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GENERAL BIOLOGY

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## Association of Atlantic Hydrothermal Mytilids of the Genus *Bathymodiolus* spp. (Mollusca: Mytilidae) with the Polychaeta *Branchiopolynoe* aff. *seepensis* (Polychaeta: Polynoidae): Commensalism or Parasitism?

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A large body of data accumulated during the past 27 years of extensive studies of hydrothermal vent and cold seep communities demonstrated a widespread distribution of symbiotic Polychaeta in these communities all over the Ocean [1]. Although the list of known symbiotic polychaetes includes about 20 species, it is expected to be extended in the future. The hosts of the symbionts are commonly dominant animals of the hydrothermal communities, such as Vestimentifera and the bivalve molluscs *Bathymodiolus* spp. and *Calyptogena* spp. (family Vesicomidae); the symbiont prevalence may reach 90.5% (our observations). These data suggest that symbiotic polychaetes play a substantial role in the consumption and transfer of organic matter in hydrothermal vents. On the other hand, the biology of the symbionts is understood insufficiently. Although the role of symbionts in the structure and function of hydrothermal communities and cold seep communities is evidently important, the understanding of their importance is significantly ahead of the understanding of their biology. This discrepancy is primarily due to methodological obstacles to the studies on the biology of symbiotic deep-sea associations. The available literature [2, 3] describes the specific features of the reproductive biology and structure of the settlements of the hydrothermal symbiotic Atlantic scale worms *Branchiopolynoe seepensis*. However, the important issue of the pattern of the host–symbiont interaction in the association between polychaetes and hydrothermal bivalves remains obscure.

Because some polychaetes of the Nautiliniellidae family, symbionts of the hydrothermal bivalves (vesicomids and solemyids), have fastening hooklike chaetae, their interaction with hosts is regarded as parasitism [4]. Interaction of the *Branchiopolynoe* species (family Polynoidae) with the mytilids *Bathymodiolus* spp. is usually regarded as commensalism [5–7]. On the other hand, gill fragments of host mollusc were found in the intestine of *Branchiopolynoe symmitilidae* from the Galapagos Rift [8]. This finding may be regarded as evidence of parasitism.

The goal of this work was to analyze the host–symbiont interaction in the associations of the mytilids *Bathymodiolus* spp. with the polychaetes *Branchiopolynoe* aff. *seepensis* in the hydrothermal vents of the Mid-Atlantic Ridge.

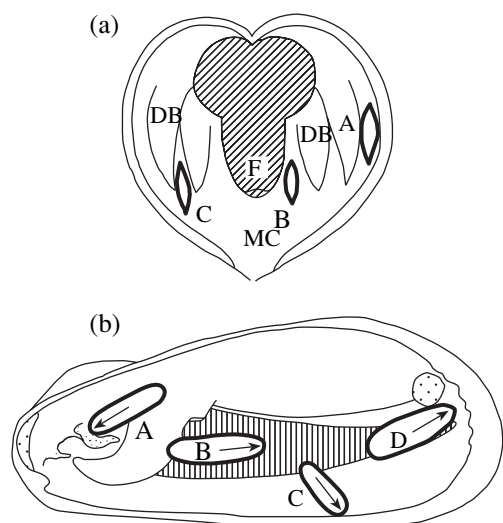
The collection of hydrothermal mytilids sampled during the expeditions of the research vessel *Akademik Mstislav Keldysh* to the hydrothermal vents of the Mid-Atlantic Ridge was used. The expeditions visited the Logatchev, Snake Pit, Lucky Strike, and Rainbow fields in 1998, 1999, and 2002. In addition, the material collected during the French expeditions to the Lucky Strike, Menez Gwen, and Snake Pit regions in 1993, 1995, and 1997 was also used. The examined material included 315 specimens of *Bathymodiolus puteoserpentis* and 725 specimens of *Bathymodiolus azoricus*, which contained 49 and 404 specimens of *Br.* aff. *seepensis*, respectively. Three methodological approaches were used to analyze the character of interaction between the species: (1) the quantitative analysis of symbiont location in the host organism. The predominant location may reflect the method or source of food consumption, interspecies or intraspecies competition, and selection of the most protected part of body surface [9]; (2) analysis of host traumas, which can be used to assess the pattern of the host–symbiont interaction and to count the total number of host specimens that are or have been affected by the symbiont; (3) examination of the intestine contents of the symbionts.

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**Fig. 1.** (a) Location of symbionts relative to the host mantle lining and gills: (A) between the mantle lining and gills; (B) between the gills and foot; (C) between the demibranch leaflets. Designations: MC, mantle cavity; F, foot; DB, demibranchs. (b) Location of the symbionts in the mollusc mantle cavity. The arrow shows the prostomium orientation: (A) towards the host palps; (B) towards the body center; (C) towards the valve edge; (D) towards the siphon.

The experimental material was treated using the following methods: the length, width, and height of the mollusc shell was measured; the shell was opened, and the number and location of symbiont polychaetes, the number of traumas, and the number of foreign bodies in host tissues were recorded. The polychaetes had been extracted under binocular microscope sexed by the number of nephridial papillae, and their body length was measured. To analyze the intestine contents of polychaetes, the animal was dissected along the dorsal side. The contents were collected with a pipette, placed in a droplet of water on a slide, and examined under a microscope.

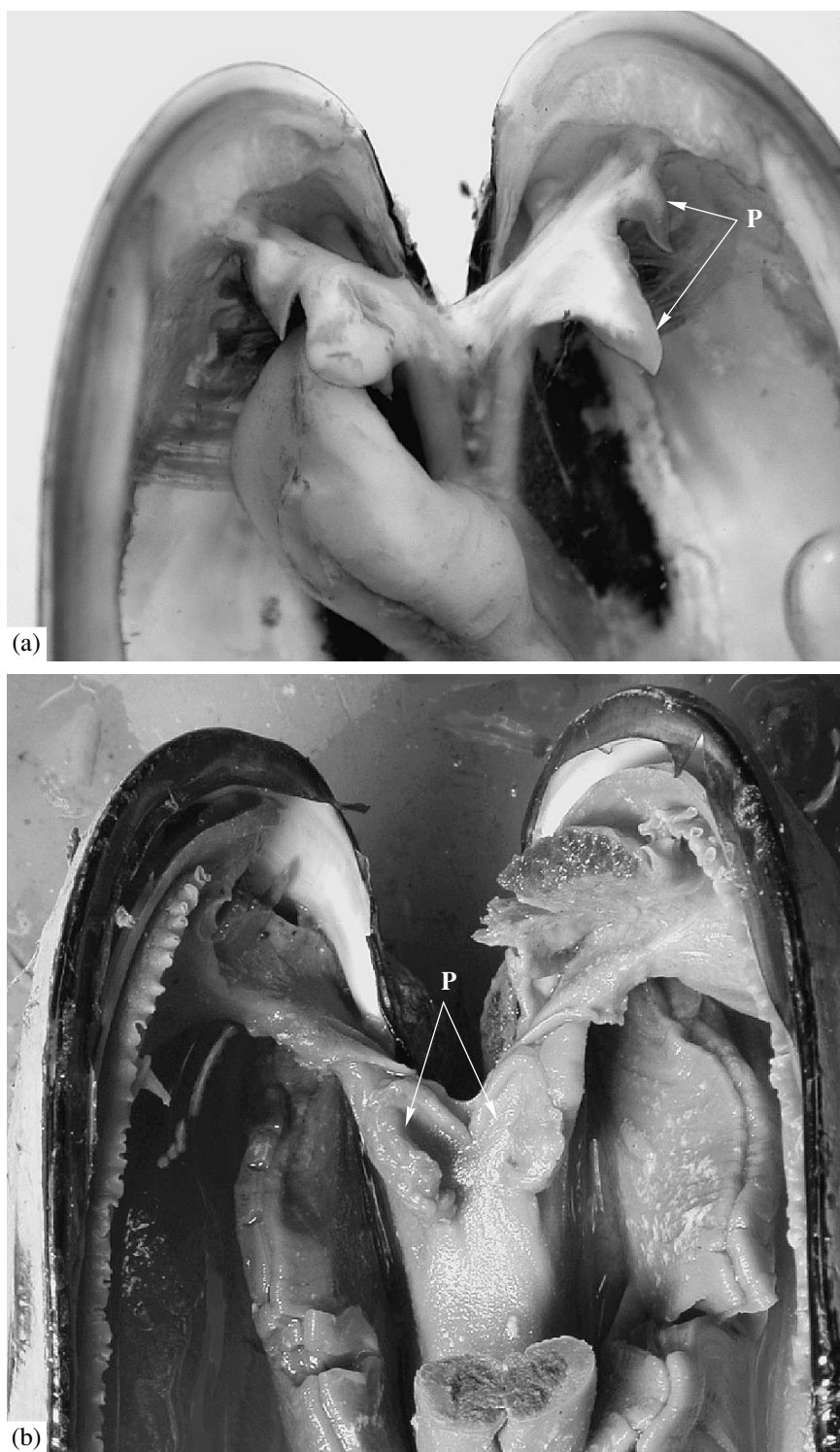
**Location.** The symbionts occupied the mantle cavity of the host mollusc, where they take up various positions (Figs. 1a, 1b). The symbionts in *B. azoricus* were most frequently located between the mantle and external demibranch (68.1%). Less often, they were located between the internal and external demibranchs (19.5%) or between the internal demibranch and the foot (12.3%,  $n = 226$  specimens; Fig. 1). If the symbionts were found between the mantle and the gills, their ventral surface was usually directed towards the mantle wall (83.8%). Less frequently, their dorsal (9.6%) or lateral (6.6%,  $n = 167$  specimens) surface faced the mantle wall. The direction of the polychaete prostomium orientation is important to understand the pattern of the trophic interaction between *Br. aff. seepensis* and the host. There are four variants of this orientation: the prostomium may be directed towards the host palps, siphon, body center, or the bottom edge of the valves (Fig. 2). It was found that the prostomium of

sexually mature specimens was more frequently directed towards the siphon opening (47.8%) or host palps (32.6%). Significantly less frequently, it took other positions (towards the body center or the bottom edge of the valves, in 17 and 2.7% animals, respectively,  $n = 224$  specimens). In 44 cases (19.3% of the total number of infested molluscs), polychaetes were found in the tubular structure formed by gill filaments and located at the lateral side of the gills or between demibranchs. Although a similar location was also typical of the *B. puteoserpentis* symbionts, the prostomium in these animals was more frequently directed towards the host palps (68.6%,  $n = 35$  specimens).

**Intestine contents.** Of 13 symbiont specimens studied, food remains were found in the intestine of six polychaetes. In most cases, the intestine was filled with detritus and particles of inorganic suspension, including ochroid particles found on the host shell surface. In addition, the chaetae of polychaetes of the same species were found in four cases, and fragments of the pelagic predatory copepods of family Oncaidae were found in one case.

**Traumatism of host soft tissues.** Morphological analysis showed that soft tissues in 34.1% ( $n = 446$  specimens) of the *B. azoricus* molluscs were damaged. The following types of morphological damages were observed: the truncation of some groups of gill filaments, foot deformation, and shortening or elimination of labial palps (Fig. 2). Palp traumas were more frequent (65.8% of the total number of traumatized molluscs,  $n = 152$  specimens) than the traumas of the gills or foot (53.3 and 9.9%, respectively). Gill traumas were more frequently located in the anterior parts of the gills. Besides, epithelial tubercle or callosity was often formed on the mollusc mantle wall along the polychaete body. Similar traumatic changes were observed in 23.7% of the *B. puteoserpentis* specimens ( $n = 135$  specimens).

To test the suggestion on the correlation of traumas with the presence of polychaetes, we compared the incidence of injured molluscs in infested and uninfested parts of the population. It was found that the incidence of traumas in molluscs infested with polychaetes was significantly higher than in uninfested molluscs. Traumas in *B. azoricus* were observed in 61.2% of infested specimens ( $n = 201$  specimens) and only 12.2% of uninfested specimens ( $n = 245$  specimens,  $F = 129.5$ ,  $p < 0.001$ ). A significant difference between the incidence of traumas in infested and uninfested specimens was also observed in *B. puteoserpentis*: 87.9% ( $n = 33$  specimens) and 2.9% ( $n = 102$  specimens), respectively ( $F = 108.8$ ,  $P < 0.001$ ). These data may be regarded as evidence for the correlation of traumatism in molluscs with the presence of symbionts in them. The traumas of uninfested molluscs could be caused by polychaetes that had escaped from the host animal before it was collected or lost during mollusc sampling.



**Fig. 2.** (a) A specimen with well-developed palps. Intact palps are indicated with arrows; (b) a specimen damaged by symbionts. Scars are seen at the sites of eliminated palps (shown with arrows). The foot of the specimen has been removed.

Probably, polychaetes are able to move inside the mollusc mantle cavity. However, their location usually remains unchanged for a long time. This is evidenced by the presence of epithelial ridges on the mollusc mantle walls along the polychaete body and tubular struc-

tures formed by the host gill filaments. We found such structures at the sites of location of polychaetes. The head-to-siphon and head-to-mouth orientations of sexually mature polychaetes in the mollusc body were found to be predominant. Probably, this orientation of

polychaetes in the mollusc body was due to the specific features of their feeding behavior. The predominant orientation of polychaetes implies that symbionts consume food (filtered and agglutinated suspension) transported with the flow of water into the host mouth or suspended organic particles transported to the siphon opening. Similar behavior is typical of other symbionts, e.g., the polychaete *Branchiosyllis exilis* associated with the brittle stars *Ophiocoma echinata* [10]; as well as the nemertine *Malacobdella grossa* and the decapod *Pinnotheres maculatus* associated with bivalve molluscs [11, 12].

The suggestion that symbionts take up suspended organic particles transported to the mollusc mantle cavity from the outside is supported by the presence of detritus and particles of inorganic suspension (including ochroid particles, which are often found on the mollusc shell surface) in the polychaete intestine. The single finding of a plankton copepod of family Oncaidae also supports this suggestion.

The correlation between the presence of symbionts in the host organism and incidence of host traumatism observed in this work is important for deeper understanding of the pattern of interaction between polychaetes and molluscs. Because the polychaetes *Br. aff. seepensis* are armed with a muscular pharynx, they quite easily can inflict damage on the host. However, analysis of the food spectrum of this species demonstrated that there were no grounds to suggest that the polychaete ate host tissues. The traumas are thought to be inflicted unintentionally during swallowing of agglutinated lumps of organic matter by the polychaetes.

The results of this study demonstrated a complicated pattern of interaction between the polychaete *Br. aff. seepensis* and *Bathymodiulus* molluscs. It is evident that the symbiont does not eat the host tissues (at least, host tissues do not play an important role in the symbiont diet). However, host traumas themselves are evidence for a negative effect of the symbiont on the host. The food of *Bathymodiulus* molluscs consists of two main components: organic matter of symbiotrophic bacterial origin and filtered seston. Polychaetes may influence negatively the metabolism of the host by catching particles of organic matter transported to the mantle cavity with the flow of water. A similar interaction between the pinnotherid crab *Pinnotheres maculatus* and the edible mussel *Mytilus edulis* has been described [12, 13]. Analysis of this association demonstrated a negative impact of the crab on the growth of the mussel [14]. Thus, the results obtained in this study

and published data of other authors on the symbiont–host interaction in similar associations suggest that the interaction between the polychaete *Br. aff. seepensis* and *Bathymodiulus* molluscs should be regarded as parasitism rather than commensalism.

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