= FOULING BIOLOGY =

Mutual Effects of Several Fouling Organisms of the White Sea (Mytilus edulis, Styela rustica, and Hiatella arctica) on Their Growth Rate and Survival

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Abstract—The mutual effects of several fouling species (the bivalves *Mytilus edulis* and *Hiatella arctica* and a solitary ascidian *Styela rustica*) on their growth rate and mortality were studied through field experiments. The interactions between *S. rustica* and *H. arctica* appeared to be the least antagonistic. In contrast, the mussel was the most "aggressive" species with regard to both competitors. It was observed that the ascidians died, because they were intensively braided and gummed up with the byssus threads of the mussels. However, in some cases the intraspecific competition was stronger than the interspecific one.

Key words: fouling communities, Mytilus edulis, Styela rustica, Hiatella arctica, growth, competition, White Sea.

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The succession of fouling communities in the White Sea is, by now, rather well studied [7, 8, 10, 12, 13, 26, et al.]. However, despite the great interest demonstrated by scientists with respect to the relationships of organisms in such communities [3, 9, 19, 22, 29, et al.], the White Sea fouling still remains beyond the confines of such interest. On the other hand, knowledge about interactions between different species is needed to understand the mechanisms of the formation and functioning of such communities, as well as the patterns of the exchange of some species with other ones. The bulk of population of fouling communities in the White Sea is constituted, in most cases, by the bivalve mollusks Mytilus edulis (Linnaeus, 1758) and Hiatella arctica (Linnaeus, 1767) and a solitary ascidian Styela rustica (Linnaeus, 1767). In this connection, the target of our project was to estimate, in the course of field experiments, the mutual effects of M. edulis, H. arctica, and S. rustica on their survivorship and growth rates.

MATERIALS AND METHODS

The animals for our experiments were collected from artificial substrates in Kruglaya Bay (Guba Chupa Bay, Kandalaksha Bay, the White Sea), located close to the Marine Biological Station of Zoological Institute RAS. Selected animals were placed into cylindrical cages 20 cm in diameter and 7 cm high made of thin perforated plastic (the holes were 3 mm in diameter). Into each of control cages we placed animals of only one species, i.e., *M. edulis*, *H. arctica*, or *S. rustica*. Into each experimental cage we placed animals of two

tested species, so that the biomass of one species was twice greater than the biomass of the other one, as follows: *M. edulis > H. arctica*; *M. edulis > S. rustica*, and *H. arctica > S. rustica* or *M. edulis < H. arctica*; *M. edulis < S. rustica*, and *H. arctica < S. rustica*. All the control and experimental cages were installed in sets of three devices each, i.e., the total number of cages equaled 27.

The total biomass of animals placed into each of the cages was approximately 300 g; the biomass of the species placed in a smaller mass and the dominating species were about 100 and about 200 g respectively; in the control the biomass of the single tested species was about 300 g. Such a large stocking density was due to our intention that the animals should not avoid direct contacts with each other. Prior to the experiments 30 specimens of each the species were numbered and measured (the specimens of *S. rustica* also were weighted).

H. arctica and S. rustica were tagged with bee tags; these were pasted onto the animals using a cyanoacry-late cement. Mussel shells were numbered and tagged using a dissection needle. In M. edulis we registered only shell length (L, mm); in H. arctica we measured shell length (L, mm), height (H, mm), and depth (D, mm). The shell of H. arctica often has an irregular shape and, depending upon particular environmental conditions, can grow disproportionately in length, height, or depth. To register the changes in the shell shape of this mollusk and estimate the increments in all three dimensions, we calculated a combined linear parameter as follows:

Variant of the experiment	Control 9.7 ± 0.55			
$H > M$ 14.8 ± 0.21	t = 2.9 $p = 0.004$	H > M		
$H < M$ 15.9 ± 2.57	t = 2.74 $p = 0.006$	t = 0.35 p = 0.73*	H < M	
$H > S 6.9 \pm 0.39$	t = 1.79 p = 0.07*	t = 4.25 p < 0.001	t = 3.92 p < 0.001	H > S
H < S 6.4 ± 1.95	t = 1.8 p = 0.07*	t = 3.98 p < 0.001	t = 3.78 p < 0.001	t = 0.13 p = 0.89*

Table 1. Mortality of *Hiatella arctica* (%) in different variants of the experiment

Note: Here and in Tables 2–5: t, empirical value of Student's test; p, significance level; * — differences are insignificant. M, Mytilus edulis, H, Hiatella arctica, S, Styela rustica.

$$L_{\text{comb}} = \sqrt[3]{LHD}$$
.

In *S. rustica* we measured the height (*H*, mm) and diameter (*D*, mm) of body that was in the maximum contracted condition. The body proportions of ascidians of this species are extremely variable; therefore we used the cube root of the body volume as a characteristic of linear size:

$$L_{\text{comb'}} = \sqrt[3]{H\pi(D/2)}^2.$$

The specimens of the same species intended for measurements were chosen to be approximately the same size. The mean shell length of mussels used in the experiments equaled 32.9 ± 0.11 mm (from 30 to 36 mm). For *H. arctica* $L_{\text{comb}} = 8.02 \pm 0.038$ mm (from 6 to 10 mm). The size of *S. rustica* ranged in wide limits due to technical difficulties in the selection of specimens of the same size; $L_{\text{comb}} = 13.7 \pm 0.15$ mm (from 7 to 20 mm).

No preliminary acclimation of animals was performed prior to the beginning of experiments, because in the cages they were maintained under same conditions and at the same point as they were living earlier. During laboratory preparation of animals prior to the experiments they were maintained in aquariums under 10°C and intensive aeration, the water was changed every day. Specimens whose condition seemed inadequate were discarded and not used in the experiments.

The cages were installed on July 3, 2003, in Kruglaya Bay, in the water column at 2.5 m depth, so that they had no contacts with bottom substrate. In early August of 2003 we performed a control inspection of the cages and found out that all ascidians maintained together with mussels had perished. On August 18, 2003 we have removed the dead animals and placed respective numbers of live ascidians into the same cages; the new animals were pasted onto cage bottoms using a cyanoacrylate cement. On June 25–27, 2004 all cages were removed from water, the tagged animals

were measured and the mortality among the animals was evaluated.

To estimate the growth rate in the surveyed species we used the relative increment of linear body size as follows:

$$\Delta L = (L_{\rm f} - L_{\rm i})/L_{\rm i},$$

where L_i and L_f are the initial and final body size respectively.

The results of the experiments were treated using methods of linear statistics. The comparison of fractions was performed using Fisher's ϕ -transformation. Standard mean errors are presented in tables and in the text as an index of variation in estimated characteristics.

RESULTS

Hiatella arctica. In the cages were this mollusk was maintained together with Styela rustica, its mortality (6.4–6.9%) was less, but did not differ significantly, from that in the control (9.7%) (Table 1). When H. arctica was maintained together with Mytilus edulis, the mortality was significantly greater (14.8–15.9%), although it showed no significant differences for different variants of the experiment (Table 1).

The relative growth increment of *H. arctica* in the cages where they were maintained in greater number compared with mussels did not differ significantly from that in the control; however, in cages, where the mass of the mussels was larger than that of *H. arctica*, the growth increment in the latter was significantly smaller (Table 2). On the other hand, mollusks that were maintained together with ascidians grew better than those in the control irrespective of the relative biomasses of these species in the cages (Table 2).

Styela rustica. Maintaining ascidians together with mussels caused the death of all the experimental specimens of *S. rustica* within the first month after the beginning of the experiment. In the other cages the majority of the ascidians remained alive at that time. In cages

Control the experiment 0.18 ± 0.015 H > Mt = 1.26H > M 0.21 ± 0.015 p = 0.21*H < Mt = 2.83t = 4.17H < M 0.13 ± 0.014 p = 0.005p < 0.001H > St = 2.91t = 1.63t = 5.98H > S 0.24 ± 0.014 p = 0.004p = 0.10*p < 0.001H < St = 3.24t = 1.99t = 6.29t = 0.38 0.25 ± 0.014 p = 0.001p = 0.048p < 0.001p = 0.70*

Table 2. Relative growth increments of Hiatella arctica (as a ratio to the initial size) in different variants of the experiment

Note: Here and in Tables 2–5: t, empirical value of Student's test; p, significance level; * — differences are insignificant. M, Mytilus edulis, H, Hiatella arctica, S, Styela rustica.

Table 3. Mortality of *Styela rustica* (%) in different variants of the experiment

Variant of the experiment	Control 73 ± 23			
S > M 100	t = 6.19 p < 0.001	S > M		
S < M 100	t = 6.19 p < 0.001	t = 0 $p = 1*$	S < M	
S > H 10 ± 6.7	t = 9.27 p < 0.001	t = 15.63 p < 0.001	t = 15.63 p < 0.001	S > H
S < H 17 ± 5.6	t = 7.77 $p < 0.001$	t = 14.14 p < 0.001	t = 14.14 p < 0.001	t = 1.30 p = 0.19*

Note: Here and in Tables 2–5: t, empirical value of Student's test; p, significance level; * — differences are insignificant. M, Mytilus edulis, H, Hiatella arctica, S, Styela rustica.

with mussels the ascidians were intensively braided with byssus threads of the mollusks, up to the formation of a kind of "cover" in some cases; the siphons of the ascidians were plastered with byssus plaques. Many ascidians appeared to be constricted by byssus threads of mussels across their bodies. All of these most likely promoted the death of ascidians, as under such conditions they could not respire and feed normally. It is pertinent to note that no such response from mussels was registered in relation to H. arctica. An assumption was made that the observed effects were mostly due to the fact that the ascidians were not attached to the substrate (they almost were not capable of reattachment). Therefore, ascidians placed into the cages as a replacement for dead animals were pasted onto the cage bottoms. However, in this case all the animals also died as a result of being heavily braided with byssus threads of the mollusks. We could not determine the precise time interval, when most animals died in this variant of the experiment; however, this happened no later than in October of 2003.

High mortality of S. rustica (73%) was also observed in the control cages. In the latter case, both the linear growth increment and body weight increment of surviving specimens appeared negative (-0.09 ± 0.011 and -0.21 ± 0.028 respectively). In cages with H. arctica the mortality of ascidians was significantly smaller than in the control and did not differ significantly in the following variants of the experiment: S. rustica > H. arctica and S. rustica < H. arctica (Table 3). The growth increment of the ascidians showed positive values and also did not differ significantly in different variants of experiments with H. arctica (t = 1.92; p = 0.06for the linear growth increment and t = 1.64; p = 0.10for the weight increment). However, a tendency was noticeable for smaller values of both linear increments $(0.04 \pm 0.012 \text{ and } 0.01 \pm 0.011 \text{ respectively})$ and weight increments $(0.16 \pm 0.042 \text{ and } 0.07 \pm 0.037 \text{ respectively})$ in the variant of the experiments where the biomass of ascidians was smaller than that of the mollusks.

Mytilus edulis. Mortality of the mussels, in almost all variants of experiments, did not differ significantly

Variant of the experiment	Control 7 ± 1.3			
M > H	t = 1.74	M > H		
2.8 ± 1.11	p = 0.08*			
M < H	t = 1.04	t = 0.14	M < H	
3 ± 2	p = 0.30*	p = 0.89*		
M > S	t = 2.33	t = 0.27	t = 0.35	M > S
1.79 ± 0.04	p = 0.02	p = 0.79*	p = 0.73*	
M < S	t = 0.005	t = 1.48	t = 0.99	t = 1.95
7.8 ± 2.22	p = 0.99*	p = 0.14*	p = 0.32*	p = 0.052*

Table 4. Mortality of *Mytilus edulis* (%) in different variants of the experiment

Note: Here and in Tables 2–5: t, empirical value of Student's test; p, significance level; * — differences are insignificant. M, Mytilus edulis, H, Hiatella arctica, S, Styela rustica.

Table 5. Relative growth increments of Mytilus edulis (as ratio to the initial size) in different variants of the experiment

Variant of the experiment	Control 0.11 ± 0.0051			
M > H	t = 6.76	M > H		
0.163 ± 0.0059	p < 0.001			
M < H	t = 8.53	t = 2.43	M < H	
0.185 ± 0.0072	p < 0.001	p < 0.016		
M > S	t = 6.66	t = 0.38	t = 1.95	M > S
0.166 ± 0.0067	p < 0.001	p = 0.70*	p = 0.053*	
M < S	t = 14.74	t = 9.99	t = 7.69	t = 9.39
0.28 ± 0.011	p < 0.001	<i>p</i> < 0.001	p < 0.001	<i>p</i> < 0.001

Note: Here and in Tables 2–5: t, empirical value of Student's test; p, significance level; * — differences are insignificant. M, Mytilus edulis, H, Hiatella arctica, S, Styela rustica.

from their mortality in the control. However, in the cages where the number of mussels was greater than that of ascidians the mortality among the mollusks was significantly smaller than in the control (Table 4). The relative growth increment of the mussels increased significantly according the following series: control—*M. edulis* > *H. arctica*—*M. edulis* < *H. arctica* (Table 5).

As *S. rustica* very rapidly died in the cages with mussels, throughout the experiments the latter were mostly living without any competitors. These cages differed from the control cages only in the smaller population density of the mussels. In the cages where the biomass of mussels exceeded that of ascidians, the relative growth increment of the mollusks was the same as in the cages where the biomass of the mussels exceeded that of *H. arctica*. On the other hand, the growth increment of mussels in the cages where their biomass was smaller than that of ascidians was significantly greater than their respective increment in both the control and all other variants of the experiments (Table 5).

DISCUSSION

Studies of the competitive relationships between sedentary organisms are one of the intensively developing lines of investigation in marine ecology. With respect to methodology, the simplest and therefore the most popular studies are those performed on colonial organisms [23, 25, 29, et al.]. Solitary animals are also used as objects for such investigations. In the latter case, somatic growth rate and mortality are used as indices of success in competition. Numerous attempts have been made to estimate competition for food resources [15, 17, 20, 21, et al.]. All these projects had the same target—to clarify the place and the role of a species in a community [24].

Several facts, such as the intensive braiding of *Styela rustica* specimens with byssus threads of *Mytilus edulis* and the following death of the former (present study); enhanced byssus production in mussels in the presence of *S. rustica* metabolites in the water [5]; as well as the results of observations on mussel behavior in aquariums with *S. rustica* and *Hiatella arctica*

[Khalaman and Lesin, unpubl.] allowed us to hypothesize that an active protective response of mussels for the presence of ascidians exists. In such a situation, the behavior of the mussels is similar to their response to predatory snails, where the mussels tried to immobilize the latter using byssus threads [18, 28, 30]. It is possible that such a usage of byssus is a non-specific response of mussels to stress and may be directed against either a predator or a competitor. However, in fouling developing on vertically arranged surfaces, such a means of competition is in all likelihood non-effective for certain purely mechanical reasons. If otherwise, then the existence of fouling communities of S. rustica in the upper 3–5 m water layer of the White Sea should be impossible. As well, it still remains unknown, how the young of S. rustica survive in fouling communities while covered with a mussel coat, which is rather common phenomenon.

The response of mussels to the presence of species that pose no direct threat to life, but which are their spatial or trophic competitors, deserves particular attention and further experimental testing. The braiding with byssus threads can appear, not as a non specific response directed at the elimination of the competitor, but rather as a side effect of a failed attempt to avoid an undesirable neighborhood. In a closed space the mollusks for a long period cannot find an appropriate place for attachment; they are continuously moving around, leaving behind many byssus threads, which braid ascidians. At the any case, the discussed phenomenon fits well with the general pattern of antagonistic relationships, which are observed between *M. edulis* and *S. rustica* in fouling communities [12, 13].

In our provisional experiments that were performed earlier [1], we had already studied the mutual effects of both *H. arctica* and *M. edulis* and *H. arctica* and *S. rustica* on their growth rates. We used a similar pattern of experiments in this case; however, the total biomass of animals in the cages was only one half as great as now. The information obtained during the present study has corroborated the results of the provisional investigations.

A comparison of incremental values for animals in the control and experimental cages showed that in the tested species the intraspecific competition often appear more important than the interspecific competition. Such a phenomenon is by no means rare and, judging from the literature, is often revealed during ecological studies [16]. In our case, the relative increment values of the mussels increased with the decrease of the biomass of these animals in cages, from the control animals (300 g), to the cages where the biomass of mussels was smaller than that of *H. arctica* (100 g). However, this does not imply that H. arctica exerts no negative effects on the mussels. The evidence for the latter conclusion is the difference between the relative growth increments of mussels in cages with equal biomass, but with either the presence of *H. arctica* or the absence of competitors (the cages with S. rustica, where the ascidians died) (Table 5).

Similar results were also obtained for *H. arctica* in the experiments with S. rustica. Despite the absence of competitors, the reduced (compared with the control values) biomass and the density of the mollusks resulted in an increase of their relative increment values. On the other hand, the absence of significant differences between the cages, where the biomass of *H. arc*tica exceeded that of S. rustica and the cages, where the biomass of the mollusks was smaller than that of ascidians, allowed us to suppose that S. rustica exerts stronger negative effects on H. arctica than H. arctica exerts on the mussels. Decrease in biomass and population density appeared to be an important factor as well for S. rustica, as it was in the case with two other species. In cages with *H. arctica* the mortality of ascidians was significantly smaller and increment values were significantly greater than those in the control. The latter fact evidently was not related to the presence of better conditions for reattachment of S. rustica, when it was maintained in cages together with H. arctica. S. rustica has almost no capability for reattachment and by the end of the experiments we did not find any attached specimens of this species.

The only case in our experiments (except for the death of ascidians in the cages with mussels), when intraspecific competition appeared to be less significant than interspecific competition was the negative effect of mussels on the growth and survival of *H. arctica*. Undoubtedly, the mussel is a stronger competitor than *H. arctica*.

The results of our experiments allowed us to suppose that among the three tested species the least intense competition is observed between the solitary ascidian *S. rustica* and the bivalve mollusk *H. arctica*. On the other hand, *M. edulis* is the most "aggressive" species in respect to both competitors. In the experiments with *S. rustica*, the mussels demonstrated a behavioral response that seems to be directed at neutralization of the competitor or, at least, that benefits the latter. *H. arctica* in all likelihood loses the competition for food resources to the mussel [4]. This fact agrees with the notion of *M. edulis* as an extremely competitive species [14, 27].

In conclusion, it is pertinent to note that in field experiments, when hydrobionts are maintained within a limited space, formal equality in biomasses and/or population densities of different species does not mean that the conditions are equally favorable for all these tested animals. For example, mussels that usually occur in dense populations appear to be the most well-adapted to maintenance under conditions with high population density; such conditions apparently are not appropriate for ascidians. The population density of mussels in benthos and fouling communities is an order of magnitude greater than that of S. rustica [2, 6, 11, 13]. The biomass of S. rustica in the communities also is smaller. Each species has its own optimum level; this significantly complicates both setting up the experiment and the interpretation of the results. Any attempts to ignore this factor lead to negative consequences. It our case the extraordinarily high mortality of *S. rustica* in the control was among such consequences.

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