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Substrate preferences of a non-colonial kamptozoan, and its interactions with bryozoan hosts

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Abstract Results of substrate preference analysis for *Loxosomella nordgaardi* Ryland (Kamptozoa: Loxosomatidae) found in association with various bryozoan species in the White Sea are presented. Local water-current patterns, for the first time observed and documented in bryozoan colonies inhabited by non-colonial entoprocts, indicate the direct dependence of kamptozoans' feeding activity on the bryozoan host. It is shown that because of the way their individuals integrate into the colony-wide water-current system both species may gain from this association. *L. nordgaardi* also demonstrates a strong preference for living bryozoan colonies relatively to other possible substrate types. It is thus probable that entoprocts are involved in specific ecological interactions with bryozoans.

Introduction

Non-colonial kamptozoans (family Loxosomatidae) are predominantly found in coexistence with various invertebrate benthic organisms. Mainly they are reported to prefer those habitats where small-scale water currents, either ambient or host-produced, are evidently present; this includes the surface of sponges, ascidians, echinoderms and bryozoans, as well as the inner space of polychaete tubes through which water is actively pumped by the worm (Ryland and Austin 1960; Nielsen and Ryland 1961; Ryland 1961; Nielsen 1964, 1971). However, several species constantly occur in habitats where the presence of water movement is much less evident, such as on the body surface of crustaceans, sipunculids and polynoid polychaetes (Atkins 1932a; Ryland and Austin 1960; Nielsen 1964, 1971; Krylova 1986). The ecology of kamptozoans is poorly known, and substrate preferences (that are seemingly present) have never been quantified for any species.

The present paper reports an attempt to describe specific substrate preferences of *Loxosomella nordgaardi* Ryland found in Chupa Bay (White Sea) and its interactions with the bryozoan host. The first point was to determine whether this kamptozoan prefers to occupy living bryozoan colonies rather than other available substrates. The second point was to estimate the abundance of associated *Loxosomella* specimens for the colonies of different bryozoan species to find out whether there are any preferences.

A kamptozoan specimen (the non-colonial one) represents a unit both similar and dissimilar to a bryozoan zooid. Though it possesses a ciliated tentacle crown resembling the bryozoans lophophore, its feeding current has an opposite direction (e.g. Atkins 1932b). Our third point was to describe the small-scale water flow observed in a bryozoan colony inhabited by entoprocts. This description would: (1) help to determine the nature of interspecific interactions within the symbiotic system studied and (2) give an example of the feeding-current patterns produced by a combination of different living water-pumping units.

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Materials and methods

Sampling was carried out in June–September 1994–1997 near the islands of Keret' archipelago and the Kartesh cape (Chupa Bay, White Sea, Fig. 1). Fourteen samples each containing several algal blades were either dredged or collected by SCUBA divers. The surface of algae was examined using binocular microscopes. For each bryozoan colony found, both the number of zooids and the number of attached *Loxosomella nordgaardi* individuals were documented. Also, all kamptozoans observed on algal surface were counted (no *Loxosomella* specimens were found anywhere, except

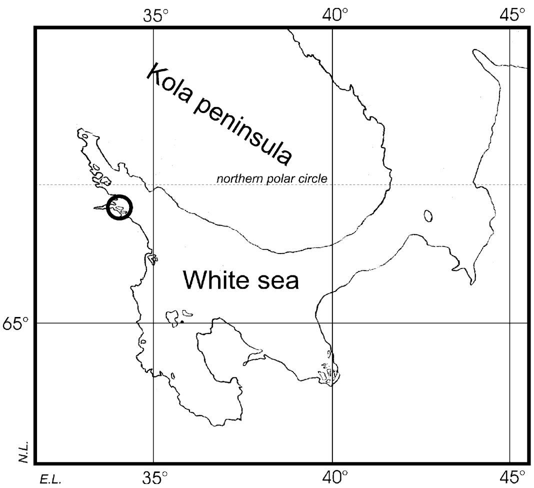

Fig. 1 Research area location (*encircled*)

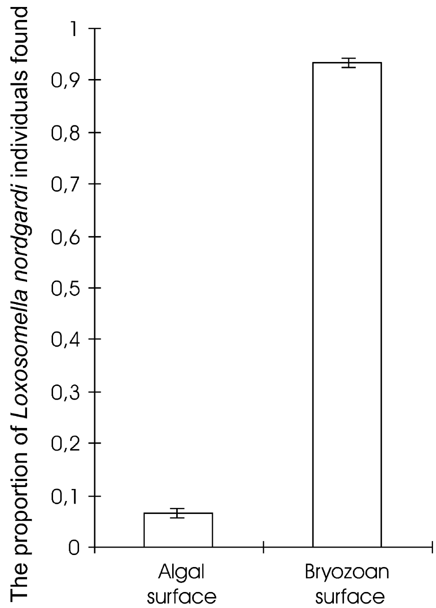

Fig. 2 *Loxosomella nordgaardi*. Proportion of individuals found on algal and bryozoan surfaces (fraction, ± SE)

on the bryozoan or algal surface). A total of 45 algal blades representing five common subtidal species [2 for *Ptilota* sp., 19 for *Odonthalia dentata* (L.), 12 for *Phycodris rubens* Batt, 6 for *Phyllophora interrupta* (Grev.) and 6 for *Ph. brodiaei* (Turn)] were examined.

The total cover of all bryozoans was estimated visually (10% precision). The quantities of *L. nordgaardi* individuals on bryozoan and algal substrata were divided by the corresponding cover values for the purpose of proper comparison. The total cover of all other macrobenthic fouling organisms (spirorbid polychaetes, hydroids and sponges) on the algal blades examined never exceeded 1%.

Feeding currents were observed on living, encrusting colonies of *Arctonula arctica* (M. Sars), *Callopora aurita* (Hincks), *Rhamphostomella bilaminata* (Hincks) and *Scrupocellaria arctica* (Busk), all densely inhabited by kamptozoans. To visualize the water motion, a coal particle suspension was added to the dish, in which living bryozoan colonies were placed. Observations were made with binocular microscopes (MBS-9, MBS-10) under 16× and 28× magnifications and documented using a portable video camera. Traces of coal particles were schematically mapped.

Frequency comparisons based on *F*-test and Pearson correlations were used to estimate the dependence of kamptozoan-occurrence frequencies and the average dimensions of bryozoan lophophores.

Results

In total, 1145 *Loxosomella nordgaardi* specimens were found on examined substrate samples. The fraction of individuals attached to the surface of bryozoan colonies ($93.5 \pm 0.70\%$) was significantly larger (*F*-test, $P \leq 0.001$) than the corresponding value for algal substrate ($6.5 \pm 0.70\%$) inhabitants. Taking into account the difference between examined areas of algal and bryozoan surfaces, of which the first ($80 \pm 2.0\%$ total cover) was four times larger than the latter ($20 \pm 2.0\%$ total cover), one may conclude that the *L. nordgaardi* population density is 60 times higher on bryozoan colonies than on algal blades (Fig. 2). This ratio results from the division of the population fraction by the average total cover estimated for the corresponding substrate type. Average total cover was as high as $19.7 \pm 2.16\%$ and $80.3 \pm 2.16\%$ for bryozoan colonies and red algal clear surface, respectively (Fig. 3). Kamptozoan individuals found on algal surfaces never demonstrated large body sizes and always lacked highly developed buds.

There was only one *L. nordgaardi* specimen found on a dead *A. arctica* colony, whereas all others were associated only with those zones of the living colonies where feeding zooids were placed. The fraction of individuals observed on living zoaria (99.9%) is thus significantly higher than the corresponding value for dead ones (0.1%). When entoprocts occur on bryozoans with erect unilaminate colonies (like those belonging to the genera *Tricellaria*, *Scrupocellaria* and *Dendrobeania*), they are observed exclusively on the frontal surface, where feeding lophophores are extruded. Of more than 200

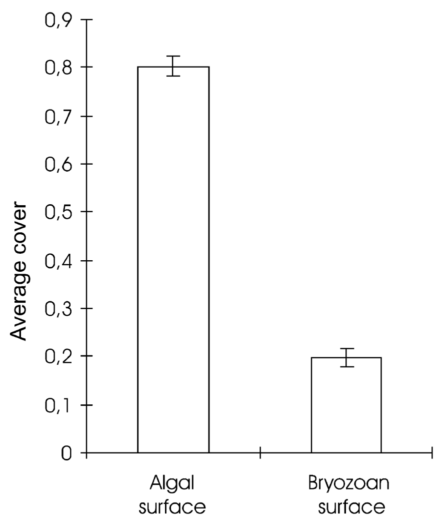

Fig. 3 Average cover of algal and bryozoan surfaces examined (fraction, ± SE)

kamptozoans found in association with these colonies, not a single specimen was attached to the basal surface.

Several bryozoan species of the 19 that we considered frequent in the research area (see Table 1) demonstrate a relatively high fraction of *Loxosomella*-inhabited colonies: *Rhamphostomella ovata* (Smitt), *R. radiatula* (Hincks), *R. bilaminata* (Hincks), *Hippoporina propinqua* (Smitt), *Arctonula arctica* (M. Sars), *Callopora aurita* (Hincks), *C. craticula* (Alder), *Tegella armifera* (Hincks) and *Scrupocellaria arctica* (Busk) (Cheilostomata). Although the cheilostomes *Tricellaria gracilis* (Ellis et Solander) and *Dendrobeania fruticosa* (Packard) are represented only by single occurrences, they have shown a relatively high density of *L. nordgaardi* on their colonial surface (measured as individuals per zooid, Table 1). Also, there are several common bryozoan species that apparently almost never attract kamptozoans, such as *Lichenopora verrucaria* (Fabricius), *Crisiella producta* (Smitt), *Crisia* sp. (Cyclostomata), *Buskia nitiens* Alder (Ctenostomata), *Cribrilina annulata* (Fabricius) and *Celleporella hyalina* (L.) (Cheilostomata). A few other species including *Electra pilosa* and *Hippoporina reticulatopunctata* (Hincks) (Cheilostomata) demonstrate an occasional association with entoprocts.

The way the ciliary activity is arranged in bryozoans forces the water first to enter the inner lophophore volume from outer space and then to filter between the tentacles moving towards the colonial surface (Fig. 4, a). In contrast, a kamptozoan pumps the water into the tentacle crown from the outside, so that it passes between the tentacles and subsequently leaves the crown inner volume in a single outgoing flow (Fig. 4, b). According to our observations, adult *L. nordgaardi* individuals never exceed one-half the height of the host bryozoan's extended polypide. Consequently, within the encrusting colony, non-colonial kamptozoan tentacle crowns are always beneath those of the bryozoans (Fig. 5). Bryozoan tentacle ciliary movement creates an incoming flow from above the colony that passes through lophophores and runs between their tentacles to the lower "underpolypide" level. There, the current partially reaches the edge of the colony, producing the colonial outgoing flow and partially (around a kamptozoan) moves up between *L. nordgaardi* tentacles. Thus, twice filtered, the water returns into the volume above the colony (Fig. 5, a). Usually young kamptozoan specimens are attached to the growing edge of the colony, where the strongest current is observed. Their tentacle crowns face the edge (away from the colony center) so that the animals are able to filter the water leaving the zoaria (Fig. 5, b). Aggregations of three to ten *L. nordgaardi* individuals were often found on those patches within the large, living, encrusting bryozoan colonies (such as *Tegella armifera*, *Callopora aurita* and *Rhamphostomella bilaminata*), where zooids do not extrude feeding lophophores. Lophohores on the borders of these zones, together with kamptozoan inhabitants here, are arranged in such a way that a noticeable water flow, directed upward outside the colony, is usually produced (Fig. 6).

Table 1 Quantities of *Loxosomella nordgaardi* on the colonial surface of different bryozoan species. : frequency in examined samples, number of colonies examined, proportion of *Loxosomella*-inhabited colonies, total number of bryozoan zooids examined, total number of *L. nordgaardi* individuals, number of *L. nordgaardi* per colony, tentacle crown diameter (mm), average number of zooids per colony

Species	Frequency in samples	No. of colonies	Proportion of inhabited colonies	No. of bryozoan zooids	Total no. of *L. nordgaardi*	No. of *L. nordgaardi* colony^{-1}	Tentacle crown diam.	Avg. no. of zooids colony^{-1}
Buskia nitiens	0.14 ± 0.049	26	0.00 ± 0.000	706	0	–	0.35	27.2
Lichenopora verrucaria	0.46 ± 0.070	215	0.00 ± 0.000	2501	0	–	0.40	11.6
Tubulipora sp.	0.46 ± 0.070	152	0.00 ± 0.000	317	0	–	0.40	2.1
Celleporella hyalina	0.06 ± 0.034	149	0.01 ± 0.007	2827	1	1.0	0.37	19.0
Cribrilina annulata	0.66 ± 0.067	270	0.01 ± 0.006	4106	5	1.7	0.67	15.2
Crisiella producta	0.76 ± 0.060	269	0.01 ± 0.006	769	9	3.0	0.35	2.9
Crisia sp.	0.42 ± 0.070	154	0.02 ± 0.011	1835	3	1.0	0.35	11.9
Calloporidae juv. sp.	0.12 ± 0.046	19	0.11 ± 0.070	120	5	2.5	–	6.3
Hippoporina reticulato-punctata	0.28 ± 0.063	23	0.13 ± 0.070	716	6	2.0	0.67	31.1
Electra pilosa	0.24 ± 0.060	22	0.14 ± 0.073	1910	3	1.0	0.50	86.8
Callopora craticula	0.56 ± 0.070	175	0.17 ± 0.028	5685	82	2.8	0.40	32.5
Rhamphostomella ovata	0.42 ± 0.070	39	0.21 ± 0.065	5380	11	1.4	0.60	137.9
Callopora aurita	0.08 ± 0.038	14	0.21 ± 0.110	583	29	9.7	0.50	41.6
Scrupocellaria arctica	0.22 ± 0.059	15	0.27 ± 0.114	609	> 500	> 33	0.80	40.6
Rhamphostomella radiatula	0.18 ± 0.054	14	0.29 ± 0.121	545	12	3.0	–	38.9
Rhamphostomella bilaminata	0.22 ± 0.059	28	0.32 ± 0.088	1296	16	1.8	0.60	46.3
Hippoporina propinqua	0.20 ± 0.057	12	0.33 ± 0.136	516	75	18.8	0.70	43.0
Tegella armifera	0.24 ± 0.060	17	0.35 ± 0.116	1462	152	25.3	0.65	86.0
Arctonula arctica	0.58 ± 0.070	92	0.41 ± 0.051	6562	510	13.4	0.80	71.3
Dendrobeania fruticosa	0.02 ± 0.020	1	1.00 ± 0.000	450	207	207	–	450.0
Tricellaria gracilis	0.02 ± 0.020	1	1.00 ± 0.000	–	> 500	–	–	–

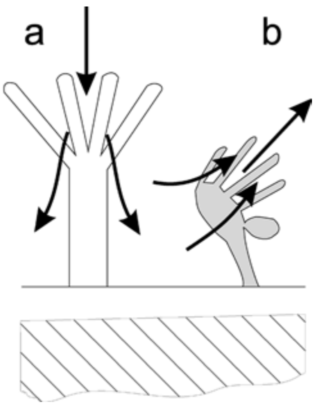

Fig. 4 Water flow, induced by a bryozoan zooid (*a*) and by a non-colonial kamptozoan (*b*)

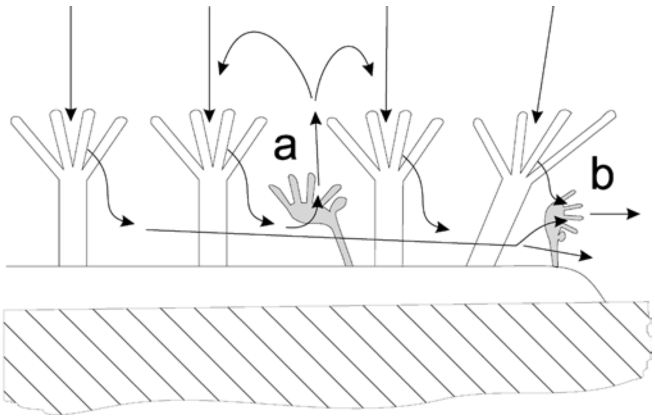

Fig. 5 Water-flow pattern for *Loxosmella nordgaardi* inhabiting an encrusting bryozoan colony: near the central part of the colony (*a*) and near the growing edge of the colony (*b*)

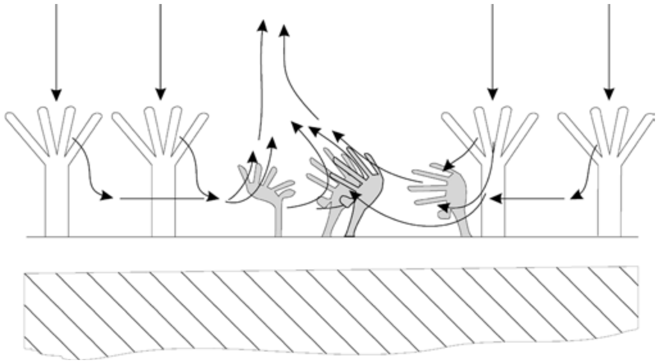

Fig. 6 Water-flow pattern for groups of *Loxosomella nordgaardi* inhabiting polypide-free zones in encrusting bryozoan colonies

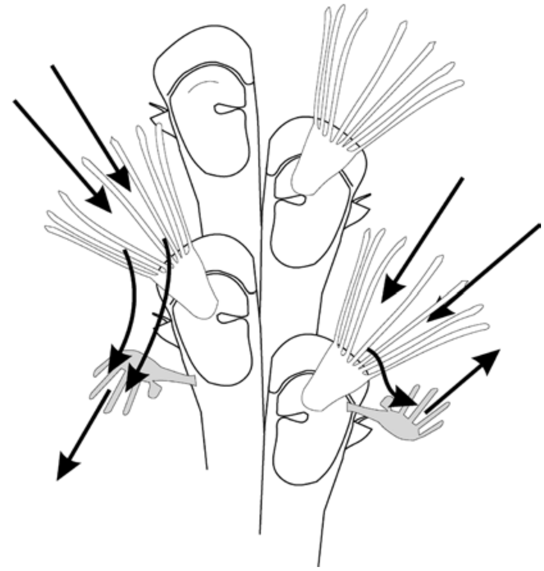

Fig. 7 Water-flow pattern for *Loxosomella nordgaardi* inhabiting a colony of the erect bryozoan species *Scrupocellaria artica*

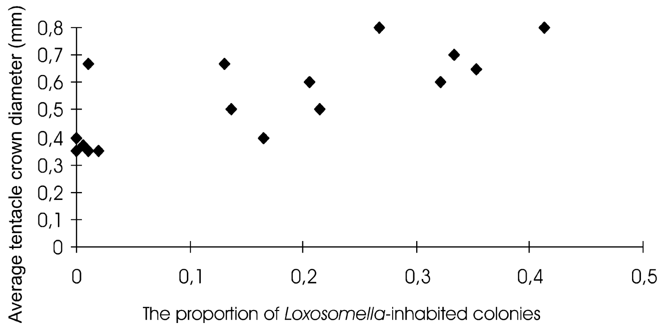

Fig. 8 Relationship between the proportion of *Loxosomella*-inhabited colonies and the average tentacle crown diameter of different bryozoan species

As to those entoprocts that inhabit erect bryozoan colonies, they are as a rule located on lateral and frontal zooidal walls around a feeding polypide, where kamptozoans orient their tentacles so that they capture the water flowing between the bryozoan tentacles (Fig. 7).

Our observations also show that *L. nordgaardi* buds, when separated from the parental individual, start crawling around the substrate surface, which often results in attachment to the same bryozoan colony their parents inhabit, or to neighboring ones.

To explain the observed spatial distribution of *L. nordgaardi*, the frequency of *Loxosomella*-inhabited colonies was compared with lophophore dimensions for different bryozoan species (Fig. 8). Bryozoans with relatively large average polypide size, e.g. *Arctonula arctica* or *Scrupocellaria arctica*, usually attract kamptozoans, whereas the species with tiny lophophores and short tentacles, such as cyclostomes and several others (e.g. the ctenostome *Buskia nitiens* and the cheilostome *Celleporella hyalina*) often lack *L. nordgaardi* population. There is a significant positive correlation (0.76 ± 0.098) between the average tentacle crown diameter and the proportion of colonies inhabited by *L. nordgaardi* for different bryozoan species. A significant positive correlation is also found between the proportion of *Loxosomella*-inhabited colonies and the average number of zooids per colony (0.60 ± 0.152).

Discussion

Substrate selectivity among epibenthic fauna may be more or less specific. Preference for a certain substratum, or at least of a certain range thereof, is known for different sessile taxa (Ryland 1962; Knight-Jones et al. 1971; Schmidt 1983; Hurlbit 1991; Orlov 1997). Strong association, for example as found between *Monobrachium parasitum* Mereschkowsky (Coelenterata) and *Macoma calcarea* (Gmelin) (Lamellibranchia), usually implies some level of symbiotic interactions between species (Ninbourg 1975). In addition to space, the substrata, when represented by a living animal or algae, may also supply its epibenthic population with food either directly (Seed and O'Connor 1981) or by facilitation of their feeding activity (Lahoinen and Furman 1986). In concordance with ecological remarks previously given for *Loxosomella nordgaardi* and several other Loxosomatidae, an association with bryozoan colonies has been noted (see Nielsen 1964). Specifically *L. nordgaardi* aggregate on large colonies formed by host species with relatively large tentacle crown diameters. Entoprocts are not attracted by representatives of various taxa with small lophophores (cyclostomes, ctenostomes and cheilostomes) or with small average colony size (found in *Cribrilina annulata*, Cheilostomata).

Both factors showing positive correlation with kamptozoan abundance (average lophophore diameter and average colony size) reflect hydrodynamic conditions near the bryozoan colony surface. The larger the polypides or the number of zooids, the greater the water volume pumped by a bryozoan per time unit. All this water enters the colony through the area proportional to the number of zooids, whereas it leaves the colony through its edge, the length of which is proportional to the square root of the number of zooids (Shunatova and Ostrovsky, unpublished results). Consequently, a suspension-feeding organism, attached near the colonial edge and filtering the bryozoan's outgoing flow, surely profits from the higher velocity of the surrounding current when inhabiting larger colonies. Visa versa, an association with larger colonies and species with larger polypides, together with a preference for living bryozoans rather than any other substrata, probably indicates a dependence on the host-produced water flow. It is also important to note that the ability of bryozoans to improve feeding conditions for the neighboring filter-feeding organisms has previously been given experimental support (Best and Thorpe 1986). The entoprocts studied here grow more robustly and therefore apparently feed more successfully where their own feeding currents are supplemented by flow generated by the host bryozan. This suggests, in general, that *L. nordgaardi* and perhaps other entoprocts benefit where their self-generated flow is supplemented by an ambient one.

As it was shown above, probably all the water that reaches *L. nordgaardi* tentacles is already filtered by the bryozoan host. The distribution of the studied entoprocts thus suggests that: (1) either there is a surplus of feeding particles suitable both for host species and its inhabitants, or (2) the particles kamptozoans and bryozoans feed on are different. We can give no evidence for either alternative, but there is at least one fact in favor of the latter one. The cilia on kamptozoan tentacles are considerably longer than those on bryozoans (Nielsen 1976). This morphological difference may reflect possible feeding segregation between coexisting entoprocts and ectoprocts by means of, for example, utilization of particles of different size. There are also observations showing that feeding bryozoans often lose particles already captured by their lophophore tentacles (Shunatova and Ostrovsky 2001). Preferential consumption of particles of a certain size is known in various suspension feeders (e.g. Young and Cameron 1989).

Sessile filter-feeding benthic invertebrates usually interact via the water flows they produce. It has been shown that the nature of interspecific competition between neighboring bryozoan colonies is in the interference of their feeding flows (Buss 1979; Best and Thorpe 1986; Okamura 1988). The presence of a filtering organism nearby may either facilitate or reduce the feeding success of a suspension feeder (Okamura 1984, 1985). An example of a similar type of competition is seen between bryozoans and ascidians (Whitlatch et al. 1995). Intraspecific feeding interference was found in barnacles (Pullen and La Barbera 1991). Colony-wide flow patterns are well documented for several bryozoan species (Cook 1977; McKinney 1989, 1991; Shunatova and Ostrovsky 2001), but there are no data on how these patterns may be modified by integration of alien active filterers.

The presence of special zones within encrusting colonies which lack feeding polypides has been reported for many bryozoan species. Because of the absence of incoming flow, which is elsewhere produced by the ciliary activity of bryozoan lophophores, the water in this case flows upwards, thus leaving the colony (Fig. 9). The described zones, usually observed in large encrusting colonies, are referred to as "chimneys" (Banta et al. 1974; Cook 1977; Cook and Chimonides 1980; Lidgard

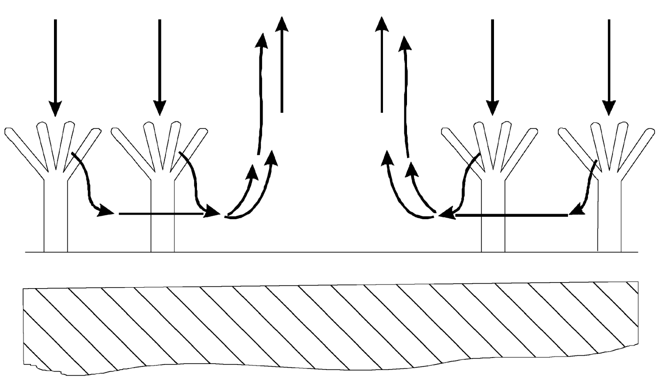

Fig. 9 Water-flow pattern in bryozoan chimneys (modified after Cook and Chimonides 1980)

1981; Dick 1987). Dick (1987) suggested that once an encrusting bryozoan colony has achieved a certain threshold of covered area, it can no longer provide sufficient outgoing flow via the edge of the zoaria. According to Dick's model any zone within a colony with relatively loose lophophore placement may turn into a chimney that produces an auxiliary "drain" establishing the water balance of the feeding bryozoan. The observed *L. nordgaardi* groups concentrated at polypide-free sites enforce an outflow. We suggest that one individual or a group of kamptozoan individuals may (after growing large enough) initiate a change in the direction of the excurrent, which commonly flows towards and along the colonial surface. Once water starts flowing upwards, further chimney development continues, with consequent morphological changes in the surrounding lophophores (Shunatova and Ostrovsky, unpublished results). Alternatively, crawling kamptozoan larvae may just concentrate inside the existing chimneys. Regardless of their origin, chimneys that include entoprocts should work more effectively than "purely bryozoan" ones, which means that not only the epibiont, but also its host may gain from their association.

Any spatial heterogeneity in sessile invertebrates may result from differential larval settlement as well as from differential asexual reproduction or mortality. Invertebrate larvae of different taxa demonstrate preferential selection of certain substrata as a result of chemical stimulation (Ryland 1959, 1962; de Silva 1962; Scheltema 1974). We suggest kamptozoan larvae use both this mechanism and *reo*-sensitive reactions during settlement, the latter having also been described for several other marine organisms (Crisp 1955, Butman et al. 1988). A particular reaction sequence may depend on the spatial scale. This behavior would result in selection of those bryozoan colonies most active in water pumping. The majority of individuals in a *L. nordgaardi* population are probably a product of budding. Perhaps an insufficient amount of food restricts budding and thus limits the ability of entoprocts to spread in locations where living conditions are unsuitable. Therefore, it is important that bryozoan species, colonies of which are frequently inhabited by kamptozoans, also demonstrate a relatively high intensity of colonization (in the amount of *L. nordgaardi* individuals per zooid) and visa versa, the intensity of colonization for the less "attractive" bryozoan species is rather low.

When epibenthic communities are studied, research is usually focused either on the result of interactions, like substrate-preference patterns (Gryshankov 1995a,b), or on their mechanisms, like larval substrate choice (Ryland 1962; Knight-Jones et al. 1971; Hurlbit 1991; Orlov 1997) and water-current interference (Buss 1979; Best and Thorpe 1986; Okamura 1988). Above we tried to combine both approaches to show the interdependence of processes and structures in an epibenthic system. Several research directions are possible to further the study of symbiotic kamptozoans: quantification of the demographic structure of kamptozoans in relation to host parameters, spatial distribution mapping both of chimneys and of entoproct individuals within bryozoan colonies and laboratory experiments with food particles of different sizes as well as comparative stomach content analyses which may help to check the presence of feeding segregation between coexisting ento- and ectoprocts.

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