# Algae versus animals in early fouling communities of the White Sea

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ABSTRACT: In epibenthic communities algae are usually predominant on sunlit substrates, while animals dominate shaded surfaces. Two possible factors that cause this are a higher competitive ability of algae and the evolutionarily defined differentiation of niches that results in animals avoiding competition with algae. We attempted to shed light on this duality by initally making the following assumption: if the key determinant for algal dominance on sunlit surfaces is niche differentiation rather than competitive exclusion, then a community already formed by animals must be impervious to algal expansion under any light conditions. This hypothesis was tested in a field experiment that used the early fouling communities developing in the upper water layer in the White Sea, Russia. Fouling communities were allowed to develop on the top sides and bottom sides of horizontal plates. After a period of exposure in water, the plates were inverted. It was shown that if the substrate orientation is reversed, the fouling community is transformed into the community that conforms to the new lighting conditions. An increased light intensity resulted in the degradation of the zoocenosis and changed its structure, whereas shading did not lead to degradation and change in the algocenosis, but caused stunting of algal growth. Our results indicate that algocenoses are more stable and have more competitive ability than zoocenoses in early fouling communities. The animal predominance on the shaded surfaces is likely to be a consequence of both competitive displacement of animals from the sunlit surfaces by algae and preferential colonization of the bottom surfaces by animals.

KEY WORDS: Alternative community states · Algal–invertebrate interactions · Substrate orientation · Competition · Biofouling · Community structure · Shading

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## INTRODUCTION

Recently, a good deal of attention has been given to the interactions between algae and sedentary animals in epibenthic communities. Canopy formed by algae is a powerful factor and can determine the nature of understorey communities (Bulleri et al. 2002, Irving et al. 2004, Clark et al. 2011). It has been demonstrated that algae have a complex, multifactorial effect on animals and the net result depends on which negative or positive influence on the animal species becomes predominant in each particular situation (Duggins et al. 1990, Bertness et al. 1999, Connell 2003). The influence can be generally neutral (Bégin et al. 2004, Beermann et al. 2013) or positive, when the algal canopy provides protection and offers more comfortable living conditions to filter-feeders compared to the bare substrates (Eckman & Duggins 1991, Irlandi & Peterson 1991, Dijkstra et al. 2012). However, it has been noted that in many cases algae have a negative effect on substrate colonization by sedentary animals and on their survival (Witman 1987, Duggins et al. 1990, Leonard 1999, Connell 2003); they may stunt the growth of animals, in par-

ticular, sponges (González-Rivero et al. 2012), and impair their physiological functions (McCook et al. 2001, Easson et al. 2014). A negative influence of algae on corals (River & Edmunds 2001, Jompa & Mc-Cook 2003), including allelopathic effects (Rasher et al. 2011, Slattery & Lesser 2014), is widely known.

According to the concept of multiple stable states (Lewontin 1969) communities dominated by algae or animals often are considered as alternative states (Barkai & Branch 1988, Knowlton 1992, Dudgeon & Petraitis 2001, Petraitis & Dudgeon 2005, Norström et al. 2009). Some researchers, however, think that these communities cannot be formed by stochastic processes and are, in fact, determined by environmental factors (Oshurkov 2000, Bertness et al. 2002) including activity of herbivory key species (Williams 1994, Benedetti-Cecchi 2000, McCook et al. 2001). In epibenthic and fouling communities, algae usually dominate sunlit substrates, while animals are predominant on shaded or hidden surfaces (Baynes 1999, Glasby 1999, Oshurkov 2000, Terlizzi et al. 2000, Irving & Connell 2002, Miller & Etter 2008, Pacheco et al. 2010). But what factor causes the predominance of algae on well-lit surfaces—their higher competitive ability or differentiation of ecological niches, such that the animals do not colonize sunlit places suitable for algal growth? Current evidence on this subject is ambiguous.

For instance, since sponges are more abundant in shaded rather than in well-illuminated habitats, it is often thought that algae outcompete sponges and displace them to shaded habitats, in which algal growth is limited due to low irradiation (Witman & Sebens 1990, Bell 2002). Preciado & Maldonado (2005), however, found that algal abundance is a reliable predictor for sponge abundance and diversity in only about 4% of cases.

Larvae of many animals are known to preferentially settle on shaded surfaces (Thorson 1964, Oshurkov & Oxov 1983, Todd & Turner 1986, Duggins et al. 1990, Durante 1991, McKinney & McKinney 2002, Darbyson et al. 2009). Young & Chia (1984) established that the settlement of tadpoles of the clubbed tunicate *Styela gibbsii* on a shaded surface is driven by the necessity to avoid the overgrowth of young tunicates by algae, because, otherwise, the algal mats would have restricted access to the siphons, causing the death of the animal. Thus this behavior can have an adaptive advantage. Nevertheless, some colonial ascidians successfully compete with algae for space (Terlizzi et al. 2000). Miller & Etter (2008) found that invertebrate recruitment is not significantly associated with the light level and

suggested that post-settlement mortality may be more important than larval phototaxis in the structure of an epibenthic community. Shading decreases post-settlement mortality of invertebrates by alleviating competition for space with algae.

Light is essential for the development of autotrophs, and shade impedes algal growth. Illumination intensity in itself cannot be the key factor for growth and development of adult animals if they do not contain autotrophic symbionts. We hypothesized that the predominance of algae on illuminated, up-facing surfaces and animals on shaded, down-facing surfaces is determined by evolutionarily defined ecological niche separation, rather than by competitive exclusion by algae. If this is the case, then an existing animal community must be impervious to algal expansion under any lighting conditions, at least during the lifetime of one generation of animals. The last clause is based on the possible cessation of recruitment of animals under light due to the preferences of larvae to settle on shaded surfaces. We attempted to verify the hypothesis using the early fouling communities that develop in the upper layer of the water column (0 to 5 m depth) in the White Sea as a model. For this purpose, we tested the following secondary hypotheses:

(1) The biological model used was appropriate for our study. In the White Sea, the early fouling communities developing on the upper well-lit surfaces of substrates are dominated by algae, whereas the shaded, down-facing surfaces are dominated by animals.

(2) There is an ecological niche separation between animals and algae. The animals predominating in the fouling communities formed on the down-facing surfaces of substrates in shaded conditions can maintain dominance and prevent algal growth even if the orientation is changed and the light conditions improved. On the other hand, if the substrate orientation changes and light conditions deteriorate, the algae predominant in the fouling communities that have formed on the upper well-lit surfaces are unable to maintain their dominance and become displaced by animals.

(3) Algae do not possess high resistance to deterioration of light condition and competitive superiority over animals. Shading leads to the degradation of the algocenosis and change in its structure. When conditions become favorable for algae, the transformation of the community towards algal dominance does not proceed faster than the transformation towards animal dominance under the opposite conditions.

## MATERIALS AND METHODS

### Study area, environmental conditions and biological background

The study was conducted at the White Biological Station of the Zoological Institute of the Russian Academy of Sciences. Kruglaya Bay, located near the station (66° 20.24′ N, 33° 38.21′ E), was chosen as the study area for the field experiment (Fig. 1).

The White Sea is a subarctic basin. Surface water temperature in summer in the study area is 12–15°C, but in exceptionally warm years it may rise for short periods to 20–25°C (Berger et al. 2001). These rises in temperature occur in small shallow inlets such as the Kruglaya Bay. The summer thermocline in the White Sea is located between 5 and 15 m depth and is determined by the hydrobiological characteristics of each individual aquatorium; Kruglaya Bay has a thermocline at 5 m (Babkov 1988, 1998). The temperature of surface water in winter varies from −0.5 to −1.4°C. Spring heating of water begins in May and rapid cooling of coastal water occurs in October (Berger et al. 2001). Reproduction and population recruitment of epibenthic organisms forming the fouling communi-



Fig. 1. Study area. 1: The White Sea Biological Station; 2: Kruglaya Bay

ties in the upper 5 m of the water column take place during the warm months from June to September (Kaufman 1977, 2015, Oshurkov & Oxov 1983, Makarov & Schoschina 1998a,b, Mikhaylova 2006).

Early fouling assemblages in the White Sea are diverse and represented by communities that may be dominated by a variety of organisms: ascidians, hydroids, bryozoans, barnacles and algae (Oshurkov 1985, 2000, Khalaman 2001, Railkin 2004). All these organisms are characterized by high growth rates and a short lifespan and can be defined as 'short-lived' organisms (Khalaman 2005a, 2013). These animals and algae make any substrate that they occupy suitable for successful settlement of larvae of the mussel *Mytilus edulis* (Linnaeus, 1758), which then becomes the dominant species and forms the next stage of succession of the fouling communities—the stage of 'long-lived' organisms (Sirenko et al. 1978, Oshurkov 1985, Khalaman 2005a, 2013). At this stage, a large proportion of early colonizers, both algae and animals, die out beneath the cover of mussels. This developmental sequence is typical in marginal seas in the temperate zones of the World Ocean (Scheer 1945, Reish 1964, Saenger et al. 1979, Chalmer 1982, Ardizzone et al. 1989, Henschel et al. 1990, Lenz et al. 2004). In the White Sea, the replacement of the community of short-lived organisms by mussels may take several months to 2 years (Oshurkov 1985, Khalaman 2013).

### Experimental design, set-up and sampling

The experimental substrates were made of ceramic plates $15 \times 15$ cm in size. The plates were fastened together in pairs in such a way that the top and bottom surfaces of this 'sandwich' were identical in physical properties. On June 9, 2013, 26 double plates were submerged in water attached to a special carrying framework (Fig. 2). The plates were positioned horizontally 1.5 m below water surface and 10–11 m above the seabed. The framework was constructed so as to allow the plates to be flipped over to reverse the top and bottom surfaces of the 'sandwich' without taking the plates out of the water. On August 4, 2013, 10 randomly chosen double plates were inverted; the orientation of 10 other plates was left unchanged. To avoid artifacts associated with rotation, the above-mentioned 10 'noninverted' double plates were vertically rotated 360° to face their original orientation. The remaining 6 double plates were taken out of the water to examine the fouling communities that had developed on the top and bottom sides of the 'sand-
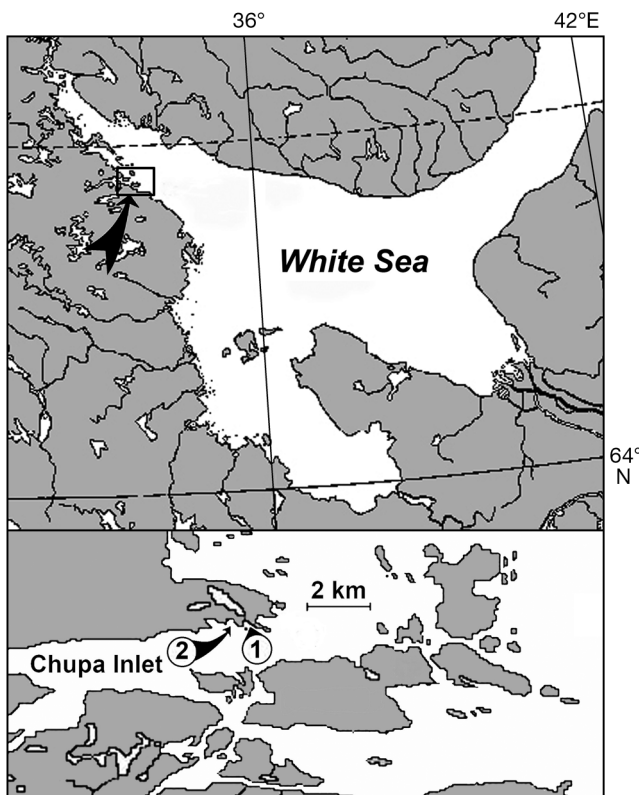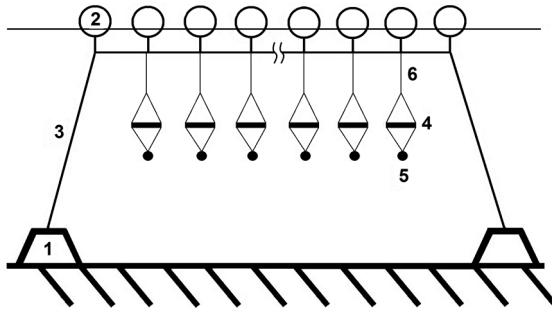
Fig. 2. Design of carrying framework for field experiment. 1: concrete anchor; 2: float; 3: main suspending rope; 4: double experimental plate; 5: weight; 6: suspending string

wich'. Ten new double plates identical to those used previously were installed on the same day. Additional plates were needed to confirm that the paths of development of early fouling communities on the up-facing surfaces and on the down-facing ones did not change after the date when some plates were inverted. Each experimental plate was numbered. The following year (from July 13 to July 26, 2014), all exposed plates were removed from the water for analysis.

The experiment, therefore, involved a group of 10 experimental plates that were inverted (hereafter referred to as ExR) and the following 3 groups of control plates: (1) 6 plates submerged in water from the beginning of the experiment until inversion of the experimental plates (CI) that indicated the initial state of the fouling communities before inversion; (2) 10 plates submerged in water throughout the experiment (CEx) that indicated the result of natural development of the fouling communities at the end of the experiment; and (3) 10 plates that were installed immediately after inversion of the experimental plates and which remained submerged in water until the end of the experiment (CA). These plates were needed to confirm that the natural development of the fouling communities starting at the date on which the plates were inverted did not differ from that at the beginning of the experiment.

Each sample was processed in the laboratory. The plates were transported to the laboratory suspended in wide buckets with sea water, making sure that the lower sides of the plates did not touch the bottoms of the buckets. In the laboratory, all fouling organisms were removed from the side edges of the plates, the 2 halves of the double plates were separated and each half (top and bottom) was processed separately. All organisms were removed from the plates, identified to species-level and counted, and their wet mass was measured to the nearest 1 mg. If the weight of an organism (usually epiphytic alga) was too small to be

measured accurately, it was recorded as 0.1 mg. We were unable to transport and process more than 3 double plates in one day. To reduce the influence of the sampling interval on the results of the experiment, experimental and control plates were examined in an alternating order.

## Measurement of light intensity

Light intensity was measured using HOBO Data Loggers UA-002-64. One detector was mounted on the top side and another on the bottom side of an additional double plate identical to those used in the experiment. This plate was installed in the same orientation and at the same place and depth as the experimental plates. The detector plate was not inverted, but detectors were periodically cleaned to remove fouling. Light intensity was measured synchronously by both detectors from June to September 2013 and was stopped after September 2013 because the regular clearing of detectors became impossible due to storm weather and freezing-over of the bay. The interval between the consecutive measurements was 15 minutes. The minimum light intensity collected by these detectors was 10.8 lux. Only those measurement pairs that did not have zero values were used to assess the difference in light intensity between the top and bottom sides.

## Statistical analysis

Fouling of the top and bottom sides in different groups of plates was assessed using the following parameters: total and relative (per plate) number of algal species, total and relative (per plate) number of animal species, total fouling biomass, algal biomass and animal biomass. Since *M. edulis* represents the next succession phase, it was excluded from all indices except the total number of species. Mean values are given with their standard errors. Data were processed using STATISTICA[TM] software (StatSoft) Release 7 and PRIMER[TM] software Version 6 (Clarke & Gorley 2006).

### Verification of appropriateness of the chosen biological model

This hypothesis was tested by comparing the state of the fouling communities that had developed on opposite sides of different groups of control plates.

For control plates (CI, CEx, CA), the effect of the plate orientation on the above indices of fouling status (dependent variables) was evaluated using split-plot ANOVA (Altman & Krzywinski 2015). The group of control plates, orientation of the fouling surface and block were selected as categorical factors, where the first was whole-plot factor, the second was a subplot factor but block indentified pairs of connected plates. The biomass of *M. edulis* was used as continuous predictor (covariant factor).

### Testing ecological niche separation between animals and algae

To reveal the niche separation between animals and algae, the effect of experimental plate inversion on the state of fouling communities needs to be estimated. The effect of experimental plate inversion on the condition of fouling communities was tested using split-plot ANOVA based on the results from experimental ExR and control CEx plates. The parameters chosen as dependent variables were the same as those used in the previous analysis. The presence or absence of inversion, orientation of the fouling surface and block were selected as categorical factors. The biomass of *M. edulis* was used as a continuous predictor. The effect of experimental plate inversion on mussel biomass was assessed based on the results from experimental ExR and control CEx plates. For this, split-plot ANOVA was used, with categorical factors: 'top side/bottom side' 'control/inverted' and 'block'.

Comparisons of the means were made using posthoc LSD test. Significance level was set at p = 0.05. Mean values were given with their standard errors. Analysis of contrasts was used to compare the difference between 2 variables with the difference between 2 other variables.

Data were first evaluated to ensure that the assumptions for ANOVA were met. Cochran's *C*-test was used to check homogeneity of variance. Normality of distribution was tested using Kolmogorov-Smirnov test. If data did not satisfy the normality, a nonparametric Mann-Whitney *U*-test was applied.

### Testing the high resistance and competitive superiority of algae over animals

To compare transformation rates of the community's structure after plate inversion, the following procedure was used. R-strategy principal component analysis (PCA) ordination with varimax raw factors rotation was performed. The analysis was based on fouling community data matrix of experimental ExR and control CEx plates. The number of taxa was initially reduced by expanding some of them to lower the number of factors and increase the amount of variation accounted for by the first components. The influence of differences in biomass between plates was reduced by using the ratio of biomass of each individual taxon to the total biomass on a given plate instead of the absolute biomass of the taxon. Before the analysis, the ratios were transformed using Fisher's φ-transformation. The results of the PCA were presented as factor loadings for each taxon and factor scores for the fouling communities on each plate for 3 factors. Only the first factor, which accounted for most variance, was used in the subsequent analysis. The average factor scores were calculated for each of the 4 groups of plates (top ExR, bottom ExR, top CEx and bottom CEx) showing the coordinates of the corresponding communities on the chosen ordination axis (first factor). The contrasts method was used to evaluate the statistical significance of differences between the positions of the communities.

To estimate the resistance of algae and animals we analyzed differences in the biomass of these groups of organisms between control CI and control CEx plates as well as between control CI and experimental ExR plates, using an LSD test. We also analyzed the similarity between cenoses developing on the control CEx plates and that developing on the experimental ExR plates. A similarity of structures of algo- and zoocenoses between the top and bottom sides of the experimental ExR plates, on the one side, and the cenoses of the top and bottom sides of the control CEx plates, on the other side, was estimated in the following way. Fouling data for the experimental and control plates were grouped into 4 samples: top side of ExR, bottom side of ExR, top side of CEx, and bottom side of CEx. The φ-transformed proportion of the species relative to the total biomass of the corresponding cenosis in the combined sample was used as a quantitative estimate of this species. Cluster analysis was performed separately for each of the cenoses (algal and animal). The measure of resemblance used was Bray-Curtis similarity. The results of the cluster analysis were verified using 1-way ANOSIM. SIMPER was used to determine the relative contribution of single taxa responsible for differences in species structure between the clusters and for a similarity within each cluster. For ANOSIM and SIMPER, the fouling data for individual plates were used

instead of those for the combined samples. ANOSIM and SIMPER were based on Bray-Curtis similarity indices, calculated from percentage data, previously φ-transformed.

### Testing the effect of mussels on early fouling communities

Although the purpose of the study was to assess the interactions between algae and animals forming early fouling communities, it was impossible under our experimental conditions to completely avoid colonization of plates by *M. edulis.* In July and August 2013, some juveniles of this species settled on the plates. The presence of mussels could dissemble the interactions between short-lived organisms because *M. edulis* is a dominant competitor that is able to suppress most early colonists. Therefore, we needed to test if the effect of mussels was weak and if the distribution of this species was homogenous throughout all plates. As mentioned above, we used the biomass of *M. edulis* as a covariant factor in ANOVA of all parameters of fouling communities. Additionally, the effects of surface orientation, group of control plates and plate inversion on mussel biomass were tested using split plot ANOVAs that were the same as those applied to other parameters of fouling communities.

### RESULTS

### Light exposure of the top and bottom sides of plates

The maximum (mean ± SE) (including zero value) light exposure recorded during the experiment for the top and bottom sides of the plates was 6200 (928 ± 15) lux and 43.1 (5.2 ± 0.13) lux, respectively. On average, light exposure for the bottom sides was 0.86 ± 0.011% of that for the top sides in measurement pairs that did not have zero values.

### Species composition

A total of 45 macrophyte species were collected from the plates: 21 species of brown algae (Phaeophyceae), 12 species of green algae (Chlorophyta) and 12 species of red algae (Rhodophyta) (Table S1 in the Supplement at www.int-res.com/articles/suppl/m553p013_supp.pdf). Of these species, 13 were identified as single finds, and 13 species of brown

algae, 8 species of green algae and 11 species of red algae were recorded as typical for the fouling community of the plates. Microalgae (cyanobacteria [2 species] and diatoms) were found in an appreciable number only on the plates of short-term exposure (CI). Diatoms were not identified.

Sedentary and sessile animals included 17 species (Table S1), of which the only sea anemone (*Metridium senile*) was very rare. One individual of this species was found on the top and bottom sides of one of the ExR plates. Total number of individuals or colonies for other species was greater, ranging from 30 to 6500.

### Verification of appropriateness of the chosen biological model

In each control group, the top sides of the plates had a greater number of algal species than the bottom sides (Table 1). A relative number of algal species (per plate) was also higher on the top sides for all control plates: CI (p = 0.001), CEx and CA (p < 0.001) (Table 2B, Fig. 3A). Although the influence of the factor 'control group' was insignificant (Table 2B), the top sides of the CI and CEx plates were significantly different in species number per sample (p = 0.016). This is consistent with the observation that the number of algal species recorded for the CI plates before their inversion was smaller than that for the CEx plates at the end of the experiment (Table 1). Cyanobacteria and diatoms were found only on the CI plates. These changes in species composition and richness most likely reflect the natural development of algocenoses.

Table 1. Species richness (total number of species) of fouling community. CI: control plates submerged in water from the beginning of the experiment to the inversion of the experimental plates; CEx: control plates submerged in water throughout the experiment; CA: control plates that were installed immediately after the inversion of the experimental plates and remained submerged in water to the end of the experiment; ExR: experimental plates submerged in water throughout the experiment and inverted once during the experiment. Top = top side, Bottom = bottom side

| —— CI —— | | —— CEx —— | | —— CA —— | | —— ExR —— | |
|---|---|---|---|---|---|---|---|
| Top | Bottom | Top | Bottom | Top | Bottom | Top | Bottom |
| **Algae** | | | | | | | |
| 20 | 12 | 30 | 18 | 30 | 13 | 33 | 22 |
| **Animals** | | | | | | | |
| 5 | 10 | 9 | 15 | 6 | 11 | 10 | 14 |

Species richness of the sedentary and sessile animals on the top and bottom sides of the control plates was inverse to that of the algae—the bottom sides of the plates had a greater number of animal species than the up-facing surfaces (Table 1). The factors 'control group' and 'top side/bottom side' had a significant effect on the relative number of invertebrate species (Table 2). The number of animal species per plate was higher for all groups of control plates on the bottom sides compared to the top sides: CI ($p = 0.006$), CEx and CA ($p < 0.001$) (Fig. 3B). The interaction of factors was also statistically significant (Table 2C). These results can be explained as follows: although the average number of animal species per sample on the top sides was only slightly different for all groups of control plates and the differences between CEx and CA were insignificant ($p = 0.85$), the relative number of animal species on the bottom sides of the CEx plates was significantly higher than that on the bottom sides of the other control groups ($p < 0.001$). The highest species richness of animals on the bottom side of the CEx plates most likely results from the largest exposure time of CEx plates.

The biomass of sedentary and sessile animals was generally higher on the bottom sides of the plates compared to the top sides (Table 2D). These differences were significant for the CI and CEx controls ($p < 0.001$), but insignificant for the plates of the CA group ($p = 0.32$), which is explained by a significantly lower animal biomass on the bottom sides of the CA plates and relatively high animal biomass on the top sides of the CA plates compared to those of the CI and CEx plates (Fig. 4A). This also explains both a significant influence of the factor 'control group' on the animal biomass and the interaction between the factors 'top side/bottom side' and 'control group' (Table 2D). It should be noted that disproportionately high animal biomass on the top sides of the CA plates was caused by seasonal development of hydroids *Obelia longissima*.

An adequate ANOVA was impossible because of the lack of a normal distribution for the algal biomass in some of the control groups. Comparison by Mann-Whitney *U*-test demonstrated that the total algal biomass was higher on the top sides compared to the bottom sides, which was true for all control groups: CI ($p = 0.004$), CEx ($p < 0.001$), and CA ($p < 0.001$) (Fig. 4A).

On the top sides of the CI and CEx plates, the algae were predominant in biomass over sedentary animals ($p < 0.01$), but on the additional control plates (CA) algal predominance was insignificant ($p = 0.16$). The latter was

Table 2. Results of split-plot ANOVA on factors affecting fouling community on control plates

| Comparison | df | SS | MS | F | p |
|---|---|---|---|---|---|
| **A. Total biomass of fouling organisms (with the exception of mussels)** | | | | | |
| Control group | 2 | 557.675 | 278.838 | 22.826 | <0.001 |
| Top side/bottom side | 1 | 447.109 | 447.109 | 26.823 | <0.001 |
| Block | 9 | 152.077 | 16.897 | 0.952 | 0.527 |
| Biomass of *Mytilus edulis* | 1 | 2.065 | 2.065 | 0.169 | 0.684 |
| Control group × Top side/bottom side | 2 | 448.466 | 224.233 | 18.356 | <0.001 |
| Top side/bottom side × Block | 9 | 160.759 | 17.862 | 1.462 | 0.212 |
| Residual | 27 | 329.831 | 12.216 | | |
| **B. Algae species richness (no. species plate$^{-1}$)** | | | | | |
| Control group | 2 | 61.622 | 30.811 | 4.284 | 0.024 |
| Top side/bottom side | 1 | 1052.377 | 1052.377 | 60.253 | <0.001 |
| Block | 9 | 218.079 | 24.231 | 1.215 | 0.387 |
| Biomass of *Mytilus edulis* | 1 | 19.554 | 19.554 | 2.719 | 0.111 |
| Control group × Top side/bottom side | 2 | 2.402 | 1.201 | 0.167 | 0.847 |
| Top side/bottom side × Block | 9 | 181.977 | 20.220 | 2.812 | 0.018 |
| Residual | 27 | 194.174 | 7.192 | | |
| **C. Animal species richness (no. species plate$^{-1}$)** | | | | | |
| Control group | 2 | 72.509 | 36.254 | 38.515 | <0.001 |
| Top side/bottom side | 1 | 139.629 | 139.629 | 80.972 | <0.001 |
| Block | 9 | 22.216 | 2.469 | 1.291 | 0.353 |
| Biomass of *Mytilus edulis* | 1 | 0.763 | 0.763 | 0.81 | 0.376 |
| Control group × Top side/bottom side | 2 | 52.691 | 26.345 | 27.988 | <0.001 |
| Top side/bottom side × Block | 9 | 17.409 | 1.934 | 2.055 | 0.072 |
| Residual | 27 | 25.415 | 0.941 | | |
| **D. Total biomass of sessile and sedentary animals (with the exception of mussels)** | | | | | |
| Control group | 2 | 376.358 | 188.179 | 19.14 | <0.001 |
| Top side/bottom side | 1 | 1022.051 | 1022.051 | 87.051 | <0.001 |
| Block | 9 | 128.654 | 14.295 | 1.172 | 0.406 |
| Biomass of *Mytilus edulis* | 1 | 4.091 | 4.091 | 0.416 | 0.524 |
| Control group × Top side/bottom side | 2 | 517.838 | 258.919 | 26.336 | <0.001 |
| Top side/bottom side × Block | 9 | 110.274 | 12.253 | 1.246 | 0.310 |
| Residual | 27 | 265.45 | 9.831 | | |
| **E. Biomass of *Mytilus edulis*** | | | | | |
| Control group | 2 | 1169.336 | 584.668 | 9.443 | <0.001 |
| Top side/bottom side | 1 | 246.129 | 246.129 | 4.928 | 0.046 |
| Block | 9 | 1453.91 | 161.546 | 3.343 | 0.043 |
| Control group × Top side/bottom side | 2 | 2..154 | 1.077 | 0.017 | 0.983 |
| Top side/bottom side × Block | 9 | 434.859 | 48.318 | 0.78 | 0.636 |
| Residual | 28 | 1733.624 | 61.915 | | |

caused by the seasonal short-term development of hydroids *O. longissima*, which is a common yearly event for Kruglaya Bay (Oshurkov 1985). On the bottom sides of the plates in all control groups, sedentary animals were predominant over algae (p < 0.001) (Fig. 4A).
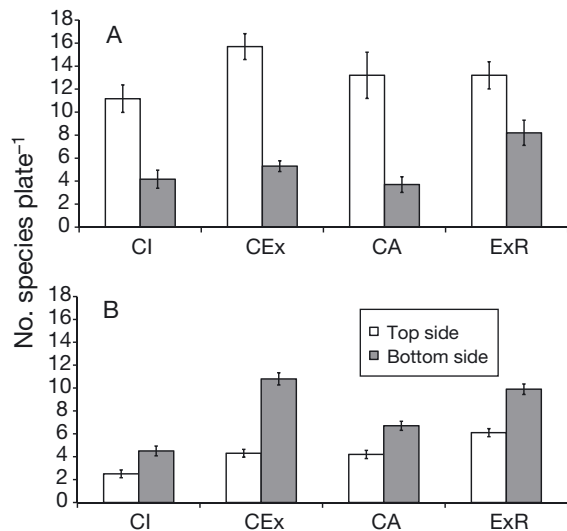


Fig. 3. Relative species richness (mean ± SE) of (A) algae and (B) animals on top and bottom sides of control and experimental plates. See Table 1 for abbreviations and treatment descriptions
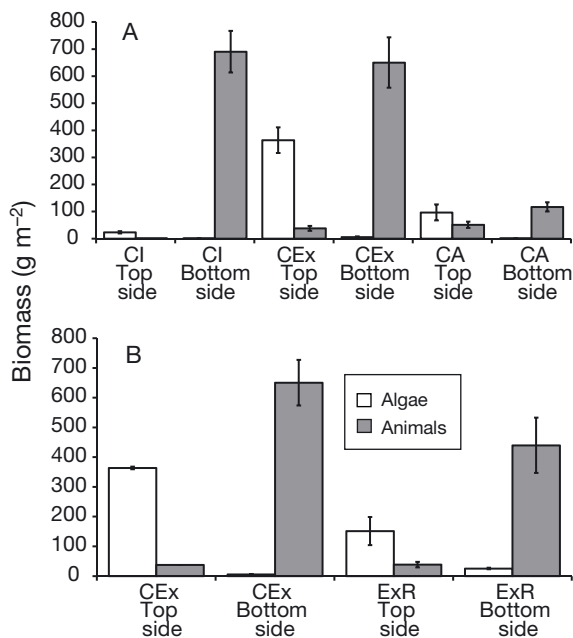


Fig. 4. Biomass (mean ± SE) of algae and animals on top and bottom sides of plates. (A) All groups of control plates. (B) Control (CEx) and experimental (ExR) plates. See Table 1 for abbreviations and treatment descriptions
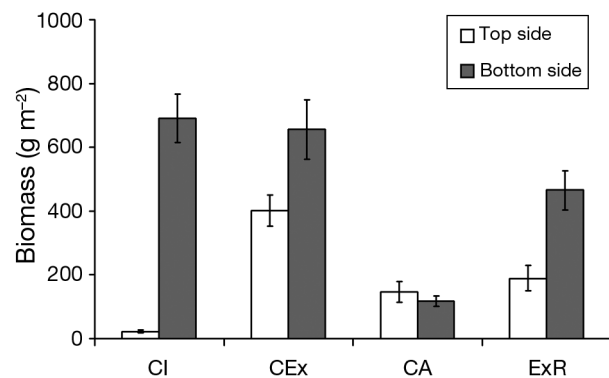


Fig. 5. Total biomass (mean ± SE) of fouling communities on top and bottom sides of control and experimental plates. See Table 1 for abbreviations and treatment descriptions

For the total biomass of fouling communities, both factors ('control group' and 'top side/bottom side') were statistically significant. The interaction of these factors was also significant (Table 2A). This latter result can be explained by the observation that, although the fouling biomass on the top sides of the CI and CEx plates was substantially lower than on the bottom sides (p < 0.001 and p = 0.001, respectively), there were no significant differences in biomass between the sides of the CA plates (p = 0.69) (Fig. 5).

Thus, in spite of some variations in species richness and biomass relating with differences in exposure time and seasonality, the chosen biological model satisfies a requirement: algae dominate and preferentially develop on the upper well-lit surfaces of substrates, whereas animals are most abundant and dominate shaded, down-facing surfaces.

## Testing the ecological niche separation between animals and algae

Comparison of the fouling status of the CEx and ExR plates at the end of the experiment showed that plate inversion resulted in a significant reduction in the total fouling biomass (Fig. 5, Table 3A). The fouling biomass was lower on the top sides of ExR plates than on the top sides of CEx plates (p = 0.025). The same pattern was also observed for the bottom sides of the ExR and CEx plates (p = 0.04). The reduction can be explained by the transformation of fouling communities on the ExR plates. However, the total fouling biomass on the bottom sides was higher than that on the top sides for both the CEx (p = 0.008) and ExR plates (p = 0.004) (Table 3A, Fig. 3).

Table 3. Results of split-plot ANOVA on factors affecting fouling community on control (CEx) and reversed (ExR) plates

| Comparison | df | SS | MS | F | p |
|---|---|---|---|---|---|
| **A. Total biomass of fouling organisms (with the exception of mussels)** | | | | | |
| Control/Reversed | 1 | 227.252 | 227.252 | 12.075 | 0.002 |
| Top side/bottom side | 1 | 322.2 | 322.2 | 19.654 | <0.001 |
| Block | 9 | 268.97 | 29.886 | 1.973 | 0.153 |
| Biomass of *Mytilus edulis* | 1 | 27.027 | 27.027 | 1.436 | 0.247 |
| Control/Reversed × Top side/ bottom side | 1 | 5.969 | 5.969 | 0.317 | 0.581 |
| Top side/bottom side × Block | 9 | 135.048 | 15.005 | 0.797 | 0.624 |
| Residual | 17 | 319.95 | 18.821 | | |
| **B. Algae species richness (no. species plate$^{-1}$)** | | | | | |
| Control/Reversed | 1 | 0.472 | 0.472 | 0.132 | 0.721 |
| Top side/bottom side | 1 | 241.154 | 241.154 | 36.352 | <0.001 |
| Block | 9 | 144.955 | 16.106 | 1.963 | 0.161 |
| Biomass of *Mytilus edulis* | 1 | 28.936 | 28.936 | 8..096 | 0.011 |
| Control/Reversed × Top side/ bottom side | 1 | 96.508 | 96.508 | 27.001 | <0.001 |
| Top side/bottom side × Block | 9 | 75.461 | 8.385 | 2.346 | 0.062 |
| Residual | 17 | 60.764 | 3.574 | | |
| **C. Animal species richness (no. species plate$^{-1}$)** | | | | | |
| Control/Reversed | 1 | 1.458 | 1.458 | 0.894 | 0.358 |
| Top side/bottom side | 1 | 171.692 | 171.692 | 105.927 | <0.001 |
| Block | 9 | 13.577 | 1.509 | 0.934 | 0.537 |
| Biomass of *Mytilus edulis* | 1 | 0.514 | 0.514 | 0.315 | 0.582 |
| Control/Reversed × Top side/ bottom side | 1 | 14.467 | 14.467 | 8.867 | 0.008 |
| Top side/bottom side × Block | 9 | 14.533 | 1.615 | 0.99 | 0.482 |
| Residual | 27 | 27.736 | 1.632 | | |
| **D. Total biomass of sessile and sedentary animals (with the exception of mussels)** | | | | | |
| Control/Reversed | 1 | 49.372 | 49.372 | 3.553 | 0.077 |
| Top side/bottom side | 1 | 766.206 | 766.206 | 54.871 | <0.001 |
| Block | 9 | 164.028 | 18.225 | 1.302 | 0.344 |
| Biomass of *Mytilus edulis* | 1 | 0.354 | 0.354 | 0.025 | 0.875 |
| Control/Reversed × Top side/ bottom side | 1 | 52.588 | 52.588 | 3.785 | 0.068 |
| Top side/bottom side × Block | 9 | 126.033 | 14.004 | 1.008 | 0.471 |
| Residual | 27 | 236.206 | 13.895 | | |
| **E. Total biomass of algae** | | | | | |
| Control/Reversed | 1 | 64.776 | 64.766 | 14.243 | 0.002 |
| Top side/bottom side | 1 | 94.683 | 94.683 | 20.568 | <0.001 |
| Block | 9 | 41.932 | 4.659 | 1.006 | 0.493 |
| Biomass of *Mytilus edulis* | 1 | 33.568 | 33.568 | 7.381 | 0.015 |
| Control/Reversed × Top side/ bottom side | 1 | 93.989 | 93.989 | 20.666 | <0.001 |
| Top side/bottom side × Block | 9 | 41.718 | 4.635 | 1.019 | 0.463 |
| Residual | 27 | 77.315 | 4.548 | | |
| **F. Biomass of *Mytilus edulis*** | | | | | |
| Control/Reversed | 1 | 71.548 | 71.548 | 1.118 | 0.304 |
| Top side/bottom side | 1 | 756.874 | 756.874 | 6.937 | 0.027 |
| Block | 9 | 4179.246 | 464.361 | 4.256 | 0.021 |
| Control/Reversed × Top side/ bottom side | 1 | 136.423 | 136.423 | 2.131 | 0.162 |
| Top side/bottom side × Block | 9 | 981.973 | 109.108 | 1.705 | 0.16 |
| Residual | 18 | 1152.101 | 64.006 | | |

Plate inversion had no significant influence on the number of algal species per sample, whereas the plate orientation at the end of the experiment had a significant effect on this index (Table 3B). The relative species richness for algal species on the top sides was higher than on the bottom sides of both ExR (p < 0.001) and CEx (p < 0.001) plates (Fig. 3A). The interactions between the factors of plate orientation ('top side/bottom side') and the presence of inversion ('control/inverted') were statistically significant (Table 3B). These results were expected because the top sides of the CEx and ExR plates did not statistically differ in the number of algal species per plate (p = 0.06), but the bottom sides of the ExR plates had a higher relative number of algal species than those of the CEx plates (p = 0.03). At the same time, the differences in relative number of algal species between the top (13.2 ± 1.18) and the bottom (8.2 ± 1.09) sides of the ExR plates were significantly smaller (p < 0.001) than between the top (15.7 ± 1.13) and the bottom (5.3 ± 0.47) sides of the CEx plates.

Plate inversion did not have any significant effect on the relative species richness of animals, but plate orientation was a significant factor (Table 3D). The number of animal species on the bottom sides of the plates was higher than on the upper sides of both ExR (p < 0.001) and CEx plates (p < 0.001) (Fig. 3B). This situation was opposite to that observed for the relative species richness of algae. The interaction between the factors 'top side/bottom side' and 'control/inverted' (Table 3D) was caused by the lack of differences in relative animal species richness between the bottom sides of the CEx and ExR

plates (p = 0.13) and the presences of these differences between the top sides of the same plates (p = 0.004). The difference in the relative animal species richness between the bottom (9.9 ± 0.46) and the top (6.1 ± 0.35) sides of the ExR plates was significantly smaller (p < 0.001) than between the bottom (10.8 ± 0.53) and the top (4.3 ± 0.33) sides of the CEx plates.

ANOVA did not reveal any significant effect of plate inversion on the biomass of sedentary and sessile animals (Table 3D). However, while the top sides of the CEx and ExR plates did not differ in this parameter (p = 0.99), the animal biomass on the bottom sides of the ExR plates was significantly lower than that on the bottom sides of the CEx plates (p = 0.012) (Fig. 4B). Animal biomass on the bottom sides of the inverted plates was only 68% of that on the bottom sides of the CEx plates. The biomass of sedentary animals for both ExR and CEx plates was higher on the bottom than on the top sides (p < 0.001) (Table 3D). The difference in animal biomass between the bottom (439 ± 57 g m$^{-2}$) and the top (39 ± 6.3 g  m$^{-2}$) sides of the ExR plates was significantly smaller (p < 0.001) compared to the CEx plates (650 ± 93 and 38 ± 9.2 g m$^{-2}$, respectively).

The influence of the plate inversion and orientation on the algal biomass as well as interaction of these factors was significant (Table 3E). The algal biomasses on the bottom sides of the CEx plates and ExR plates showed no significant differences (p = 0.63), but the algal biomass was significantly higher on the top sides of the CEx plates than on the top sides of the ExR plates (p < 0.001) (Fig. 4B). The algal biomass on the top sides of the ExR plates was only 42% of that on the top sides of the CEx plates. Algae were more abundant on the top sides of both ExR and CEx plates (p = 0.004 and p < 0.001, respectively). The difference in algal biomass between the top (151 ± 37 g m$^{-2}$) and the bottom (25 ± 8.7 g m$^{-2}$) sides of the ExR plates was smaller (p < 0.001) than between those of the CEx plates—364 ± 47 and 6 ± 2.6 g m$^{-2}$, respectively.

Both the ExR and CEx plates showed algal dominance over animals on the top sides (p < 0.001) and the dominance of sedentary and sessile animals over algae on the bottom sides (p < 0.001) (Fig. 4B).

Thus, the hypothesis about the resistance of animals to algal expansion under well-lit conditions, which was designed to demonstrate niche separation between animals and algae, was not confirmed. Results of plate inversion show that the predominance of algae on illuminated, up-facing surfaces and animals on shaded, down-facing surfaces can be determined by competitive exclusion by algae.

## Testing the high resistance and the competitive superiority of algae over animals

### The dynamics of biomasses

Animal biomass was 0.41 ± 0.191 g m$^{-2}$ on the top sides of the CI plates, but was much (p = 0.005) higher at the end of the experiment on the bottom (formerly top) sides of the ExR plates (440 ± 57 g m$^{-2}$) Similarly, the algal biomass on the top (formerly bottom) sides of the ExR plates (151 ± 37 g m$^{-2}$) was significantly higher (p = 0.003) than on the bottom sides of the CI plates (0.2 ± 0.14 g m$^{-2}$). Thus, the change in orientation of plates towards conditions that were favorable for either algae or animals had the same result for algae or animals. However, a change towards worse conditions led to different results for algae and animals. Animal biomass on the bottom sides of CI plates before their inversion was 691 ± 77 g m$^{-2}$, and, at the end of the experiment, was significantly (p < 0.001) lower (39 ± 6.3 g m$^{-2}$) on the top (formerly bottom) sides of the ExR plates. At the same time, the algal biomasses on the top sides of the CI plates (23 ± 4.5 g m$^{-2}$) and on the bottom (formerly top) sides of the ExR plates (26 ± 8.7 g m$^{-2}$) showed no significant differences (p = 0.83) (Fig. 4).

### Rate of community transformation on the top- and bottom sides of inverted plates

The results of the PCA for the community data matrix of the ExR and CEx plates showed that the vast majority of animal taxa on the first principal component (PC1) had positive factor loadings. One of the exceptions was the hydroid *O. longissima*. The factor loadings for barnacles were slightly negative. All algal taxa had significant negative factor loadings on this component (Fig. 6). PC1 accounted for 39% of variance. Since algae were predominant on the top sides and animals on the bottom sides, PC1 can be interpreted as an ordination axis between the communities of the top and bottom sides of the plates. The average factor scores for the top sides of the CEx plates were −0.95 ± 0.077, and those for the top sides of the ExR plates were −0.87 ± 0.091. At the same time, the average factor score for the bottom sides of the CEx plates was 1.22 ± 0.145 and for the ExR plates 0.6 ± 0.1. The difference in factor scores between the top sides of the CEx and ExR plates was significantly smaller (p = 0.0015) than between the bottom sides of the CEx and ExR plates. This indicates a faster transformation of the communities on those sides that be-

came up-facing after plate inversion compared to those sides that became down-facing. In other words, if the conditions become favorable, the algocenosis develops faster than zoocenosis. The difference in fouling status between the bottom sides of the CEx plates and the top sides of the ExR plates was larger than between the top sides of the CEx plates and the bottom sides of the ExR plates (p < 0.001). This can be interpreted as evidence of a more substantial degradation of zoocenosis compared to algocenosis under unfavorable conditions.

### Conformity between the control and inverted plates in the structure of algo- and zoocenoses

The cluster analysis demonstrated that the structures of zoocenoses on the equally oriented sides of the CEx and ExR plates are similar, but the structures of the zoocenoses on the opposite sides sharply differ (Fig. 7A). ANOSIM confirmed the differences in structure of animal assemblages between the top and bottom sides of the plates (R = 0.82, p < 0.001). The average similarity of zoocenoses on the top sides was 64.48%. The greatest contribution to this similarity (69.11%) was made by the hydroid *O. longissima*. The average similarity between zoocenoses of the bottom sides was 83.06%, 69.26% of which comprised the ascidian *Molgula citrina*. Both these species combined accounted for 71.89% of the average dissimilarity in the structures of zoocenoses on the opposite sides of the plates, which was 62.81%.

Based on the distribution of the fouling animals on the top and bottom sides of the control and experi-



Fig. 6. Position of algae (○) and animals (●) on principal components I and II for control (CEx) and experimental (ExR) plates. See Table 1 for abbreviations and treatment descriptions
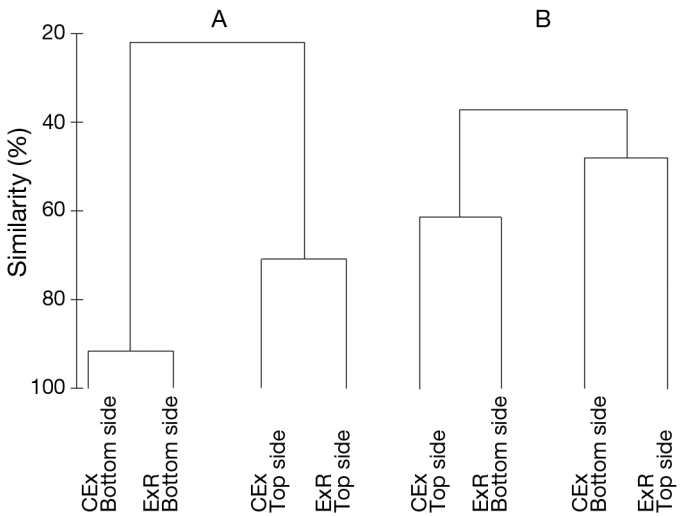


Fig. 7. Results of cluster analysis. (A) Assemblages of animals (zoocenoses); (B) assemblages of algae (algocenoses). See Table 1 for abbreviations and treatment descriptions

mental plates (Fig. 8), all these organisms can be subdivided into the following groups: (1) sessile animals initially settled on the bottom sides and disappearing from the now top sides after inversion (ascidian *M. citrina*, polychaetes of the family Spirorbidae, and bryozoans); (2) sessile animals preferring the bottom sides of the plates which were not eliminated by plate inversion (*Heteranomia* sp. and Cirripedia); (3) the bivalve *Hiatella arctica*, which preferred to live on the bottom sides of the plates before and after plate inversion; most individuals of this bivalve probably migrated to the side that became down-facing after inversion; (4) animals that had no apparent preference for the sides (sedentary polychaete *Neoamphitrite figulus* and the hydroid *O. longissima*); after plate inversion, both species continued to live successfully on the side that was facing downward. The sponge *Halichondria panicea* cannot be assigned with certainty to any of the above groups, because it was found only on the bottom sides of some CEx plates. The most abundant species were *M. citrina* and *O. longissima*. The former accounted for up to 90% of biomass of the zoocenosis on the bottom sides and the latter accounted for 77% of biomass on the top sides; these species were the main determinants of the differences in the zoocenosis structure on the opposite sides of the plates.

Unlike zoocenoses, structures of algocenoses on the equally oriented sides of the CEx and ExR plates were not the same. The algocenoses on the top sides of the CEx plates and on the bottom sides of the ExR plates were clustered in one group, while those on
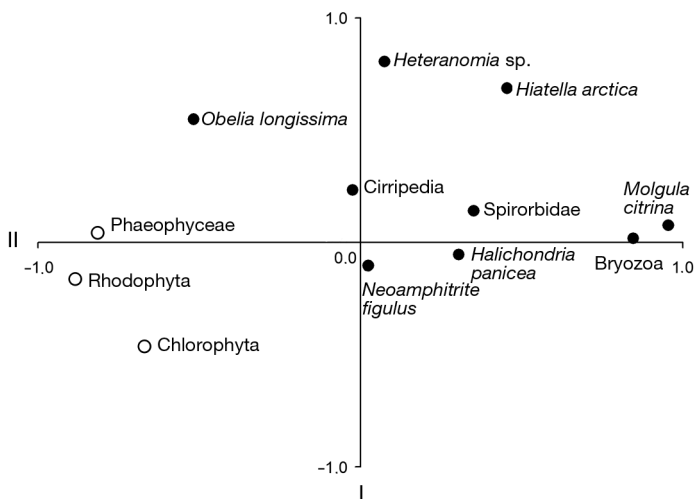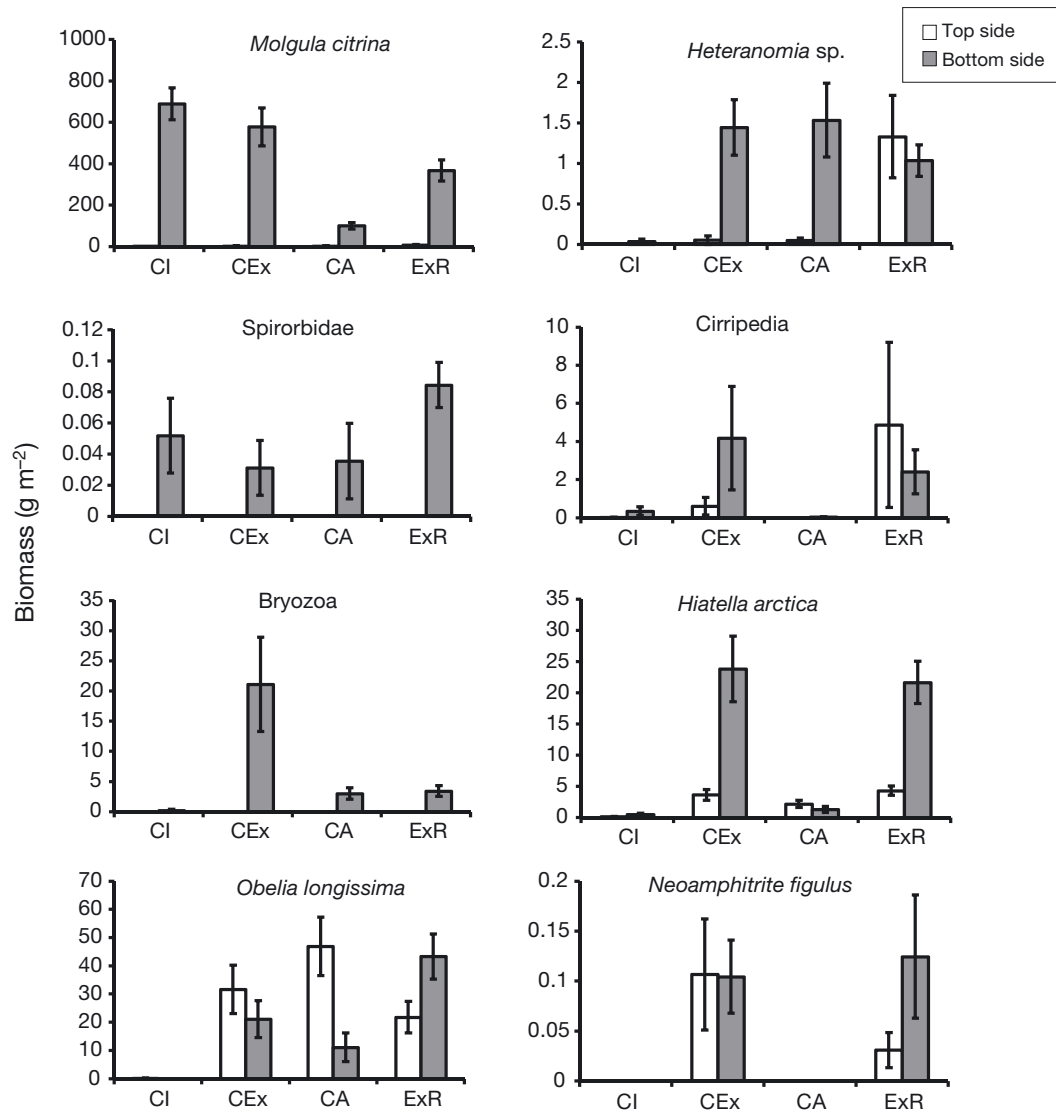
Fig. 8. Biomass (mean ± SE) of some species of animals on top and bottom sides of control and experimental plates. See Table 1 for abbreviations and treatment descriptions

the bottom sides of the CEx plates and on the top sides of the ExR plates formed another group (Fig. 7B). ANOSIM confirmed the differences in the structure of these algal assemblages (R = 0.23, p < 0.001), but the differences between these 2 groups and similarities within each group were minor. The average similarity of algocenoses that developed on the top sides of the CEx plates and on the bottom (formerly top) sides of the ExR plates was 51.86%. The greatest contribution (29.36%) to this similarity was made by the red alga *Polysiphonia fucoides*. The average similarity between algocenoses on the bottom sides of the CEx plates and on the top (former bottom) sides of the ExR plates was 42.49%, 49.47%

of which was contributed by the red alga *P. stricta*. Both these species of the genus *Polysiphonia* accounted for 35.07% of the average dissimilarity between the structures of algocenoses within the 2 groups, which was 59.25%. *P. fucoides* contributed 34 and 29% of biomass to the algocenoses of the top sides of the CEx plates and the bottom sides of the ExR plates, respectively. On the bottom sides of the CEx plates and on the top sides of the ExR plates, *P. stricta* accounted for 19 and 32% of the total algal biomass, respectively. Both species of *Polysiphonia*, which became the dominant forms by the end of the experiment, were low in biomass before plate inversion. The biomass of *P. stricta* was $0.07 ± 0.037$ g m$^{-2}$
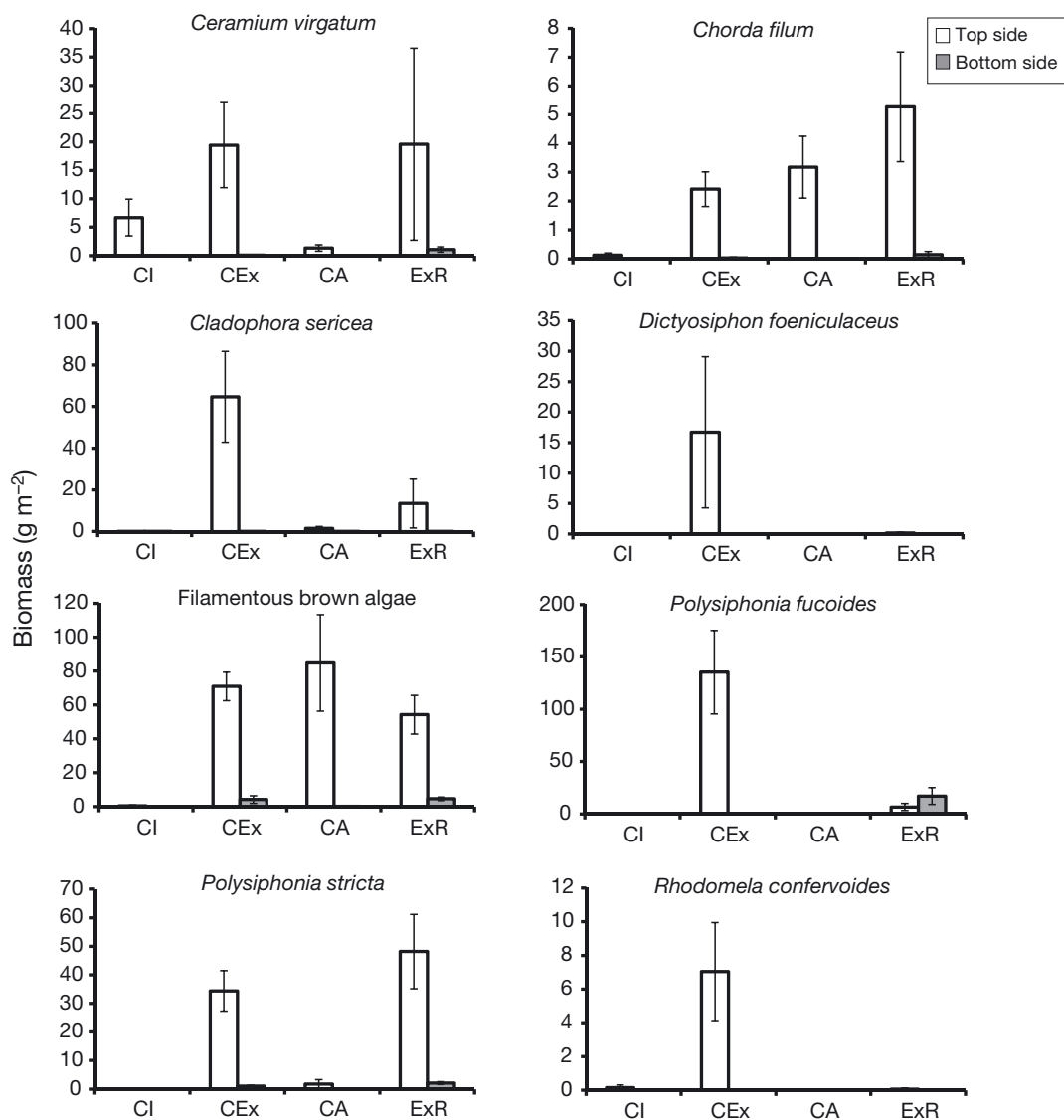
Fig. 9. Biomass (mean ± SE) of some species of algae on top and bottom sides of control and experimental plates. See Table 1 for abbreviations and treatment descriptions

on the top sides, and 0.01 ± 0.007 g m$^{-2}$ on the bottom sides. *P. fucoides* was found on the top side of only one plate (0.01 ± 0.01 g m$^{-2}$).

Although algae had considerably higher biomasses and species diversity on the sunlit top sides of the plates compared to the bottom sides (Figs. 3A, 4A & 9, Table 1), the majority of common algal species were present in considerable biomasses not only on the top but also on the bottom sides of the plates. This was the case for *Ceramium virgatum*, *Chorda filum*, *P. fucoides*, *P. stricta* and filamentous brown algae (*Ectocarpus siliculosus + Haplospora globosa + Pylaiella littoralis + P. varia*) (Fig. 9). The prevalence of *Cladophora sericea*, a common algal species, on

the bottom sides of the plates was high (61%), but its biomass was low (0.001 ± 0.0009 to 0.135 ± 0.058 g m$^{-2}$) (Fig. 9). The reduced light intensity due to plate inversion probably caused a decrease in the growth rates of these algae, but did not lead to their complete disappearance. Only a few of the common algal species, such as the red alga *Rhodomela confervoides*, brown algae *Dictyosiphon foeniculaceus* (Fig. 9) and *Fucus vesiculosus* proved to be unable to exist on the shaded, down-facing surfaces. Also, no microscopic epiphytic brown or red algae were found on the bottom sides, except for some isolated finds of *Hecatonema terminale* and *Rhodochorton purpureum*.
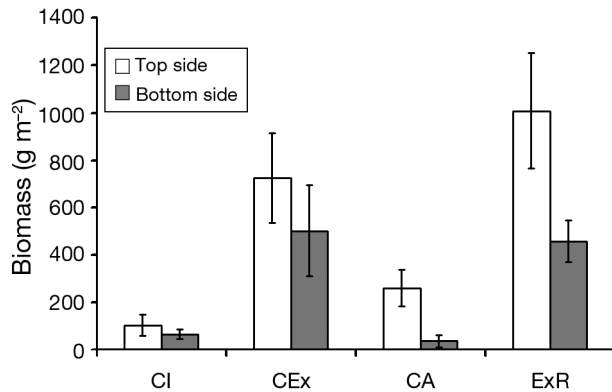
Fig. 10. Biomass of *Mytilus edulis* on top and bottom sides of control and experimental plates. See Table 1 for abbreviations and treatment descriptions

## Effect of mussels on the early fouling communities

At the end of the experiment, the settlement density of mussels on the plates was relatively low and was, on average, $7100 \pm 830$ ind. m$^{-2}$ for both CEx and ExR plates. The biomass of mussels did not have a significant relationship with parameters of fouling communities (Tables 2A–D & 3A,C,D) with the exception of relative algal species richness (Table 3B) and algal biomass (Table 3E) that were calculated for CEx and ExR plates. However the correlation between mussel biomass and these algal indices was not high, ranging from $r = 0.32$ ($p = 0.045$) to $r = 0.48$ ($p = 0.002$). This relationship may be explained by the fact that mussel biomass was generally higher on the top sides than on the bottom sides and the influence of the factor 'top side/bottom side' was significant for both control and experimental plates (Tables 2E & 3F). However, pairwise comparison of mussel biomasses on the top and bottom sides of the control plates did not reveal any significant differences (CI: $p = 0.85$; CEx: $p = 0.17$; CA: $p = 0.16$) but it was found for the ExR plates ($p = 0.003$) (Fig. 8). Regarding other factors, it should be noted that plate inversion had no effect on mussel biomass (Table 3F), but the biomass of *M. edulis* was different in different groups of control plates (Table 2E, Fig. 10), which was, most likely, caused by their different exposure in water. Thus, it can be concluded that the presence of mussels had no significant effect on early fouling organisms and the results of our experiment.

## DISCUSSION

Our experiment confirmed the hypothesis that the fouling assemblages that develop on the up-facing and down-facing surfaces of substrates in the upper water layer of the White Sea are different. The algae were predominant on the top sides of the plates, in terms of both species richness and biomass, while the bottom sides were dominated by animals. These results are in good agreement with the existing view that the nature of an epibenthic community depends on substrate orientation (Hatcher 1998, Baynes 1999, Glasby 1999, 2000, Oshurkov 2000, Glasby & Connell 2001, Terlizzi et al. 2000, Pacheco et al. 2010). In our experiment, the predominance of autotrophic organisms on sunlit surfaces indicated that the key determinant for the composition of the fouling community was not the substrate orientation itself, but rather an associated factor—the intensity of light falling on this substrate. Despite the fact that the sedimentation closely relating with the substrate orientation can influence the development of fouling communities, we did not estimate this effect. As shown by Irving & Connell (2002), the effect of sedimentation is considerably weaker than the effect of light. In Kruglaya Bay, where we held our experiment, the rate of sediment accumulation was 0.3 to 0.5 g m$^{-2}$ d$^{-1}$ at a depth of 20 m (Mityaev et al. 2012, 2015). This value is greatly less than 50 to 350 g m$^{-2}$ d$^{-1}$ that was observed by Irving & Connell (2002). Moreover, our experimental plates were suspended at a depth of 1.5 m, where the velocity of tidal current reached 0.1 to 0.15 m s$^{-1}$ (Babkov et al. 1985). Both the minimal depth and the tidal current were additional factors that could reduce sediment accumulation on control and experimental plates. Based on the above statements, we disregarded the effect of sedimentation in our study.

Although the study was carried out on early fouling communities only, our results also reflected some succession phenomena. For instance, the cyanobacteria and diatoms were present in appreciable quantity only on CI plates, which had the shortest exposure time. The communities dominated by these groups of autotrophs are typical for the initial phases of substrate colonization (Bondarchuk & Kulakowski 1988, Tuchman & Stevenson 1991, Railkin 2004, Fricke et al. 2016). By contrast, the red algae, such as *Polysiphonia fucoides* and *P. stricta*, were abundant only on the CEx and ExR plates, which were exposed in seawater for the longest period. The observation that, of all the control groups, the highest number of species of both animals and algae was recorded on the CEx plates can be explained by a well-known tendency for an increase in species richness with the increasing exposure time of the substrate (Schoener 1974, Chapman 2007).

Plate inversion resulted in restructuring of the fouling communities and established the algal predominance on the previously down-facing surfaces that became up-facing, with animals gaining dominance on the surfaces inverted to the down-facing orientation. In other words, the fouling community responded to the environmental changes and transformed towards the community corresponding to the new environmental conditions. The results of our experiment are not entirely consistent with the results of a similar experiment performed by Irving & Connell (2002) near the shores of Australia. At the end of this experiment, the communities that had developed on the top sides of the inverted plates were still more similar to the communities on the bottom sides than to those on the top sides of the intact plates. This apparent inconsistency, however, is likely due to a longer period of exposure following plate inversion in our experiment. The observed transformation process agrees with the idea that abiotic conditions determine the nature of the epibenthic community (Bertness et al. 2002, Irving & Connell 2002) and that in this case the communities under study cannot be regarded as alternative as asserted by the concept of multiple stable states (Lewontin 1969).

The transformed communities (ExR plates) differed from the corresponding control plates (CEx) in having a lower total biomass and a lower biomass of the predominant group (algae or animals). Moreover, differences in the species number and in the biomass of both algae and animals between the opposite sides of the inverted plates were smaller than those between the opposite sides of the control plates. These characteristics of the transformed communities are likely to have resulted from their initial state before inversion and from a shorter time interval that the transformed communities had for their development compared to the communities on the control plates.

It can thus be concluded that, although it is true that under low light intensity algae become suppressed and animals gain dominance, the assumption that the fouling community formed by animals remains stable when placed under lighting conditions favoring algae proved to be false.

We presumed that an increase in light intensity should not have a detrimental effect on the survival of adult individuals of most animal species, although it could have affected the recruitment of juveniles, because the larvae of some animals prefer to settle on shaded substrates (Thorson 1964, Oshurkov & Oxov 1983, Todd & Turner 1986, Duggins et al. 1990, McKinney & McKinney 2002, Darbyson et al. 2009). The expected result was obtained for Cirripedia and bivalves of the genus *Heteranomia*. In our fouling community, however, these animals were rare, which explains the low significance of the results, especially with regards to the Cirripedia. When the light intensity was increased after plate inversion, many animals (bryozoans, polychaetes of the family Spirorbidae, and *Molgula citrina*) essentially disappeared from the community or, like the bivalve *Hiatella arctica*, reduced their numbers substantially. It should be noted that the members of the family Spirorbidae are known as abundant early colonizers, but they have a low competitive ability (Connell & Keough 1985). The shift in abundance of *H. arctica* can be explained by migration of this bivalve to the side that became down-facing after inversion. This species leads a cryptic lifestyle and prefers sheltered places (Khalaman 2005b).

The most pronounced effect on the structure of zoocenosis was exerted by the disappearance of the dominant species, the ascidian *M. citrina*. The exact cause of this disappearance is unknown. It is possible that the elimination of ascidians resulted from a combined action of several factors. First, it may have been caused by a detrimental effect of illumination. For instance, it is known that the colonial ascidian *Didemnum* sp. grows more intensively on shaded, rather than sunlit, surfaces (Kennelly 1989). The elimination of ascidians could have been influenced by mussels *Mytilus edulis* that settled on the experimental substrates. It has been shown for the ascidians *Styela rustica* that mussels may cluster around these animals and kill the ascidians by covering them with byssus (Khalaman & Komendantov 2007, Khalaman & Lezin 2015). However, we did not find any evidence of this kind of activity of mussels on the plates. The presence of *M. citrina*, unlike that of *S. rustica*, does not induce byssus production in mussels (Khalaman et al. 2009). Moreover, the mussels were rare on the plates and were small in size and so had hardly a decisive influence on the ascidians. The most likely cause of elimination of *M. citrina* was algal mat formed by a tangle of red and filamentous brown algae, which could have prevented normal functioning of the ascidians (Young & Chia 1984); other contributors may have been the sediment and microscopic silt, which could have accumulated as a consequence of surface orientation and because of the presence of algae that limited the scouring of the sediment (Kennelly 1989). Algae can also have a negative influence on animals through abrasion (Dayton 1971) and allelopathy (Rasher et al. 2011, Amsler 2012, Slattery & Lesser 2014).

The hydroid *Obelia longissima* was the only animal that was abundant on the top sides of the plates. Based on our results, we cannot make a firm conclusion as to whether this species prefers the top or bottom surfaces. It is, however, known that the hydroids of the genus *Obelia* can settle on the surfaces of any orientation and compete successfully with other fouling organisms (Oshurkov & Oxov 1983, Brault & Bourget 1985, Oshurkov 2000, Railkin et al. 2012). As an erect form, *O. longissima* rises considerably above the substrate and must experience a less negative effect from algae than encrusting or barrel-shaped animals. It is probably the similarity in ecological forms and body size of *O. longissima* and the algae predominant in our experiment that allowed this hydroid to compete successfully with algae for substrate.

Interestingly, the biomass of animals that settled on the bottom sides decreased considerably after plate inversion, while the biomass of algae that colonized the top sides did not change to any noticeable degree. As a consequence, after lighting conditions improved, the zoocenosis degraded, but no degradation of algocenosis was observed following the reduction in light intensity, although algal growth declined. At the same time, an increase in light intensity led to the growth of algae and shading resulted in animal growth. The results of the PCA demonstrated that the transformation rates of the fouling community, i.e. the establishment of the algal dominance on the surfaces that became up-facing after inversion, were higher than the transformation rates on the bottom sides leading to the animal dominance. This difference can be explained by the ability of algae to withstand shading and by elimination of many animals from the top sides of the inverted plates.

Plate inversion led to significant changes in the structure of zoocenoses. Among the animals, the ascidian *M. citrina* was predominant on the bottom sides of both control and inverted plates, while the top sides were dominated by *O. longissima*. In contrast with zoocenoses, the structures of the previously formed algocenoses remained essentially unchanged after plate inversion. Algal growth was either impeded or stimulated without replacement of dominant forms, depending on changes in light intensity. These results confirm the existing opinion that algae are more resistant to stress than animals (Lenz et al. 2004).

The initial structure of the algocenosis is most likely determined by the level of light intensity, due to the existence of both photophilic and shade-tolerant algal species (Clark et al. 2004, Hanelt & Figueroa 2012). Based on the results of the experiment, *Polysiphonia fucoides*, which predominated in the algocenosis of the top sides of the control plates, can be defined as photophilic, while *P. stricta*, the most abundant species on the bottom sides of the same plates, is shade-tolerant. Concurrently, the macrophytes living on the bottom surfaces were represented not only by the common representatives of the deep part of the photic zone adapted to low light conditions, such as *Coccotylus truncatus*, species of the genus *Polysiphonia*, *Derbesia marina*, and *Spongamorpha aeruginosa*, but also by the typical members of a well-lit littoral zone: *Cladophora sericeae*, *Chaetomorpha tortuosa*, *Rhizoclonium riparium*, and *Ceramium virgatum* (Smirnova & Mikhailova 2013). It is possible that plate colonization by algae was determined not only by the illumination of the surface, but also by other unknown factors or was at least partially stochastic in nature.

In our analysis of the experiment, we took into account only those animals that belonged to the early colonizers. These are mostly relatively fast-growing and short-living species. The only notable exception was the long-living and slow-growing *Hiatella arctica* (Sejr et al. 2002). This mollusc, however, leads a cryptic lifestyle and is not a dominant competitor in fouling communities of the White Sea (Khalaman 2005b). Early colonizers, both animals and algae, facilitate the settlement of mussel larvae (Chalmer 1982). As they continue growing, the mussels occupy the available space and most colonizers, except *H. arctica* and *Neoamphitrite figulus*, die out under their cover (Oshurkov 1985, Khalaman 2001, 2005a, 2013). Some species of early colonizers can eventually colonize this place again, but then usually as mussel epibionts (Khalaman 1989, Mikhailova et al. 2014). It should be noted that *N. figulus* is more likely to be a member of associated fauna rather than foundation fouling organisms. Judging from the observations made in the laboratory, this worm can quickly restore and build its mud tube adapting it to the changing environment (V. V. Khalaman unpubl. data).

In our opinion, the presence of mussels, whose settlement was impossible to prevent, could not have affected the results of our experiment to any significant extent. First, the biomass and settlement density of mussels were insignificant throughout the experiment and they did not form any continuous cover or even clusters. Second, there were no notable differences in mussel biomass between the top and bottom sides of the plates and between the control and inverted plates. This gave us enough

reason to consider the effect of mussels to be equal in all parts of the experiment. Third, the positive correlation between mussel biomass, on the one hand, and species diversity and algal biomass, on the other hand, was not strong. It can probably be explained by preferential mussel settlement on the filamentous substrate (Seed 1969, Railkin & Zubakha 2000). If the settled mussels did have a stronger negative effect on algae than on animals, it would have resulted in underestimation of growth rates of algocenosis. However, the adjustment for this effect does not challenge our conclusions, but rather makes them more reliable.

To conclude, in the White Sea, algae predominate in the early fouling communities developing on the upper sunlit surfaces, while animals are dominant on the shaded down-facing substrates. If the substrate orientation is reversed and, as a consequence, light intensity is changed, the fouling community transforms into the community that conforms to the new lighting conditions. An increased light intensity results in the degradation of zoocenosis and changes its structure, whereas shading does not lead to the degradation of algocenosis or any significant change in its structure, but causes stunting of algal growth. When the conditions become favorable for algae, the transformation of the community towards algal dominance proceeds faster than the transformation towards animal dominance under the opposite conditions. Our results indicate that algocenoses are in general more stable and have more competitive ability than zoocenoses. The animal predominance on the shaded surfaces is likely to be a consequence of 2 processes: (1) competitive displacement of most animals from the sunlit surfaces by algae; (2) niche diversification between algae and animals. Some animals such as Cirripedia and the bivalve *Heteranomia* sp. were much more abundant on the bottom sides of the control plates than on the top sides in spite of their high resistance to algae. Plate inversion and subsequent algal development on the top side of the ExR plates did not eliminate the mentioned animals. These facts may be evidence of preferential colonization of the bottom surfaces of the substrates by these species. However these animals had no noticeable influence on the overall low resistance of zoocenoses against algae in our experiment. It is likely that those animals which are less resistant to algae appear to prefer colonization of the bottom side of substrate. However, the results of our experiment do not allow us to unequivocally state that. This can only be evaluated by means of experiments with larvae of these animals.

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