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The Bryozoan Diversity Mystery: Why Do We Have About 1000 Species in Japanese Waters?

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ABSTRACT

Bryozoans are clonal and colonial organisms that have a species-specific biological potential to perform tactial (reactive) growth alterations. These biological potentials subdivide encrusting bryozoan morphotypes into several different pathways of individuality of morphoprocesses, a term introduced by V. N. Beklemishev (1890–1962), and applied to bryozoans with various degrees of colony integration. The frequency distribution of these morphotypes (z-/m-/c-/s-laminae) has been studied in bryozoans occurring in the vicinity of 5 Japanese marine biology stations, located along the latitudinal gradient in Japan from cool-temperate to (marginally) tropical. With increasing light influx and temperature, substrate occupation and thickness of biofilms increase, and filamentous microalgae and cyanobacteria gradually replace diatoms. Likewise, the warmer the water, the more frequent became s- and c-laminae. Both are the morphotypes with the best relative potential to perform tactical response and to overgrow biomats. In warmer water, bryozoan coverage tends to decrease benthic microbial diversity. In cool waters, the opposite is often the case. This indicates that biofilms contribute to differentiate the substrate surface into various bryozoan microhabitats, and thus contribute to the overall bryozoan diversity present in Japanese waters.

Keywords: Bryozoa, Biofilms, Morphoprocess, Latitudinal gradients

INTRODUCTION

Bryozoans represent a phylum of colonial, suspension feeding animals. They are abundantly found in Japanese coastal waters. This is hardly a surprise since, in general, the Western Pacific represents the global hot spot of bryozoan diversity [1].

Repeated budding of genetically but not always morphologically identical zooids forms bryozoan colonies of physiologically connected modules. Each zooid is delimited by a cuticular and often calcified covering of the body wall. Bryozoan polypides consist of a U-shaped gut and a ring of tentacles. The alimentary canal forms a deep loop inside the coelomic cavity. Intestine and rectum rise to the anus, which is situated near the mouth but outside the lophophore. There are no special respiratory organs, and no circulatory or excretory systems [2]. The latter is of special importance since this implies a significant size limitation in the growth of bryozoan zooids.

In feeding position, the polypides are protruded from their rigid zooidal skeleton (zooecium). The zooecial chamber is very small (in most species not larger than 0.5 mm). The protrusion of the tentacle bell is controlled by the muscular contraction of

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membranes and the increase of hydrostatic pressure of the coelomic fluid. Spatial and functional arrangement of membranes, zooecial walls and annular or parietal muscles is a criterion in bryozoan classification up to the level of orders and infraorders (see [2–4]) (Fig. 1).

Bryozoan colonies have many distinct shapes, and various colony forms and growth strategies can be distinguished. Furthermore, large numbers of encrusting species are able to co-exist, even though they are often in direct competition for settling space and food. There has been little research why so many species—sometimes several hundred at a given site—are able to co-exist [6], and which role bryozoans play in maintaining the health of shallow marine ecosystems [7]. The question is not only which factor(s) actually control(s) biodiversity, but also the biodiversity itself, since our taxonomical record of the species is still far from being complete.

In 1988, it was estimated that only 50% of bryozoan species that dwell in the Indopacific are known [8]. An increase in taxonomic resolution due to the now-routine use of scanning electron microscopy and molecular biology, and a paradigm shift in how taxonomists view geographic variation has revealed that in the western Pacific, the percentage of bryozoan fauna known today is even less. The high proportion of new species in recent studies in the Pacific is thus attributable to generally low previous taxonomic effort throughout much of the region.

TAXONOMY STUDIES ON JAPANESE BRYOZOA

For the Japanese region, systematic knowledge of the bryozoan fauna dates back to the year 1890. In the very first taxonomical descriptions of bryozoans from Japan, 137 species mainly from Sagami Bay have been described, 85 of them new [9]. Today, the study on bryozoans of the Sagami Bay is continued by one of the authors (M. H.).

In the 20th century, Y. Okada and S. Mawatari added new species to the taxonomical records of Japan. For example, in 1955, 78 species of cyclostomes have been listed from Japanese waters [10] (typically, there are 2–3 cheilostome species per cyclostome species in a given association; [6]). Although the total number of bryozoans in Japanese waters is still unknown, we feel safe to estimate the diversity at a level of well over 1,000 species.

Aside from a nationwide view, we also need to know the regional differences of bryozoans along the Japanese coasts. The latitudinal gradient in Japan from cool temperate to (marginal) tropical contributes significantly to the richness of the Japanese fauna, but the magnitude of this diversity gradient is still subject to speculation. Traditionally, bryozoan research focussed on the warm temperate regions of Honshu, while the higher and lower latitudes received comparatively less attention. However, this has changed recently. In the northern part of Hokkaido, 39 cheilostome species have been recorded recently, found among more than 7000 specimens

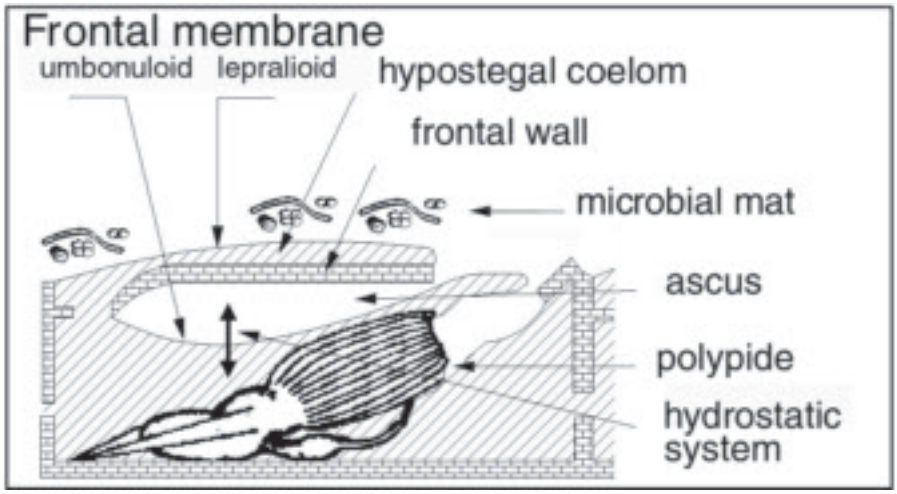

Fig. 1 Diagram of a bryozoan zooid of the suborder Ascophora. The hydrostatic system is based on the presence of the inner compensation sack (ascus): when parietal muscles pull down the frontal membrane, water can flow into the ascus, and the polypide is extruded. The process is reversible by contraction of the retractor muscle. The calcified frontal shield protects the flexible membranes from microbial colonization (indicated on top). Redrawn from Ref. 5.

collected at 10 intertidal sites in rocky habitats along the shore of Akkeshi Bay. Nine species (23% of total) are described as new [11].

In the southern regions of Japan at Sesoko Island, Okinawa, one of the authors (S. F. M.) reported 20 species [12]. In another study, 25 species have been collected, several of them for the first time recorded from Japanese waters [13]. Most probably, the true diversity in the hermatypic habitats of the Ryukyu Islands may reach several hundred species of bryozoans, judging from the experience in similar habitats in the Philippines and Indonesia where 725 species were reported [14].

MATERIAL AND METHODS

Bryozoan specimens settling on disarticulated and living bivalve shells were collected either by dredging or by hand at several sites around Japan between May and June 2000 and in October 2002. Water depths ranged from the intertidal zone to 17 metres, depending on the availability of bryozoan colonized substrata. In order to minimize bathymetric patterns that might interfere with latitudinal patterns, and which are known from tropical settings [15–16], small to medium-sized unstable substrata subjected to transport by bottom currents, or wave action, have been selected.

In order to outline whether the different hydrographic and biological settings of the respective sites in Japan and New Zealand may be influencing diversity and species records, three bryozoan collection sites with different water temperatures were selected. These were: Akkeshi (cool-temperate), Shimoda (subtropical) and Okinawa (marginally tropical) (see Fig. 3). In October 2002 samples from Akkeshi and Shimoda were taken again from the same sites.

Furthermore, we based our study exclusively on bryozoans that were found encrusting bivalve shells. A shell is a rather simple bryozoan habitat, compared to the fractal surfaces of rocks. Therefore, a more or less standardized natural bryozoan habitat is compared across the latitudes.

From each of the stations, 300 colonies of encrusting laminar bryozoans were examined and categorized in seven types of growth as outlined below. When more than one colony of a single species was present on one shell, each colony was counted separately. Total species diversity and taxonomical observations are presented elsewhere [12–13, 17].

Parts of the collection were fixed in 5% formalin-seawater. Additional samples were air-dried. All colonies were examined with a binocular microscope in order to study optical signals of microbial interaction, and both bleached and CPD (Critical Point Dried) samples were documented using an scanning electron microscope.

BRYOZOAN ECOLOGY AND LATITUDINAL GRADIENTS

Bryozoans have traditionally been used as indicators of environmental conditions in both recent and fossil environments ([3], with review of literature). In most species, the functional attributes are well represented in a great diversity of skeletal features. Since bryozoans have an excellent fossil record, they became an ideal example for the study of evolution, and thus had an important role in shaping the "punctuated equilibrium" theory (Ref. 18, with review of literature).

Despite of considerable abundance and coverage of marine surfaces, bryozoans are small and inconspicuous animals that henceforth are often overlooked. In most of the encrusting taxa, frontal surface and orifice are situated only about 100 to 200 μm above substrate level. Therefore, in spreading over solid surfaces, bryozoan basal and lateral zooidal walls are exposed to microbenthic organisms such as bacteria and fungi, while, the frontal surfaces are also open to a flux of energy, organic and inorganic matter, and other controlling factors from the water column (nutrients, larvae, sediment load, larger organisms such as predators, grazing fishes etc.). Accordingly, microbial mats and biofilms represent some of the most important control factors influencing bryozoan settlement and distribution. Contrary to what occasionally has been stated in marine biology textbooks, there are many laminar bryozoan species that compete successfully with weedy "algal mats" [19–20].

Moreover, bryozoans actively control microbial distribution patterns. As early as 1929, Canu and Bassler described as "the reteporidan mystery" that "Never is a complete colony encrusted by another organism... No larva has been able to develop here and disturb the harmony..." This is one of the very first observations that some (phidoloporid) bryozoans are able to actively control or inhibit what settles on them [21].

Due to the demands of biotechnology research, it is well known that bryozoan coelomic cavities provide nanohabitats for a great variety of Bacteria ([22–23], with review of literature). In some bryozoan species, even the larvae contain symbiotic bac-

teria (Ref. 4, with review of literature), and in several species of marine ctenostome and cheilostome Bryoza, calcofluor-white staining revealed the presence of numerous hyphae of endozoic fungi [25]. Bryozoans are thus a good example for the "Theory of the Global Morphoprocess" by Vladimir N. Beklemishev (1890–1962), and his quotation "Every organism is in the nature of semi-parasitic, semi-mutualistic community. Life of the wholeness is based on the conflict and destruction of the parts" [26]. Actually, the theoretical system of Beklemishev has been applied to bryozoan biosystems, characterized as periodic and aperiodic morphoprocesses, and showing various degree of individuality of the colony modules, and of the colony itself [27–29].

To a certain degree, microorganisms control the spatial occurence of bryozoan species and thus bryozoan diversity. Judging from earlier data collected in New Zealand, the Philippines, and the Gulf of Aqaba, the latitudinal and also bathymetric occurrence of various bryozoan growth types is mainly linked to the competitive pressure of biofilms and microbial mats in shallow waters, and the interaction with epizoic mats in shaded microhabitats [5, 30].

When we compare the different collections, it becomes evident that the latitudinal gradient is clearly expressed by the distribution patterns not only of bryozoan species but also in the distribution of bryozoan growth morphologies. Laminar encrusting species that are able to produce giant buds are becoming more abundant in shallow water, and warm temperate to (sub-) tropical latitudes, whereas encrusters lacking giant buds are more abundant in the cool temperate region, or in cryptic microhabitats.

For example, in the fauna collected from Sesoko Island in Japan, growth morphologies show many features typical for tropical bryozoans. There are abundant sheets of various species that produce giant buds at their colonial margins. These buds are separated spaces which have not built a polypide yet [31]. Their walls are weakly calcified so the colonial margin remains flexible, which enables the colony to expand over substrate or competitors for space; afterwards the distal walls and the polypide are built. Apparently, this growth form has a higher energy demand because there are no feeding polypids in marginal areas. Aside from that, the new zooids cannot not be assigned to a single parent zooid of the former generation [31].

Fig. 2 Vladimir N. Beklemishev (1890–1962). Image courtesy of George S. Levit, St. Petersburg, Russia.

One of the adaptive values of giant buds is their ability to overgrow microbial mats. Therefore, we have quantified those laminar colonies that produce giant buds, and compared them with another type that does not. The latter has been classified as z-lamina, whereas the first is classified as an s-lamina. They represent opposite ends among the four possible sheet morphologies (the other two types are not considered here, and discussed in Ref. 5 and 27. Z- and s-laminae can be defined as follows:

1) z-laminae (zooid-laminae)

In zooidal laminae, growth is mainly determined by the structural polarity of a single zooid. The spatial orientation of the new bud is determined by the distal or angular distolateral position of pore chambers. The potential to react to opponents is very low. During interaction with biofilms and microbial mats, growth usually stagnates; but, if possible, growth might also be diverged away from the contact zone. The budding frequency at some selected areas of the colonial margin may decrease or increase, thereby influencing the outer shape of the zoarium. The advantage of this mode of growth is that a new feeding polypide is generated in a short period of time.

2) s-laminae (sheet-laminae)

Sheet laminae show a much more environmentally induced way of growth, with various types or sizes of giant buds, stolonal outgrowths, or weakly calcified zoarial margins concealing the structural polarity of the single colonial module. Colonies with giant buds longer than at least two autozooid lengths belong to the category s-laminae. They have a very much improved biological potential of elevating their flexible, weakly calcified, and very broad growth margins. For example, the tropical species *Parasmittina parsevalii* (Audouin, 1826) is able to generate giant buds reaching the length of 8 regular autozooids. Since the colonial margin is devoid of

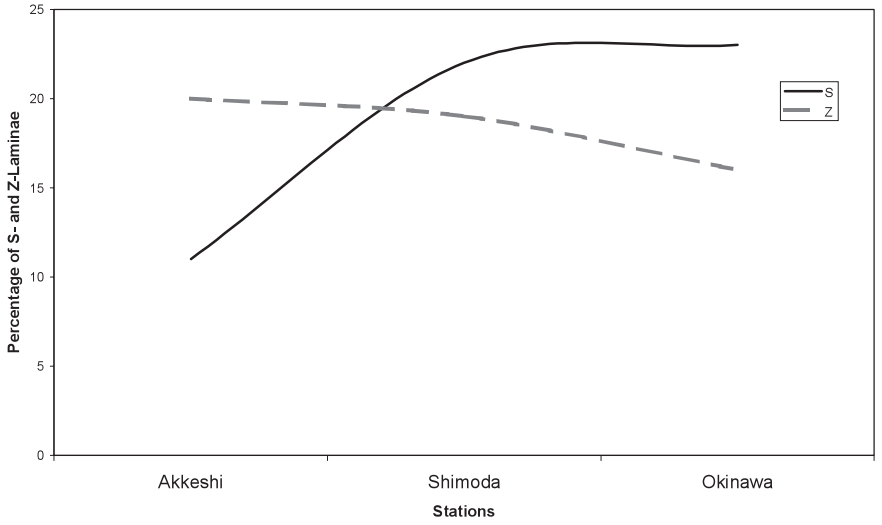

Fig. 3 Comparison of relative abundance of z- and s-laminae (percentage of all bryozoan colonies recorded; n = 900) from Akkeshi, Hokkaido, in the North, towards Okinawa in the South. S-laminae dominate in subtropical to tropical waters whereas in cool-temperate water, z-laminae are more important.

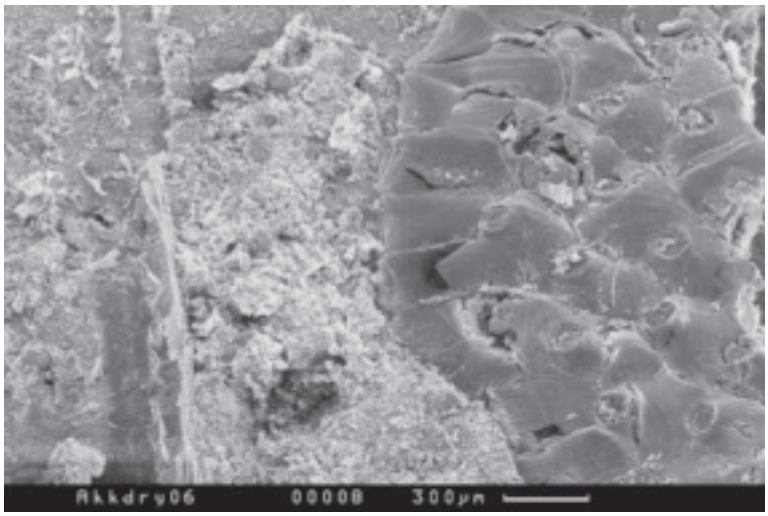

Fig. 4 A cool-temperate association of *Schizomavella punctigera* (MacGillivray) and diatom biofilms from Akkeshi, Hokkaido; SEM image of Critical-Point-Dried sample. Photograph courtesy of Jürgen Kaselowsky.

feeding autozooids, and thus has to be supported by the whole colony, the s-type is both highly integrated and highly energy-demanding. In substrata characterized by a high degree of overgrowth competition and abundance of microbial or sponge mats, bryozoan colonies with the potential to build s-type laminae are more successful in settling, than most of the other bryozoans.

In Okinawa, the percentage of s-laminae is very high, when compared to other sites studied in Japan such as the bryozoans off the Oshoro and Akkeshi marine stations, Hokkaido University. On the other hand, there is some similarity to the tropically influenced bryozoan fauna of the Shimoda Marine Research Center, Tsukuba University, situated at the tip of the Izu Peninsula (see Fig. 3). This is certainly also an effect of the taxonomical similarity of both faunas (but not exclusively, since several bryozoan species produce laminae of various types of morphology, depending on external stimuli).

Biofilms also show some correlation with latitudinal gradients in Japan from cool-temperate to subtropical and tropical waters. Diatom films become replaced by filamentous cyanobacteria towards low-

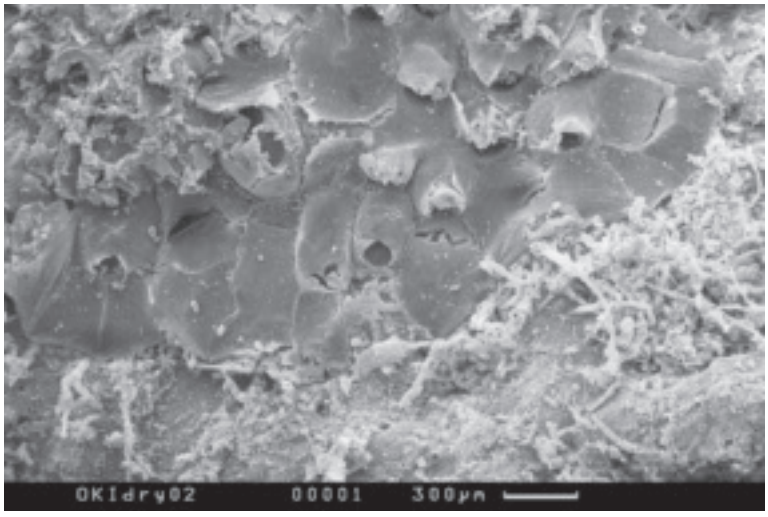

Fig. 5 A marginal tropical association of *Celleporaria sibogae* WINSTON & HEIMBERG and biofilms (composed e.g. of filamentuous Cyanobacteria) from Sesoko Island, Okinawa. Photograph courtesy of Jürgen Kaselowsky.

er latitudes, and the biofilms are becoming thicker (Figs. 4 & 5). In contrast, biofilms settling on the living sediments of the bryozoan frontal walls decrease in warm water settings. The decrease of microbial fouling of bryozoan surfaces towards lower latitudes parallels findings in which bryozoan lamina types comparatively strong in overgrowth competition increased towards lower latitudes. Details on taxonomy and morphology of benthic microorganisms co-occurring with bryozoans have been presented elsewhere [22, 23].

Looking at tropical to warm temperate bryozoans, we may adopt some lines of SHAKESPEARE (HAMLET): Bryozoans are "taking arms against a sea of troubles", and competition becomes a dominant control factor of bryozoan diversity once it gets warm.

The "sea of troubles" unfolded at the beginning of the Upper Cretaceous when the mucilage secretion by biofilms attached to interfaces, binding particles and rocks increased, due to the growing abundance of benthic diatoms since Aptian/Albian times [32–34]. Diatoms might have triggered the great radiation of ascophorine and interior walled cyclostome bryozoan species and morphologies in the Upper Cretaceous [5]. This idea is not really a new one.

As early as 1969, the great bryozoologist Gilbert Larwood (1930–1997) wrote about the innovations in the calcified frontal wall of certain Upper Cretaceous bryozoans: "It acts as a coarse outer filter to the zoarium precluding penetration by larger organisms or by coarse detritus and it may even be effective in retaining a certain amount of gradet detritus forming a further protection over the surface of the zoarium" [35].

Detritus attached to bryozoan surfaces usually indicates the presence of a biofilm. Accordingly, what Larwood had foreseen is the antagonistic-mutualistic "Beklemishev" world of bryozoans and biofilms, contributing ever since the Cretaceous to shape the modern bryozoan communities occurring in Japanese waters, and elsewhere.

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