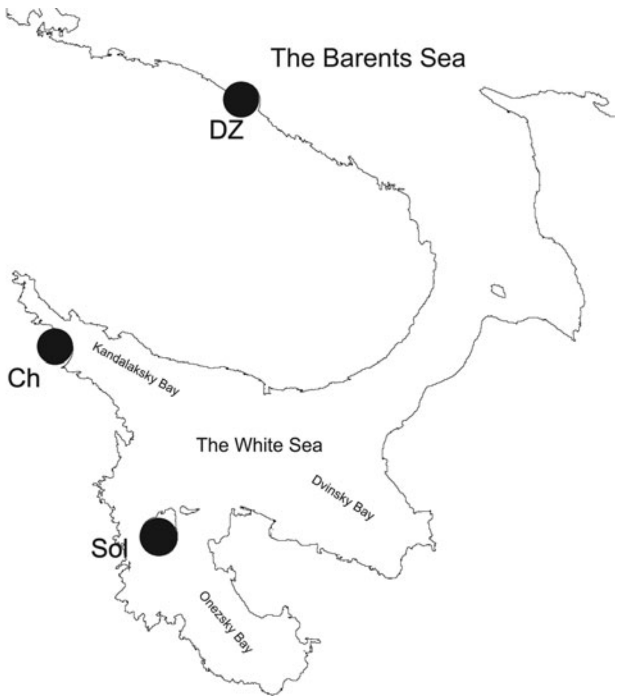

Fig. 2. Map showing the collecting sites. DZ, Dalnezelentskaya Inlet (East Murman Region, Barents Sea); Ch, Chupa Inlet (Kandalaksha Bay, White Sea); Sol, Solovetski archipelago (Onega Bay, White Sea).

'average' (typical) forms of ancestrulae on stones versus those on *O. dentata* are shown on Figure 6.

Comparison of ranges of variation of ancestrulae length on different substrata showed the length of the shortest ancestrula on stones was greater than the shortest ancestrula on algae. The length of the longest ancestrula on *O. dentata* was also less than the length of the longest ancestrula on stones.

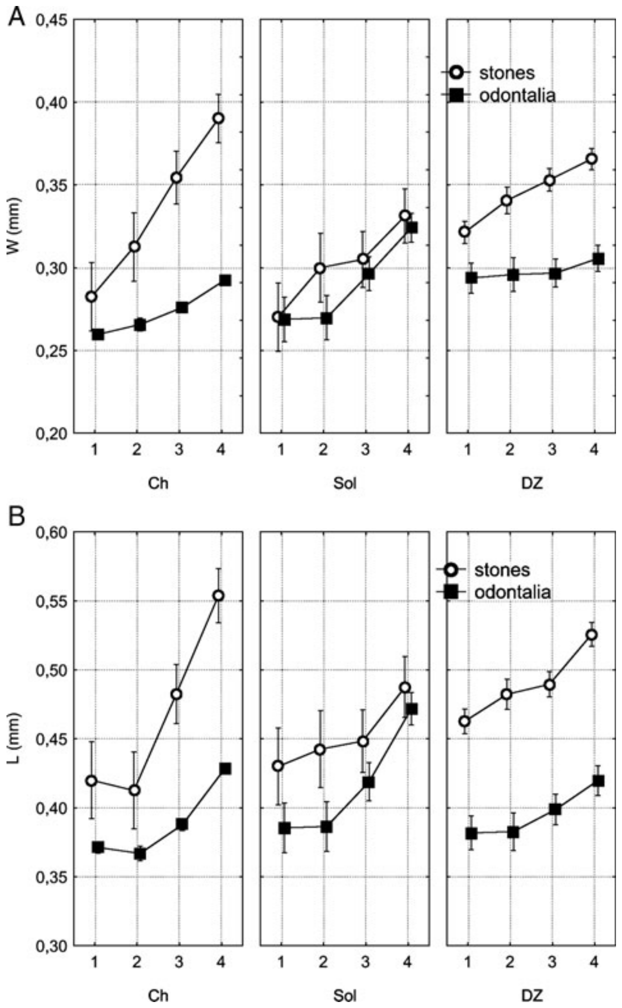

Fig. 3. Habitat variability of sizes in the first zooidal generations of *Cribrilina annulata* in three regions. (A) Width variability; (B) length variability (samples from 2002). The numbers on the abscissa axis correspond to the zooidal generation: 1, ancestrula; 2–4 sequential generations of zooids (see Figure 1).

DISCUSSION

Comparison of colonies of the cheilostome bryozoan *Cribrilina annulata* living on two different substrata in the White and Barents Seas showed that the type of substratum essentially affects the zooidal size. Length of zooids is more sensitive to the type of substratum than their width. In general zooidal length varies more than width (Taylor & Furness, 1978; Taylor, 1988). It has been suggested that zooidal width depends on surrounding factors to a lesser degree than their length, and is determined mainly by the position of zooid in the colony and by the shape of its neighbours (O'Dea & Okamura, 1999). Our results confirmed higher stability of zooids' width in a species and environment different to those previously studied, suggesting this finding to be robust.

Table 1. Number of measured zooids in colonies of *Cribrilina annulata* collected from two different substrata in each of three regions during 2002 and 2006.

Year, region	**2002**			**2006**
	DZ	**Ch**	**Sol**	**DZ**
Stones	358	57	51	22
Odontalia	223	1596	144	14

DZ, Dalnie Zelenzi (Barents Sea); Ch, Chupa Inlet (White Sea); Sol, Solovetskiy archipelago (White Sea).

Our research did not reveal significant 'geographical' variability of zooidal size. The early colony formation occurs during summer when the water temperature near the surface in the White Sea is higher than in the Barents Sea (8–15°C and 7–8°C correspondingly). The annual average temperature in the Ch region is also higher than in the DZ region (Kuznetsov, 1960; Climatic Atlas of the Barents Sea, 1998). The colonies collected in the Barents Sea with lower water temperature had, on average, larger zooids. This, at first sight, confirms the 'temperature rule' for dimensional changes (see O'Dea & Okamura, 2000; O'Dea & Jackson, 2002; O'Dea, 2005 and references therein). However, comparisons carried out separately for different substrata and different generations of zooids, did not show the same differences between colonies from the White and Barents Seas. Also, we suggest that the differences in salinity do not play an important role in the zooidal size determination. The salinity is 30–34‰ in the DZ region and 20–24‰ in the

Table 2. Results of three-factor ANOVA of zooidal size variability in *Cribrilina annulata* (samples of 2002).

Factors	Width of zooids						Length of zooids					
	SS	df	MS	F	*P*	Influence portion (%)	SS	df	MS	F	*P*	Influence portion (%)
Substratum	0.26	1	0.26	232.88	0.000	5.24	0.78	1	0.78	387.80	0.000	7.93
Region	0.10	2	0.05	43.60	0.000	1.96	0.04	2	0.02	8.88	0.000	0.36
Generation	0.26	3	0.09	77.85	0.000	5.25	0.61	3	0.20	101.33	0.000	6.22
Substratum*region	0.05	2	0.03	23.71	0.000	1.07	0.09	2	0.05	23.18	0.000	0.95
Substratum*generation	0.03	3	0.01	9.36	0.000	0.63	0.01	3	0.00	2.18	0.088	0.13
Region*generation	0.05	6	0.01	7.39	0.000	1.00	0.08	6	0.01	6.79	0.000	0.83
Substratum*region* generation	0.02	6	0.00	3.39	0.002	0.46	0.06	6	0.01	4.65	0.000	0.57

Substratum, stones/*Odontalia dentata*; region, Ch/Sol/Bar; generation, generation of zooids; *, denotes composition of the factors.

Ch region, but geographical differences appeared to be much weaker than habitat ones. On the other hand, we must admit that our approach may have not detected geographical variability due to the similar subarctic nature of the two study areas.

There are some well-known general rules concerning differences between fouling communities on algae and on solid substrata. The major characteristics of a substratum are its longevity and physical properties (e.g. its flexibility) (Manriquez & Cancino, 1996). Habitat conditions on firm substrata are considered to be more stable (Seed & O'Connor, 1981). These conditions allow prevailing of those species of bryozoans that have greater sizes of colonies, thicker zooids, and higher growth intensity, forming larger ovicells and producing more larvae per colony (Hillmer *et al.*, 1975; Herrera & Jackson, 1996). These species are often perennial, and show high ability to regenerate a colony from a fragment (Hughes & Cancino, 1985). The

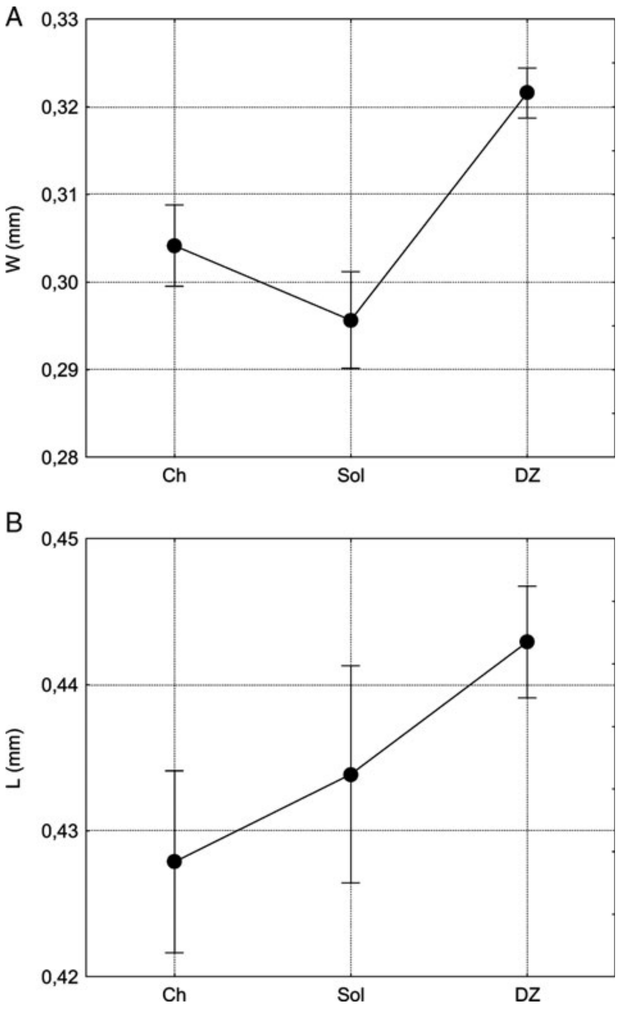

Fig. 4. Average sizes of zooids in early astogeny of *Cribrilina annulata* in three regions. (A) Width variability; (B) length variability (samples from 2002).

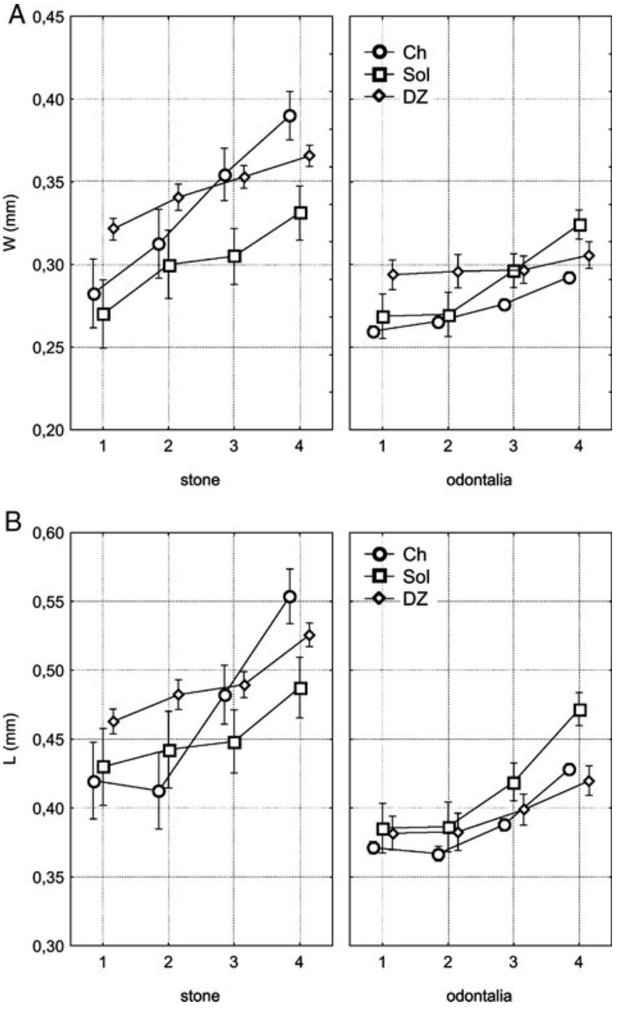

Fig. 5. Geographical variability of size in the first zooidal generations of *Cribrilina annulata* collected on two different substrata. (A) Width variability; (B) length variability (samples from 2002). The numbers on the abscissa axis correspond the zooidal generation: 1, ancestrula; 2–4 sequential generations of zooids (see Figure 1).

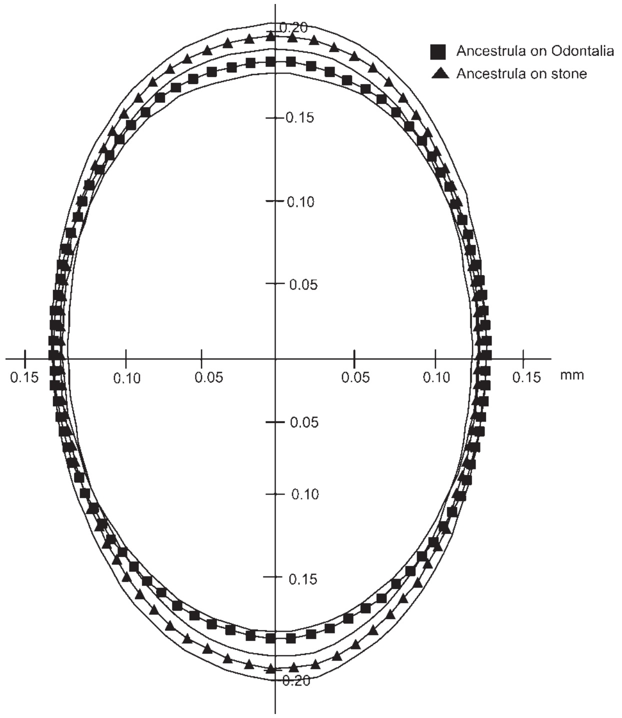

Fig. 6. Scheme showing an 'average, ancestrulae of *Cribrilina annulata* forming on two different substrata' (samples from 2006, Barents Sea).

species living on unstable substrata are characterized by an inverse set of properties. Strong calcification of encrusting colonies is considered as an obstacle for living on soft and flexible algae (Seed & O'Connor, 1981).

Our results show that similar rules can be observed at intraspecific level too. We found that zooids in colonies on stones were larger than in colonies growing on algae. Since differences are apparent as early as the ancestrulae stage, they are unlikely to be caused by temperature, feeding conditions or substratum longevity. We suggest it could be connected with settlement and metamorphosis of larvae.

The substratum influence on larvae (settling or just settled) can be both direct (the surface properties or emission of metabolites), and indirect—by change of hydrodynamic conditions or the intensity of sediment accumulation (Wahl, 1989; Manriquez & Cancino, 1996; Harvey & Bourget, 1997; Lapointe & Bourget, 1999). This influence may act before settlement (during larval seeking of the place for settlement), during metamorphosis or growth (Qian, 1999). We considered three competing hypotheses to explain the substrate influence on size of ancestrula. The first hypothesis assumes that the substratum influences only have bearing when larvae choose a place for settling. The second hypothesis assumes that the substratum affects only the survival of the ancestrulae and colonies. In the third we assume that the substratum affects only larval metamorphosis.

If the first hypothesis is correct then the larvae settling on stones should be larger than on algae (Figure 7A). It has been shown that larval size correlates with the size of ancestrula (Marshall & Keough, 2003), and the size of ancestrula with the size of zooids and the entire colony. Larger colonies are known to produce larger larvae (Marshall & Keough, 2004a). Hence, larvae produced by the colonies living on stones should be, on average, larger than larvae of colonies on algae. The probability of settling on stones where their parental colonies live is again higher for these larger larvae. As a consequence of such processes a partial genetic isolation of colonies growing on these two substrata is possible.

If we assume that small and large larvae are uniformly settled on both substrata, then the size differences of ancestrulae may be either a result of their differential mortality (hypothesis 2; Figure 7B) or change of size during metamorphosis (hypothesis 3; Figure 7C).

Colonies of *Bugula neritina* grown from larger larvae survived better in laboratory experiments. In contrast, in natural conditions better survival has been shown for colonies of the same species formed from smaller larvae (Marshall & Keough, 2004b). In other words, larvae of the same species of different sizes may be more viable in different conditions. Therefore colonies from ancestrulae of different sizes may survive to reach the reproductive phase better on different substrata: colonies from large ancestrulae survive better on stones, and colonies from small ancestrulae preferentially persist on algae. If this is true, colonies from one substratum should produce mainly small, and from the other, mainly large larvae. For both groups of larvae the probability of survival is higher when they settle on a 'parental' substratum. Thus, in this case, as well as in the first, it is possible to expect partial genetic isolation of colonies growing on these two different substrata.

Could the type of substratum affect a process of metamorphosis? In this case (Figure 7C) it is assumed that larvae of

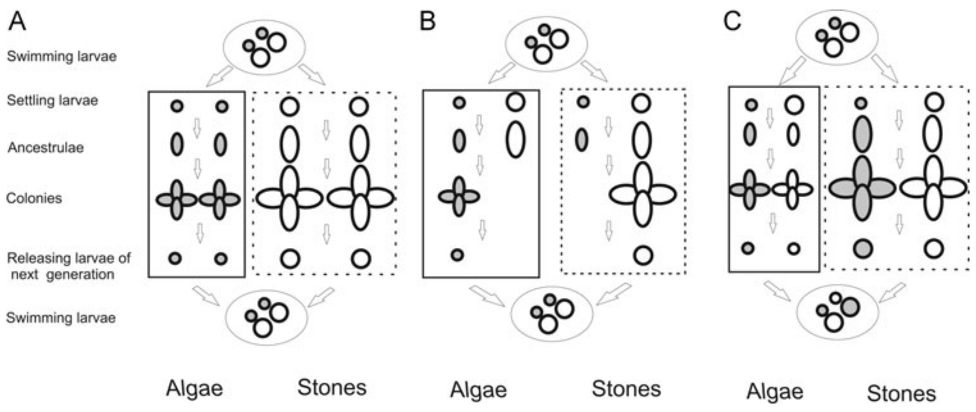

Fig. 7. Scheme representing three hypotheses of possible origin of size differences in zooids of *Cribrilina annulata* in colonies living on two different substrata. (A) 'larger larvae settle on stones'; (B) 'only larger ancestrula survive on stones'; (C) 'even small larvae become large ancestrulae on stones'.

the different sizes settle uniformly on both types of substrata. Then the differences in the ancestrulae size should indicate that metamorphosis itself varies, resulting in formation of ancestrula of different sizes on different substrata. Such an assumption does not contradict the high correlation between sizes of larvae and ancestrulae. High correlation between sizes of larvae and ancestrula may indicate the precision of linear dependence between these sizes, but it does not show coefficients of the linear regression itself. One may assume that larger ancestrula will be generated on stones rather than on algae from larvae of the same size. In this case the size of the ancestrula (especially, its length) becomes only a phenotypic characteristic defined by environmental conditions. All three hypotheses agree well with the general understanding of fouling organisms on stones and algae: i.e. larger sizes of colonies and zooids occur on stones, and they tend to have stronger calcification (Hillmer *et al.*, 1975; Herrera & Jackson, 1996).

A rough (rugose) substratum (each as a typical stone) is traditionally considered as more attractive for settlement of larvae than a smooth one (Marshall & Keough, 2003). So, other factors being equal, higher densities of ancestrulae might be expected on a rough substratum (Marshall & Keough, 2003). In addition larger larvae are considered to have higher chances to reach the most attractive substratum for settlement, therefore their average sizes should be higher on an optimal substratum (Bennett & Marshall, 2005). These facts argue that stones are better substrate for *C. annulata* than algae. However, it is known that colonies of *Cribrilina annulata* on stones in the Solovetsky Archipelago region are rare, and on thalli of *Odontalia* in the same region they are rather abundant (Grishankov, 1995). Our observations (unfortunately, only qualitative, not quantitative) confirm this result. Furthermore, the same situation was observed in the Chupa Inlet. Hence, it seems that stones are not an optimal substratum for settling larvae of *C. annulata* in both of the investigated regions in the White Sea (Ch and Sol). Noteworthy, Barnes & Clarke (1995) observed that stones are not the best substrate for some Antarctic bryozoans as well. In the areas studied by these authors the species diversity was lower on stones in contrast with brachiopod shells of the same size. As to the Dalnie Zelenzi (DZ) region, colonies of *C. annulata* on the stones were very abundant there. We cannot explain these geographical differences in larvae preferences. We have only an idea about this phenomen. In the White Sea (Ch and Sol) stones and *Odontalia* were very close to each other. In the Barents Sea (DZ) colonies have been collected on stones on the lower boundary of the intertidal zone where red algae are absent. Probably for this reason colonies on stones in the Barents Sea were rather abundant.

All the above-stated gives us some arguments to doubt that a stone is a more attractive substratum for settling of larvae than *Odontalia*. Thus, in our investigation the larger ancestrulae were found on a substratum that we consider less attractive for larvae. If we accept the first hypothesis ('larger larvae settle on stones', see Figure 7A), then we are forced to reject the thesis 'the probability to settle on the best substratum is higher for larger larvae'.

Generally the suitability of a substratum for habitation of a colony does not denote its attractiveness for settling of larva and vice versa. Comparison of the second ('only larger ancestrulae survive on stones', Figure 7B) and the third ('even small larvae become large ancestrulae on stones', Figure 7C) hypotheses leads to opposite conclusions about stones as an optimal substratum for colonies. The second hypothesis assumes, that smaller ancestrula perish on stones, and the third, that they develop successfully. The fact that size differences of zooids from different substrata are stronger for the zooids of later generations (Figure 3) supports the third hypothesis.

Examination of the second versus two other hypotheses may be done by comparison of ancestrulae size: (1) right after settling of larvae; and (2) in survived colonies. If the first or the third hypotheses are true, then size of ancestrulae on stones and algae should differ right after metamorphosis as in survived colonies. If the second hypothesis is true, then the average size of ancestrulae should be the same on both substrata right after metamorphosis, and differ when comparing the survived colonies. One more method to check these hypotheses is a genetic analysis since the first and the second hypotheses necessarily involve partial genetic isolation of colonies living on different substrata. Additional research is planned to check these suggestions.

We suggest that stones are not an optimal substratum for the settlement of larvae of *Cribrilina annulata*. As the astogeny of encrusting colonies is less stable on stones, than on algae (Yagunova, 2006), stones are probably not an optimal substratum for habitation of colonies of *Cribrilina annulata* either. We found that the shortest ancestrulae were on *Odontalia*, and the longest ones on stones. Two reasons are suggested for this allocation of ancestrulae. Firstly, it is more difficult for a larger larva to attach to the flexible thin thallus of algae. Secondly, irregularities of the rough stone surface make it inconvenient for small larvae. Therefore we conclude that a stone is the best substratum for settling of largest larvae, and alga is an optimum for the smallest larvae. If so, then the principal cause of the size differences of ancestrulae should be the difference in sizes of settling larvae choosing different substrata (the first hypothesis). Size difference of ancestrulae is determined by the optimal substrata for larvae of different sizes being different.

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REFERENCES

Abelson A. (1997) Settlement in flow: upstream exploration of substrata by weakly swimming larvae. *Ecology* 78, 160–166.

Barnes D.K.A. and Clarke A. (1995) Epibiotic communities on sublittoral macroinvertebrates at Signy Island, Antarctica. *Journal of the Marine Biological Association of the United Kingdom* 75, 689–703.

Bennett C.E. and Marshall D.J. (2005) The relative energetic costs of the larval period, larval swimming and metamorphosis for the ascidian *Diplosoma listerianum*. *Marine and Freshwater Behaviour and Physiology* 38, 21–29.

Bishop J.D.D. (1988) Disarticulated bivalve shells as substrates for encrustation by the bryozoan *Cribrilina punctarata* in the Plio-Pleistocene Red Crag at Eastern England. *Palaeontology* 2, 237–253.

Bishop J.D.D. (1989) Colony form and the exploitation of spatial refuges by encrusting Bryozoa. *Biological Reviews* 64, 197–218.

Boaden P.J.S., O'Connor R.J. and Seed R. (1975) The composition and zonation of a *Fucus serratus* community in Strangford Lough, Co. Down. *Journal of Experimental Marine Biology and Ecology* 17, 111–136.

Boardman R.S. and Cheetham A.H. (1969) Skeletal growth, intracolony variation, and evolution in Bryozoa: a review. *Journal of Paleontology* 43, 205–233.

Buss L.W. (1979) Habitat selection, directional growth and spatial refuges: why colonial animals have more hiding places. In Larwood G.P. and Rosen B.R. (eds) *Biology and systematics of colonial organisms*. London, New York: Academic Press, pp. 459–497. [Systematics Association Special vol. 11]

Cadman P.S. and Ryland J.S. (1996) The characters, reproduction, and growth of *Alcionidium mytili* Dalyell, 1848 (Ctenostomatida). In Gordon D.P., Smith A.M. and Grant-Mackie J.A. (eds) *Bryozoans in space and time*. Wellington, NZ: National Institute of Water and Atmospheric Research Ltd, pp. 69–79.

Climatic Atlas of the Barents Sea. (1998) Temperature, salinity, oxygen. *International Ocean Atlas Series*. Volume 1, NOAA Atlas NESDIS 26.

Grishankov A.V. (1995) *Fauna and some peculiarities of the structure of benthic communities in Solovetskiy Bay*. PhD thesis, University of St Petersburg, St Petersburg, Russia. [In Russian.]

Grunbaum D. (1995) A model of feeding currents in encrusting bryozoans shows interference between zooids within a colony. *Journal of Theoretical Biology* 174, 409–425.

Håkansson E. and Winston J.E. (1985) Interstitial bryozoans: unexpected life forms in a high energy environment. In Nielsen C. and Larwood G.P. (eds) *Bryozoa: Ordovician to Recent*. Fredensborg: Olsen and Olsen, pp. 125–134.

Harmelin J.G. (1997) Diversity of bryozoans in the Mediterranean sublittoral cave with bathyal-like conditions: role of dispersal process and local factors. *Marine Ecology Progress Series* 153, 139–152.

Harvey M. and Bourget E. (1997) Recruitment of marine invertebrates onto arborescent epibenthic structures: active and passive processes acting at different spatial scales. *Marine Ecology Progress Series* 153, 203–215.

Herrera A. and Jackson J.B.C. (1996) Life history variation among 'dominant' encrusting cheilostomate Bryozoa. In Gordon D.P., Smith A.M. and Grant-Mackie J.A. (eds) *Bryozoans in space and time*. Wellington, NZ: National Institute of Water and Atmospheric Research Ltd, pp. 29–38.

Hillmer G., Gautier T.G. and McKinney F.K. (1975) Budding by intrazooecial fission in the stenolaemate bryozoans *Stenoporella, Reptomulticava* and *Canalipora*. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 44, 123–132.

Hughes R.N. and Cancino J.M. (1985) An ecological overview of cloning in Metazoa. In Jackson J.B.C., Buss W. and Cook R.E. (eds) *Population biology and evolution of clonal organisms*. New Haven: Yale University Press, pp. 153–186.

Jebram D. (1973) Preliminary observation on the influences of food and other factors on the growth of bryozoans. *Kieler Meeresforschungen* 29, 50–57.

Jebram D. (1978) Preliminary studies on «abnormities» in bryozoans from the point of view of experimental morphology. *Zoologische Jahrbücher, Abtheilung für Anatomie und Ontogenie der Tiere* 100, 245–275.

Jebram D. and Rummert H.D. (1978) Influences of different diets on growth and forms of *Conopeum seurati* (Canu) (Bryozoa: Cheilostomata). *Zoologische Jahrbücher. Abteilung für Systematik, Okologie und Geographie der Tiere* 105, 502–514.

Kuklinski P., Gulliksen B., Lønne O.G. and Weslawski J.M. (2006) Substratum as a structuring influence on assemblages of Arctic bryozoans. *Polar Biology* 29, 652–661.

Kuznetsov V.V. (1960) *The White Sea and the biological features of its flora and fauna*. Moscow–Leningrad: Nauka. [In Russian.]

Lapointe L. and Bourget E. (1999) Influence of substratum heterogeneity scales and complexity on a temperate epibenthic marine community. *Marine Ecology Progress Series* 189, 159–170.

Lombardi C., Cocito S., Occhipinti-Ambrogi A. and Hiscock K. (2006) The influence of seawater temperature on zooid size and growth rate in *Pentapora fascialis* (Bryozoa: Cheilostomata). *Marine Biology* 149, 1103–1109.

Manriquez P.H. and Cancino J.M. (1996) Bryozoan–macroalgal interactions: do epibionts benefit? *Marine Ecology Progress Series* 138, 189–197.

Mariani S. (2003) Recruitment in invertebrates with short-lived larvae: the case of the bryozoan *Disporella hispida* (Fleming). *Helgoland Marine Research* 57, 47–53.

Marshall D.J. and Keough M.J. (2003) Variation in the dispersal potential of non-feeding invertebrate larvae: the desperate larva hypothesis and larval size. *Marine Ecology Progress Series* 255, 145–153.

Marshall D.J. and Keough M.J. (2004a) Variable effects of larval size on post-metamorphic performance in the field. *Marine Ecology Progress Series* 279, 73–80.

Marshall D.J. and Keough M.J. (2004b) When the going gets rough: effect of maternal size manipulation on larval quality. *Marine Ecology Progress Series* 272, 301–305.

Nikulina E.A. (1999) Substrate reactions of bryozoans of class Euristomata in connection with formation of their colonies. *Ontogenesis* 30, 245–254. [In Russian.]

Nikulina E.A. (2001) Sequence of buds development of bryozoan zooids (Cheilostomata) and the bidimensional organization of their colonies. *Zoological Journal* 80, 210–209. [In Russian.]

O'Connor R.I., Seed R. and Boaden P.J.S. (1979) Effect of environment and plant characteristics on the distribution of Bryozoa in a *Fucus serratus* L. community. *Journal of Experimental Marine Biology and Ecology* 38, 151–178.

O'Dea A. (2005) Zooid size parallels contemporaneous oxygen isotopes in a large colony of *Pentapora foliacea* (Bryozoa). *Marine Biology* 146, 1075–1081.

O'Dea A. and Jackson J.B.C. (2002) Bryozoan growth mirrors contrasting seasonal regimes across the Isthmus of Panama. *Palaeogeography, Palaeoclimatology, Palaeoecology* 185, 77–94.

O'Dea A. and Okamura B. (1999) Influence of seasonal variation in temperature, salinity, and food availability on module size and colony growth in the estuarine bryozoan *Conopeum seurati*. *Marine Biology* 135, 581–588.

O'Dea A. and Okamura B. (2000) Intracolony variation in zooid size in cheilostome bryozoans as a new technique for investigating palaeoseasonality. *Palaeogeography, Palaeoclimatology, Palaeoecology* 162, 319–332.

Okamura B. (1987) Seasonal changes in zooid size and feeding activity in epifaunal colonies of *Electra pilosa*. In Ross J.R.P. (ed.) *Bryozoa: present and past*. Bellingham: Western Washington University, pp. 197–203.

Ostrovsky A.N. (1998) Comparative studies of ovicell anatomy and reproductive patterns in *Cribrilina annulata* and *Celleporella hyalina* (Bryozoa: Cheilostomatida). *Acta Zoologica (Stockholm)* 79, 287–318.

Pachut J.F., Cuffey R.J. and Anstey R.L. (1991) The concept of astogeny and ontogeny in stenolaemate bryozoans, and their illustration in colonies of *Tabulipora carbonaria* from the Lower Permian from Kansas. *Journal of Paleontology* 65, 213–233.

Partridge J.C. and Okamura B. (1999) Suspension feeding adaptations to extreme flow environments in a marine bryozoan. *Biological Bulletin. Marine Biological Laboratory, Woods Hole* 196, 205–215.

Powell N.A. (1967) Sexual dwarfism in *Cribrilina annulata* (Cribrilinidae–Bryozoa). *Journal of the Fisheries Research Board of Canada* 24, 1905–1910.

Qian P.Y. (1999) Larval settlement of polychaetes. *Hydrobiologia* 402, 239–253.

Sebens K.P. (1979) The energetic of asexual reproduction and colony formation in benthic marine invertebrates. *American Zoologist* 19, 683–697.

Seed R. and O'Connor R.J. (1981) Community organization in marine algal epifaunas. *Annual Review of Ecology and Systematics* 12, 49–74.

Stebbing A.R.D. (1972) Preferential settlement of a bryozoan and serpulid larvae on the younger parts of *Laminaria* fronds. *Journal of the Marine Biological Association of the United Kingdom* 52, 765–772.

Taylor P.D. and Furness R.W. (1978) Astogenetic and enviromental variation of zooid size within colonies of *Stomatopora* (Bryozoa, Cyclostomata). *Journal of Paleontology* 52, 1093–1102.

Taylor P.D. (1988) Colony growth pattern and astogenetic gradients in the Cretaceous cheilostome bryozoan *Herpetopora*. *Palaeontology* 31, 519–549.

Wahl M. (1989) Marine epibiosis. I. Fouling and antifouling: some basic aspects. *Marine Ecology Progress Series* 58, 175–189.

Yagunova E.B. (2002) Some laws of development of encrusting bryozoan *Cribrilina annulata* (Fabricius, 1780). *Journal of General Biology* 63, 62–67. [In Russian.]

Yagunova E.B. (2005) Astogeny of *Cribrilina annulata* (Fabricius, 1780) (Bryozoa, Cheilostomata): norm and anomaly. *Invertebrate Zoology* 2, 36–50. [In Russian.]

and

Yagunova E.B. (2006) *Colony of encrusting bryozoan* Cribrilina annulata *(Fabricius, 1780) as multilevel living system: the organization, dynamics, variability*. PhD thesis, University of St Petersburg, St Petersburg, Russia. [In Russian.]

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