ISSN 0001-4370, Oceanology, 2021, Vol. 61, No. 2, pp. 244–253. © Pleiades Publishing, Inc., 2021.
Russian Text © The Author(s), 2021, published in Okeanologiya, 2021, Vol. 61, No. 2, pp. 276–285.

MARINE BIOLOGY

Effects of *Cystoseira* Sensu lato (Fucales: Phaeophyceae) on Species Richness, Composition, and Biomass of Abrau Peninsula Shelf Macrophytobenthic Communities (Black Sea)

D. F. Afanasyev[a], * **and V. V. Akatov**[b]

[a] *Azov–Black Sea Branch, Russian Federal Research Institute of Fisheries and Oceanography, Rostov-on-Don, 344002 Russia*
[b] *Maikop State Technological University, Maikop, 385000 Russia*
**e-mail: dafanas@mail.ru*

Received February 13, 2020; revised September 9, 2020; accepted September 15, 2020

Abstract—Field observations were applied to study the macrophytobenthos of the Abrau Peninsula of the Black Sea and the effect of the two most common and largest species of brown algae of the Black Sea sublittoral, *Cystoseira bosphorica* and *Treptacantha barbata* (*Cystoseira* sensu lato), on species richness and phytocenosis biomass, as well as biomass and the occurrence of related macroalgae species of different ecological groups. In total, 48 species of macroalgae were found in *Cystoseira* assemblages, including 27 species of Rhodophyta; 11 species of Ochrophyta, Phaeophyceae; and 10 species of Chlorophyta. It was shown that two- to fourfold decrease in the *Cystoseira* biomass in communities as a whole does not significantly affect their species richness but leads to a decrease in the total biomass of these cenoses and a multidirectional change in participation (biomass, occurrence) of many species of macroalgae. The response of the cenoses to a decrease in biomass of *C. bosphorica* and *T. barbata*, as well as its negative character—a decrease in productivity and species richness—was more pronounced at greater depths.

Keywords: Black Sea, Abrau Peninsula, macrophytobenthos, *Cystoseira* sensu lato, species richness, biomass, epiliths, epiphytes

DOI: 10.1134/S0001437021020028

INTRODUCTION

Out of the 46 valid species of *Cystoseira* sensu lato dominant on the shelf of the Mediterranean Sea and adjacent areas of the Atlantic Ocean [29, 36], only five were found in the Black Sea and only two species were widespread: *Cystoseira bosphorica* (previously identified here as *C. crinita*) and *Treptacantha barbata* (=*C. barbata*) [15, 16, 29, 40]. Both species grow in a wide range of depths (from 0.2–0.3 to 10–15 m) and play a significant role in the formation of benthic plant communities, accounting for the larger fraction of their biomass [5, 10, 12, 33, 34]. However, in recent decades, as a result of the impact of many factors (a decrease in the water transparency, eutrophication, introduction of alien species, destruction of biotopes, increase in recreational load, climate change, etc.), the penetration depth, area, and total biomass of the *Cystoseira* tangle are decreasing; in addition, the phytodiversity of large areas of the Black Sea shelf is decreasing [3–5, 8–10, 12–14, 17, 33, 34, 43].

Degradation (decrease in productivity and species richness) of *Cystoseira* communities can be the result of both a synchronous (independent) response of populations of dominants and associated species to unfavorable changes in habitat and a decrease in the participation of *C. bosphorica* and *T. barbata* in their formation. At the same time, the role of the second factor in this process remains unclear, for at least three reasons. First, *Cystoseira* can have both negative (competition) and positive (as shelter, substrate) effects on other species. Second, they can dominate at different depths, and the nature of the influence of dominants on the species richness of phytocenoses may differ under different environmental conditions. It is known that the more severe these conditions, the weaker the competitive effect of dominants on the accompanying species, but the stronger the protective functions of such species are manifested [1, 2, 18, 19]. There is evidence that this pattern is typical of both terrestrial and aquatic (benthic marine) communities [19, 25, 30, 45]. Third, studies on Black Sea phytobenthos, with a few exceptions [20, 34], hardly investigated at all interspecific relations, including the influence of dominants on the state of other macroalgae species populations.

The aim of our study was to quantitatively assess the joint influence of species of the genus *Cystoseira* sensu lato on accompanying macroalgae species, species richness, composition, and biomass of communities in general, by comparing areas of cenoses (samples) with relatively high and low biomasses of these species.

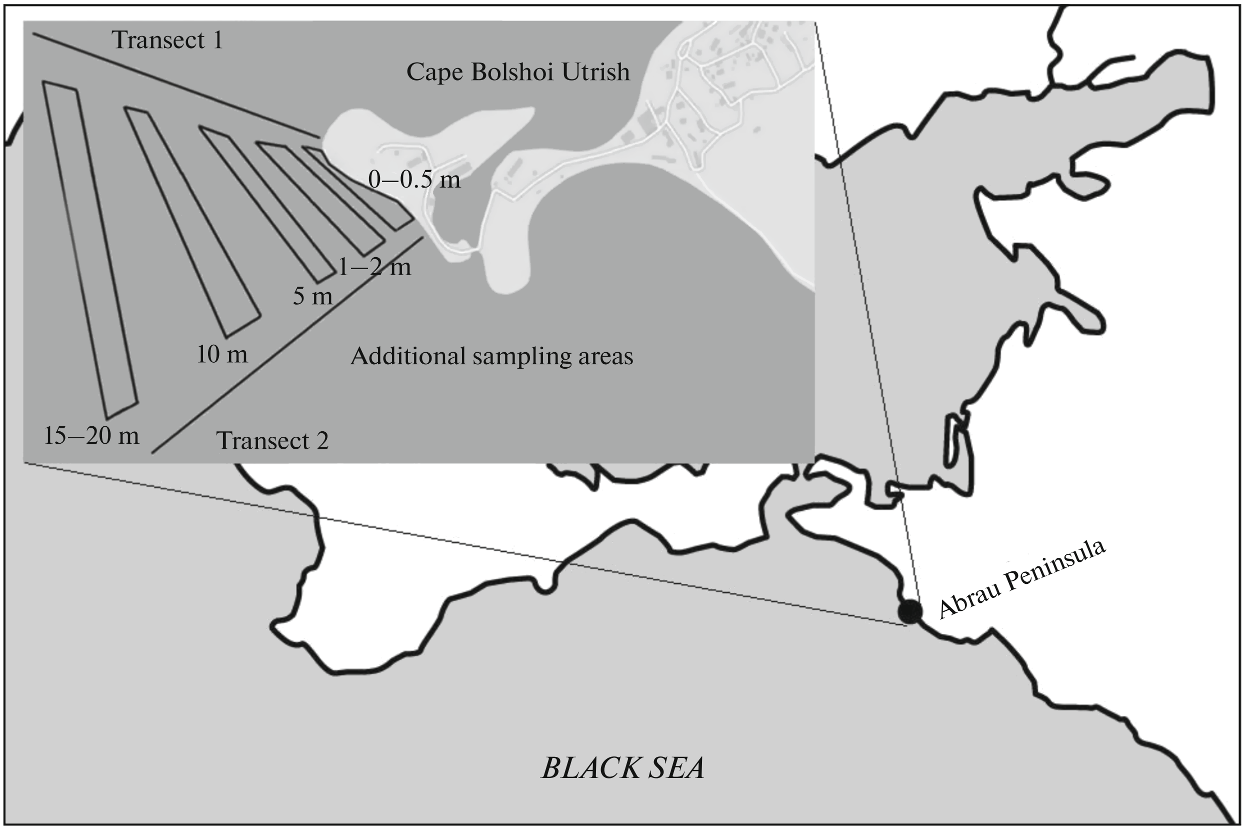

Fig. 1. Study area and sampling map.

MATERIALS AND METHODS

Methods for Collecting Factual Material

The study is based on 155 samples of the macrophytobenthos taken from June 29 to August 8, 2018, on the shelf of the Black Sea near Cape Bolshoi Utrish (Krasnodar krai; Abrau Peninsula) (Fig. 1). One hundred and ten samples were taken in *Cystoseira* communities (0.3–10 m), 29 at shallower depths (0 and 0.15 m, dominant *Ceramium ciliatum*), and 16 at a depth of 15–20 m (dominants *Codium vermilara* and *Phyllophora crispa*). In *Cystoseira* communities, samples were taken at depths of 0.3–0.5 (25 samples), 1–2 (38), 5 (26), and 10 m (21).

Samples were taken from an area of 0.25 m^2 in homogeneous habitats. The majority of the samples at each depth were taken in a regular way on two transects of ten sites. Samples taken on transects at the same depth were at a distance from 1 to 8–10 m from each other, depending on the bottom topography. Additionally, several more samples were taken to increase the contrast of the sampling between transects. In this case, the plots were established in the areas of communities with the highest and lowest projective cover of *C. bosphorica* and *T. barbata*, which was assessed visually. All macrophytic algae from each frame were collected in a separate gauze bag using a set of scrapers. Then each sample was sorted according to species, dried with filter paper, and each species was weighed [35]. Cortical algae and microepiphytes were not considered.

Analysis Methods

Analysis of the factual material included the following steps:

(1) For each sample (site), the values of the following indicators were calculated: (1) total wet algal biomass per 1 m^2 (W); (2) biomass of each species (W_i); (3) joint biomass of *C. bosphorica* and *T. barbata* (W_C); (3) total biomass of accompanying species ($W_S = W - W_C$); (4) number of accompanying macroalgae species per 0.25 m^2 (S_S, local species richness).

(2) Samples with dominant *Cystoseira* from each depth were ranked according to increasing total biomass of these species (W_C), then divided into two equal or approximately equal (with a difference of one sample) groups: with biomass values above the median (high biomass, HBC) and with biomass values below the median (low biomass, LBC). For each selected group, the following was determined: total number of accompanying species (N_S), average values of the above characteristics (Table 1), average values of the

biomass of each species (taking into account samples in which the species was not present) (W_A), as well as their occurrence (proportion of samples in a group with the presence of a species to the total number of samples, F). The average values of the biomass of the species are shown in Table 2; their occurrence values are shown in Table 3.

(3) In order to assess the nature of changes in the occurrence and biomass of accompanying species with decreased participation of *Cystoseira* (synchronous or compensatory), we compared the values of characteristics W_A and F for each species in groups of samples with low and high *Cystoseira* density. The statistical significance of the differences between the W_A values was estimated using one-way analysis of variance (ANOVA); between F values, using Student's *t*-test.

(4) If a decrease in participation of *Cystoseira* affects the distribution and occurrence of accompanying macroalgae species, then this may affect the degree of homogeneity of the species composition of algocenoses at different depths. As an indicator of the species similarity of the studied areas of the communities, we used the Sorensen coefficient (K_s = 2C/(A + B), where A and B are the number of species in the groups of samples from two compared areas (depths); C is the total number of species in the compared areas). Species similarity between all sites was estimated, and individual estimates were obtained for variants with low and high *Cystoseira* participation. The significance of their difference (mean similarity values) was determined by ANOVA.

RESULTS AND DISCUSSION

In total, 48 macroalgae species were identified in the studied *Cystoseira* cenoses, including 27 species of red (Rhodophyta), 11 brown (Ochrophyta, Phaeophyceae), and 10 green (Chlorophyta).

The values of indicators characterizing whole macrophytobenthos communities with high and low *Cystoseira* biomass are shown in Table 1. The following can be seen from Table 1:

(1) The total biomass of *C. bosphorica* and *T. barbata* was maximum at depths of 1–2 m. At shallower (0.3–0.5 m) and greater depths (5 and 10 m), it was lower. At all depths, the total biomass of samples with HBC on average was statistically significantly higher than that with LBC.

(2) In the upper phytal zone (from 0.3 to 2 m), a high abundance of accompanying species was observed in samples with a low participation of *Cystoseira*. Conversely, at depths of 5 and 10 m, a high biomass of accompanying species was found in samples with a high biomass of *Cystoseira*. The share of biomass of accompanying species in samples with LBC was higher than in cenoses with HBC, and at shallow depths, the difference was statistically significant; at great depths it was not (Table 1).

It also follows from the table that in areas with a low density of *Cystoseira* in the composition of accompanying species dominance of epiliths was observed (76–99% of the biomass of accompanying species at all depths, except 5 m). The increase in abundance of basiphytes (*Cystoseira*) was accompanied by an increased role of epiphytes.

(3) At the shallowest (0.3–0.5 m) and deepest (10 m) areas, the contribution of species of different ecological groups (epiphytes and epiliths) to the biomass of associated species of communities with HBC was approximately the same. Epiphytes prevail at depths of 1–2 and 5 m. A decrease in the biomass of *Cystoseira* by 2.2–3.9 times in groups with LBC led to a significant decrease in the participation of epiphytes (by 1.8–13.1 times) and an increase in the participation of obligate epiliths (by 1.3–10.1 times). As a result, in most areas with LBC, obligate epiliths were the dominant group among the associated species in terms of biomass.

(4) For most depths, the number of epiphyte species recorded in samples with LBC was lower, and epiliths were both higher and lower than in samples with a high participation of *Cystoseira*. As a result, at most depths, the total number of species recorded in samples with LBC was slightly lower than in samples with their high participation. In general, for all depths, 35 species were recorded in the first group, and 39 species were revealed in the second. At depths from 0.3 to 5 m, samples with low participation of *Cystoseira* were characterized by higher average values of local richness (S_S) than samples with a higher biomass of these species; however, these differences were not statistically significant. At a depth of 10 m, on the contrary, a decrease in the biomass of *Cystoseira* corresponded to a decrease in S_S, and the difference was statistically significant.

Tables 2 and 3 present data on the average biomass (W_A) and occurrence (F) of accompanying macroalgae species in communities with different participation of *Cystoseira*. Clearly, the species have different reactions to a decrease in the *Cystoseira* biomass and, according to these characteristics, can be combined into three groups: (1) species that increase the biomass and occurrence at most depths (compensatory or positive response); (2) species that reduce the values of these characteristics (synchronous or negative response) and (3) species with an indeterminate response (having approximately the same or both higher and lower W_A and F values in the samples of the compared groups).

The first group consists of eight species (17% of the total number of accompanying species). These are obligate (*Padina pavonica*, *Dictyota fasciola*, *Phyllophora crispa*, *Cladostephus spongiosum,* and *Cladophoropsis membranacea*) and facultative (*Ceramium ciliatum*, *Gelidium crinale*, and *Laurencia coronopus*) epiliths, which have predominantly competitive rela-

Table 1. Biomass and species richness of communities of the Abrau Peninsula of Black Sea with high and low biomass of *C. bosphorica* and *T. barbata*

Indexes	Samples with high *Cystoseira* biomass				Samples with low *Cystoseira* biomass			
Depth, m	0.3–0.5	1–2	5	10	0.3–0.5	1–2	5	10
Number of samples	13	19	13	11	12	19	13	10
Cystoseira biomass (g/m^2)	3087.0 ± 353.3	4318.9 ± 313.2	3245.1 ± 151.0	718.3 ± 41.3	785.0 ± 143.5*	1602.9 ± 159.2*	1510.1 ± 161.8*	197.9 ± 47.0*
Total biomass (g/m^2)	3227.0 ± 392.8	4540.8 ± 323.5	3439.0 ± 162.1	763.5 ± 41.8	1063.2 ± 133.5*	1955.5 ± 145.1*	1600.2 ± 160.2*	218.8 ± 48.7*
Biomass of accompanying species (g/m^2), including:	140.0 ± 56.8	221.9 ± 30.4	193.8 ± 39.8	45.2 ± 12.2	278.2 ± 71.3	352.6 ± 74.4	90.1 ± 15.4*	20.9 ± 5.7
epiliths	94.2 ± 35.3	114.0 ± 31.2	7.3 ± 2.3	26.8 ± 12.4	274.7 ± 73.4*	292.4 ± 79.6*	31.7 ± 11.1*	15.9 ± 6.5*
epiphytes	45.7 ± 26.1	107.9 ± 29.2	186.5 ± 40.1	18.4 ± 5.0	3.5 ± 0.6	60.2 ± 25.0	58.4 ± 12.3*	5.0 ± 1.8*
Share of biomass of accompanying species, %	4.3 ± 0.04	4.9 ± 0.5	5.6 ± 1.0	5.9 ± 0.1	26.2 ± 5.0*	18.0 ± 0.9*	5.6 ± 0.1	9.6 ± 4.0
Mean number of accompanying species per 0.25 m^2 (S_S)	7.5 ± 0.4	7.4 ± 0.5	6.9 ± 0.5	7.9 ± 0.6	8.4 ± 0.8	7.9 ± 0.3	8.5 ± 0.7	5.9 ± 0.6*
Total number of accompanying species (N_S), including:	22	31	21	24	19	25	29	20
epiliths	12	15	9	14	14	14	17	12
epiphytes	10	16	12	10	5	11	12	8
Total number of species in all samples	39				35			

* Statistically significant difference in mean values of characteristics in groups of samples with high and low *Cystoseira* biomass (ANOVA, *F*-criterion, p 0.05); mean values are shown with standard errors.

Table 2. Average biomass of algal species (W_A, g/m^2) in different communities of Abrau Peninsula of Black Sea

Species	Communities with dominance of *Ceramium ciliatum*		Communities with dominance of *C. bosphorica* and *T. barbata*								Communities with dominance of *Phyllophora crispa* and *Codium vermilara*
			samples with high *Cystoseira* biomass				samples with low *Cystoseira* biomass				
Depth, m	0	0.15	0.3–0.5	1–2	5	10	0.3–0.5	1–2	5	10	15–20
Cystoseira bosphorica	4.69	320.73	1994.40	3339.81	2485.46	405.93	605.90	1020.62	1108.38	109.77	2.75
Treptacantha barbata			1092.58	979.10	759.66	312.36	179.10	582.24	401.68	88.16	0.06
Species with a predominantly compensatory response (group 1)											
Ceramium ciliatum	1699.33	1225.18	0.54	–	–	–	**11.30***	**0.02**	–	–	0.01
Padina pavonica	–	1.35	–	–	–	–	**136.85***	**2.42***	**0.85***	–	–
Dictyota fasciola	–	2.32	0.15	–	–	0.37	**2.71**	**0.88***	**0.67**	**0.51**	0.01
Phyllophora crispa	–	–	–	–	–	–	–	–	**2.69***	**5.49***	149.83
Gelidium crinale	–	–	1.18	1.44	–	**0.23**	**27.94***	**3.52***	**0.80***	0.16	0.01
Laurencia coronopus	0.87	20.21	0.79	0.63	1.47	**0.23**	**1.62**	**0.84**	**2.95**	–	–
Cladostephus spongiosum	–	–	**25.13**	14.91	0.01	3.05	20.65	**94.33**	**15.62***	**4.16**	0.14
Cladophoropsis membranacea	–	–	**22.37**	65.81	0.05	**0.14**	16.54	**181.04***	**1.09***	–	–
Species with a predominantly synchronous response (group 2)											
Laurencia obtusa	–	–	**0.09**	**8.24**	**18.17**	**3.84***	0.05	3.19	11.72	1.33	0.03
Ceramium deslongchampsii	–	–	–	**15.06***	**20.26***	**3.11***	–	–	–	–	–
Sphacelaria cirrosa	–	–	**10.96**	**7.97**	**3.07**	**0.91**	3.02	5.12	1.82	0.17	0.01
Chaetomorpha linum	–	–	**0.22**	**0.18**	**0.09**	**0.06**	0.05	0.11	0.03	0.01	0.01
Ceramium siliquosum var. *elegans*	–	–	**24.69**	**11.31**	**4.44**	–	–	7.59	2.06	–	0.01
Vertebrata subulifera	–	–	**3.69**	1.06	**44.99**	**4.97**	0.16	**26.76**	12.63	0.30	0.03
Polysiphonia opaca	–	–	**0.96**	**4.48**	**2.49**	–	–	–	–	–	–
Stilophora nodulosa	–	–	**0.06**	**0.38**	**0.47**	–	–	0.18	0.05	–	–
Polysiphonia sanguinea	–	–	–	**54.53**	**88.81**	**4.32**	**0.01**	11.57	22.57	2.83	–
Ceramium diaphanum	–	–	**0.49**	**2.98**	0.45	**0.01**	–	0.01	**1.52**	–	–
Palisada paniculata	–	–	**1.43**	–	**0.97**	–	–	–	–	–	–
Species with indefinite response and/or low biomass (group 3)											
Ellisolandia elongata	–	–	**1.44**	2.74	**2.12**	**0.95**	0.29	**6.00**	1.28	0.54	0.01
Gelidium spinosum	–	–	**0.05**	0.47	**0.71**	**0.17**	0.01	**1.36**	0.26	0.12	0.02
Ceramium virgatum	–	–	**4.31**	1.87	**2.59**	–	–	**3.01**	0.63	–	0.01
Cladophora albida	281.08	287.09	**8.86**	**5.44**	–	–	4.00	1.64	**0.08**	**0.01**	0.01
Ectocarpus siliculosus	–	–	**0.12**	–	–	**8.29**	–	–	**0.95**	0.50	0.04
Ulva sp.	–	–	32.43	**15.96**	–	–	**35.30**	–	**0.05**	–	–
Cladophora sp.	–	–	–	**0.47**	**0.38**	**0.04**	**0.02**	0.02	–	0.03	–
Pterothamnion plumula	–	–	–	**0.37**	–	**0.66**	–	0.20	**0.26**	0.05	–
Codium vermilara	–	–	–	–	–	**6.91**	–	–	–	3.82	337.88
Apoglossum ruscifolium	–	–	–	–	–	**6.29**	–	–	**4.53***	0.50	0.04
Jania rubens	–	–	–	–	0.07	**0.13**	–	**0.95**	**0.12**	0.01	0.01
Florideophyceae indet.	–	–	–	**0.42**	–	0.24	–	–	**4.85**	**0.25**	–
Chondria capillaris	–	–	–	–	–	**0.17**	–	–	–	0.10	–
Cladophora liniformis	–	–	–	**0.42**	–	**0.02**	–	–	–	0.01	–
Jania virgata	–	–	–	–	**0.03**	**0.05**	–	–	–	–	–

Species found in single quantities only in communities with a high *Cystoseira* biomass: *Vertebrata reptabunda*, *Osmundea pinnatifida*, *Stilophora tenella*, *Ulva rigida*, *Punctaria tenuissima*, *Chondria dasyphylla*, *Striaria attenuata*?. Species found in single quantities only in communities with a low *Cystoseira* biomass: *Chaetomorpha aerea*, *Bryopsis plumosa*, *Ceramium secundatum*, *Hypnea musciformis*?, *Lomentaria clavellosa*?.
Higher values of W_A in groups of samples with different participation of *Cystoseira* are highlighted in bold;
Species of neighboring communities not found in *Cystoseira* communities are not shown in table.

Table 3. Occurrence of algal species (F) in different communities of Abrau Peninsula of Black Sea

Species	Communities with dominance of *Ceramium ciliatum*		Communities with dominance of *C. bosphorica* and *T. barbata*								Communities with dominance of *Phyllophora crispa* and *Codium vermilara*
			samples with high *Cystoseira* biomass				samples with low *Cystoseira* biomass				
Depth, m	0	0.15	0.3–0.5	1–2	5	10	0.3–0.5	1–2	5	10	15–20
Cystoseira bosphorica	0.67	1	0.85	1	1	1	**0.92**	1	0.92	0.90	0.06
Treptacantha barbata			**0.46**	0.74	0.85	1	0.25	**0.9**	0.85	1	0.13
Species with a predominantly compensatory response (group 1)											
Ceramium ciliatum	1	1	0.23	–	–	–	**0.67***	**0.11**	–	–	0.13
Padina pavonica	–	–	–	–	–	–	**0.54**	**0.11**	**0.15**	–	–
Dictyota fasciola	–	0.75	0.15	–	–	0.18	**0.25**	**0.26***	**0.14**	**0.3**	0.06
Phyllophora crispa	–	–	–	–	–	–	–	–	**0.15***	**0.4**	0.75
Gelidium crinale	–	–	**0.85**	0.37	–	0.18	0.83	**0.79***	**0.46***	**0.2**	0.06
Laurencia coronopus	0.67	0.75	0.15	0.11	0.23	**0.18**	**0.42**	0.11	**0.31**	–	–
Cladostephus spongiosum	–	–	0.54	0.42	0.08	**0.36**	**0.58**	**0.63**	**0.46***	**0.3**	0.13
Cladophoropsis membranacea	–	–	**0.85**	0.32	0.08	**0.18**	0.75	**0.79***	**0.62***	–	0.06
Species with a predominantly synchronous response (group 2)											
Laurencia obtusa	–	–	0.08	**0.42**	0.54	**0.91***	**0.08**	0.32	**0.77**	0.5	0.06
Ceramium deslongchampsii	–	–	–	**0.42***	**0.62***	**0.55***	–	–	–	–	–
Sphacelaria cirrosa	–	–	**0.92**	0.84	1	1	0.92	**1**	1	1	0.13
Chaetomorpha linum	–	–	**0.77**	0.58	**0.46**	**0.36**	0.58	**0.68**	0.39	0.2	0.13
Ceramium siliquosum var. *elegans*	–	–	**0.08**	**0.32**	**0.54**	–	–	0.16	0.23	–	0.13
Vertebrata subulifera	–	–	0.08	0.16	0.39	**0.46**	0.08	**0.21**	**0.62**	0.4	0.31
Polysiphonia opaca	–	–	**0.08**	**0.05**	**0.08**	–	–	–	–	–	–
Stilophora nodulosa	–	–	**0.08**	0.05	0.15	–	–	0.05	0.15	–	–
Polysiphonia sanguinea	–	–	–	**0.47**	**0.62**	0.36	**0.33**	0.32	0.39	**0.5**	–
Ceramium diaphanum	–	–	**0.15**	**0.16**	0.08	**0.09**	–	0.11	0.08	–	–
Palisada paniculata	–	–	**0.15**	–	**0.08**	–	–	–	–	–	–
Species with indefinite response and/or low biomass (group 3)											
Ellisolandia elongata	–	–	0.77	**0.9**	0.77	**0.82**	**0.83**	0.84	0.77	0.6	0.06
Gelidium spinosum	–	–	0.15	0.21	**0.46**	0.09	**0.17**	**0.42**	0.23	**0.1**	0.19
Ceramium virgatum	–	–	**0.08**	0.11	**0.39**	–	–	0.11	0.08	–	0.13
Cladophora albida	1	1	**0.85**	0.42	–	–	0.75	**0.58**	**0.08**	**0.1**	0.06
Ectocarpus siliculosus	–	–	**0.08**	–	–	**0.46**	–	–	**0.08**	0.2	0.38
Ulva sp.	–	–	**0.31**	**0.11**	–	–	0.25	–	**0.15**	–	–
Cladophora sp.	–	–	–	**0.21**	0.08	0.09	**0.08**	0.05	–	**0.1**	–
Pterothamnion plumula	–	–	–	0.05	–	**0.18**	–	0.05	**0.07**	0.1	–
Codium vermilara	–	–	–	–	–	0.09	–	–	–	**0.2**	1
Apoglossum ruscifolium	–	–	–	–	–	**0.55**	–	–	**0.31***	0.3	0.06
Jania rubens	–	–	–	–	0.15	**0.27**	–	**0.05**	**0.39**	0.1	0.13
Florideophyceae indet.	–	–	–	**0.05**	–	0.09	–	–	**0.07**	**0.1**	–
Chondria capillaris	–	–	–	–	–	**0.18**	–	–	–	0.1	–
Cladophora liniformis	–	–	–	**0.05**	–	**0.18**	–	–	–	0.1	–
Jania virgata	–	–	–	–	**0.07**	**0.09**	–	–	–	–	–

Higher F values in groups of samples with different *Cystoseira* participation are in boldface.
* Statistically significant difference in F in groups of samples with high and low *Cystoseira* participation ($p < 0.05$, t-test).
Species of neighboring communities not found in *Cystoseira* communities are not shown in table.

tionships with *Cystoseira*. Most of them (six out of the eight species) have a very low abundance in communities with a high participation of *Cystoseira* or they almost never occur in them. In particular, *Ceramium ciliatum* and *Phyllophora crispa* penetrate into the sparse *Cystoseira* tangle from adjacent cenoses (from shallower and deeper areas), where they are dominant.

Another two species from this group, *Cladostephus spongiosum* and *Cladophoropsis membranacea,* have a less definite response to a decrease in participation of *Cystoseira*. As follows from our data, at depths from 1 to 10 m, they clearly preferred areas with a low density of *Cystoseira*, while at 0.3–0.5 m, this effect is not pronounced. It can be assumed that in shallow waters, under conditions of high wave activity, these species use the *Cystoseira* canopy as shelter, and at great depths, they compete with them for substrate. Interestingly, *Cladophoropsis membranacea* has demonstrated an increase in occurrence and biomass in recent decades compared to the 1950s–1970s. [34]. Therefore, it is possible that the increase in occurrence of this species is associated with a weakening of topical competition with *Cystoseira*.

Group 2 included 11 species (24% of the total number of associated species). These were mainly epiphytes (*Sphacelaria cirrosa*, *Laurencia obtusa*, *Vertebrata subulifera* etc.), which were expected to respond negatively to a decrease in the total biomass of *Cystoseira* and two species that are capable of epilithic growth (*Chaetomorpha linum* and *Polysiphonia opaca*). Most of the species of this group are considered characteristic and constant for *Cystoseira* communities [6, 7].

The third group consists of 15 species (33%) belonging to different ecological groups (obligate and optional epiliths, epiphytes). It can be suggested that these are macroalgae more or less indifferent to the effect of the considered factor, as well as species that were less abundant in our study (*Ellisolandia elongata*, *Gelidium spinosum*, *Ceramium diaphanum*, *C. virgatum*) the response of which to changes in *Cystoseira* biomass is difficult to determine. The group also included *Codium vermilara*, which rarely grows in *Cystoseira* communities, regardless of the degree of their dominance at the sites.

Lastly, we found some species in single samples (listed in the caption to Table 2). Seven of them were found only in samples with a high *Cystoseira* biomass, and five, in samples with a low biomass. This was a heterogeneous group, consisting of rare species, as well as species confined to other habitats and uncharacteristic of *Cystoseira* communities.

In general, as follows from Tables 2 and 3, among the ten obligate epiliths found in all areas, half were characterized by a higher occurrence and biomass in areas with LBC. The rest of the epiliths showed no particular preference in this regard. Among the 20 epiphytes that we identified at all depths, only 9 clearly preferred the areas of communities with a high *Cystoseira* biomass. At the same time, among the 16 species capable of growing both as epiliths and as epiphytes, only one-third showed a positive or negative response to a change in *Cystoseira* abundance.

It also follows from Tables 2 and 3 that at depths of 0.3–0.5 m, six species (a quarter of the total number of species identified at this depth) have a well-pronounced response (positive or negative) to a change in participation of *Cystoseira*; at depths of 1–2 m, 12 species (one-third of species identified at this depth); at depth of 5 m, 14 species (41%); and at depth of 10 m, 11 species (42%). Thus, the proportion of such species increased with depth. However, at depths of 0.3–5 m, the number of species responding positively to a decrease in *Cystoseira* biomass was somewhat higher than the number of species with the opposite response. At a depth of 10 m, the response of species to this effect was predominantly negative (in nine versus two species). This may mean that the role of *Cystoseira* as a species forming cenosis increases with depth.

The average values of the Sorensen species similarity coefficient between the sites of cenoses with HBC were 0.68 ± 0.02, $n = 6$; with LBC, 0.70 ± 0.04, $n = 6$. As can be seen, the difference between them is small and not statistically significant (ANOVA, $F_{4.96} = 0.31$, $p = 0.05$). This suggests that a two- to fourfold change in the participation of *Cystoseira* did not significantly affect the degree of species homogeneity (differentiation) of macrophytobenthos along the depth gradient.

The phenomenon when a decrease in the abundance or loss of some species from communities is accompanied by an increase in the number of others is known as the density compensation effect (DCE) [24, 28, 31]. It can be accompanied by a niche (spectrum of occupied habitats) expansion of the remaining species and, in this case, it is part of a broader concept: the ecological release effect [24, 28]. It was assumed that the DCE can contribute to stabilization of the functional parameters of ecosystems with a decrease in their species richness and is one of the indicators of the role of interspecies competition in the structuring of communities [21, 28, 48]. It was shown that the exchange surface in the basiphyte–epiphyte system remains at a relatively constant level in the eutrophication and water mobility gradient: a decrease in productivity of Black Sea *Cystoseira* is compensated by an increase in the role of production (and biomass) of epiphytes [11].

Thus, if we interpret our results using this concept, we can conclude that both the niche expansion effect (penetration of new species into communities at their upper and lower boundaries) and DCE (the decrease in *Cystoseira* biomass by 50–75% was accompanied by an increase in biomass of obligate epiliths) were revealed in the studied communities. However, the degree of their manifestation can be considered low, since in absolute values the compensatory growth of the epilithic biomass was significantly lower on the whole than the decrease in total *Cystoseira* biomass: at depths of 0.3–0.5 m, by 16 times; 1–2 m, by 14 times; 5 m, by 87 times; and 10 m, by 168 times. Moreover, as can be seen from these data, the intensity of compensatory processes decreased with depth. It is also known that the lower phytal zone underwent the most intense degradation during the period of global restructuring of the Black Sea ecosystem [14, 17, 33, 34].

In the Mediterranean Sea, species with similar importance, in addition to *T. barbata* (*C. bosphorica* is most likely absent in the Mediterranean Sea [22]), are other species of the genus *Cystoseira* and related genera of brown algae (*Cystoseira* sensu lato): *C. compressa*, *C. amentacea* var. *stricta*, *C. usneoides*, *Carpodesmia tamariscifolia*, *C. crinita*, *C. zosteroides*, *Treptacantha sauvageauana*, *T. ballesterosii*). All these species have thalli with a developed three-dimensional structure, which ensures the formation of additional habitats and ecological niches for plants and animals settling here [37, 38, 42, 44]. All these species of *Cystoseira* sensu lato are dominants of associations of the same name at depths from 0.5 to 10–15 m and deeper [26, 27, 39]. In recent decades, in the Mediterranean Sea, due to warming and anthropogenic impact, *Cystoseira* have become rarer and their disappearance has been accompanied by a significant decrease in species diversity of the cenoses [23, 32, 41, 46, 47]. The main accompanying species able to inhabit the vacant niches and form new communities are *Padina pavonica*, *Dictyota dichotoma*, *Ellisolandia elongata*, and *Halopteris scoparia* [23], e.g., species (or their vicar analogs) that in our study also demonstrated an exclusively positive (*Padina pavonica*, *Dictyota fasciola*) or positive at some depths (*Ellisolandia elongata*) response to a decrease in the proportion of *Cystoseira* in the cenosis (*Halopteris scoparia* in the Black Sea is now encountered very rarely).

Such observations in weakly perturbed and slightly polluted regions of the Black Sea are rare; among them is the discovery of a significant reduction of *T. barbata* tangle on the Mary Magdalene Bank by the beginning of the 21st century and distribution of *Cladostephus spongiosum* [34], which also agrees with our data.

Thus, our results show that a two- to fourfold decrease in the participation of *Cystoseira* in the macrophytobenthic communities of the Russian Black Sea shelf unassociated with a significant change in the quality of the environment generally has no significant effect on the species richness of communities and the degree of homogeneity (differentiation) of vegetative cover along the depth gradient. However, this leads to a decrease in the total biomass of these cenoses and multidirectional change in the participation (biomass, occurrence) of many accompanying macroalgae species. In this case, negative consequences were observed for about 50% of the epiphytic species of these communities; positive consequences were revealed for the species of adjacent cenoses at shallower and greater depths, as well as for about half the epilithic species. At the same time, the response of cenoses to decreased biomass of *C. bosphorica* and *T. barbata*, as well as its negative character (decrease in productivity and species richness), was more pronounced at greater depths.

ACKNOWLEDGMENTS

The authors are sincerely grateful to the reviewers for their critical comments, which significantly improved the article.

FUNDING

The study was financially supported by the Russian Foundation for Basic Research (project nos. 16-04-00228 and 20-04-00364).

COMPLIANCE WITH ETHICAL STANDARDS

This article does not contain any studies involving animals or humans performed by any of the authors.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

REFERENCES

1. V. V. Akatov, T. V. Akatova, and C. G. Chefranov, “The relationship of dominance and evenness with productivity and species richness in plant communities with different organization models,” Russ. J. Ecol. **49**, 296–305 (2018).
2. V. V. Akatov, T. V. Akatova, and S. G. Chefranov, “Plant communities in harsh and favorable environments: characteristics of their organization, their dominant structure and its relationship to species richness,” Biol. Bull. Rev. **10**, 215–229 (2020).
3. D. F. Afanasyev, “Reserves of some species of macrophytes on the Russian shelf of the Black Sea: current state, long-term dynamics, and analysis of the dynamics,” Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. **155**, 161–168 (2008).
4. D. F. Afanasyev, “Assessment of reserves and distribution of some species of macrophytes on the Russian shelf of the Black Sea,” Rastit. Resur. **45** (3), 51–59 (2009).
5. D. F. Afanasyev and I. G. Korpakova, *Macrophytobenthos of Russian Azov-Black Sea Basin* (Azov-Black Sea Branch, All-Russian Scientific Research Institute of Marine Fisheries and Oceanography, Rostov-on-Don, 2008) [in Russian].
6. D. F. Afanasyev, Sh. R. Abdullin, and M. M. Sereda, “Ecological-floristic classification of bottom vegetation of the Russian shelf of the Black Sea,” Izv. Samar. Nauchn. Tsentra, Ross. Akad. Nauk **14** (1), 963–966 (2012).
7. D. F. Afanasyev, A. N. Kamnev, D. V. Seskova, and E. G. Sushkova, “Seasonal dynamics of *Cystoseira crinita* Duby, 1830 (Fucales: Phaeophyceae)–dominated communities in the northeastern Black Sea,” Russ. J. Mar. Biol. **43**, 425–435 (2017).

8. E. I. Blinova, M. Yu. Saburin, and O. A. Belenkina, "Conditions of phytocenosises and growing *Cystoseira* in the Black Sea," Rybn. Khoz. (Moscow), No. 12, 42–45 (1991).
9. O. Yu. Vilkova, "Modern reserves of *Cystoseira* spp. in the Russian part of the Black Sea," in *Marine Coastal Ecosystems: Algae, Invertebrates, and Their Processing Products* (VNIRO, Moscow, 2005), pp. 20–22.
10. V.V. Gromov, Doctoral Dissertation in Biology (Komarov Botanical Institute, Russian Academy of Sciences, St. Petersburg, 1998).
11. S. E. Zavalko, "Epiphyting of marine macrophytes as an adaptation to eutrophication and water mobility," Biol. Morya (Vladivostok), No. 6, 36–42 (1988).
12. A. A. Kalugina-Gutnik, *Phytobenthos of the Black Sea* (Naukova Dumka, Kiev, 1975) [in Russian].
13. A. A. Kalugina-Gutnik, "Development of phytobenthos studies," in *Marine Biological Studies* (Kovalevsky Institute of Biology of the Southern Seas, Sevastopol, 1994), pp. 65–80.
14. O. V. Maksimova and N. P. Luchina, "The current state of macrophytobenthos near the coast of the North Caucasus: the phytal zone reaction to the eutrophication of the Black Sea basin," in *Complex Studies in the Northeastern Part of the Black Sea* (Nauka, Moscow, 2002), pp. 297–308.
15. N. A. Mil'chakova, "Red algae (Rhodophyceae) of the Black Sea: taxonomic composition and distribution," Int. J. Algae **5** (4), 1–13 (2003).
16. N. A. Mil'chakova, "New species of macrophytes of the Black Sea flora," Ekol. Morya, No. 62, 19–24 (2002).
17. N. A. Mil'chakova, "Macrophytobenthos," in *The Current State of Biological Diversity of Coastal Waters of Crimea (the Black Sea Sector)* (EKOSI-Gidrofizika, Sevastopol, 2003), pp. 152–208.
18. B. M. Mirkin and L. G. Naumova, *The Current State of General Scientific Concepts about Vegetation* (Gilem, Ufa, 2012) [in Russian].
19. V. G. Onipchenko, *Functional Phytocenology: Synecology of Plants* (Krasand, Moscow, 2013) [in Russian].
20. U. V. Simakova, "Influence of the sea bottom relief on the *Cystoseira* communities of the North Caucasian coast of the Black Sea," Oceanology (Engl. Transl.) **49**, 672–680 (2009).
21. P. B. Adler and J. B. Bradford, "Compensation: an alternative method for analyzing diversity-productivity experiments," Oikos **96**, 411–420 (2002).
22. D. Berov, E. Ballesteros, M. Sales, and M. Verlaque, "Reinstatement of species rank for *Cystoseira bosphorica* Sauvageau (Sargassaceae, Phaeophyceae)," Cryptogam.: Algol. **36** (1), 65–80 (2015).
23. M. Catra, G. Alongi, R. Leonardi, M. Negri, R. Sanfilippo, F. Sciuto, D. Serio, A. Viola, and A. Rosso, "Degradation of a photophilic algal community and its associated fauna from eastern Sicily (Mediterranean Sea)," Mediterr. Mar. Sci. **20** (1), 74–89 (2019).
24. K. L. Crowell, "Reduced interspecific competition among the birds of Bermuda," Ecology **43**, 75–88 (1962).
25. A. M. Ellison, "Foundation species, non-trophic interactions, and the value of being common," iScience **13**, 254–268 (2019).
26. G. Giaccone, G. Alongi, F. Pizzuto, and A. Cossu, "La vegetazione marina bentonica fotofila del Mediterraneo: II. Infralitorale e Circalitorale: proposte di aggiornamento," Boll. Sedute Accad. Gioenia Sci. Nat. Catania **27** (346), 111–157 (1994).
27. G. Giaccone, G. Alongi, F. Pizzuto, and A. Cossu, "La vegetazione marina bentonica sciafila del Mediterraneo: III: Infralitorale e Circalitorale: proposte di aggiornamento," Boll. Sedute Accad. Gioenia Sci. Nat. Catania **27** (346), 201–227 (1994).
28. A. Gonzalez and M. Loreau, "The causes and consequences of compensatory dynamics in ecological communities," Annu. Rev. Ecol. Evol. Syst. **40**, 393–414 (2009).
29. M. D. Guiry and G. M. Guiry, AlgaeBase, National University of Ireland, Galway, 2020. http://www.algaebase.org.
30. B. B. Hughes, "Variable effects of a kelp foundation species on rocky intertidal diversity and species interactions in central California," J. Exp. Mar. Biol. Ecol. **393**, 90–99 (2010).
31. R. H. MacArthur, J. M. Diamond, and J. R. Karr, "Density compensation in island faunas," Ecology **53**, 330–342 (1972).
32. F. P. Mancuso, E. M. A. Strain, E. Piccioni, O. De Clerck, and G. Sarà, "Status of vulnerable *Cystoseira* populations along the Italian infralittoral fringe, and relationships with environmental and anthropogenic variables," Mar. Pollut. Bull. **129** (2), 762–771 (2018).
33. O. V. Maximova and N. A. Moruchkova, "Long-term anthropogenic transformation and contemporary state of the North Caucasian macrophytobenthos (Black Sea)," Oceanology (Engl. Transl.) **45**, S168–S175 (2005).
34. O. V. Maximova, N. A. Moruchkova, and U. V. Simakova, "The state of macrophytobenthos. Northeastern (Russian) shelf area," in *State of the Environment of the Black Sea (2001–2006/7)* (Commission on the Protection of the Black Sea Against Pollution, Istanbul, 2008), pp. 233–239.
35. G. G. Minicheva, D. F. Afanasyev, and A. B. Kurakin, *Black Sea Monitoring Guidelines: Macrophytobenthos* (Istanbul, 2014).
36. S. Orellana, M. Hernández, and M. Sansón, "Diversity of *Cystoseira* sensu lato (Fucales, Phaeophyceae) in the eastern Atlantic and Mediterranean based on morphological and DNA evidence, including *Carpodesmia* gen. emend. and *Treptacantha* gen. emend.," Eur. J. Phycol. **54** (3), 447–465 (2019).
37. J. Otero-Schmitt and J. L. Pérez-Cirera, "Epiphytism on *Cystoseira* (Fucales, Phaeophyta) from the Atlantic coast of northwest Spain," Bot. Mar. **39** (1–6), 445–466 (1996).
38. J. M. Pérès and J. Picard, *Nouveau Manuel de Bionomie benthique de la Mer Méditerranée* (Station Marine d'Endoume, Aix-en-Provence, 1964).
39. G. Reilni and G. Giaccone, "Priority habitats according to the SPA/BIO protocol (Barcelona Convention) present in Italy. Identification sheets," Biol. Mar. Mediterr. **16** (1), 365 (2009).
40. M. A. Ribera, A. Gómez-Garreta, T. Gallardo, M. Cormaci, G. Furnari, and G. Giaccone, "Check-

list of Mediterranean seaweeds. I. Fucophyceae (Warming 1884)," Bot. Mar. **35**, 109–130 (1992).

41. M. Sales and E. Ballesteros, "Shallow *Cystoseira* (Fucales: Ochrophyta) assemblages thriving in sheltered areas from Menorca (NW Mediterranean): relationships with environmental factors and anthropogenic pressures," Estuarine, Coastal Shelf Sci. **84**, 476–482 (2009).
42. R. Sanfilippo, A. Rosso, F. Sciuto, D. Serio, and M. Catra, "Serpulid Polychaetes from *Cystoseira* communities in the Mediterranean Sea," Vie Milieu **67** (3–4), 217–226 (2017).
43. A. Sburlea, "The state of macrophytobenthos. Romanian shelf area," in *State of the Environment of the Black Sea (2001–2006/7)* (Commission on the Protection of the Black Sea Against Pollution, Istanbul, 2008), pp. 223–227.
44. F. Sciuto, A. Rosso, R. Sanfilippo, G. Alongi, and M. Catra, "First data on ostracods and foraminifera living in *Cystoseira* communities in western Ionian Sea (southern Italy, Mediterranean Sea)," Mediterr. Mar. Sci. **18**, 393–405 (2018).
45. J. Templado, "Future trends of Mediterranean biodiversity," in *The Mediterranean Sea: its History and Present Challenges* (Springer-Verlag, Dordrecht, 2014), pp. 479–498.
46. T. Thibaut, A. Blanfune, C. F. Boudouresque, and M. Verlaque, "Decline and local extinction of Fucales in the French Riviera: the harbinger of future extinctions?" Mediterr. Mar. Sci. **16**, 206–224 (2015).
47. T. Thibaut, S. Pinedo, X. Torras, and E. Ballesteros, "Long-term decline of the populations of Fucales (*Cystoseira* spp. and *Sargassum* spp.) in the Albères coast (France, North-western Mediterranean)," Mar. Pollut. Bull. **50**, 1472–1489 (2005).
48. W. M. Tonn, "Density compensation in *Umbra–Perca* fish assemblages of Northern Wisconsin lakes," Ecology **66**, 415–429 (1985).

Translated by V. Mittova