



Diversity and structure of epibenthic communities of the red algae zone in the White Sea

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Abstract

At high latitudes, the marine transitional zone between the highly productive kelp communities and the devoid of vegetation deep-waters is occupied mainly by number of red algae species, both encrusting and cespitose, which associate with rich and diverse fauna. However, zoologists and botanists never scrutinized these communities in equal manner up to present. We investigated the transition red algae zone in the White Sea in summer 2016 and 2017 using scuba equipment. The photic depth is limited to 18–23 m at different locations. Sessile species prevail among 315 epibenthic organisms in species number (~80%) and biomass (~90%). Communities of the red algae zone are rich in species (from 54 to 177). The most distinct differences were observed between the communities of Kandalaksha and Onega Bays. Vertical heterogeneity of the red algae zone was revealed; at most locations, Rhodophyta predominate in the upper subzone and Cirripedia predominate in the lower parts of the red algae zone. At the investigated depths, shallow-water and deep-water sets of species were defined. Interspecific spatial interactions between sessile organisms are revealed: $72.2 \pm 3.5\%$ of them were recorded as epibionts, and $29.1 \pm 2.5\%$ were registered as basibionts. These interactions provide evidence of the increase of species diversity: $32.7 \pm 6.8\%$ of sessile taxa were recorded exclusively as epibionts. Algae *Phycodrys rubens*, *Odonthalia dentata*, and *Coccotylus truncatus*, ascidian *Styela rustica*, barnacles *Balanus crenatus*, *Verruca stroemia*, and polychaete *Pista maculata* are foundation species, each supporting multi-level suites (up to four levels) of dependent species.

Keywords Hard bottom · Red algae · Biodiversity · Epibiosis · White Sea

Introduction

Arctic seas are increasingly studied lately. Since the end of the 1980s, studies of the Arctic seas (Greenland, Barents, Kara, Laptev, Bering, Chukchi and Beaufort Seas, and Baffin

Bay) have been carried out as part of a number of international projects related to global climate change (Piepenburg 2005). These researches were mainly interested in either off-shore shelf and deep-sea environments (Piepenburg and Schmid 1996a, b, 1997; Piepenburg et al. 2001; Włodarska-Kowalczyk and Pearson 2004; Kędra et al. 2013), or intertidal and kelp communities (Dunton et al. 1982; Mikhaylova 2000, 2012; Bulleri et al. 2012; Bird et al. 2013; Naumov 2013; Scrosati 2017). At the same time up to the present, the lower part of the photic zone of Arctic seas occupied mainly by diverse species of red algae was not well scrutinized. There is only fragmentary information about the flora and fauna of these depths (Derjugin 1928; Blinova 1962, 1964, 1969; Vozzhinskaya 1967; Golikov et al. 1982, 1985a, b; Naumov 2001, 2017; Yakovis et al. 2008; Uryupova et al. 2012; Wiencke and Amsler 2012; Voronkov et al. 2013; Kent et al. 2017; Mikhaylova et al. 2017). Meanwhile, it was shown that the coralline red algae play an important

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role as support for rich epibenthic communities and nursery grounds (Jørgensbye and Halfar 2017).

Additionally, joint studies of flora and fauna were more often carried out in experimental works and focused on the succession and ecological interactions (competition, grazing, facilitation, and trophic cascades) between the most important representatives (Schultze et al. 1990; Oshurkov and Ivanjushina 1993; Christie et al. 1998; Jørgensen and Christie 2003; Waage-Nielsen et al. 2003; Norderhaug 2004; Carlsen et al. 2007; Yakovis et al. 2008; Nikishina et al. 2014; Khalaman et al. 2016; Schaal et al. 2016; Scrosati 2017). Unfortunately, only a few studies of undisturbed natural marine benthic communities have taken into account animals and seaweeds in an equal manner and with sufficient taxonomic resolution (Myagkov 1974; Naumov et al. 2017; Bertolini 2018). Therefore, for both zoologists and botanists, the transitional zone between the highly productive kelp communities and the devoid of vegetation deep-water zone is still *terra incognita*.

The goal of our work is to describe the species diversity, structure of epibenthic communities, and spatial relationships between the macrobenthic organisms within the red algae zone in the White Sea. Previous studies of the White Sea showed a significant differentiation of abiotic conditions in its different parts, which causes contrasts in overall

communities' structure of the White Sea bays as well as distributions of species (Golikov et al. 1985a, b; Naumov et al. 2003). Thus, we also expect to encounter interregional heterogeneity within the surveyed red algae zone.

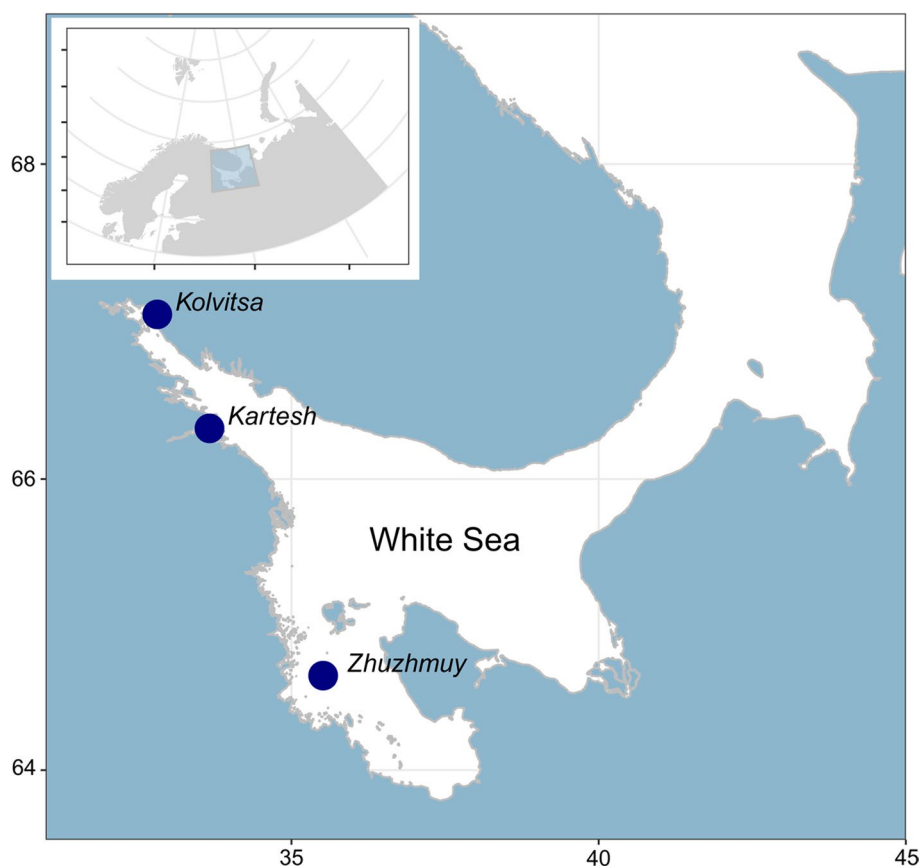
Material and methods

Study areas and sampling

The study was conducted in July 2016 and 2017 at the White Sea Biological Station “Kartesh” of the Zoological Institute of the Russian Academy of Sciences. Two of the study areas are located in Kandalaksha Bay: Kolvitsa Inlet (2016), 67°04' N, 32°49' E, and Kartesh Cape in Chupa Inlet (2016–2017), 66°20' N, 33°40' E. A third study area is located in Onega Bay: specifically, Bol'shoy Zhuzhmuy Island (2017), 64°40' N, 35°31' E. The study areas are hereinafter referred to as Kolvitsa, Kartesh, and Zhuzhmuy, respectively (Fig. 1).

Temperature, salinity, and turbidity were measured by MIDAS CTD+ oceanographic probe (Valeport Ltd., UK) and Cyclops-6 multi-sensor platform (Turner Designs, USA); water transparency was measured by Secchi disk. Divers using photo and video cameras determined the

Fig. 1 Map of the study areas in the White Sea



boundaries of the surveyed zone visually. The higher boundary of the red algae zone was considered at the depth where the kelp canopy disappeared and cespitose red algae were predominant; and the lower boundary was considered at the depth where algae were no longer visible. Sampling stations were arranged in the range from 6 to 18 m depth with an interval of 1–3 m and with 3–4 replicates. The sampling area is sufficient and the most important for a reliable quantitative assessment of epibenthos (macrophytobenthos and epifauna), unlike the significance of the sample volume for infauna (Raz-Guzman and Grizzle 2001). The epibenthic samples were collected by scuba divers using mostly diver-operated grab (0.05 m²) equipped with a net bag with mesh size 0.5 mm (Gruzov and Pushkin 1967). At the sites with rocky ground (or stones and boulders more than 15 cm in diameter), all epibenthic organisms were collected either by cutting within a frame (0.04 m²) from boulders (rock) or by picking up small stones (15–20 cm in diameter) including all overgrown epibenthos with each stone's surface area being subsequently measured (see below). To avoid the escape of vagile fauna, each sample (stone or benthos cut within a frame) was put in a 0.5-mm mesh bag. In total, 36 samples were collected: 8 and 10 samples from Kolvitsa and Zhuzh-muy, 18 samples from Kartesh (6 of them were collected in 2017 only from 13 m depth).

Processing

In the case of quantitative sampling without grab or frame (when a stone was collected as a sample), we estimated areas of stone that could be the substrate to have grown over by wrapping it tightly in thin aluminum foil. Extra foil, including that from folds, was removed. The rest was weighed accurately to 1 mg; the surface area was estimated using a previously derived relationship between the foil's area and weight, which obtained by weighing a series of pieces of aluminum foil with known surface areas (Marsh 1970).

Specimens were squeezed slightly on a dry paper towel to remove extra water and were wet weighed to the nearest 1 mg using spring (BT-500) and electronic balance (Adventure Pro RV313). Subsequently, the species biomass from different ways collected samples was recalculated per 1 m². The percentage cover of encrusting epibenthic organisms was evaluated visually.

All algae and macrofauna were identified to the lowest possible taxonomic level using light microscope (Levenhuk D670T, magnification $\times 100$ –400) and stereoscopic microscopes (MBS 1, 9, 10, magnification $\times 4.8$ –56). All taxa names and their classifications were accepted according to the works of Botanical and Zoological Institutes RAS experts and verified by reference to World Register of Marine Species (WoRMS Editorial Board 2018) and Algae-Base (Guiry and Guiry 2018).

To describe the direct spatial interspecific interaction between epibionts and basibionts, we recorded substrates occupied by every species for each sample. For reporting the structure of multi-level epibiosis, all previous substrates were also recorded. We defined several categories of basibionts and epibionts. The basibiont was considered as *the principal basibiont*, if more than 20 species of its epibionts at a certain site were recorded. The epibiont was considered as *the principal epibiont*, if it was recorded in the site with a frequency of occurrence greater than 50%, if it was recorded on the stone with a frequency of occurrence less than 50%, and if it was recorded on the living substrate with a frequency of occurrence greater than 50%. The basibiont was considered as *the preferable basibiont*, when certain facultative epibiont was recorded on this host with a frequency of occurrence greater than 50%. The epibiont was considered as *the prevalent epibiont*, if it was recorded on the separate host with frequency of occurrence more than 50%. *The foundation species* is the basibiont forming multilevel epibiosis with a biomass more than 10% from total epibiotic biomass at the site.

Data preparation and statistical analysis

Simpson's diversity index (Magurran 1988) and evenness index of oligomixness (Naumov 1991, 2013) were used to describe community structure and diversity. Frequency of occurrence of epibionts and basibionts at each site was calculated as the percentage of samples in which a species was found in the total number of samples. Biological traits (habitat and mobility) of the species were accessed via a "Marine benthos" database elaborated by several of the authors of this paper (Zarodov et al. 2017). Species lists from samples of each site were combined, and then, the resulting lists were compared using Sørensen index (Magurran 1988).

To compare the community composition and structure, we prepared two data matrices for qualitative (presence–absence) and quantitative sample' description where columns were species and rows were samples. In the quantitative data matrix, we used biomass (g m⁻²) as a dependent variable. However, the biomass of some species was below measurements accuracy. Hence, we added a "dummy" biomass of 0.0001 g to such species to perform the necessary calculations. In multivariate analyzes to reduce matrix heterogeneity, all raw biomass values were log-transformed and Wisconsin double standardization was performed (Minchin 1987; Anderson et al. 2006). The dissimilarity between samples was measured using Czekanowski index, recently often referred as Bray–Curtis index (Naumov 2013), for quantitative matrix and Sørensen index for the quality one. After that non-metric multidimensional scaling (MDS) was performed on two prepared matrices (see above). An optimal solution was reached after 999 random permutations using

the metaMDS function implemented in the vegan R-package (Oksanen et al. 2017).

We performed permutational multivariate analysis of variance (PERMANOVA) to test the impact of site and depth on community structure, using the adonis function implemented in the vegan R-package (Oksanen et al. 2017). Partitioning of dissimilarity matrix between samples measured by scaled species biomass or frequency of occurrence was done with the surveyed Site, Depth and interaction between the predictors.

To obtain the contribution of species to interregional differences, similarity percentage (SIMPER) analysis (Clarke 1993) was performed using the eponymous function in the vegan R-package (Oksanen et al. 2017). The method does not support the presence–absence matrix, so species with unknown biomass (encrusting organisms) were excluded from this analysis.

The contribution of species to depth pattern was obtained by redundancy analysis (RDA), with eponymous function in the vegan R-package (Oksanen et al. 2017); all dissimilarities were constrained to predictor Depth nested in Site. We then used 5% from the head and 5% from the tail of the ranged RDA species scores to select “shallow” and “deep” ones correspondingly.

To reveal the communities at the surveyed red algae zone at each site, we performed cluster analysis by hclust function (R Core Team 2018), and the agglomeration method was average linkage. Then, each site-restricted biomass data subset was used to cluster samples from different depths. We used various methods of agglomeration (average and complete linkages) with Czekanowski similarities to adjust clear depth clusters at different sites. For cluster analysis, we used all data except dataset from 2017 at Kartesh.

Calculations were made by using the R software environment for statistical computing and graphics (R Core Team 2018) with RStudio v. 1.0.136, and Microsoft Excel 2010.

Throughout the text, standard error for all mean values is given.

Results

Abiotic conditions

Detailed measurements of seawater column characteristics were taken at Kolvitsa and at Kartesh (Table 1). Storm conditions did not allow obtaining similar data at Zhuzhmuy, where temperature and salinity were measured only at the depth of 10 m and on the water surface (Table 1). Waters of the shallow Onega Bay are not stratified by temperature and salinity due to intensive mixing by tidal and wind currents (Kravets and Polupanov 1991). The usual summer water temperature in the bay is circa 9 °C, and salinity is about 27 psu (Babkov 1998; Berger and Naumov 2001).

Sediments in the surveyed depth range are different at each of the studied areas. At Kolvitsa, the sea bottom is represented by silty mud with rare boulders; at Kartesh it is mainly rocky cliff and sand along with small stones (10–20 cm in diameter), and rare boulders at Zhuzhmuy. The angles of the bottom slope are 2°, 30°, and 1° at Kolvitsa, Kartesh, and Zhuzhmuy, respectively.

General description of the red algae zone

At the studied sites, erected algae occur up to the depth of 15 m, with encrusting calcareous red algae spread deeper down to the lowest boundary of the phytal zone. In total, 315 taxa were found. Algae in general and bryozoans were characterized by greatest number of species, $32.4 \pm 2.3\%$ and $26.5 \pm 1.0\%$, respectively. A list of all encountered species and higher order taxa can be reached at Online Resource 1.

Table 1 Hydrological characteristics of sea-water column at surveyed areas

Sites	Kolvitsa	Kartesh	Zhuzhmuy
Depth range of the red algae zone (m)	7–18	7–23	7–18
Date of hydrological sampling	July 16–21, 2016	July 23–26, 2016	July 23–25, 2017
Surface temperature (°C)	16.6	18	10
Depth range of thermocline (m)	10–22	10–17	No thermocline
Depth of maximum temperature gradient (m)	12	13	No thermocline
Temperature at surveyed range (°C)	14–4	15–6	9
Surface salinity (psu)	18	24	26
Depth range of halocline (m)	10–15	5–20	No thermocline
Depth of maximum salinity gradient (m)	12	15	No thermocline
Salinity at surveyed range (psu)	21–24	25–26	26
Turbidity (FTU, formazin turbidity units)	11–13	10–11	–
Water transparency measured by Secchi disk (m)	–	–	4

Dashes are absence of the data

Hereafter we give brief descriptions of the peculiarities of the assemblage composition and structure at each site.

At Kolvitsa the surveyed red algae zone thrives from 7 to 17–18 m depth. In total, 153 species were found here. Among these, 32 occurred in more than 50% of the samples. Average total biomass was $282.3 \pm 57.1 \text{ g m}^{-2}$. Three algal species, which contributed to 53% of the total biomass here, were red algae: *Coccotylus truncatus* (21%), *Odonthalia dentata* (19.8%), and *Polysiphonia stricta* (11.8%). Simpson's diversity index was 0.34 ± 0.04 , and oligomixness evenness index was 0.57 ± 0.03 . Sessile organisms were represented by 112 taxa. Algae (including calcareous red ones), sponges, and bryozoans represented the encrusting tier (in total 23 species). Bryozoans were the richest in species, and brown alga *Pseudolithoderma extensum* was the most abundant in percentage cover (up to 45%). The main primary substrate holders were algae *O. dentata*, *C. truncatus*, *P. extensum*, and polychaete *Pista maculata*.

At Kartesh, the red algae zone encounters from 7 to 22–23 m depth. In total, 206 species were recorded. Among these, 47 were obtained in more than half of the samples. Average total biomass was $408.4 \pm 122.6 \text{ g m}^{-2}$. Just two animal species contributed to 62% of the total biomass: *Modiolus modiolus* (39.8%) and *Styela rustica* (22.5%). The values of diversity and evenness indices were as follows: Simpson's diversity 0.36 ± 0.05 and oligomixness 0.57 ± 0.04 . Sessile organisms were represented by 165 taxa. Algae (including calcareous red ones), sponges, bryozoans, and colonial ascidians represented the encrusting tier (in total 27 species). Bryozoans were the richest in species. Brown alga *P. extensum* was the most abundant in percentage cover (up to 40%). The percentage cover of colonial ascidian *Didemnum albidum*, sponge *Hymedesmia* sp. and calcareous red algae *Clathromorphum compactum*, *Lithothamnion glaciale*, *Leptophytum laeve* reached 10% for each. The main primary substrate holders were ascidian *S. rustica* and bivalve *Hiatella arctica* in the shallow part and algae *C. truncatus*, encrusting *P. extensum*, *L. glaciale*, and serpulide *Chitino-poma serrula* in the deeper part.

At Zhuzhmuy, the surveyed zone extends from 7 to 17–18 m depth. In total, 220 species were found at this site. Among these 60 occurred in more than half of the samples. Average total biomass was $1482.4 \pm 278.0 \text{ g m}^{-2}$. Two species contributed to 59.7% of total biomass: barnacle *Balanus crenatus* (46.9%) and red alga *Phycodrys rubens* (12.8%). Simpson's diversity index was 0.53 ± 0.06 , and oligomixness index was 0.71 ± 0.04 . Sessile organisms were represented by 160 taxa. Algae (including calcareous Rhodophyta), sponges, and bryozoans represented the encrusting tier (in total 13 species). Brown algae *P. extensum* was the most abundant in percentage cover (up to 30%). The main primary substrate holders were red algae *P. rubens* and barnacle *Verruca stroemia* in the shallow part and cirripedians *V.*

stroemia and *B. crenatus* followed by bivalve *Heteranomia squamula* in the deeper part.

Interregional differences and depth patterns

Similarity of species composition measured by the Sørensen index between sites was not high (Kolvitsa to Kartesh: 0.61, Kolvitsa to Zhuzhmuy: 0.56, Kartesh to Zhuzhmuy: 0.61). Ninety-six taxa were common for all sites. The richest in species number were algae (33.3%) and bryozoans (28.1%). Among the common species, only 14 were recorded with a frequency of occurrence greater than 50%. They are the most typical representatives of the red algae zone: algae (*C. truncatus*, *P. rubens*, *P. stricta*, and *Battersia arctica*), Bivalvia (*Musculus discors* and *H. arctica*), Polychaeta (*P. maculata*), Bryozoa (*Cribrillina annulata*, *Crisiella producta*, *Esharella ventricosa*, *Hippoporina reticulatopunctata*, and *Lichenopora* sp.), and Porifera (*Leucosolenia complicata* and *Sycon* sp.).

According to PERMANOVA, the observed sites differed significantly in biomass (PERMANOVA, pseudo- $F_2 = 8.43$, $p = 0.001$) and frequency of occurrence (PERMANOVA, pseudo- $F_2 = 7.32$, $p = 0.001$) of encountered species. Similar to these results, depth has a lesser but still significant impact (biomass: PERMANOVA, pseudo- $F_1 = 3.77$, $p = 0.001$; frequency of occurrence: PERMANOVA, pseudo- $F_1 = 3.11$, $p = 0.001$) as well as with interaction of sites and depth (biomass: PERMANOVA, pseudo- $F_2 = 2.71$, $p = 0.001$; frequency of occurrence: PERMANOVA, pseudo- $F_2 = 2.64$, $p = 0.001$). These results are clearly illustrated by MDS analysis (Fig. 2).

According to SIMPER analysis, the overall difference in species biomass between Kolvitsa and Kartesh was 87.5%. Over half (58.5%) of that difference was supported by six species. Among these, red algae *C. truncatus* (12.6%), *O. dentata* (8.6%), *P. stricta* (5.5%), and acorn barnacle *B. crenatus* (5.2%) were more abundant at Kolvitsa while horse mussel *M. modiolus* (16.3%) and the ascidian *S. rustica* (10.3%) predominated at Kartesh. Similar results were obtained comparing Kolvitsa and Zhuzhmuy: the overall difference of 93.9% was supported by five species (73.9%): *B. crenatus* (39%), *P. rubens* (10.4%), *V. stroemia* (10.4%), *O. dentata* (7.4%), and *M. modiolus* (6.7%). All of these were more abundant at Zhuzhmuy. Overall difference in species biomass between Kartesh and Zhuzhmuy was 96.3%. Five species contributed the greater part (76.6%) to that difference: barnacle *B. crenatus* (38.6%), clam *M. modiolus* (12.7%), red alga *P. rubens* (10.2%), the cirripedian *V. stroemia* (9.9%), and red alga *O. dentata* (5.2%). All of these except *M. modiolus* were more abundant at Zhuzhmuy.

According to RDA, depth explains only 12.7% of the overall variance of species biomass at Kolvitsa. The nine most sensitive species, which showed the clearest depth

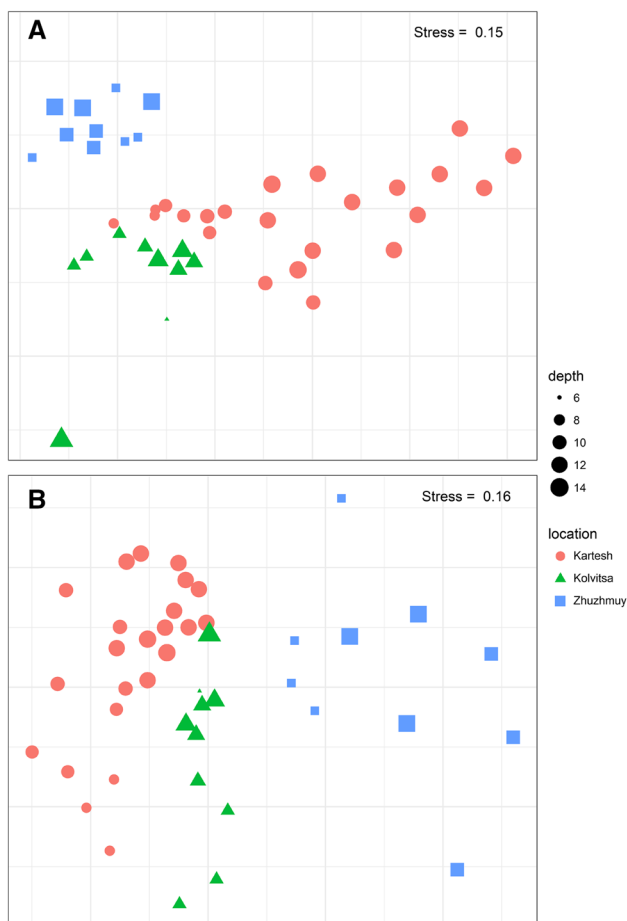


Fig. 2 Non-metric multidimensional scaling (MDS) ordination based on Czekanowski similarities of macrobenthos biomasses (**A**) and frequencies (**B**) in samples. Data were standardized by log-transformation

pattern, were *C. truncatus*, *M. discors*, *O. dentata*, *Ophiopholis aculeata*, *Ophiura robusta*, and *P. stricta*, which predominated at the upper part of the red algae zone, and *B. crenatus*, *Euthora cristata*, and *H. arctica*, which inhabited deeper patches. Thirty-one percent of the overall variance of species biomass at Kartesh was explained by depth. The nine most sensitive species, which showed the clearest depth pattern, were *C. truncatus*, *O. aculeata*, *O. robusta*, *P. rubens*, *P. stricta*, *S. rustica* (“shallow” group), and *Dendrodoa grossularia*, as well as *Tonicella marmorea* and *V. stroemia* (“deep” group). Depth explains 19.6% of the overall variance of species biomass at Zhuzhmuy. The 11 most sensitive species showed the clearest depth pattern. The “shallow” species were *C. truncatus*, *O. dentata*, *P. rubens*, *P. stricta*, *Ptilota gunneri*, and *Ptilota serrata*. The biomass of *B. crenatus*, *Flustra foliacea*, *H. arctica*, *D. grossularia*, and *V. stroemia* increased depthward.

The frequency of occurrence of species at different depths was compared at each site. Depth explains 16.9% of

the overall variance of species occurrence at Kolvitsa. *Callopora lineata*, *Derbesia marina*, *Rhizoclonium riparium*, and *Tegella armifera* were added to “shallow” species at this site, meanwhile *Membranipora membranacea*, *Lichenopora* sp., and *T. marmorea* added to “deep” species. Depth explains 20.6% of the overall variance of species occurrence at Kartesh. *Chaetopterus plumosa*, *Harmothoe imbricata*, *Vertebrata fucoides*, and *Rhodomela confervoides* decreased their occurrence depthward, while *Buccella granulata*, *C. serrula*, *D. albidum*, and *Spirorbis tridentatus* demonstrated the opposite pattern. Depth explains 20.5% of the overall variance of species occurrence at Zhuzhmuy. Species *Caprella linearis*, *Meiodiscus spetsbergensis*, *P. extensum*, and *Arctonula arctica* were found mostly at the higher part of the zone. *Antithamnionella floccosa* and *Styela coriacea* were added to the list of “deep” species at this site.

Community structure

The cluster analysis showed that the samples could be divided into upper, middle, and lower subzones at each site (Fig. 3). We described communities of these subzones on the base combining samples from this analysis results. The main members and characteristics of each community are shown in Table 2.

As a rule, Rhodophyta predominated in the upper part of the red algae zone. The only exception is the ascidian *S. rustica* at Kartesh, so red algae were subdominant here. In the middle subzone, algae were rarely dominant. Into the middle and the lower subzones, *M. modiolus* and Cirripedia are the most abundant in biomass of the epibenthic assemblage (Fig. 4). However, *M. modiolus* was distributed rather sporadic as evidenced by large standard error values (Table 2); therefore, we cannot define this species as dominant. An increase in depth led to a reduction in total biomass, as well as an abundance of seaweeds. The maximum overall biomass was recorded at Zhuzhmuy, and oligomixness index was higher than in other locations.

Sessile organisms predominated among epibenthic species both in species number ($79.8 \pm 1.9\%$) and in overall biomass ($88.8 \pm 3.8\%$). At Kolvitsa and Kartesh, the maximum biomass of sessile organisms (94–96%) was recorded in the upper part of the red algae zone, while in the middle subzone the biomass of vagile fauna comprises 20–30% of the total biomass, largely due to the high abundance of ophiurian species. The biomass of latters reached 16–25% of the total biomass of epibenthos. Despite the large number of species of vagile fauna at Zhuzhmuy (27, 46, and 17 species in the upper, middle, and lower subzones, respectively), their biomass was very low (< 1–2% of total biomass). This is explained by the complete absence of brittle stars here.

Algae (including calcareous red ones), sponges, bryozoans, and sometime colonial ascidian represented the

Table 2 Species composition, species average biomass (g m^{-2}) and characteristics of epibenthic communities into upper, middle, and lower subzones at the surveyed sites

Species/taxa and characteristics of communities	Upper subzone	Middle subzone	Lower subzone
Kolvitsa			
Depth range (m)	7–8	8–10	10–17
Number of samples	2	4	2
<i>Odonthalia dentata</i> (R)	213.3 ± 39.8	33.0 ± 28.3	
<i>Polysiphonia stricta</i> (R)	138.4 ± 125.2	9.9 ± 3.7	
<i>Musculus discors</i> (Bv)	111.2 ± 20.7		9.1 ± 9.1
<i>Ophiura robusta</i> (E)	11.4 ± 8.8	23.0 ± 3.9	16.7 ± 5.3
<i>Coccotylus truncatus</i> (R)	10.0 ± 4.9	120.4 ± 58.2	26.0 ± 6.8
<i>Saccharina latissima</i> (Ph)	9.3 ± 9.3		
<i>Nereis pelagica</i> (P)	8.4 ± 8.3		
<i>Pista maculata</i> (P)	5.6 ± 3.2	8.7 ± 3.7	
<i>Ophiopholis aculeata</i> (E)		9.3 ± 5.4	10.2 ± 2.8
<i>Balanus crenatus</i> (C)		5.5 ± 5.5	100.7 ± 54.0
Porifera indet. (Po)			17.5 ± 15.0
<i>Phycodryas rubens</i> (R)			11.1 ± 7.0
Total biomass	531.0 ± 124.2	232.6 ± 75.9	207.4 ± 79.4
Species richness	89	119	62
Simpson Index	0.36 ± 0.08	0.36 ± 0.07	0.28 ± 0.04
Oligomixness Index	0.59 ± 0.07	0.58 ± 0.06	0.51 ± 0.04
Kartesh			
Depth range (m)	7–10	10–11	11–22
Number of samples	4	6	2
<i>Styela rustica</i> (A)	296.7 ± 193.2		
<i>Phycodryas rubens</i> (R)	56.2 ± 24.9	5.2 ± 2.8	
<i>Polysiphonia stricta</i> (R)	28.5 ± 7.4		
<i>Boltenia echinata</i> (A)	22.8 ± 13.3		20.6 ± 20.0
<i>Coccotylus truncatus</i> (R)	22.2 ± 8.9	13.0 ± 4.5	13.9 ± 3.5
<i>Musculus discors</i> (Bv)	13.3 ± 6.2		
<i>Styela coriacea</i> (A)	13.0 ± 6.3		
<i>Ophiopholis aculeata</i> (E)	10.9 ± 3.8	16.8 ± 3.2	
<i>Molgula</i> sp. (A)	9.4 ± 4.3		
<i>Ophiura robusta</i> (E)	8.5 ± 3.6	10.6 ± 3.2	
<i>Odonthalia dentata</i> (R)	5.3 ± 5.2		
<i>Modiolus modiolus</i> (Bv)		323.1 ± 225.0	
Total biomass	516.3 ± 185.8	407.3 ± 232.8	49.0 ± 29.5
Species richness	124	145	54
Simpson Index	0.34 ± 0.12	0.46 ± 0.12	0.32 ± 0.01
Oligomixness Index	0.55 ± 0.10	0.62 ± 0.11	0.48 ± 0.02
Zhuzhmuy			
Depth range (m)	7–8	8–11	11–17
Number of samples	3	5	2
<i>Phycodryas rubens</i> (R)	584.4 ± 335.7	28.4 ± 9.0	
<i>Modiolus modiolus</i> (Bv)	435.2 ± 433.4		7.6 ± 7.5
<i>Odonthalia dentata</i> (R)	374.4 ± 304.3	36.9 ± 30.6	
<i>Laminaria digitata</i> (Ph)	125.6 ± 125.6		
<i>Balanus crenatus</i> (C)	104.7 ± 66.6	1295.7 ± 350.4	245.9 ± 99.7
<i>Verruca stroemia</i> (C)	64.0 ± 29.7	78.1 ± 36.5	289.5 ± 13.6
<i>Coccotylus truncatus</i> (R)	32.6 ± 24.5		
<i>Buccinum undatum</i> (G)	17.9 ± 17.9		
<i>Ptilota serrata</i> (R)	10.5 ± 6.9		

Table 2 (continued)

Species/taxa and characteristics of communities	Upper subzone	Middle subzone	Lower subzone
<i>Ptilota gunneri</i> (R)	5.3±3.7		
<i>Flustra foliacea</i> (Br)		33.4±13.8	16.9±5.1
Porifera indet. (Po)		19.8±9.6	11.3±7.5
<i>Heteranomia squamula</i> (Bv)		17.0±8.5	
<i>Musculus discors</i> (Bv)		5.1±4.9	
<i>Hiatella arctica</i> (Bv)		5.0±2.3	
<i>Halocynthia pyriformis</i> (A)			131.4±131.4
<i>Hemithiris psittacea</i> (Bch)			10.3±10.3
<i>Dendrodoa grossularia</i> (A)			8.1±8.1
<i>Halichondria</i> sp. (Po)			7.2±7.2
Total biomass	1780.0±723.1	1557.7±351.2	760.9±246.5
Species richness	113	177	105
Simpson Index	0.45±0.08	0.66±0.07	0.33±0.05
Oligomixness Index	0.66±0.06	0.80±0.04	0.56±0.04

Only species whose biomass is more than 5 g m⁻² were presented in this table. Standard error of average (SE) indicated as ± after biomass parameters

A Ascidiacea, Bch Brachiopoda, Br Bryozoa, Bv Bivalvia, C Cirripedia, E Echinodermata, G Gastropoda, P Polychaeta, Ph Phaeophyceae, Po Porifera, R Rhodophyta

encrusting tier. The most abundant was *P. extensum* (Phaeophyceae); its percentage cover into the middle part at Kolvitsa and Kartesh reached 40–45%, into the upper part at Zhuzhmuy, 30%. At Kartesh into the middle subzone, calcareous red algae (*C. compactum*, *L. glaciale*, *L. laeve*) and sponge *Hymedesia* sp. were also relatively abundant with percentage cover of about 10% for each; at the middle and the lower subzones there were also ascidian *D. albidum* (percentage cover of about 10%).

Direct epibiotic interactions

Most sessile organisms were attached to each other and only several main holders (4–6 species at the each site) occupied the primary substrate (rock, boulders, stones). To describe interspecific epibiotic interactions, we focus on aspects of the general diversity of epibionts, features of the primary living substrate (basibionts), and preferences.

The epibionts were represented by algae, bryozoans, sponges, ascidians, hydroids, bivalve molluscs, polychaetes, cirripedians, actinarians, and kamptozoans. These comprise 72.2±3.5% of sessile organisms. In total, 171 taxa of epibionts were found: 80, 110, and 127 at Kolvitsa, Kartesh, and Zhuzhmuy, respectively, and 52 taxa were common to all sites. The highest taxonomic richness was recorded for bryozoans (37.7±0.8%) and algae (38.0±2.3%), among them for Rhodophyta (20.8±2.1%). While 28 from 60 epibiotic bryozoan's taxa were recorded in epibiosis only, most algae were recorded both on living and rocky substrates. Moreover, mass representatives of red algae demonstrated mainly

a preference for rocky substrates, except for filamentous *P. stricta*. Only 10 of 51 algal epibiotic species were recorded exclusively in epibiosis; in particular, these were small filamentous brown and red algae. In total, 32.7±6.8% of sessile organisms were found only as epibionts.

Totally 31 taxa of the principal epibionts were found: 20, 7, and 17 at Kolvitsa, Kartesh, and Zhuzhmuy, respectively. They were algae, bryozoans, sponges, hydroids, bivalvia, and polychaetes (Spirorbidae). Taxa of Bryozoa predominated among the principal epibionts at all sites (45%, 71.4%, and 76.5%), and also algae were plentiful at Kolvitsa (30%). Only two taxa (Bryozoa) were common for all sites—*C. annulata* and *Lichenopora* sp.

In total, 86 taxa of basibionts were found: 27, 50, and 53 at Kolvitsa, Kartesh, and Zhuzhmuy, respectively. They made up 29.1±2.5% of sessile organisms. Only 11 basibionts were common for all sites. Among the general number of basibionts, 10 principal basibionts were recorded: 6, 7, and 9 at Kolvitsa, Kartesh, and Zhuzhmuy, respectively (Table 3). Five of these were common for all sites: *C. truncatus*, *O. dentata*, *P. rubens*, *P. stricta* (Rhodophyta), and *P. maculata* (Polychaeta). The largest numbers of common epibionts for all sites were recorded for *C. truncatus* (15 species—14.6% from total epibionts of this host), *O. dentata* (11 species—15.1%), *P. rubens* (19 species—18.4%), and *P. stricta* (8 species—14.5%). Therefore, the number of epibiotic species common to all sites did not exceed 20% for each basibiont. There were also five specific principal basibionts for separate sites: *S. rustica* (Ascidiacea) at Kartesh, *B. crenatus*, *V. stroemia* (Cirripedia), *F. foliacea* (Bryozoa), and *P. serrata* (Rhodophyta) at Zhuzhmuy.

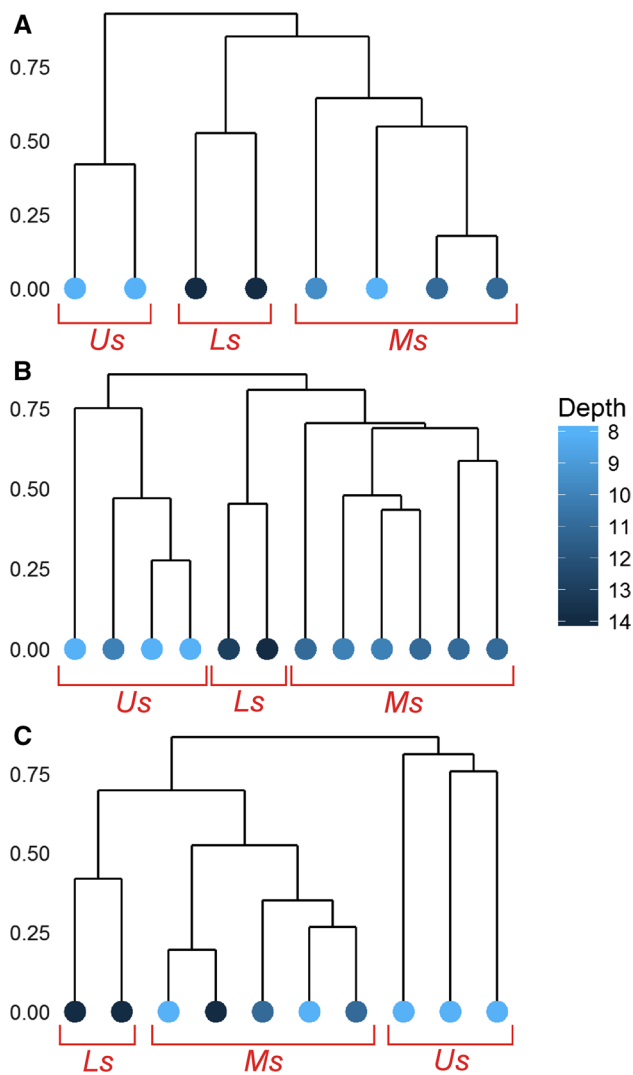
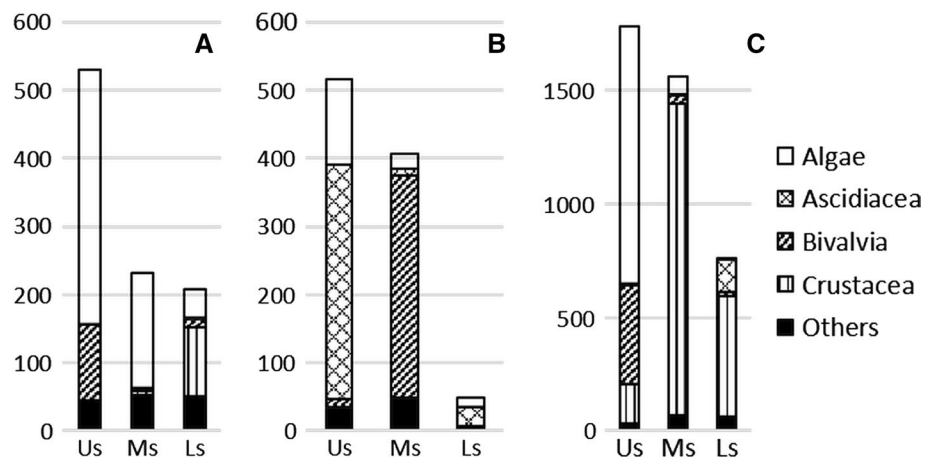


Fig. 3 Results of cluster analysis, showing the depth effect on the community structure. Rare species (with unitary occurrence) were excluded from this analysis. Numbers denote dissimilarity level (%). Us, Ms, and Ls are upper, middle, and lower subzones correspondingly at Kolvitsa (A), Kartesh (B), and Zhuzhmuy (C)

Fig. 4 Biomass (g m^{-2}) of main macrobenthic taxa of the red algae zone at different subzones. Us, Ms, and Ls are upper, middle, and lower subzones correspondingly at Kolvitsa (A), Kartesh (B), and Zhuzhmuy (C)



On the principal algal basibionts, the highest taxonomic richness was recorded for Bryozoa ($40.1 \pm 2.6\%$), and on the principal animal basibionts, the highest taxonomic richness was recorded for algae ($50.4 \pm 5.7\%$) (Fig. 5), mainly for Rhodophyta ($31.0 \pm 2.6\%$). Furthermore, a total of 53 species of bryozoans was recorded for the principal algal basibionts and 33 for the principal animal basibionts. However, similar numbers of algal species were recorded both for the principal algal and animal basibionts (43 and 41).

As a rule, each principal basibiont had one or more the prevalent epibionts. The most plentiful sets of the prevalent epibionts were inherent for *C. truncatus* at Kolvitsa and Kartesh, for *O. dentata* at Kolvitsa, for *P. rubens* at Kolvitsa, Kartesh, and Zhuzhmuy, and for *B. crenatus* at Zhuzhmuy (Table 3). The prevalent epibionts sets of the same basibionts varied at the different sites. Red alga *P. rubens* carried the prevalent epibionts sets at all sites, but from these only two species were common: *C. annulata* (Bryozoa) and *P. stricta* (Rhodophyta). Moreover, red algal species predominated in the prevalent epibionts sets of *C. truncatus* and *P. rubens* (50% for each) at Kolvitsa, while Bryozoa predominated on the same principal basibionts at Kartesh (50% and 57.1%). Bryozoa also predominated in the prevalent epibionts sets of *P. rubens* (62.5%) at Zhuzhmuy.

All of the prevalent epibionts had preferences to one or several hosts. Herewith, permanent relationships were recorded only for obligate species-specific partially or completely endophytic algae (*Choreocolax polysiphoniae*, *Coccotylus hartzii*, *Harveyella mirabilis*, and *Chukchia endophytica*), which penetrated into the tissues of the host (*Polysiphonia*, *Coccotylus*, *Rhodomela*, and algae from order Laminariales, respectively). For facultative epibionts in total, seven preferable basibionts were recorded: *C. truncatus*, *P. rubens*, *O. dentata*, *P. stricta*, *B. crenatus*, *H. squamula*, and *F. foliacea*. The most preferable basibionts were *C. truncatus* at Kolvitsa and Kartesh, and *P. rubens* at Zhuzhmuy.

Table 3 Number of the epibionts species (total/prevalent) on the principal species-basibionts at all sites

Principal basibionts	Sites		
	Kolvitsa	Kartesh	Zhuzhmuy
Algae			
<i>Coccotylus truncatus</i>	57/14	79/8	37/1
<i>Odonthalia dentata</i>	42/16	28/1	39/2
<i>Phycodrys rubens</i>	42/6	55/14	69/16
<i>Polysiphonia stricta</i>	23/2	40/0	21/1
<i>Ptilota serrata</i>	–	16/1	20/0
Animalia			
<i>Balanus crenatus</i>	3/0	–	61/9
<i>Flustra foliacea</i>	–	–	21/2
<i>Pista maculata</i>	31/4	19/0	12/1
<i>Styela rustica</i>	–	49/2	0
<i>Verruca stroemia</i>	0	0	35/2

Dashes are absence of the principal basibionts at site

Multi-level epibiosis

The maximum number of levels in epibiosis is four. In total, we found 20 basibionts forming multi-level suits both with direct and indirect interactions: 3, 16, and 9 at Kolvitsa, Kartesh, and Zhuzhmuy, respectively. *O. dentata* (Rhodophyta) and *P. maculata* (Polychaeta) were common to all sites. However, only 7 from 20 above-mentioned basibionts were foundation species whose epibiosis makes up a significant proportion (more than 10%) of total epibiotic biomass at each site (Table 4). These are the facilitators of the first order.

The distribution of different taxonomic groups of epibionts in the first level of the foundation species was analogical to the distribution of the direct epibionts on the principal

basibionts (Fig. 5): the richness of bryozoan's species was the highest on the algal foundation species and the richness of algal species was the highest on the animal foundation species. A significant fraction of bivalve biomass (mainly *M. discors*) was recorded on the algal foundation species, and also ascidians could be abundant on *C. truncatus*, while algae were abundant in biomass on *P. rubens* (Fig. 6). Algae were also abundant on the animal foundation species with the exception of *V. stroemia*, which was occupied by Crustacea, mainly by *B. crenatus* (Fig. 6).

Facilitators of the second order were attached to the foundation species and also carried on themselves the sets of dependent species. These were algae (especially red algae), cirripedians (especially *V. stroemia*), ascidians (especially *S. rustica*), bryozoans (especially Flustridae, Bugulidae, and Crisiidae), and hydrozoans (especially *Obelia*).

On the second level of the foundation species, the richness of bryozoan's species was the highest ($48.7 \pm 4.6\%$). Only small organisms or young stages grew on the third and fourth levels of the foundation species. The richest species composition and highest biomass of the third-level epibionts were recorded on the barnacles (Table 4). Facilitators of higher orders were recorded only at Zhuzhmuy: *P. rubens* was the facilitator of the third and *V. stroemia* was the facilitator of the third and fourth orders.

Discussion

In the present paper, we focus on the red algae zone in the White Sea, to which not so much attention has been paid so far. This zone extends in the White Sea shallows from 7 to approximately 20 m in depth, where the appropriate substrate of hard rock, pebbles, or boulders exists, and the depths ranged from 15 to 20 m are occupied mainly by

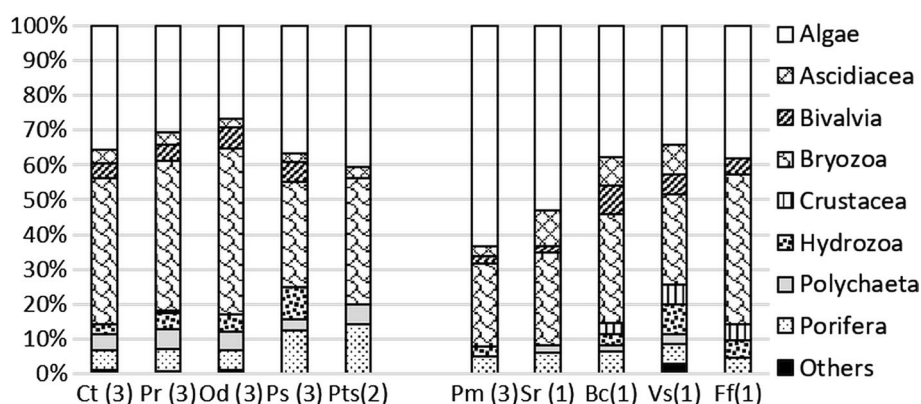


Fig. 5 Relative species richness in different taxonomic groups of epibionts on algal and animal principal basibionts. *Ct* *Coccotylus truncatus*, *Pr* *Phycodrys rubens*, *Od* *Odonthalia dentata*, *Ps* *Polysiphonia stricta*, *Pts* *Ptilota serrata*, *Pm* *Pista maculata*, *Sr* *Styela rustica*, *Bc*

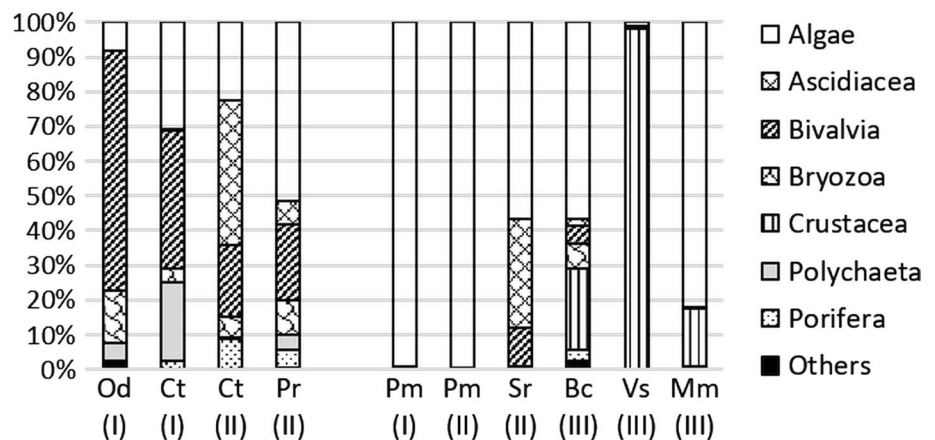
Balanus crenatus, *Vs* *Verruca stroemia*, *Ff* *Flustra foliacea*. In brackets—the number of sites for which data were averaged. An empty space separates algal and animal basibionts

Table 4 Features of foundation species

	1	2	3	4	5	6	7	8	9	10	11
Kolvitsa											
<i>Odonthalia dentata</i>	38.1	3	44	42	9	1	–	99.50	0.50	0.00	–
<i>Pista maculata</i>	42.6	3	44	32	16	1	–	99.24	0.76	0.00	–
<i>Coccotylus truncatus</i>	15.7	2	60	60	4	–	–	99.79	0.21	–	–
Others living substrates	3.6										
Kartesh											
<i>Phycodrys rubens</i>	13.4	4	54	49	22	2	1	93.85	6.08	0.06	0.01
<i>Pista maculata</i>	13.9	4	33	14	22	2	1	97.14	2.83	0.03	0.00
<i>Coccotylus truncatus</i>	27.7	3	71	67	30	1	–	97.60	2.39	0.00	–
<i>Styela rustica</i>	34.1	3	58	46	34	5	–	97.39	2.58	0.03	–
Others living substrates	10.8										
Zhuzhmuy											
<i>Balanus crenatus</i>	35.2	4	83	62	52	12	2	94.41	5.45	0.11	0.03
<i>Verruca stroemia</i>	49.0	4	44	28	22	9	2	99.46	0.41	0.12	0.00
Others living substrates	15.8										

Titles of columns: 1 percentage of epibiotic cascade biomass of this basibiont in total epibiotic biomass at site, 2 number of epibiosis levels, 3 total number of epibionts species, 4–7 number of epibionts species in 1st, 2nd, 3rd, and 4th levels, respectively, 8–11 fraction of epibionts biomass of 1st, 2nd, 3rd, and 4th levels in total biomass epibiotic suit of this basibiont, respectively. Dashes are absence of epibionts

Fig. 6 Biomass fraction of epibionts in different taxonomic groups on the first level of epibiosis on the algal and animal foundation species. *Od* *Odonthalia dentata*, *Ct* *Coccotylus truncatus*, *Pr* *Phycodrys rubens*, *Pm* *Pista maculata*, *Sr* *Styela rustica*, *Bc* *Balanus crenatus*, *Vs* *Verruca stroemia*, *Mm* *Modiolus modiolus*. In brackets: I—Kolvitsa, II—Kartesh, III—Zhuzhmuy. An empty space separates algal and animal basibionts



rhodolites. Rich and diverse epibenthic communities are formed at these depths with a prominent portion of Rhodophyta species. The depth range of red algae distribution in the White Sea somewhat differs from the Antarctic (up to 29 m) (Brouwer et al. 1995) and southeast Alaska (beyond the 25 m) (Estes et al. 1978) but generally resembles that of the Baltic Sea (Johansson and Snoeijs 2002), which has low water transparency similarly to the White Sea (Naumov et al. 2003).

Worldwide comparison shows that in the Aegean Sea (Greece), 1171 hard-bottom species have been recorded. Surprisingly, the number of macrobenthic species obtained in the present study resembles the number of species, specific to clear-water photophilic communities (388) (Chintiroglou et al. 2005). Over 550 epibenthic species were found on the Australia coast in the depth range of 5–12 m, although

there are red-brown algae mixed communities at these depths (O'Hara 2001). Among six macroalgal species, 105 macrobenthic species were found in the Spitsbergen subtidal zone (Lippert et al. 2001). The White Sea flora is richer than the flora of various regions of the Arctic region (Zinova 1950). Our data support this view. For instance, total marine flora of Kongsfjorden and Isfjorden (Spitsbergen) (Hop et al. 2012; Fredriksen et al. 2015) includes a quantity of species (62 and 88, respectively) similar with what we detected in a narrow range of depths in the White Sea (80 species). Therefore, obviously, our data contradict the opinion of the poor biodiversity of the White Sea (Derjugin 1928).

The number of obtained species is approximately 100 below the total registered number of species in Kandalaksha and Onega Bays. However, in a narrow depth range, we found 50–100 species more than have been recorded to

date over the whole phytal zone (Naumov 2001). We also, in particular, found two times more amphipod species than amphipods' assemblages living in the red algae communities in Velikaya Salma Strait (Kandalaksha Bay, the White Sea) in the depth range of 3–11 m (Uryupova et al. 2012). We suggest that this result is connected with an insufficient knowledge of the biota in this species-rich White Sea zone up to the present study and a low taxonomic resolution in algae description in the past.

According to the results, the surveyed assemblages may be characterized as polymix and mesomix at different depths (Table 2). These data throw the light on our knowledge about communities of the phytal zone of the White Sea (Naumov 1991, 2001). On the taxonomic structure of zoobenthos: similarly to the study of subtidal macrobenthos of the Kongsfjorden (Spitsbergen) (Voronkov et al. 2013), the Bryozoa in our survey were the richest taxa of animals.

Though the phenomena of depth-related community change in the White Sea (Golikov et al. 1982, 1985a, b; Khalaman 1998; Naumov 2001) as well as in other bodies of water (Logan et al. 1984; Terlizzi et al. 2007) have been widely discussed, up to the present sufficient data about depth-related community shift in this zone of the White Sea have been almost completely absent (Mikhaylova et al. 2017). The revealed zonation in the distribution of epibenthic organisms fills this gap.

Despite the above-mentioned common features, we found clear interregional differences among the surveyed red algae zone. The most distinct features of the different sites include the dominance of red algae in the upper and middle parts of the red algae zone at Kolvitsa and Zhuzhmuy, *S. rustica* in the upper subzone at Kartesh and Cirripedia in the middle and lower subzones at Zhuzhmuy (Fig. 4). Different factors were proposed to explain the individual traits of epibenthic assemblages, focused primarily on several sources of variation: abiotic conditions (Vance 1988; Khalaman et al. 2016, 2018), biotic interactions, such as the effect of predators and grazers (Underwood 1980; Breitburg 1985; Nydam and Stachowicz 2007; Yakovis and Artemieva 2017) as well as species competition (Dürr and Wahl 2004), and patterns in recruitment of foundation species (Bruno and Bertness 2001). All these factors can vary in time, creating the mosaic, complicated by succession processes. We cannot unambiguously reject possible succession processes due to the brevity of our observations. However, similar to the animal dominants were noted earlier at the same locations and depths for the Kandalaksha (*S. rustica*) and the Onega (*B. crenatus* and *V. stroemia*) bays (Golikov et al. 1985b; Solyanko et al. 2011). This fact increases our reliance that communities we found are rather stable. We suggest that observed interregional differences were linked with peculiarities of hydrology regimes and sediments at surveyed sites.

The abiotic factors such as currents, stratification, and turbidity as well as bottom inclination and type of sediments obviously have a great impact on algae distribution ranges and patterns (Witman and Dayton 2001). Strong tidal currents and the mixing of water caused by winds and storms lead to vertical homothermy and homohalinity in many parts of the Onega Bay, which create favorable conditions here for the thriving of cirripedians (Berger and Naumov 2001; Naumov et al. 2003; Solyanko et al. 2011). Significant differences between the communities of Kandalaksha (Kolvitsa and Kartesh) and Onega Bays (Zhuzhmuy) are mainly associated with the high biomass of cirripedians (Figs. 2, 4). The results we obtained in the zone of red algae cogently confirm the available information on the heterogeneity of benthos in different regions of the White Sea (Golikov et al. 1985a, b; Naumov et al. 2003).

It is usually considered that horizontal and gently sloping substrates are generally dominated by macroalgae, whereas vertical rock walls are covered by epifaunal invertebrates (Witman and Dayton 2001). Substrate slope is, therefore, one of the fundamental determinants of local community structure, that is, dominance by algae versus invertebrates so the large differences in invertebrate cover between horizontal and vertical surfaces are among the most striking and general features of rocky subtidal communities worldwide. In our opinion, the prevalence of invertebrates over algae in the upper and middle subzones at Kartesh, especially *S. rustica*, is linked with the larger incline at this area.

The significance of secondary substrates is strengthened by a deficiency of the primary (Lohse 1993; Gutt and Schickan 1998). Epibiosis plays an important role in positive interactions inside communities of the red algae zone of the White Sea, because only a few species of the many found occupy the primary substrate at all investigated sites. More than half of all epibenthic taxa and almost three quarters of sessile species were recorded in epibiosis. With rare exceptions, all of these are facultative epibionts. These are mainly algae and bryozoans. The latter demonstrate a greater preference for settling in epibiosis. The fact of the greatest diversity of bryozoans on algal substrate is due to their possible preference for such a substrate (Manriquez and Cancino 1996; Yagunova and Ostrovsky 2008, 2010).

Currently, there have been reports of facilitators in marine communities, which can be bivalves, their dead shells, ascidians, barnacles, etc. (Rees et al. 2008; Yakovis et al. 2008; Thomsen et al. 2016; Kent et al. 2017; Yakovis and Artemieva 2017). According to our data in total 11 species contributing to facilitation were revealed: 7 species are foundation species, 10 species are principal basibionts, 7 species are preferable basibionts, and some of them combine these functions (Tables 3, 4). Such species as a rule are mass representatives of different communities and also are a favorable substrate for epibionts (Yakovis and Artemieva 2017).

Therefore, a number of sessile invertebrates and algae use the surfaces of the dominants to live on. However, some relatively abundant species were poorly overgrown (ascidians *Boltenia echinata*, *S. coriacea*, *D. grossularia*) or had no epibionts at all (ophiurians, bivalve mollusc *M. discors*, ascidian *Halocynthia pyriformis*). Obviously, not only the large surface area of species allows them to perform the facilitation function. Some important species of basibionts are neither dominants nor mass representatives of communities. For instance, *P. maculata* at Kolvitsa and Kartesh, *O. dentata* at Kartesh and *F. foliacea* and *H. squamula* at Zhuzhmuy. Their facilitating function is determined not by their abundance, but the suitable texture of their surface, which provides favorable conditions for the attachment of numerous different epibionts. Furthermore, the tubes of *P. maculata* permit red algae to form a significant biomass on them; consequently, this polychaete performs the function of a foundation species.

Four algal species are common principal basibionts for all sites. Three of these are also the foundation species at two sites simultaneously (*C. truncatus*, *O. dentata*, and *P. rubens*). Moreover, *C. truncatus* and *P. rubens* were registered as the most preferable basibionts. Until now, the role of distinct species of cespitose red algae as foundation species in the marine benthic communities has been underestimated because of the insufficient knowledge of various biotopes (Bates and DeWreede 2007; Yakovis et al. 2008).

Facilitators in marine environment support a diversity and stability of communities (Bertness and Callaway 1994; Yakovis et al. 2008; Angelini et al. 2011; Hughes et al. 2014). Within the red algae zone of the White Sea, we found large number of basibionts providing space for numerous organisms and supporting multi-level epibiosis (the principal basibionts and the foundation species). These basibionts perform an undoubted facilitative function increasing the taxonomic diversity of Bryozoa and providing additional environment for algae, hydroids, and sponges.

Red algae, *P. maculata*, *S. rustica*, and cirripedians are facilitators with different functions. The decline of any foundation species can pull the ecosystem out of its current state, causing changes to the local environment, abundance, and diversity of dependent organisms (Ellison et al. 2005). In our case, degradation of *P. maculata* at Kolvitsa, *S. rustica* at Kartesh, and cirripedians at Zhuzhmuy can lead to structural rearrangements in the macrobenthos. At the same time, algal foundation species have a similar taxonomic composition of epibionts (Fig. 5). Thus, these algae perform equal facilitation function. We assume that presence of several foliose algae species creates more persistent systems, and if any of these is eliminated, another one could replace it.

Foundation species carry on their surface multiple hierarchical levels of epibionts. The first level accommodates both the greatest number and biomass of epibionts. Some

epibionts of the first level (algae, ascidians, cirripedians, bryozoans, and partly hydrozoans) are also facilitators of the second order. Therefore, several facilitators operate at more than one order (red algae, *S. rustica*, and *V. stroemia*), increasing the overall system diversity.

According our findings in the White Sea, the transitional zone between the highly productive kelp communities and the devoid of vegetation deep-waters, so-called the red algae zone, inhabited by rich and diverse epibenthic communities. Diversity is due to the complexity of the spatial organization of communities, expressed in direct and indirect interspecific interactions. Red algae here perform functions of producers, substrate holders, and facilitators.

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Compliance with ethical standards

Conflict of interest We have no conflicts of interest to disclose.

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