Vegetation of the red algal belt of the White Sea (European Arctic, Russia)

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Abstract. In 2016–2018, during the summer period, the first detail studies of the red algal belt of the White Sea were carried out time with SCUBA diving at the Chupa Inlet, near the Cape Kartesh, and at the Kolvitsa Inlet (the Kandalaksha Bay), in the vicinity of Sonostrov Island (the White Sea Basin) and Bolshoy Zhuzhmuy Island (the Onega Bay). The upper boundary of the red algal belt lies at a depth of about 7 m, and the lower boundary, at a depth of about 20 m. In the White Sea, the algae distribution in the lower part of the photic zone depends on the geomorphological structure of the bottom and on the composition of the accompanying sedentary fauna, so the lower boundary may vary in the depth range from 14 down to 23 m. In total, 87 species of algae belonging to the three large taxonomic groups have been registered: Chlorophyta (13), Phaeophyceae (33), and Rhodophyta (41). Significant richness of the species composition, vertical zoning, and a variety of phytocoenoses of the red algal belt in different parts of the White Sea have been found. Phytocoenoses of the red algal belt refer to three associations: ass. *Odonthalia dentata*(–*Pseudolithoderma extensum*), ass. *Phycodrys rubens*+*Coccotylus truncatus*(–*Pseudolithoderma extensum*), and ass. *Lithothamnion glaciale*. Nineteen species of macrophytes were the most common and characteristic representatives of the red algal belt, including thirteen species of red algae, four species of brown algae, and two species of green algae. It has been found that abundant and characteristic species of the red algal belt have an additional edificatory function in the studied phytocoenoses, being the consorts that carry rich epiflora and form favorable conditions for increasing the species diversity of algae in the lower phytal zone. The observed rapid shrinkage of the depth range of the kelp and red algal belts, as well as the changes in the vertical distribution of some other algal species in the White Sea, require specific attention concerning altering of their habitat conditions.

Keywords: biomass, lower phytal zone, phytocoenoses, seaweeds, size and age structure of coenopopulations, zonal distribution, White Sea.

Растительность пояса красных водорослей Белого моря (Европейская Арктика, Россия)

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Резюме. Первые детальные исследования пояса красных водорослей Белого моря проведены с применением водолазного оборудования в летний период 2016–2018 гг. в губе Чупа, вблизи м. Картеш, и в губе Колвица (Кандалакшский залив), в районах островов Соностров (Бассейн Белого моря) и Большой Жужмуй (Онежский залив). Установлено, что верхняя граница пояса залегает на глубине около 7 м, а нижняя — на глубине около 20 м. Распределение растительности нижней части фотической зоны Белого моря зависит от геоморфологической структуры дна и состава сопутствующей седентарной фауны, в связи с чем расположение нижней границы пояса может варьировать в диапазоне глубин от 14 до 23 м. Всего отмечено 87 видов водорослей: 13 — Chlorophyta, 33 — Phaeophyceae, 41 — Rhodophyta. Выявлено значительное флористическое богатство, вертикальная зональность и разнообразие фитоценозов пояса красных водорослей в различных участках моря. Фитоценозы относятся к трем ассоциациям (асс.): асс. *Odonthalia dentata*(*–Pseudolithoderma extensum*), асс. *Phycodrys rubens* + *Coccotylus truncatus* (*–Pseudolithoderma extensum*) и асс. *Lithothamnion glaciale*. Наиболее характерными представителями пояса являются 19 видов макрофитов, 13 из которых — красные, 4 — бурые и 2 вида — зеленые водоросли. Установлено, что массовые и характерные представители пояса выполняют дополнительную эдификаторную функцию в фитоценозах как консорты, несущие богатую эпифлору и формирующие условия для увеличения видового разнообразия водорослей нижней фитали. Отмеченное поднятие нижних границ распределения отдельных видов и элементов растительности требует внимания к оценке изменений в условиях обитания в Белом море.

Ключевые слова: биомасса, морские водоросли, нижняя фиталь, размерная и возрастная структура ценопопуляций, фитоценозы, зональность, Белое море.

The vertical distribution of the macroalgae in the Arctic Ocean and in the northern Atlantic Ocean is generally well known. Mainly *Fucus* L. and *Ascophyllum* Stackh. algae inhabit coastal or intertidal zone that is drained during the ebb. The species of *Laminaria* J. V. Lamour. and *Saccharina* Stackh. inhabit greater depths and form laminarian zone; some researchers also distinguish deeper the *Desmarestia* J. V. Lamour. zone in the Barents Sea represented by *Desmarestia aculeata* (L.) J. V. Lamour. and *D. viridis* (O. F. Müll.) J. V. Lamour. (Blinova, 1964a, 1964b, 1965; Wiencke, Amsler, 2012). Red algal belt is the lowest one; it limits the macrophyte distribution down to the boundary of the photic zone. These groups (belts or zones) combine the formations with numerous smaller communities, so-called associations.

The diverse phytocoenoses of the large brown algae have been studied in detail by both Russian and foreign researchers (Kalugina, 1957, 1958; Blinova, 1962, 1964a, 1964b, 1965, 1969; Vozzhinskaya, 1967, 1986; Dolgacheva, 1975; Kain, 1975; Ninburg, Shoshina, 1986; Mikhaylova, 2000a, 2000b, 2006, 2014; Wiencke *et al.*, 2004; McNeill, 2010). Meantime, intertidal communities, due to their easy accessibility, are the most popular for the studies by marine biologists (Stephenson, Stephenson, 1949, 1972; Blinova, 1962; Ellis, 2003; Malavenda *et al.*, 2017; Bertolini, 2018).

At the same time, a more deep-lying zone remains relatively poorly studied in terms of both algae abundance and the species composition. There is sketchy information about the maximum depth of distribution of various species. It is known, for example, that in the region of Spitsbergen, red algae communities are predominantly formed by the species *Coccotylus truncatus* (Pall.) M. J. Wynne et J. N. Heine and *Phycodrys rubens* (L.) Batters, and the latter may descend down to a depth of 60 m (Wiencke, Amsler, 2012).

The first information on the lower part of the photic zone of the White Sea was obtained on the basis of the samples collected by means of hydrobiological dredges, i. e. without visual control (Sinova, 1922; Derjugin, 1928). Particularly, the elitorial boundary, i. e. the lowest part of the photic zone, was set in the White Sea at a depth of 45 m and even lower, at 60 m depth in the vicinity of the Solovetsky Islands (Sinova, 1922).

The studies of the structure of algal communities of the White Sea began in the second half of the 20th century and continue to nowadays (Kalugina, 1957, 1958; Blinova, 1962; Vozzhinskaya, 1967, 1986; Dolgacheva, 1975; Ninburg, Shoshina, 1986; Mikhaylova, 2000a; Mikhaylova *et al.*, 2017). Using SCUBA diving for algae sampling made it possible to assess the characteristics of the vegetation visually and to determine the composition of species and their quantitative ratio at specific depths with more accuracy. It has been reported earlier that the algal cover in the lower part of the photic zone is strongly rarefied, with the exception of red coralline algae (Vozzhinskaya, 1967). At the same time, fairly high algal biomass has been described for the depth range of 15–30 m by the same author (Vozzhinskaya, 1967): for example, the biomass of two species of the genus *Ptilota* C. Agardh was 0.8 kg/m^2, and the total biomass of the red algae reached almost 2 kg/m^2.

In the 1980s, the hydrobiologists studied the bottom biocoenoses at the whole depth range in the Basin, in the Kandalaksha and Onega Bays (Golikov *et al.*, 1982, 1985a, 1985b). These biocoenoses were defined in regard to the dominant species, often by benthic invertebrates: therefore, according to these data, it is not always possible to determine the distribution boundary of the autotrophic organisms.

The results of the first investigation targeted specifically on the lower part of the photic zone in the Kolvitsa Inlet, the Kandalaksha Bay (Mikhaylova *et al.*, 2017) showed that the red algal belt extended there from 7 down to 17–18 m, and it was characterized by a clear zonal distribution. The association of *Odonthalia dentata* (L.) Lyngb. developed in the uppermost part (7–9 m), *Coccotylus truncatus* association inhabited the middle part (9–15 m); meantime, the monodominant phytocoenosis of latter association were distributed within the depth range from 9 down to 11–12 m, and the phytocoenosis of *C. truncatus*+*Phycodrys rubens* (two dominating species), from 11–12 down to 14–15 m. In the lower part of the red algal belt (deeper than 15 m), a few species of crustose algae grew, mainly representatives of coralline red algae. Phytocoenoses formed by bushy forms were quite rich, they include from 26 to 35 algae species (Mikhaylova *et al.*, 2017).

The goal of our work is to describe the species diversity and structure of vegetation of the red algal zone at different areas of the White Sea. The data from the latest detailed studies prompted us also to test the hypothesis of high species richness and vertical heterogeneity of the vegetation of the red algal belt in the other areas of the White Sea.

Material and methods

The material was sampled in 2016–2018: in the Kolvitsa Inlet (67°04'N, 32°49'E, the Kandalaksha Bay, July 2016), near the Cape Kartesh, the Chupa Inlet (66°20'N, 33°40'E, the Kandalaksha Bay, July 2016–2017), in the vicinity of the Sonostrov Island (66°11'N, 34°13'E, the White Sea Basin, July 2018), and in the vicinity of the Bolshoy Zhuzhmuy Island (64°40'N, 35°31'E, the Onega Bay, July 2017).

The water temperature and salinity were measured using the MIDAS-500 and Cyclops automatic probes. Initial survey of the red algal belt and defining of its boundaries were performed by SCUBA divers using an Olympus Pen E-PL3 underwater camera equipped with an Olympus lens (14–42 mm/3.5–5.6) and an Olympus UFL-2 flashlight, and a video camera Magiceye hdss100. The survey started at the depth of 6 m, and then the divers went deeper to the lower boundary of the algae distribution; the maximum depth, where the observations were made, was 24–25 m. The sampling stations were planned on the base of photo and video material analysis. The samples were collected by SCUBA divers in the depth range from 6–7 to 14–18 m using a 0.04 m^2 frame and a 0.05 m^2 diving core designed by Gruzov and Pushkin (1967). If it was impossible to use the diving core and the frame, the samples were taken by collecting the entire stone. In this case, during further processing, the area of the stone was measured by wrapping the overgrown surface with aluminum foil and removing its sections from the folds (Marsh, 1970). The area was recalculated through the weight of the foil, for which the «area/weight» ratio was previously established. In total, 72 samples were collected. The initial processing of the collected samples showed that some of them were collected outside the red algal belt and therefore were not used in the further analysis. The species composition and the algal communities of the red algal belt were argued from 54 samples: at each site, from 8 to 19 samples have been collected.

Algae were identified to the species level using light microscopic technic. In the absence of the necessary taxonomic attributes, the samples were determined to the genus level (Table). The frequency of occurrence of the particular species at the site was calculated as the ratio of the number of samples, where the species was encountered, to the total number of the samples collected at this site. The biomass (g/m^2) of all species (with 1 mg accuracy of wet weight), the population density (ind./m^2), the size and age (Schoschina, 1996; Shoshina, 1990a, 1990b) of the dominant species were determined, the percentage cover degree (PCD) has been visually determined for the crustose algae. When comparing the species composition of algae at different sites, the Sørensen index was applied (Magurran, 1988). The species abundance (number of species per 1 m^2) was calculated according to the logarithmic relationship (Gleason, 1917, 1926). The selected examined specimens were collected for deposit in the Herbarium of the Komarov Botanical Institute of the Russian Academy of Sciences (LE).

The data obtained earlier in the Kolvitsa Inlet, but not included in the previous publication (Mikhaylova *et al.*, 2017), are used here for comparison with the other studied sites and for the data generalization.

Results

Environmental conditions. Generally, the hydrological conditions in the studied areas are quite similar. In the studied range of the depths, the water temperature in July decreased uniformly from 13–15 down to 4–10 °C, the water salinity gradually increased with the depth from 21.0 up to 26.0 ‰ in the Kolvitsa Inlet (Mikhaylova *et al.*, 2017), and from 24.5 up to 26.0 ‰ in the areas of Cape Kartesh and in the vicinity of Sonostrov and Bolshoy Zhuzhmuy islands.

The bottom sediments in the Kolvitsa Inlet are presented by silty mud with rare boulders (Mikhaylova *et al.*, 2017). In the area of Cape Kartesh, the sea bottom is represented by rocky cliff. In the area of the Sonostrov Island, gravel-pebble deposits on a sandy base are distributed down to a depth of 14 m; the rock substrate is absent at the deeper areas, and the sediments are sands. In the vicinity of Bolshoy Zhuzhmuy Island, there is a stream gravel on the sandy bottom; at the depths exceeding 15 m, the stones lie on the sandy-muddy bottom.

Phytocoenoses of the Kolvitsa Inlet. The red algal belt extends from 7 m down to 17–18 m. The quantitative composition of phytocoenoses of all studied areas is presented in the Table. The two-layer phytocoenoses of the upper parts of the belt have been described earlier (Mikhaylova *et al.*, 2017). It can also be added to the published data that the red algae *Grania efflorescens*, *Meiodiscus spetsbergensis*, *Phycodrys rubens*, *Scagelia pylaisei*, brown algae *Battersia arctica*, *Ectocarpus siliculosus*, and green algae *Chaetomorpha tortuosa*, *Derbesia marina*, and *Rhizoclonium riparium* are also characteristic species (frequency of occurrence 100 %) in the phytocoenosis *Odonthalia dentata+Coccotylus truncatus+Polysiphonia stricta* (7–9 m depth). In the phytocoenosis of *Coccotylus truncatus* (9–12 m depth), red algae *Euthora cristata*, *Grania efflorescens*, *Meiodiscus spetsbergensis*, *Rhodochorton purpureum*, *Rhodomella confervoides*, *Scagelia pylaisei*, brown algae *Battersia arctica*, *Ectocarpus siliculosus*, *Pseudolithoderma extensum*, *Stictyosiphon tortilis*, and green algae *Chaetomorpha tortuosa*, *Cladophora rupestris*, *C. sericea*, and *Derbesia marina* belong to the characteristic species, in addition to the subdominants indicated earlier. In the phytocoenosis of *Coccotylus truncatus+-Phycodrys rubens* (12–14 m depth), the characteristic species are also red algae *Euthora cristata*, *Leptophytum leave*, *Meiodiscus spetsbergensis*, *Polysiphonia stricta*, *Rhodochorton purpureum*, *Rhodomela confervoides*, *Scagelia pylaisei*, brown algae *Battersia arctica*, *Ectocarpus siliculosus*, *Pylaiella littoralis*, *Stictyosiphon tortilis*, and green algae *Chaetomorpha tortuosa*, *Cladophora rupestris*, and *C. sericea*. The depth range from 14–15 m down to 17–18 m is inhabited by poorly developed single-layer phytocoenosis of the crustose algae *Lithothamnion glaciale+Leptophytum laeve*, that are characterized by low percentage cover degree (PCD) of 10–20 % and include 3–4 algal species.

In the red algal belt, a synusia of epiphytes has been found; it included 29 species at this site. Epiphytes settle on 12 basiphyte species. Three of them (*Coccotylus truncatus*, *Odonthalia dentata*, and *Phycodrys rubens*) host more than 10 epiphyte species. Such basiphytes may be considered as the most significant members of the community.

Table. Species composition (with average biomass, gm^{-2}± standard error) of phytocoenoses in the red algal zone in the White Sea.

Locations / Depths, m / Taxa	Kolvitsa Inlet			Cape Kartesh		Sonostrov Island			Bolshoy Zhuzhmuy Island		
	7–9	9–12	12–14	8–11	11–14	7–9	9–11	11–14	7–9	9–12	12–17
1	2	3	4	5	6	7	8	9	10	11	12
Phylum CHLOROPHYTA											
Acrosiphonia arcta (Dillwyn) Gain	+					+	+	+	+	+	+
A. flagellata Kjellm.						+					
A. incurva Kjellm.						+	+			+	+
A. sonderi (Kütz.) Kornmann										+	
Chaetomorpha melagonium (F. Weber et D. Mohr) Kütz.	+			0.1±0.1	+	0.2±0.1	+		+	+	
C. tortuosa Kütz.	+	+	+	+	+			+		+	
Cladophora rupestris (L.) Kütz.	+	0.7±0.4	0.1±0.1	0.1±0.0	+	0.5±0.4	+	+		+	
C. sericea (Hud.) Kütz.	+	+	0.2±0.1	+	+		+	+	+	+	
Derbesia marina (Lyngb.) Solier	+	+		+		+			+	+	
Rhizoclonium riparium (Roth) Harv.	+	+		+	+	+					
Spongomorpha aeruginosa (L.) Hoek		+				+	+	+			
Ulva prolifera O. F. Müll.	+	+	+								
Urospora penicilliformis (Roth) Aresch.				+							

Продолжение таблицы

1	2	3	4	5	6	7	8	9	10	11	12
Phylum OCHROPHYTA											
Class PHAEOPHYCEAE											
Ascophyllum nodosum (L.) Le Jol.										0.1±0.1	
Battersia arctica (Harv.) Draisma, Prud'homme et H. Kawai	+	0.1±0.1	+	0.1±0.1	+	+	+	+	+	+	+
Chaetopteris plumosa (Lyngb.) Kütz.		+		0.5±0.3	0.1±0.1	2.5±1.5	+	+	0.1±0.0	0.1±0.0	0.1±0.1
Chorda filum (L.) Stackh.	+	0.3±0.2		+	+				0.1±0.1	+	+
Chukchia endophytica (S. Lund) R. T. Wilce, P. M. Pedersen et S. Sekida										+	
Desmarestia aculeata (L.) J. V. Lamour.			+	+		0.3±0.3			0.3±0.2	0.6±0.5	+
D. viridis (O. F. Müll.) J. V. Lamour.							+		+	+	0.1±0.1
Dictyosiphon chordaria Aresch.				+	+		+				
D. foeniculaceus (Huds.) Grev.				+	+		0.1±0.1			+	
Dictyosiphon sp.					+						
Ectocarpus fasciculatus Harv.						+	+	+			
E. siliculosus (Dillwyn) Lyngb.	+	+	0.4±0.4	+	+	+	+	+		+	+

Продолжение таблицы

1	2	3	4	5	6	7	8	9	10	11	12
Ectocarpus sp.					+						
Elachista sp.				+							
Fosliea curta (Foslie) Reinke										+	
Fucus vesiculosus L.									0.1±0.1		
Fucus sp.					+	+					+
Haplospora globosa Kjellm.						+	+	+	+		+
Hincksia ovata (Kjellm.) P. C. Silva	+				+	+					
Laminaria digitata (Huds.) J. V. Lamour.									94.2±94.2		
Laminariocolax tomentosoides (Farl.) Kylin										+	
Petalonia fascia (O. F. Müll.) Kuntze				0.6±0.6							
Pseudolithoderma extensum (P. Crouan et H. Crouan) S. Lund	++	++	++	++	++	++	++	++	++		
Punctaria plantaginea (Roth) Grev.		+								+	
Pylaiella littoralis (L.) Kjellm.	+		+	+		+	+		+	+	+
P. varia Kjellm.		+		+	+	+	+		+	+	+
Ralfsia fungiformis (Gunnerus) Setch. et N. L. Gardner				++							
R. verrucosa (Aresch.) Aresch.						++	++				

Продолжение таблицы

1	2	3	4	5	6	7	8	9	10	11	12
Saccharina latissima (L.) C. E. Lane, C. Mayes, Druehl et G. W. Saunders	6.2±6.2			0.7±0.4	+	+			0.2±0.1	+	
Sphacelaria cirrosa (Roth) C. Agardh					+	+					
Sphacelaria sp. 1				+							
Sphacelaria sp. 2							+				
Stictyosiphon tortilis (Gobi) Reinke	+	+	+		+		+	+		+	
Phylum RHODOPHYTA											
Acrochaetium secundatum (Lyngb.) Nägeli						+	+				
Ahnfeltia plicata (Huds.) Fr.				0.5±0.3	0.3±0.3	0.3±0.3	+		0.2±0.1	0.2±0.1	+
Antithamnionella floccosa (O. F. Müll.) Whittick									+	+	+
Ceramium deslongchampsii Chauv. ex Duby				+	+				+		
C. virgatum Roth	+	+		+	+	+			0.1±0.1	+	+
Choreocolax polysiphoniae Reinsch		+		+	+					+	
Clathromorphum compactum (Kjellm.) Foslie					++			++			
Coccotylus brodiei (Turner) Kütz.						74.2±60.8					

Продолжение таблицы

1	2	3	4	5	6	7	8	9	10	11	12
C. hartzii (Rosenvinge) Le Gall et G. W. Saunders	+	+	+	+	+	+				+	
C. truncatus (Pall.) M. J. Wynne et J. N .Heine	30.4±20.6	136.8±77.0	26.0±6.8	22.3±5.7	7.8±2.1	8.8±8.8	5.0±2.9	0.1±0.1	24.5±19.1	2.5±1.2	0.5±0.1
Corallina officinalis L.				0.2±0.1	+	2.5±2.5					
Cystoclonium purpureum (Huds.) Batters						0.1±0.1			+		
Euthora cristata (C. Agardh) J. Agardh	0.1±0.1	0.1±0.1	3.8±0.3	2.4±1.6	+	2.4±1.2	+	+	0.2±0.1	1.7±0.9	+
Fimbrifolium dichotomum (Lepech.) G. I. Hansen						4.9±3.9	+		0.2±0.1	0.2±0.2	0.1±0.1
Grania efflorescens (J. Agardh) Kylin	+	+	+	+	+	+	+		+	+	+
Haemescharia hennedyi (Harv.) K. L. Vinogr. et Yacovleva					++	++	++	++	++		
Harveyella mirabilis (Reinsch) F. Schmitz et Reinke										+	
Hildenbrandia rubra (Sommerf.) Menegh.			++		++	++	++	++	++	++	++
Leptophytum foecundum (Kjellm.) W. H. Adey					++		++				
L. laeve (Foslie) Adey			++		++		++	++	++		
Leptophytum sp.					++						
Lithophyllum crouaniorum Foslie					++	++	++	++	++	++	++

Продолжение таблицы

1	2	3	4	5	6	7	8	9	10	11	12
Lithothamnion glaciale Kjellm.	++	++		++	++	++	++	++	++	++	
Meiodiscus spetsbergensis (Kjellm.) G. W. Saunders et McLachlan	+	+	+	+	+	+	+	+	+	+	
Membranoptera fabriciana (Lyngb.) M. J. Wynne et G. W. Saunders	+	1.3±1.3	+								
Odonthalia dentata (L.) Lyngb.	181.3±39.4	4.9±4.8	+	3.6±3.5	+	108.9±66.7	+		320.5±221.8	8.7±4.1	0.3±0.1
Palmaria palmata (L.) F. Weber et D. Mohr						0.1±0.1					
Phycodrys rubens (L.) Batters	4.8±2.2	3.5±1.9	11.1±7.0	40.6±18.7	3.2±2.0	28.1±27.0	7.2±2.4	0.2±0.2	445.0±275.4	35.4±13.4	5.0±2.2
Phymatolithon purpureum (P. Crouan et H. Crouan) Woelk. et L. M. Irvine			++								
Plumaria plumosa (Huds.) Kuntze				+	+	+	+	+	+		
Polyides rotunda (Huds.) Gaillon		0.2±0.2		+	+						
Polyostea arctica (J. Agardh) Savoie et G. W. Saunders	+			+			0.4±0.4				
Polysiphonia stricta (Mert. ex Dillwyn) Grev.	96.6±83.5	8.9±5.1	0.1±0.0	21.4±6.4	+	0.3±0.1	1.5±1.3	+	3.2±2.1	1.3±0.5	0.4±0.1
Porphyra purpurea (Roth) C. Agardh						5.5±3.4				+	

Продолжение таблицы

1	2	3	4	5	6	7	8	9	10	11	12
Ptilota gunneri P. C. Silva, Maggs et L. M. Irvine				1.2±1.1	+	5.5±3.4	1.1±1.0		4.1±2.9	3.4±1.4	0.4±0.3
P. serrata Kütz.				2.2±1.6	0.1±0.1	15.5±14.9	0.1±0.1		7.9±5.6	0.1±0.1	0.7±0.4
Ptilota sp.					+						
Rhodochorton purpureum (Lightf.) Rosenv.	+	+	+	+	+	+	+		+	+	+
Rhodomela confervoides (Huds.) P. C. Silva	0.1±0.1	0.8±0.6	+	0.2±0.1	+	+	+		+	+	+
Scagelia pylaisaei (Mont.) M. J. Wynne	+	+	+	0.1±0.0	+	+	+		0.2±0.1	0.2±0.2	+
Vertebrata fucoides (Huds.) Kuntze		+	+	0.1±0.1	+	+	+		+	+	0.1±0.1
Number of samples	3	3	2	6	13	5	6	6	4	3	3
Total species number	31	32	26	45	50	50	44	24	41	48	30
Total biomass	319.5±69.6	157.7±92.6	41.9±1.1	97.0±27.5	11.5±2.7	255.4±85.0	15.6±5.3	0.4±0.3	900.8±597.0	54.6±19.1	7.8±2.3

Note. Biomass less than 0.1 gm^{-2} is indicated as +. The contribution of crustose algae were assessed in terms of projective cover only, the presence of such species is marked as ++.

Phytocoenoses near the Cape Kartesh. The red algal belt here spreads from the depths of 7–8 m down to 22–23 m. At the depths from 8 to 10–11 m, two-layer phytocoenosis *Phycodrys rubens+Coccotylus truncatus+Polysiphonia stricta–Pseudolithoderma extensum* included 45 species (38.5 ± 0.9 species/m^2). The first layer is represented by bushy and filamentous forms up to 10–15 cm height; it includes 42 species, the biomass here is 97.0 ± 27.5 g/m^2. The layer of crustose algae is poorly developed, it is represented by the three species; the brown alga *P. extensum* dominates here (PCD 5–20 %). At these depths, several species are the most characteristic representative species of the phytocoenosis, which encountered in each sample: red algae *Ahnfeltia plicata*, *Vertebrata fucoides*, *Rhodomela confervoides*, *Scagelia pylaeaei*, brown algae *Battersia arctica*, *Chaetopteris plumosa*, and green algae *Cladophora rupestris*, *C. sericea*, and *Rhizoclonium riparium*. The abundant representative of zoobenthos, ascidia *Styela rustica* L., 1767, is one of the main holder of the primary stony substrate together with algae.

At a depth of 11–14 m, the phytocoenosis *Coccotylus truncatus+Phycodrys rubens–Lithothamnion glaciale* is formed; it includes 50 species (16.6 ± 2.9 species/m^2). The first layer is represented by bushy forms up to 5–10 cm height; it includes 41 species, the biomass is 11.5 ± 2.7 g/m^2. Most species have negligible biomass. The crustose algae layer is formed by 9 species, their total PCD is 40–55 %. The most common species is red coralline alga *L. glaciale* (average PCD 20–30 %); *Pseudolithoderma extensum* (PCD 10–20 %) is the second most important species of this layer.

At the depth of more than 14–15 m, only crustose algae (5 species) are noted. Although, they are most abundant down to the depths of 17–18 m, where *Lithothamnion glaciale* (PCD 50–80 %) and *Lithophyllum crouaniorum* (PCD 10–30 %) dominate. In the lowest part of the belt, the PCD of algae does not exceed 10 %.

The synusia of epiphytes in this area includes 32 species that settle on 25 species-basiphytes. The most significant basiphytes are *Coccotylus truncatus*, *Phycodrys rubens*, and *Polysiphonia stricta*.

Phytocoenoses near the Sonostrov Island. The red algal belt stretches at the depth range from 7–8 m to 13–14 m. The two-layer phytocoenosis *Odonthalia dentata+Coccotylus brodiei–Pseudolithoderma extensum*, comprising 50 species (43.5 ± 6.0 species/m^2), is formed in the upper part of the belt (7–9 m depth). The first layer is represented by large bushy forms that are up to 15–20 cm height; it includes 44 species, the biomass is 255.4 ± 85.0 g/m^2. *Phycodrys rubens* and *Ptilota serrata* are also quite abundant inhabitants of the first layer; their biomass exceeds 10 g/m^2. The crustose layer is formed by six species, the total PCD is 65–85 %, brown algae *P. extensum* (PCD 50–75 %) and *Ralfsia verrucosa* (PCD 5–25 %) prevail. Several species have been found in each sample, and so they can be classified as the characteristic representative species of phytocoenoses at these depths. These are the red algae *Euthora cristata*, *Fimbrifolium dichotomum*, *Polysiphonia stricta*, *Meiodiscus spetsbergensis*, and brown algae *Battersia arctica*, *Chaetopteris plumosa*, and *Saccharina latissima*; the last species has been found at the stage of germlings.

The middle part of the belt (9–11 m depth) is occupied by a two-layer phytocoenosis *Phycodrys rubens+Coccotylus truncatus–Pseudolithoderma extensum+Lithophyllum crouaniorum*, comprising 44 species (33.7 ± 3.8 species/m^2). The first layer is represented by bushy forms about 5 cm high; it includes 36 species, the biomass is 15.6 ± 5.3 g/m^2. The crustose layer is formed by 8 species, the total PCD is 60–70 %; brown alga *Pseudolithoderma extensum* (PCD 25–35 %) and red coralline alga *Lithophyllum crouaniorum* (PCD 20–30 %) dominate. The most characteristic representative species of phytocoenosis (frequency of occurrence is 100 %) at these depths are red algae *Lithothamnion glaciale*, *Meiodiscus spetsbergensis*, *Polysiphonia stricta*, and *Ptilota serrata*.

The lower part of the belt is occupied by the phytocoenosis of the crustose algae *Lithothamnion glaciale+Lithophyllum crouaniorum*, which includes 24 species (12.7 ± 2.7 species/m^2). The total PCD is 30–45 %, the two dominant species contributes 10–15 % each. In addition to the crustose algae, the phytocoenosis includes also 17 species of bushy forms, which are rare and are characterized by insignificant quantity, so they do not form an independent layer.

The synusia of the epiphytes at the studied site includes 42 species that settle on 25 species-basiphytes. Nine of them are the most important: *Coccotylus brodiei*, *C. truncatus*, *Odonthalia dentata*, *Phycodrys rubens*, *Polysiphonia stricta*, *Ptilota serrata*, *Corrallina officinalis*, *Chaetopteris plumosa*, and *Cladophora rupestris*.

Phytocoenoses near the Bolshoy Zhuzhmuy Island. The red algal belt occupies here the depths from 7–8 m down to 17–18 m. Two-layer phytocoenosis *Phycodrys rubens+Odonthalia dentata–Pseudolithoderma extensum* are formed in the upper part of the belt and include 41 species (37.3 ±1.6 species/m^2). The first layer is represented by large bushy forms up to 15–20 cm height and includes 35 species; biomass here is 900.8 ±597.0 g/m^2. *Coccotylus truncatus* is a relatively abundant species of this phytocoenosis, its biomass reaches more than 10 g/m^2. The biomass of the other species is low. The crustose layer is formed by six species, the total PCD is 15–40 %, and *P. extensum* dominates (PCD 10–30 %). The most characteristic representative species of phytocoenosis (frequency of occurrence of 100 %) at these depths are red algae *Euthora cristata*, *Grania efflorescens*, *Meiodiscus spetsbergensis*, *Polysiphonia stricta*, *Ptilota gunneri*, *Scagelia pylaeaei*, and the germlings of brown alga *Saccharina latissima*.

The middle part of the belt (depths of 9–12 m) is occupied by a two-layer phytocoenosis of *Phycodrys rubens*; 48 species (41.2 ± 3.4 species/m^2) are registered for this community. The species richness of the phytocoenosis is provided mostly by the species of the first layer (45 species). The height of the algae here is mainly 7–10 cm, rare it exceeds 15 cm. The total biomass is 54.6 ± 19.1 g/m^2. The biomass of non-dominant algae is insignificant. The crustose layer is extremely poor: three found here species form small spots; their PCD does not exceed 1–3 %. The most characteristic representative species of phytocoenosis (frequency of occurrence 100 %) at these depths are red algae *Antithamnionella floccosa*, *Coccotylus truncatus*, *Euthora cristata*, *Grania* *efflorescens*, *Meiodiscus spetsbergensis*, *Odonthalia dentata*, *Polysiphonia stricta*, *Ptilota gunneri*, *Rhodomela confervoides*, *Scagelia pylaisaei*, and brown algae *Battersia arctica*, *Chaetopteris plumosa*, and *Desmarestia aculeata*. Along with algae inhabiting this range of depths, barnacles (*Balanus crenatus* Brug., 1789 and *Verruca stroemia* (O. F. Müll., 1776)) are also the main holders of the primary stony substrate here.

Depths from 12–13 m down to 17 m are actually occupied by the same phytocoenosis of *Phycodrys rubens*, but it comprises less species (30 species) and has a lower biomass (7.8 ± 2.3 g/m^2). The height of the algae here does not exceed 5 cm. The abundance of barnacles is also high, especially of *Verruca stroemia*.

The synusia of epiphytes in this area includes 34 species that settle on 24 basiphyte species. The most important basiphytes are *Coccotylus truncatus*, *Odonthalia dentata*, *Phycodrys rubens*, *Polysiphonia stricta*, and *Ptilota serrata*.

Structure of coenopopulations of dominant species. The species *Odonthalia dentata* is a typical representative of the red algal belt, it develops in masse only in the upper part of the belt, where it is the single dominating species or one of the dominants in the algal community. The only exception is the site in the vicinity of the Cape Kartesh area, where this species has been observed in small quantities (Table). The population density of this species varies from 100 to 300 ind./m^2, and rarely reaches 500 ind./m^2. In most of the studied coenopopulations inhabiting the depths of 7–9 m, large plants (more than 5 cm long) have a significant proportion (Fig. 1, *a*). The maximum size of this alga was registered in the Kolvitsa Inlet and in the vicinity of Bolshoy Zhuzhmuy Island (20.5 and 21.5 cm, respectively). As a rule, the life span of the species is 3–4 years; a small number of algae aged 5+ years are noted in the vicinity of the Sonostrov Island; in the area close to the Cape Kartesh, the age spectra is limited to 2+ years (Fig. 1, *c*). The size and age spectra of the coenopopulations narrow as the depth increases (Fig.1, *b*, *d)*: at a depth of 9–11 m, the age of algae does not exceed 3+ years; 50 % and more of the specimens do not exceed a length of 5 cm. This species is rarely found deeper than 10–11 m, usually as a few germlings.

Phycodrys rubens is a characteristic representative of the red algal belt at all depths. In the vicinity of the Bolshoy Zhuzhmuy Island, this species is characterized by much higher biomass (Table) and population density. In the upper part of the belt (depths of 7–9 m), the average population density of this species in most areas varies from 250 to 450 ind./m^2 and reaches about 3000 ind./m^2 in the vicinity of Bolshoy Zhuzhmuy Island. In the coenopopulations inhabiting this range of depths, the contribution of the large algae (more than 5 cm long) to the total abundance is significant, 20–40 % (Fig. 2, *a*); here the largest plants are noted: 22.4 cm and 16.8 cm in the vicinity of the Bolshoy Zhuzhmuy Island and the Cape Kartesh, respectively. As a rule, the life span of this species reaches 3+ years (Fig. 2, *d*), but the algae of 0+ and 1+ age prevail here (75–85 %). At the depths of 9–11 m, the average population density at most sites varies from 100 to 300 ind./m^2; in the vicinity of the Bolshoy Zhuzhmuy Island, it is 1300 ind./m^2. The length of the plants decreases here: as a rule, it does not ex-

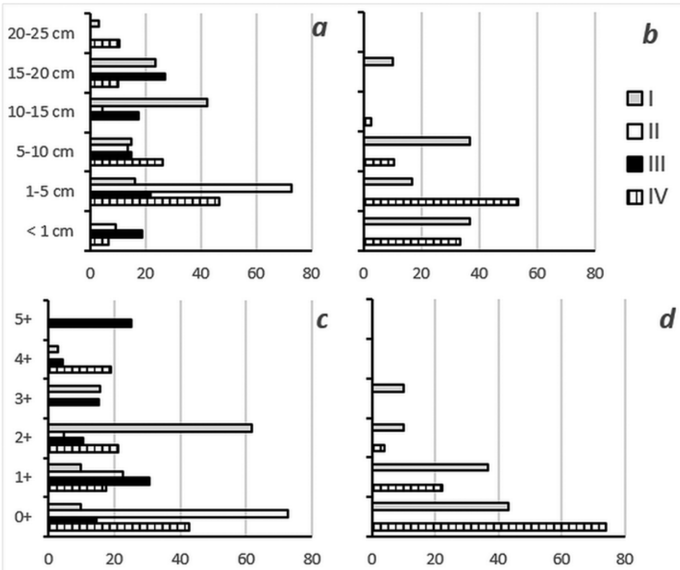

Fig. 1. Size structure (*a*, *b*) and age structure (*c*, *d*) of *Odonthalia dentata* coenopopulations from the different sites at the depths 7–9 m (*a*, *c*) and 9–11 m (*b*, *d*). X-axis: percentage of plants in coenopopulation, %; Y-axis: size groups (*a*, *b*) and age (*c*, *d*). Legend: I–VI — Kolvitsa Inlet, Cape Kartesh, Sonostrov Island and Bolshoy Zhyzhmuy Island, respectively.

ceed 10 cm; in the coenopopulations small (less than 5 cm in length) and young algae predominate (90–98 % and 75–95 %, respectively) (Fig. 2, *b*, *e*). At the depths of 11–14 m, the population density is significantly reduced: in the most areas, from 5 to 30 ind./m². but in the vicinity of the Bolshoy Zhuzhmuy Island, it is about 300 ind./m². In the coenopopulations inhabiting these depths, small plants of 0+ and 1+ age prevail, the large plants (about 10 cm in length) of the two-year-old algae were found among single specimens only in the area of the Cape Kartesh (Fig. 2, *c*, *f*).

The species *Coccotylus truncatus* is a typical representative of the red algal belt and is one of the most abundant species at different depths, including the deepest zone of the distribution of the bushy forms: down to the depths of 14–15 m. In the upper part of the belt (depths of 7–9 m), the average population density of this species varies from 200 to 500 ind./m². As a rule, for the coenopopulations inhabiting this range of depths, a large number of big-size algae (more than 5 cm in length) are usual: from 5–10 up to 25 % (Fig. 3, *a*). At the depths of 9–11 m, the average population density increases, it varies from 250 to 1000 ind./m². However, the overwhelming majority of the algae do not exceed 5 cm in length (Fig. 3, *b*); only in the Kolvitsa Inlet, there was noted a high percentage of large algae (more than 30 %). At the depths of 11–14 m the population density decreases again, varying from 80 to 500 ind./m². The size of algae also decreases: in this range of depths, most algae do not exceed 1 cm in length (Fig. 3, *c*).

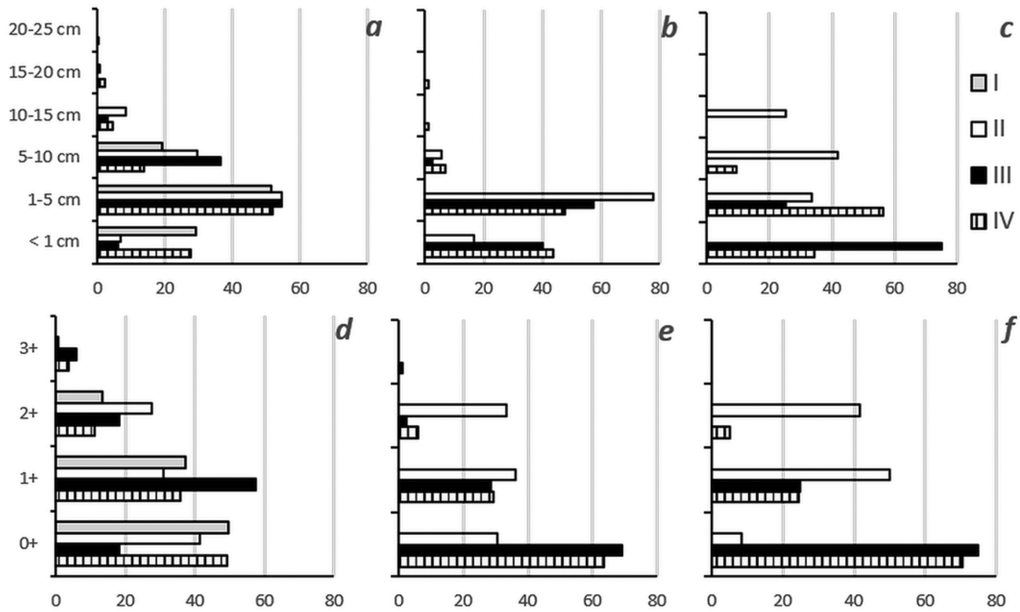

Fig. 2. Size structure (*a–c*) and age structure (*d–f*) of *Phycodrys rubens* coenopopulations from the different sites at the depths 7–9 m (*a*, *d*), 9–11 m (*b*, *e*) and 11–14 m (*c*, *f*). X-axis: percentage of plants in coenopopulation, %; Y-axis: size groups (*a–c*) and age (*d–f*). Legend as in Fig. 1.

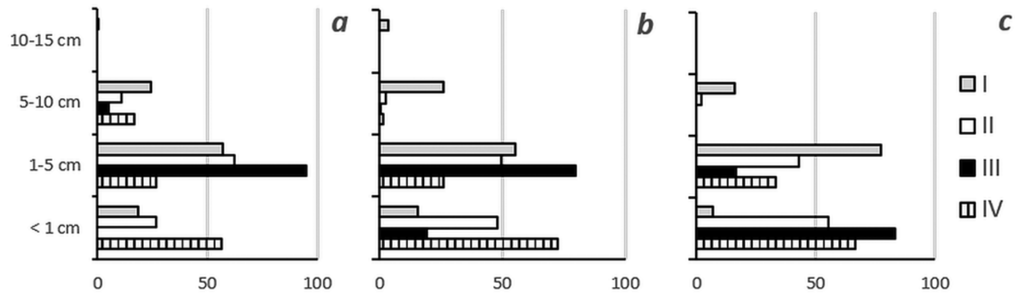

Fig. 3. Size structure of *Coccotylus truncatus* coenopopulations from the different sites at the depths 7–9 m (*a*), 9–11 m (*b*) and 11–14 m (*c*). X-axis: percentage of plants in coenopopulation, %; Y-axis: size groups. Legend as in Fig. 1.

An exception is the sampling site in the Kolvitsa Inlet, where about 90 % of the algae of the coenopopulation are relatively large and belong to the size groups of 5–10 cm (~20 %) and 1–5 cm (~70 %) (Fig. 3, *c*).

The species *Coccotylus brodiei* is found in the red algal belt only in the vicinity of the Sonostrov Island and only at the depths of 7–9 m, where this species is a subdominant by biomass. Its distribution is patchy, the average density of plants is 96.0 ± 58.8 ind./m^2. Different size groups of this species are presented uniformly in the coenopopulation; the maximum length of the alga here is 23.4 cm.

Discussion

The red algal belt in the White Sea follows immediately after the laminarian zone. In the studied areas, the laminarian zone ended at a depth of about 6 m, only single specimens of large kelps were found deeper. At the studied sites, the lowest boundary of the distribution of marine algae referred in the most of cases at the depths of about 20 m. According to our observations, the depth limitation of the algal distribution can be associated with various factors, both abiotic and biotic. For instance, in the vicinity of the Cape Kartesh, where the rock substrate in the deep-water zone was represented sufficiently, the crustose algae were found down to a depth of 22–23 m. On the contrary, in the vicinity of the Sonostrov Island, the rock substrate and, accordingly, the red algal belt were distributed only down to a depth of 13–14 m. In the Kolvitsa Inlet, a pronounced silting prevent the algae spreading down to the margin of the photic zone, and in the vicinity of Bolshoy Zhuzhmuy Island, the rock substrate was almost completely occupied by dense colonies of barnacles. According to the published data, in some areas of the White Sea, the lower boundary of the laminarian zone lies at the depths of 8–12 m, sometimes reaching 15 m (Vozzhinskaya, 1967; Golikov *et al.*, 1882; Golikov *et al.*, 1985a, b; Mikhaylova, 2000b; Pronina, Repina, 2005); the lower limit of the algae distribution goes down to the depths of 25–30 m (Vozzhinskaya, 1967). Taking into account the diversity of the numerous biotopes of the White Sea, it cannot be ruled out that under conditions of sufficient transparency, in the presence of rocky grounds at greater depths, and at the absence of competition from the sedentary animals, the red algal belt may lie deeper and occupy a slightly different depth range comparing to our data.

In the red algal belt, 87 species of algae belonging to the three large taxonomic groups were noted at the studied sites: Chlorophyta (13), Phaeophyceae (33), Rhodophyta (41). Of these, 42 species were observed in the Kolvitsa Inlet, 55 in the vicinity of the Cape Kartesh, 59 in the vicinity of the Sonostrov Island, and 57 species in the vicinity of Bolshoy Zhuzhmuy Island. Twenty-nine species (a third of the total number of species) were common for all the studied sites. Of these, three species of Rhodophyta (*Coccotylus truncatus*, *Phycodrys rubens*, *Polysiphonia stricta*) and one species of Phaeophyceae (*Battersia arctica*) were noted at all sites with a frequency of more than 50 %. Red microscopic alga *Meiodiscus spetsbergensis* has been encountered with similar frequency at three sites. In two of the four studied areas, nine species of Rhodophyta (*Ceramium virgatum*, *Euthora cristata*, *Grania efflorescens*, *Lithothamnion glaciale*, *Odonthalia dentata*, *Rhodochorton purpureum*, *Rhodomela confervoides*, *Scagelia pylaisaei*, *Vertebrata fucoides*), three species of Phaeophyceae (*Chaetopteris plumosa*, *Ectocarpus siliculosus*, *Pseudolithoderma extensum*), and two species of Chlorophyta (*Cladophora rupestris*, *C. sericea*) have been found with high frequency. The remaining

10 common species have been found frequently only at one of the studied sites. Thus, in our opinion, the nineteen species common for all studied sites are the most characteristic for the red algal belt, they are found with high frequency at least in two sites of four studied.

The lowest similarity is observed between the most remote areas — the Kolvitsa Inlet on one hand, and at the vicinities of Sonostrov and Bolshoy Zhuzhmuy islands on the other: the Sørensen coefficient is the same (0.69). On the contrary, the highest similarity (0.74) is noted between the two areas of the Kandalaksha Bay (between Kolvitsa Inlet and Cape Kartesh) and the sites located in the Basin and the Onega Bay (between the Sonostrov and Bolshoy Zhuzhmuy islands).

Phytocoenoses of the red algal belt refer to three associations: (1) association *Odonthalia dentata*(–*Pseudolithoderma extensum*), (2) association *Phycodrys rubens*+*Coccotylus truncatus*(–*Pseudolithoderma extensum*), and (3) association *Lithothamnion glaciale*. The phytocoenoses of the first two associations are two-layered, and sometimes the crustose layer can be slightly expressed; the phytocoenoses of the third association are single-layered.

The association *Odonthalia dentata*(–*Pseudolithoderma extensum*) is common in the upper part of the belt. *Phycodrys rubens*, *Polysiphonia stricta*, *Coccotylus brodiei*, and *C. truncatus* are co-dominants and/or subdominants of the phytocoenoses of this association.

As a rule, the phytocoenoses of the association *Phycodrys rubens*+*Coccotylus truncatus*(–*Pseudolithoderma extensum*) inhabit the middle part of the belt. In some cases, they spread to the upper (Kartesh) and lower (Kartesh, Zhuzhmuy) parts of the belt. In the phytocoenoses of this association, either one of the species may dominate, or both species may act as co-dominants. *Polysiphonia stricta* may be also a subdominant. The mono- and bi-dominant phytocoenoses *Coccotylus truncatus* and *C. truncatus*+*Phycodrys rubens* described in the Kolvitsa Inlet, were mistakenly attributed earlier as the association of *Coccotylus truncatus* (Mikhaylova *et al.*, 2017). In fact, they refer to the association *Phycodrys rubens*+*Coccotylus truncatus*; at this particular site, they are only a special case of the association widespread in the White Sea.

The association *Lithothamnion glaciale*, which includes single-layer phytocoenoses of crustose algae, is distributed in the lower part of the belt. Coralline algae *Lithophyllum crouaniorum* and *Leptophytum laeve* are the subdominants in these phytocoenoses.

In our opinion, the replacement of some associations by other ones or the reduction of particular dominants in the phytocoenoses (Fig. 4) resulted largely from the interrelations with some certain species of the sedentary invertebrates. Thus, the depressed state of vegetation in the upper part of the belt in the area of the Cape Kartesh is due to the fact that the biocoenosis with the dominance of the ascidian *Styela rustica* is developed there. As a result, we observe not only a low algal biomass unusual for this depth range, but also an unusually low biomass of the species *Odonthalia dentata* (Fig. 4), which usually thrives at these depths and forms an independent association. Rough leathery tunic

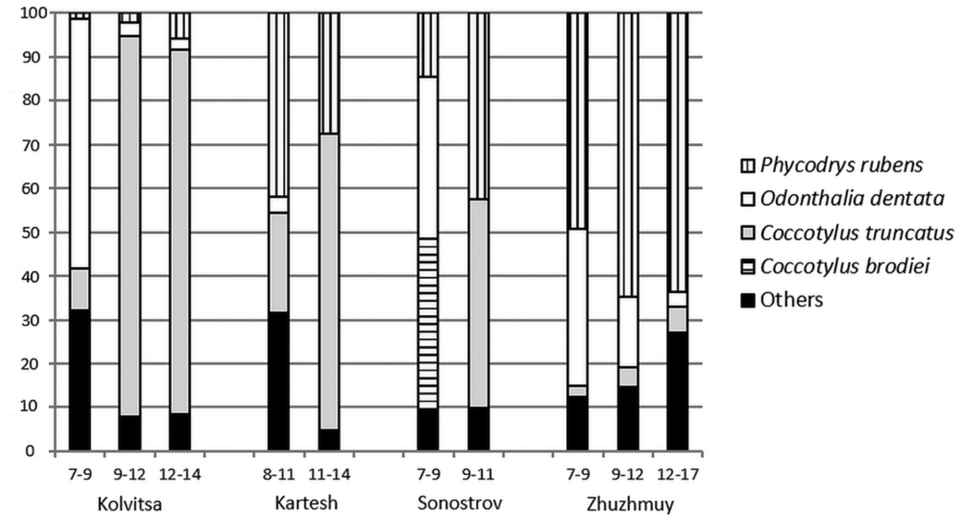

Fig. 4. Contribution of dominant species to the total biomass of phytocoenoses in the red algal belt in the White Sea. X-axis: depth range (m) and locations; Y-axis: percentages.

of ascidians, which are a good substrate for many species of algae (*Phycodrys rubens*, *Coccotylus truncatus*, *Polysiphonia stricta*, etc.), are unsuitable for the development of the long-living large thallus of *O. dentata*. Probably, periodic contractions of the animal's body lead to a breakdown in the strength of the connection with the large holdfast of this algal species and thus do not allow it to develop to an adult state.

Another example is the displacement of algae by the barnacles *Balanus crenatus* and *Verruca stroemia* in the vicinity of Bolshoy Zhuzhmuy Island. This applies not only to crustose algae. According to our observations, the species *Coccotylus truncatus*, unlike *Phycodrys rubens*, is found extremely rare on the barnacle shells and prefers to grow on a stony substrate. At this site, the biomass of *C. truncatus* in the middle and lower parts of the red algal belt is significantly lower when compared to the other sites studied (Fig. 4) due to the almost complete occupation of the substrate by barnacles at this particular depth range.

Finally, the insignificant biomass of the *Phycodrys rubens* in the upper parts of the red algal belt in the Kolvitsa Inlet may be preconditioned by the high abundance of the polychaete *Pista maculata* Marenzeller, 1884. These polychaetes build their tubes using the sand grains. The adhesive substance used by these polychaetes to build their tubes attaches with the same success both to the rocky substrate and to the thalli of the filamentous and foliose algae, so the conglomerates of interconnected algae are formed. The thick blades of *Odonthalia dentata* and *Coccotylus truncatus* are able to hold such tubes, but the thin leaf-like blades of *P. rubens* easily come off. The abundance of *P. rubens* slightly increases only at a depth of 12–14 m (Fig. 4), accompanied by a simultaneous decrease in the abundance of *P. maculata*.

The edificatory function of the dominant species in the red algal belt of the White Sea is not limited to the function of the holders of the substrate; these species are also the most important basiphytes. The basiphyte-epiphyte consortiums, formed by dominant species, provide the species richness of the entire synusia of the epiphytes of the lower part of the phytal zone, increasing the species diversity of the entire belt as a whole.

Generalizing the data obtained, the features of the vertical distribution of the main dominant species are revealed. *Coccotylus truncatus* is a characteristic representative of the red algal belt. According to our observations, it appears in the subtidal zone at a considerable depth of 7–8 m and reaches the depths of 13–15 m almost everywhere.

The species *Coccotylus brodiei* in the White Sea inhabits both in the lower littoral and in the sublittoral zones. According to the literature data, this species was often registered in the red algal belt (Vozzhinskaya, 1967; Golikov *et al.*, 1982, 1985a, 1985b). However, in the areas studied within the present work, and also in accordance with previous original observations, this species rarely goes deeper than 7–8 m. Generally, it is a typical representative of the associations of *Fucus/Ascophyllum* and *Laminaria/Saccharina* algae. In our material sampled at the four geographically distinct sites, it was met only in the vicinity of the Sonostrov Island, on the boundary between the laminarian zone and the red algal belt. In the zone of ecological overlap between the two species of the genus *Coccotylus* (7–9 m), their morphology has similar features.

Our data also do not prove the high abundance of *Polyostea arctica* and species of the genus *Ptilota* (Vozzhinskaya, 1967), as well as *Palmaria palmata* (Golikov *et al.*, 1985b) in the red algal belt of the White Sea. Despite these species have been found at the studied sites, they are not the dominant species there. Moreover, they do not even refer to the characteristic and frequently encountered species of the red algal belt.

Phycodrys rubens and *Odonthalia dentata* are the typical representatives of both the laminarian zone and the red algal belt. The distribution of *P. rubens* down to the depths of 14–15 m in the subtidal zone, its abundance and life span in our collections fits nicely to the data previously reported for the White Sea (Schoschina, 1996; Shoshina, 1990a). At the same time, our data do not support the previous results on the depth distribution of *O. dentata* in the White Sea. Particularly, Shoshina (1990b) marks this species as dominant in the red algal belt of the White Sea down to a 15 m depth. According to our data obtained at the four sites located in different regions of the White Sea, this species prefers the depths that do not exceed 8–9 m and rarely descends deeper than 11 m. The life span of *O. dentata* in our collections generally corresponds to the age range indicated in the published data (Shoshina, 1990b), but the maximum age for this alga reported for the White Sea (7+ years) was not recorded within this study. Taking into account that Shoshina (1990b) sampled the algae in a shallower zone (depths of 2–5 m), the full age spectrum is characteristic for the coenopopulations of this species that inhabit the associations of laminarian algae, where it is abundant.

For the last fifty years, the kelp belt boundaries has shifted to the shallower depths, as well as the overall lower boundary of the marine vegetation distribution did; in addition, several species in the red algae belt are nowadays characterized by significantly lower abundance than it has been reported in 1960s–1980s (Vozzhinskaya, 1967; Golikov *et al.*, 1882, 1985a, 1985b; Mikhaylova, 2000b; Shoshina, 1990b). Such evidence is a warning signal about the ongoing change in the ecological state of the White Sea.

Conclusion

At all the studied sites, the upper boundary of the red algal belt lies at a 7 m depth. The lower boundary of the belt refers to different depths: 14 m in the vicinity of the Sonostrov Island, 17–18 m in the Kolvitsa Inlet and in the vicinity of Bolshoy Zhuzhmuy Island, and 22–23 m in the vicinity of the Cape Kartesh. The boundaries of the red algal belt in other parts of the White Sea may vary depending on the characteristics of the biotopes.

Algae distribution in the red algal belt of the White Sea depends on the geomorphological structure of the bottom and on the composition of the accompanying sedentary fauna. The vegetation of the red algal belt is characterized by considerable species richness and diversity in various parts of the White Sea.

In total, in the red algal belt, 87 species of algae belonging to the three large taxonomic groups were noted at the studied sites: Chlorophyta (13), Phaeophyceae (33), Rhodophyta (41). Of these, 42 species were observed in the Kolvitsa Inlet, 55 in the vicinity of the Cape Kartesh, 59 in the vicinity of the Sonostrov Island, and 57 species in the vicinity of Bolshoy Zhuzhmuy Island. Nineteen species are the most characteristic for the red algal belt of the White Sea, including thirteen species of red algae, four species of brown algae, and two species of green algae.

Phytocoenoses of the red algal belt refer to three associations: association *Odonthalia dentata*(–*Pseudolithoderma extensum*), association *Phycodrys rubens*+*Coccotylus truncatus*(–*Pseudolithoderma extensum*), and association *Lithothamnion glaciale*.

The peculiarities of the vertical distribution of the dominant species of the red algal belt have been revealed in the White Sea, these data substantially supplement the earlier conceptions. An additional edificatory function of the algae has been found, especially of the key and the most characteristic representatives of the belt: they serve as the consorts bearing a rich epiflora and forming conditions for increasing the species diversity of the lower phytal zone.

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