Solitary entoprocts living on bryozoans - Commensals, mutualists or parasites?

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ABSTRACT

To assess the effects of interspecific interactions on community structure it is necessary to identify their sign. Interference in sessile benthic suspension-feeders is mediated by space and food. In the White Sea solitary entoproct *Loxosomella nordgaardi* almost restrictively inhabits the colonies of several bryozoans, including *Tegella armifera*. Since both entoprocts and their hosts are suspension-feeders, this strong spatial association suggests feeding interference of an unknown sign.

We mapped the colonies of *T. armifera* inhabited by entoprocts and examined stomachs of both species for diatom shells. Distribution of *L. nordgaardi* was positively correlated with distribution of fully developed and actively feeding polypides of *T. armifera*, i.e. areas of strong colony-wide currents. We compared diatom shells found in their stomachs and observed a diet overlap, especially in the size classes <15 μm. Size spectra of the diatom shells consumed by *T. armifera* and average number of diatom shells per gut were not affected by the presence of *L. nordgaardi*. According to these results, *L. nordgaardi* is a commensal of *T. armifera*.

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1. Introduction

Marine benthic communities are driven by environmental conditions and biotic interactions. The structuring effect of the latter increases at smaller spatial scale, since organisms often interfere at the distances comparable to their size (Paine, 1994). According to the net outcome, biotic interactions can favor, harm or have neutral effect on the organisms involved.

Positive or facilitative interactions are defined as beneficial for at least one side and harmful for none (Bruno and Bertness, 2001). Negative ones are harmful for one or all of the organisms, while none of them benefits. Finally, there are interactions in which one organism receives benefit at the expense of the other, namely predation and parasitism.

In epibenthic communities, where most organisms are attached to the substratum, space is often a limiting factor (Buss, 1980; Connell, 1961; Paine, 1994). Spatial interactions are inevitable between organisms permanently living close to each other. Since many of them are suspension-feeders, food-mediated interactions and hydrodynamical interference may also arise and affect the communities (e.g. Buss, 1980, 1981; Okamura, 1985; Russ, 1982).

Food competition may be mitigated by flow-mediated facilitation, or become more acute because of interference of feeding currents. The most effective competitor is usually the one with the strongest feeding currents that disrupt currents generated by others (Best and Thorpe, 1986; Okamura, 1984). This effect, however, is greatly

Ambient flow, however, may reverse the effect. Under certain conditions, competitors with weaker currents may receive facilitation, not suppression, from their stronger neighbors (Okamura, 1985, 1988).

Loxosomella nordgaardi (Entoprocta, Loxosomatidae) and *Tegella armifera* (Bryozoa, Cheilostomata) are suspension-feeders, often found in association. *L. nordgaardi* is an epibiont, inhabiting the surface of the host colonies of *T. armifera*. Both species employ crowns of ciliated tentacles (often called lophophores) to produce food-bearing currents, however the generated water flow patterns are quite different.

Lophophore of *T. armifera* works as "upstream-collecting system" (Nielsen, 1987, 1989, 1995) with water current entering the lophophore from above and leaving obliquely downwards between the tentacles (Atkins, 1932; Larsen and Riisgard, 2002). In case of *L. nordgaardi*, the direction is opposite ("downstream-collecting system"). Water passes between tentacles and leaves obliquely upwards from the frontal side of the animal. Due to the low number and shortness of the tentacles, number of cilia is relatively small in entoprocts. Therefore generated water currents are likely to be relatively weak (see Best and Thorpe, 1986; Riisgard and Manriquez, 1997).

Entoprocts of the family Loxosomatidae are small solitary animals. They often inhabit the surface of other invertebrates that produce water currents (ascidians, polychaetes, bryozoans, sponges, etc.— Arroyo and Benito, 2000; Hyman, 1951; Iseto et al., 2008; Nielsen, 1989). According to a previous study, *L. nordgaardi* forms associations with only a limited number of cheilostome bryozoans (Yakovis, 2002). On rare occasions separate individuals may be found on the surface of the red algae.

T. armifera is one of the most common subtidal bryozoans of the White Sea, and also one of the most preferred host species for

entoprocts. At our research site in Keret' Archipelago about 30% of its colonies are occupied with *L. nordgaardi*. *T. armifera* forms unilaminar, rounded or fan-shaped, encrusting sheets of tightly packed zooids. Height of *T. armifera* lophophores and introverts is around 700 μm (Kluge, 1975). Individuals of *L. nordgaardi* are 1.5 times smaller, up to 470 μm (Nielsen, 1989). Thus entoprocts form a separate layer beneath the canopy of expanded lophophores.

Feeding currents of symbionts seem to be complimentary: the water that left hosts' lophophores may then enter epibionts' feeding apparatus and later be expelled upwards and away from the colony. Together with the strong association of *L. nordgaardi* with *T. armifera*, this indicates that the interactions are beneficial for entoprocts. As the net effect of *L. nordgaardi* on its host may be positive, negative or neutral, we may find mutualistic, commensal or parasitic interactions. We have tested predictions of three hypotheses about the nature of these interactions:

H1. *L. nordgaardi* individuals do not depend on the host feeding currents.

Colonies of *T. armifera* display pronounced zoning and colony-scale variation of flow conditions. Polypides of *T. armifera* undergo a fixed degeneration–regeneration cycle. They are capable of generating water currents and feeding only when fully developed. The primary area of incurrents is a part of a colony where developed polypides are concentrated. Areas occupied by polypides not yet, or already unable to feed are the areas of more or less strong excurrents. If there is no effect of host feeding currents on epibiont, there would be no correlation in spatial distribution of feeding zooids and *L. nordgaardi* individuals.

H2. Diet of *L. nordgaardi* does not differ from that of *T. armifera*.

As the primary food sources for suspension-feeders are essentially similar (Ryland, 1970), their diets are often discriminated by the size of ingested food (Hughes, 2000; Lesser et al., 1992). Diatoms are good natural markers of food size spectra. These algae dominate the White Sea waters both in abundance and biomass (Gogorev, 2005; Ilyash et al., 2003) and cover a widest range of size classes (2–200 μm, Round et al., 1990). Their siliceous shells are resistant to digestive enzymes and have characteristic shape. Diatoms serve as a good food source, even with undamaged shells, owing to the layer of extracellular products and associated bacterial communities (Decho and Fleeger, 1988).

Diatoms had successfully been used to identify diets and food particle size preferences of meiobenthic grazers in a number of studies (Azovsky et al., 2005 and references therein; Decho and Fleeger, 1988). Our preliminary study indicated that both focus species feed on diatoms (Tamberg et al., 2007). Overlapping size spectra of diatoms in the stomachs of *L. nordgaardi* and *T. armifera* would indicate the similarity of their diets, and a possibility of competition for the same food resources (given they are limited). Non-overlapping diets mean they do not directly compete for some particular resource, though they still can hinder or facilitate each-other's feeding in different ways.

H3. Presence of *L. nordgaardi* does not affect host feeding.

Whether their food size spectra overlap or not, epibionts may affect the hosts' feeding process by changing the surrounding hydrodynamic conditions. If there is no flow-mediated effect, size spectra of diatoms from free and occupied colonies would be identical. Moreover, the gut fullness (i.e. number of ingested diatoms) would also remain unchanged despite the presence of entoprocts. To test these predictions, we compared the colony-wide spatial distribution of entoprocts and bryozoan zooids of different types. We also measured and counted the diatoms ingested by *L. nordgaardi* individuals and separate polypides from the occupied and unoccupied host colonies.

Rejection of 1st and 3rd hypotheses means that net interactions in this system are not neutral (rejection of the 2nd one can only indicate as much). Details of how epibionts and hosts are affected would reveal the nature of interactions: facilitative or parasitic.

2. Material and methods

2.1. Sampling and bryozoan colonies used

Keret' Archipelago at the mouth of Keret' River close to Chupa Bay in Kandalaksha Gulf of the White Sea (Fig. 1) consists of several islands separated by shallow straits. We took samples on September 19 and 25, 2009 in the strait between the Karelian shore and Matryonin Island within a 40 m² circle centered at 66°18.557′ N; 33°37.845′ W. Two species of kelp, *Laminaria digitata* and *Saccharina latissima*, cover the stony bottom of the 5–6 m deep sampling site. Co-dominating red algae *Rhodimenia palmata*, *Phycodrys rubens*, *Odonthalia dentata*, *Phyllophora interrupta* and *Ptilota plumosa* grow on holdfasts and stalks of the kelp. We collected kelp with a grapnel and picked all the colonies of *T. armifera* on the blades of red algae attached. Most colonies were found on *R. palmata*. To stop the digestion and thus avoid changes to the gut contents we fixed these colonies immediately after collecting (in the boat) with 4% formaldehyde in seawater.

In the laboratory we selected and preserved 20 *T. armifera* colonies with 10 or more *L. nordgaardi* individuals attached (BO hereafter) and 31 ones without any entoprocts (BF hereafter). Among 20 occupied colonies 12 were collected on 19.09 and 8 on 25.09. From 31 free colonies, 20 and 11, respectively, were collected on these days. Colonies varied in size: both free and occupied ones contained 60–510 zooids with 30–350 living polypides. Size difference between BF and BO colonies was non-significant (Wilcoxon test p = 0.136; F-test p = 0.634).

2.2. Colony mapping and spatial distribution of entoprocts

To check the hypothesis about the importance of host feeding currents for *L. nordgaardi* we studied zoning of host colonies and epibionts'
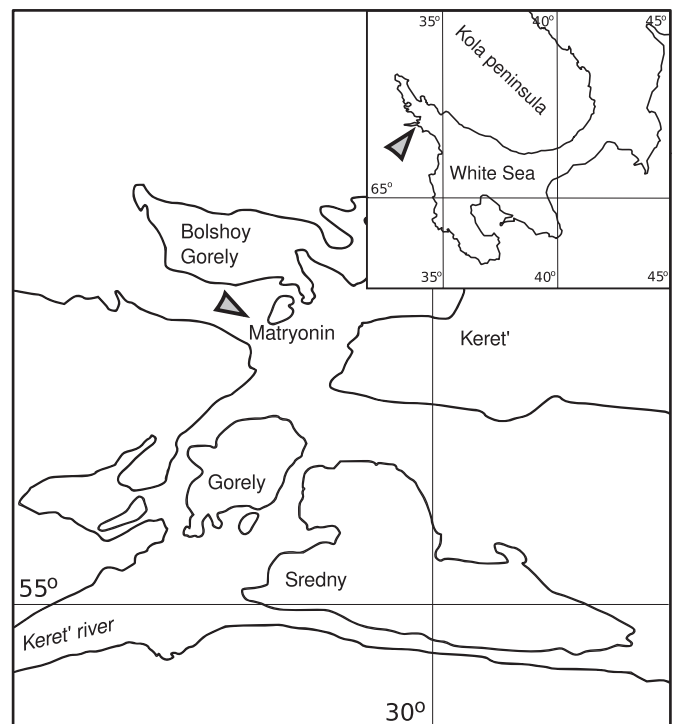

Fig. 1. Map of the study area.

spatial distribution. We photographed 31 free and 11 occupied colonies under binocular microscope with a digital camera (Leika M 250 C and Leika DCF 420) and mapped all the polypides and *Loxosomella* individuals.

Colony growth in *T. armifera* is essentially centrifugal, and is implemented by marginal budding. We recognized concentric rows of zooids starting with outermost growing margin of the colony. We recorded the position of each polypide in terms of distance in zooids from the growing margin and identified four polypide cycle stages (compare with Barnes and Clarke, 1998; Dyrynda and Ryland, 1982; Shunatova and Ostrovsky, 2002):

(1) growing (at the colony edge);
(2) actively feeding;
(3) degenerating polypides and
(4) empty zooids.

Location of each *Loxosomella* individual was recorded in a similar fashion.

We obtained spatial distribution of epibionts calculating their number per zooid, i.e. their density, in each zooid row. Likewise we calculated densities of different polypide types. After averaging these numbers across colonies we proceeded to calculate Spearman's rank correlation coefficients. We compared the average density distribution of *L. nordgaardi* individuals with those of growing, feeding, degenerating polypides and empty zooids.

We also studied correlations between the row size (number of zooids in a row) and distribution of different polypide types. The total number of zooids from a given colony formed 100%, from which we calculated their fraction in each row. Thus we normalized the data for different colony sizes. Likewise, we obtained percentages of polypides of each type, separately for all colonies. We calculated Spearman's correlation coefficients between these percentages.

2.3. Stomach content

To test the hypotheses about feeding interference we used 20 free and 20 occupied bryozoan colonies and examined their stomach contents. From each BF colony we obtained 10 polypides, dissecting them from cystides. From 9 to 14 entoprocts were picked from the surface of each BO, together with 10 neighboring polypides. In both cases, we used only completely developed polypides, neither too young, nor degenerating. We made separate temporary slides from individual polypides and entoprocts, and studied them under stereomicroscope (12×40; Decho and Fleeger, 1988). We recorded and measured two largest dimensions of each diatom. To ensure this, we applied some pressure to the cover glasses so that the diatoms became oriented as flat as their shape allowed. This also reduced the possibility of overlooking small diatoms in the folds of digestive tract, as it became a smear, not a thick clump of tissue.

We used this mild method to preserve smallest lightly silicified diatoms, especially those with already damaged valves. In our preliminary studies (Tamberg et al., 2007) we employed a standard method used in algology (Round et al., 1990): boiling in 40% peroxide with KCr_2O_7. We found that for diatoms smaller than 15 μm, species of genera *Cyclotella*, *Fragillaria* and *Parlibellus* accounted for 69% of the cells in BO and BF stomachs. Among diatoms larger than 15 μm, 60% of the cells belonged to species of genera *Navicula*, *Cocconeis*, *Amphora* and *Fragillaria*. However this method is aggressive, and later we found that about 60% of diatoms were lost in the process: either dissolved or crumbled beyond recognition. Our preliminary results (2007) are, thus, at least partly incorrect. In the present study we dismissed this damaging technique to get accurate shell counts, although undissolved bryozoan tissues and bad condition of smallest diatoms made species identification impossible.

We performed type III sum of squares two-way ANOVA with factors Sampling Date (random) and Entoprocs' Presence (fixed) on

diatom lengths to assess the effect of *L. nordgaardi* on average length of diatoms consumed by its host. Similarly, we estimated effect of entoprocts on feeding efficiency of the host comparing mean numbers of diatoms of all sizes inside digestive systems of BF and BO. In both cases we checked homogeneity of variances with median-centering Fligner–Killeen test (Conover et al., 1981; p = 0.06 and p = 0.13 for Diatom Lengths and Diatom Numbers, respectively). We used lengths and counts of diatoms averaged by colony as independent observations. To identify the relationship between the length and proportions of diatom shells we calculated Spearman's correlation coefficient between their length and length to width ratio. All statistical analyses were performed with R 2.9.1 (R Development Core Team) (2009).

3. Results

3.1. Colony zoning and spatial distribution of entoprocts

Polypides from 11 occupied and 31 free colonies of *T. armifera* were mapped row by row and 352 individuals of *L. nordgaardi* were registered. Size of the colonies varied between 60 and 510 zooids and from 5 to 11 zooid rows respectively. Nevertheless, all the colonies demonstrated a generally similar trend of zooid distribution (Fig. 2). Outermost row was dominated by developing polypides. In the next four rows most of the polypides were actively feeding. Towards the center of the colony their fraction gradually decreased. Almost only degenerated polypides and empty zooids were present from the 6th row on.

Correlation coefficients between the fractions of growing and feeding polypides in a row and the size of that row were 0.62 (p < 0.001) and 0.76 (p < 0.001) respectively. Together, these polypide types were the most numerous—76% of all zooids.

Distribution of *L. nordgaardi* individuals greatly resembled one of actively feeding polypides. There was a strong positive correlation between them (Spearman's rank correlation coefficient = 0.91, p-value < 0.001). Correlation between distributions of epibionts and
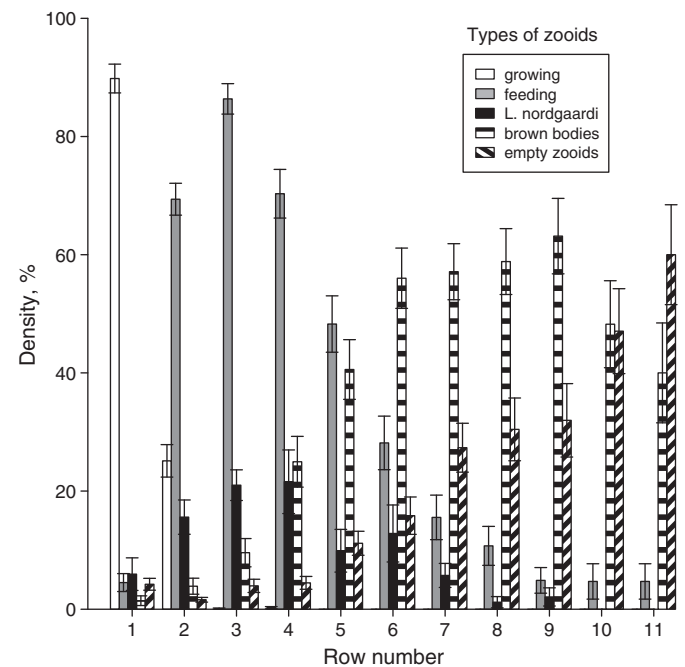

Fig. 2. Zoning of colonies of *T. armifera* and spatial distribution of *L. nordgaardi*. Zooid rows are numbered starting with the youngest (row 1), towards the ancestrula. Fractions of zooid types are averaged among colonies (T. armifera: BO+BF colonies, n = 42; L. nordgaardi from BO colonies, n = 11, error bars are S.E.).

growing polypides, although positive, was less strong (0.62, p = 0.04). Correlations between distribution of L. nordgaadi and those of degenerating polypides and empty zooids were negative (−0.49, p > 0.1 and −0.91, p < 0.001 respectively).

3.2. Stomach contents

3.2.1. Diatom size spectra

We studied the total of 200 and 200 zooids of *T. armifera* (BF and BO, respectively), and 244 individuals of *L. nordgaardi*. There were 1951, 1856 and 778 diatoms in BF, BO and *L. nordgaardi*, correspondingly. Size spectra of diatoms found inside the guts of bryozoans and their epibionts overlapped. Both consumed cells from 3 to 70 μm, but generally below 36 μm (which is 95th percentile for *T. armifera* and 99th for *L. nordgaardi*; Fig. 3).

Individuals of *L. nordgaardi* mainly contained diatoms of very small size, roughly 80% of them being below 15 μm. *T. armifera* ingested relatively small (below 15 μm, 40%) as well as large diatoms.

Length distribution of the diatoms in *T. armifera* stomachs was bimodal, with the depression at 15 μm (Fig. 3). Length to width ratios, i.e. proportions, of the diatoms were distributed in a similar fashion (Fig. 4). We found a strong positive correlation between the diatoms' size and shape (Spearman's correlation coefficients: 0.85, p ≪ 0.001 for BF and 0.84, p ≪ 0.001 for BO). Small diatoms were generally rounded or square-shaped, with their length to width ratio around 1:1. Larger cells were often elongated, with length to width ratios of 6–8:1.

ANOVA (Table 1) revealed that the presence of entoprocts did not affect the mean length of diatoms ingested by BF and BO, while the effect of sampling date was significant.

3.2.2. Gut fullness

Number of diatoms found inside each zooid varied from 0 (empty) to 50 (Fig. 5). Mean values were 9.76 ± 1.44, 9.28 ± 1.45 and 3.19 ± 0.49 for BF, BO and *L. nordgaardi*, correspondingly. In the entoprocts we found the least gut fullness, and also the highest number of empty stomachs (28%). Analysis of variance demonstrated that only the sampling date and not the presence of entoprocts affected the mean number of diatoms inside BF and BO stomachs (Table 1).
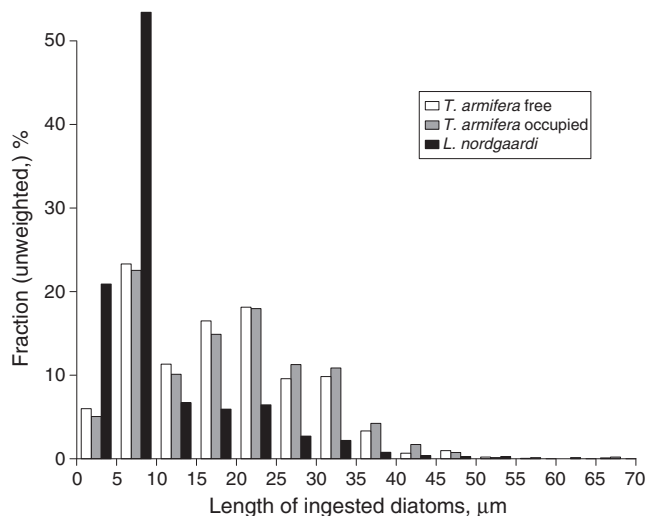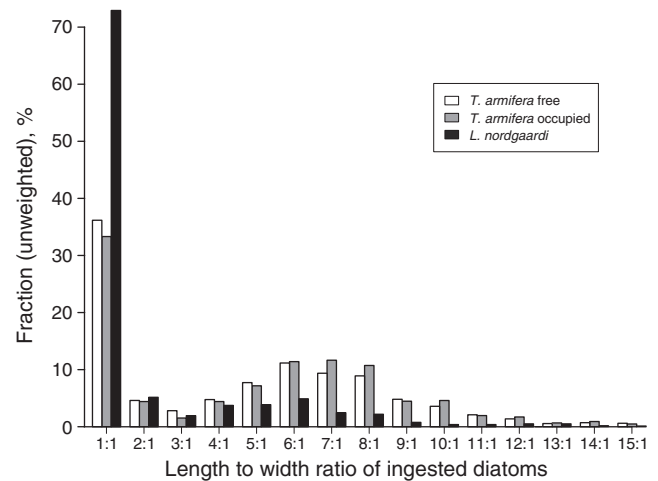

Fig. 4. Proportions of ingested diatoms (length to width ratio). Fractions of size classes are unweighted, n = 1951 for BF, n = 1856 for BO and 778 for *L. nordgaardi*.

4. Discussion

4.1. Colony zoning of T. armifera and spatial distribution of L. nordgaardi

Spatial distribution of *L. nordgaardi* individuals was positively correlated with that of fully developed and actively feeding polypides (Fig. 2).

T. armifera generally inhabits relatively long-living red algae attached to stones or kelp stalks and can survive more than one winter. Life cycle of this particular species has never been studied. Nonetheless, it probably resembles the cycles of other long-living species in seasonal climates (Barnes and Clarke, 1998; Dyrynda and Ryland, 1982; Kluge, 1975; Marcus, 1926a,b; Shunatova and Ostrovsky, 2002), with spawning in early autumn. We collected colonies in the middle and late September, well after the onset of degeneration of polypides. Zoning of the colonies at that time had already been well developed.

Loxosomatides are generally short-living, with the lifespan of 6–10 weeks (Emschermann, 1993a). They reproduce and disperse mainly by budding. Newly released buds of *Loxosomella* species are capable of slow creeping movements for a short period (up to 2 days), while adults are permanently attached. Our qualitative observations indicate that the highest budding rate occurs in individuals from the most populated ring-shaped areas of colonies. According to Yakovis (2002), general direction of bud migration is towards the growing margin of the same colony. As buds at the growing margin attach and grow, so does the colony, and by the time *L. nordgaardi* individuals reach adulthood, their host polypides become fully developed and actively feeding.

However, the precise budding rate of either species is unknown. The underpopulation of the youngest rows is probably caused by this rate difference. But in case of identical budding rate, the lack of migration when *L. nordgaardi* buds attach alongside the parent individuals may produce the same pattern.

Fig. 3. Size distribution of diatoms ingested by *L. nordgaardi* and *T. armifera*. Fractions of size classes are unweighted, n = 1951 for BF, n = 1856 for BO and 778 for *L. nordgaardi*.

Table 1
Sum of squares (SS) values from two-way ANOVA comparisons of (A) mean lengths and (B) mean numbers of diatoms from digestive systems of free and occupied *Tegella armifera*, sampled on two dates. Lengths and counts averaged by colony represent individual data points in the analysis.

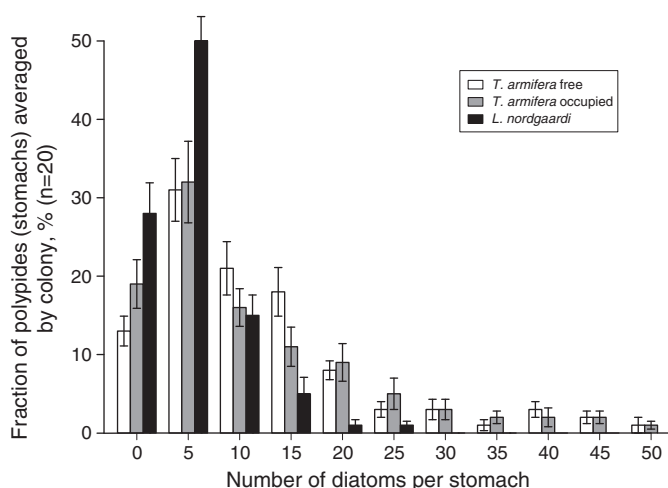| Source:	Sampling date (random)	Presence of *L. nordgaardi* (fixed)	Interaction (random)	Error
df	1	1	1	36
(A) Diatom lengths	105.7[***]	0.0	18.0	213.4
(B) Diatom numbers	327.12[***]	17.29	51.07	798.89

[***] p < 0.001.

Fig. 5. Number of diatoms, ingested by all three consumers. Fractions are averaged among colonies, n = 20 for BF, BO and *L. nordgaardi*.

Spatial distribution of feeding polypides in a given row is closely associated with the size of that row. We cannot prove that distribution of epibionts is caused by their preference for feeding polypides and not simply because they are the most numerous, and thus provide most space for attachment. However, the negative correlations with non-feeding and empty zooids indicate that *L. nordgaardi* does not occupy host colonies uniformly, regardless of the state of the polypides.

We cannot accept the hypothesis that colony-wide water currents do not affect distribution of *L. nordgaardi*. Entoprocts occur at the sites with stronger currents like growing margin with its strong outflow and a 'ring' of feeding zooids where chimneys are formed.

There are indications of similar, flow-dependent, preferences of entoprocts inhabiting other bryozoan species: erect branching *Scrupocellaria arctica* (Yakovis, 2002) and free-living lunulitiform species (families Selenariidae and Cupuladriidae: Cook, 1963; Cook and Chimonides, 1994). The latter, as well as *T. armifera*, demonstrate pronounced colony zoning. Group of closed, non-feeding zooids at the top of the colony acts as 'chimney'. Entoprocts are abundant on the upper sides, and even more on the top parts of these colonies (Cook, 1963; Cook and Chimonides, 1994), probably because of favorable flow conditions. Other fouling suspension feeders may occupy similar places (Chimonides and Cook, 1981).

A model integrating entoprocts into the hydrodynamical system of the feeding bryozoan colony had been proposed in the literature (Shunatova and Ostrovsky, 2002; Yakovis, 2002). In unoccupied bryozoan colony incurrents generated by many adjacent lophophores are quite strong, and therefore need to be balanced (Grünbaum, 1995; Larsen and Riisgard, 2002; Pratt, 2004). Balance is maintained by passive outflow along the edge of the colony (Taylor, 1999) and by 'chimneys'—regularly spaced zones of excurrent within the lophophore canopy (Cook, 1977; Cook and Chimonides, 1980, 1994; Dick, 1987).

T. armifera in particular creates 'temporary chimneys'. Scattered groups of 10–12 neighboring polypides withdraw for some time (up to 1 h), so that water leaves the space below lophophores that surround the 'chimney' upwards. Excurrents also appear in central regions of colonies if zooids there are degenerated or dead (Shunatova and Ostrovsky, 2001).

According to aforementioned authors, entoprocts may become involved into chimney formation, thus facilitate the excurrents. This in turn is beneficial since the higher speed of excurrent ensures that filtered water is carried away by ambient flow and not become re-filtered. However *T. armifera* chimneys have temporary nature: groups of polypides withdraw at intervals and only for short periods of time (Shunatova and Ostrovsky, 2002; our observations). When zooids involved in 'temporary chimneys' resume feeding, activity of

epibionts may become disadvantageous for the host. Water, already depleted of food particles by both host and epibiont and directed upwards by entoprocts, returns to the space right above the colony and may be drawn into the lophophores again (see Grünbaum, 1995).

4.2. Stomachs contents

4.2.1. Size and shape spectra of ingested diatoms

Diet, i.e. kinds and numbers of food particles, captured by each of symbionts, is not completely identified. Specific evidences from culturing, feeding experiments and in situ analysis of available food are rather scarce (see Ryland, 1970). Analysis of the gut contents is also of a limited assistance, since the digestion is quite fast: from 30 to 80 min for bryozoans (Best and Thorpe, 1987; Bullivant, 1968; Menon, 1974); and about 60 min in entoprocts (Hyman, 1951). The content of the guts cannot be visually identified because of the delicate nature of the food, with the exception of skeletal groups: diatoms and dinoflagellates.

Size spectra of the diatoms found in the present study are in a good agreement with previous works on bryozoans (Riisgard and Goldson, 1997; Riisgard and Manriquez, 1997) and with general prediction by Barnes and Clarke (1998) about nanoplankton size-range of particles taken by polar species. Diet of the ectoprocts is substantially less studied, still our results agree with exiting sparse data (Emschermann, 1993a,b; Hyman, 1951).

Diatoms serve as a good food source despite their resistant shells. It is often possible to open the shell and digest the protoplast with enzymes alone, without mechanically damaging the valves. Moreover, diatom cells are covered with more or less thick extracellular mucus layer which is itself a source of food (Chen, 2007; Decho and Fleeger, 1988). In culture many invertebrates, including bryozoans, are successfully reared and fed on diatoms.

Together with dinoflagellates, diatoms dominate polar seas, including the White Sea, throughout the year (Ilyash et al., 2003). Surface waters of Kandalaksha Bay (0–10 m) have consistently high levels of primary production from mid July to early September (Martynova et al., 2011). Range of potential food sources for filter-feeders is rather limited in Kandalaksha Bay. In August, the "production:destruction" ratio of the organic matter exceeded 1.0 in the surface water layer, which indicates the autotrophic status of the phytoplankton community. Specifically, the impact of the heterotrophic algae did not exceed 7% of the total plankton biomass (Ilyash et al., 2011).

In 2002 the most abundant group of late August plankton was Bacillariophyta (210 cells/mL, 70% on 21.08 and 75 cells/mL, 40% on 31.08). Without specific data on composition of planktonic communities for mid and late September of 2009, we may extrapolate from general observations that diatoms play an important role in autumn phytoplankton (Gogorev, 2005; Ilyash et al., 2003).

Being by no means the sole food source, diatoms are nonetheless an important one. Combined with the great size diversity, it makes them good markers of the diet. We believe that conclusions derived from this study may be applied to the whole diet range of the animals, except for bacteria and non-particulate organic matter.

Observed bimodal distribution may represent the distribution of the diatom cells in the seawater, reflect some feeding preferences of the bryozoan, or alternatively, indicate imperfection in their capturing mechanism. Among adaptations to planktonic life employed by diatoms are (1) small cell size and (2) elongated shape, with length to width ratio of 7 to 1. Indirectly, they may indicate that bryozoan gut contents indeed reflect two groups of planktonic cells. Alternatively, relatively low abundance of 15 μm diatom shells in the stomachs may be caused by high density of other food particles of the same size (see Best, Thorpe, 1994). Only the data on diatom size spectra from seawater directly surrounding *T. armifera* colonies may clarify the issue.

Bryozoans ingested both "small rounded" and "large elongated" diatoms, while entoprocts mainly contained small rounded cells (Figs. 4, 5). Notable overlap exists only in the smaller size classes of the food (less than 15 μm; Fig. 3). Thus, the food competition is possible, and we fail to accept the original hypothesis of independence of diets. The magnitude of such competition, is, however, a subject for a further study. It must also be held in mind, that diatoms form only a part of the diet of both consumers. Numbers of other ingested food particles are unknown. An important overlap or segregation of diets may remain unnoticed.

We focus on the effect of *L. nordgaardi* on its host, but there is a possibility of an opposite influence. Lack of larger particles in the stomachs of epibionts may be not due to their food preferences, but to the influence of the host. *T. armifera* may remove most of the large particles from the water flow, thus depriving its epibionts this food source. To answer this question, size preferences of free-living entoprocts would have been of most help, but *L. nordgaardi* almost never occur separately. Thus the study of diatom size spectra from stomachs of *L. nordgaardi* associated with other host species and from surrounding waters may be necessary.

Our next hypothesis stated that the presence of *L. nordgaardi* does not affect the feeding of the host. If interspecific food competition is present, one may expect to find some segregation between competitors (Begon et al., 2006; Hughes, 2000), in this case a drop in number of diatoms smaller than 15 μm in occupied colonies. However, comparison of the size-shape spectra (Fig. 5) of free and occupied colonies does not support this suggestion. Epibionts did not induce differences in size and proportions of ingested diatoms in their occupied hosts.

4.2.2. Gut fullness

Another indication of the effect *L. nordgaardi* may have on its host is the total amount of food ingested by free and occupied colonies. Zero effect would result in zero differences in the "gut fullness" between BF and BO colonies.

Entoprocts in the present study consumed very low quantities of diatoms. Our results are in a good agreement with previous data (Emschermann, 1993b; Hyman, 1951). Compared with bryozoan polypides, *L. nordgaardi* individuals ingested approximately three times less diatoms. Moreover, variability was much lower in entoprocts (Fig. 5).

Fullness of stomachs was similar in free and occupied colonies (see above, Fig. 5). Analysis of variances (Table 1) demonstrated that the presence of entoprocts does not change overall feeding success of the host.

Entoprocts may be involved in chimney formation and facilitate outflow. Their spatial distribution partly supports this proposition. Alternatively, entoprocts may deprive the host polypides of food particles, and interfere with colony water balance. But we found no compelling evidences for either of the effects. Therefore, if at all present, they are extremely weak and may cancel each other out.

Entoprocts and their bryozoan hosts may completely avoid trophic interference. *L. nordgaardi* individuals consume less food than a bryozoan polypides and bryozoan lophophores cannot remove every particle from the flow (Riisgard and Manriquez, 1997). It is possible that the water already filtered by the host still satisfies feeding requirements of the epibiont.

As we found no noticeable positive or negative effects of *L. nordgaardi* on its host, we conclude that these entoprocts are commensals of bryozoans.

5. Summary

L. nordgaardi tends to occupy cystides of fully developed and actively feeding zooids of its host, *T. armifera*. This is probably a result of preference of specific, favorable flow conditions at these areas.

Size ranges of diatom shells found in the stomachs of *T. armifera* and *L. nordgaardi* overlapped, especially in the size classes <15 μm. Numbers of ingested diatoms were different in entoprocts and their hosts. Entoprocts ingested, on average, 3 times less diatoms than polypides of *T. armifera*.

Presence of *L. nordgaardi* had no effect on size spectra and number of ingested diatoms. We suggest that *L. nordgaardi* is a commensal of *T. armifera*.

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