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Article

The phytomass and dominant complex of benthic producers in the hydrological natural monument "Coastal aquatic complex at Cape Sarych" (the Black Sea)

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Abstract. Phytobenthos studies in the waters of Cape Sarych suggest that Heterokontophyta is the basic producer among the divisions and *Ericaria crinita*, *Gongolaria barbata*, *Vertebrata subulifera*, *Phyllophora crispa* among the species. Indicators of benthic phytomass vary widely, being the least at great depths. By-depth changes of the cenosis phytomass and Heterokontophyta demonstrate similarity. Location of the phytomass maximum (0.5 m for Chlorophyta and 5 m for the rest) clearly indicates its dependence on light regime at the horizons and photopigment composition in species of different divisions. In terms of intra-annual dynamics, phytomass peak is noted in spring for Chlorophyta and Heterokontophyta, while for Rhodophyta and the entire phytocenosis in summer. It is characterized by strong manifestation. Long-term observations at the reference site show a threefold increase (over 20 years) in the benthic phytomass due to the Heterokontophyta development. Productional heterogeneity of the cenosis, estimated from the Shannon and Pielou indices, is lower in time than in space. By indicators of halobity and saprobity, marine and oligosaprobic species dominate by phytomass and species diversity. Brackish-water, poly- and mesosaprobic species develop en masse in sites with anthropogenic pressure.

Keywords: macrophytobenthos, biomass, occurrence, spatiotemporal variability, indicator groups, Crimea

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Научная статья

Фитомасса и доминантный комплекс бентосных продуцентов гидрологического памятника природы «Прибрежный аквальный комплекс у мыса Сарыч» (Черное море)

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Аннотация. Исследование фитобентоса акватории мыса Сарыч показало, что базовым продуцентом среди отделов является Heterokontophyta, среди видов – *Ericaria crinita*, *Gongolaria barbata*, *Vertebrata subulifera* и *Phyllophora crispa*. Фитомасса бентоса варьирует широко с минимумом на больших глубинах. Направленность изменений фитомассы ценоза и Heterokontophyta по глубинам идентична. Локация максимума фитомассы (0.5 м – у Chlorophyta, 5 м – у остальных) наглядно подтверждает зависимость от светового режима на горизонтах и состава фотопигментов у видов разных отделов. Для внутригодовых изменений фитомассы характерен ее весенний максимум у Chlorophyta и Heterokontophyta, летний – у Rhodophyta и всего фитоценоза, а также высокая степень проявления. Многолетние наблюдения в реперной точке показывают, что за 20 лет фитомасса бентоса увеличилась втрое за счет Heterokontophyta. Продукционная неоднородность ценоза, оцененная по индексам Шеннона и Пиелу, во времени ниже, чем в пространстве. Среди индикаторов галобности и сапробности среды по фитомассе и видовому разнообразию лидируют морские и олигосапробные виды, на участке с антропогенным прессом массово развиваются солоноватоводные, поли- и мезосапробные.

Ключевые слова: макрофитобентос, биомасса, встречаемость, пространственно-временная изменчивость, индикаторные группы, Крым

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Introduction

The development of a new paradigm for biota protection, based on the idea of biodiversity conservation, started in the late 1980s. The concept of vegetation as an integral form of structural and functional organization of phytobiota in two manifestations, i.e. qualitative (floristic) and quantitative (phytocenotic) should be the theoretical basis of the new approach. The emerging problem of planning and developing the methods for exploitation and protection of marine bottom vegetation requires the creation of a database on the phytocenoses structure at the local and regional levels. The information on the qualitative and quantitative indicators of biotas in the protected natural areas is of particular importance. The absence of such information makes formal the process of regional econetworks establishment (Belich et al., 2019; Evstigneeva and Tankovskaya, 2022; Sadogursky et al., 2019) that hinders the development of the system of criteria for identifying the marine areas in need of protection (Darbyshire et al., 2017; Edgar et al., 2008; Heino, 2010).

The regional hydrological natural monument (NM) "Coastal aquatic complex at Cape Sarych" (CAC) serves as an example of the protected natural area. NM, being a part of Laspi Bay, is located in the southwest of the Crimea. The bay has long been considered as one of the clean water areas in the Sevastopol region. Its open type provides dynamic activity and aeration of waters. Previously, it was less susceptible to wastewater discharges, in contrast to other bays of the Crimea southern coast. In recent years, the situation has drastically changed because of the increased interest to the bay coast as a promising building area. Multi-story buildings are currently being erected on its slopes and near Cape Sarych that causes the destruction of endangered plants, a reduction in forest areas and the activation of landslide processes (Pankeeva and Mironova, 2022). Nowadays, the growing biological oxygen consumption is observed in Laspi Bay and at Cape Sarych even at a considerable distance from the coast. In opinion of researchers, the source of pollution is wastewater discharged from the sewage treatment plant of Foros village (Zaskokov, 2017). In these conditions, it is reasonable to comply with the legally regulated principles of activities in the protected areas, among which is the conducting of investigations and monitoring of consequences of the economic development (Mokievsky, 2002).

The relevance of the study, the results of which are presented in this article, is in great importance of the data on phytomass and species differentiation (by their participation in the productional process) needed for a complete understanding of marine phytocenoses. Phytomass is an indirect characteristics of the productional potential of individual species of macroalgae and their groups (Papchenkov, 2003; Rabotnov, 1978). Besides, it is worth noting that phytocenoses are the complex systems not only of biologically, but also ecologically different plant species. By response to salinity and saprobity, we specify the indicator groups of halobity and saprobity. The level of their development and position in the structure of benthic communities allow assessing the state of benthic habitats (Kalugina-Gutnik, 1975).

The aim of the work is to study the quantitative features of the benthic phytocenosis and the composition of the dominant complex of producers, as well as to perform structural and functional analysis of the development and distribution of indicator ecological groups in the protected waters of the "Coastal Aquatic Complex at Cape Sarych".

Materials and methods

The work is based on the analysis of macrophytobenthos (MPB) collected in the summer of 2020 via using a geobotanical technique modified for the underwater research (Kalugina, 1969). Sampling was implemented with the use of the lightweight diving equipment and a small vessel. Macroalgae were harvested in quadruple replicates in three vertical hydrobotanical sections from depths of 0.5, 1, 3, 5, 10 and 15 m, at the 25×25 cm permanent quadrates. Fig. 1 shows the layout of sections.

Section **I** is located in the Tunnel Rock area, section **II** in the central part of the protected area (with a city beach and wastewater discharge site), section **III** – near Mayak (Lighthouse). For establishing their coordinates, we used GPS receiver Oregon 650. A total of 56 quantitative and 20 qualitative samples were collected. In the course of their processing, the species composition of algae was identified by means of the identification Key with regard for modern nomenclature changes (Zinova, 1967; AlgaeBase[1]). The Pielou (E) and the Shannon species diversity (H) indices calculated from the biomass of the community populations were applied to describe the phytocenosis structure (Rosenberg, 2010). Groups of dominants, subdominants, secondary and minor species of the community were specified by the E.L. Lyubarsky scale, taking into account the phytomass of individual species. The frequency of key producers' dominance was defined according to De Vries (Bakanov, 2005).

For assessing the spatiotemporal variability of the community characteristics, their mean values with a confidence interval and the variation coefficient (C_v, %) were calculated (Zhukova and Minets, 2019). Based on C_v, the level of variability of traits by the scale of G.N. Zaitsev was established as upper and lower normal, significant, large, very large, abnormally high) (Zaitsev, 1990). For description of the intra- and interannual dynamics of the productional potential of MPB in Cape Sarych, we used the results of our own research conducted at the same depth (0.5 m) in March–October 2007 and in summer of 2002–2020 within the Mayak area (section **III**).

Fig. 1. The study area: hydrobotanical sections and CAC boundaries. Section I – N 44°23.569′ E 033°43.616′, Tunnel Rock; Section II – N 44°23.475′ E 033°43.839′, the central part of NM; Section III – N 44°23.243′ E 033°44.267′, Mayak.

[1] AlgaeBase. World-wide electronic publication, National University of Ireland, Ireland. Web page. URL: http://www.algaebase.org (accessed: 20.05.2023).

Results and discussion

Section I (Tunnel Rock)

The total biomass of macroalgae at the stations of section I is not uniform and fluctuates as 1313–7773 g/m^2 (Table 1).

At depths from 1 to 10 m, Heterokontophyta (Het) species predominate followed by the representatives of Rhodophyta (Rh), leading in other horizons. Green algae (Chlorophyta, Ch) are recorded at a depth of 0.5 and 1 m. In terms of production, they occupy the second and third place after red algae. The curves describing the spatial dynamics of the absolute phytomass largely coincide for the phytocenosis and Het that emphasizes the role of the latter as key producers of MPB (Fig. 2). The spatial location of the absolute phytomass maximum differs for various divisions. With allowance made for the coefficient of variation of the absolute phytomass, the divisions and cenosis are arranged as Ch > Het > cenosis > Rh, where the Rh phytomass exhibits the greatest spatial stability.

By relative phytomass, Het are also in the lead at all horizons, except for 0.5 m. At the shallowest depth, the dominant position is occupied by Rh species.

Among divisions, the contribution of Het to the average total phytomass of the cenosis is the largest (66%) and Ch is the smallest (1.1%). The average phytomass of the latter is basically provided by *Cladophora sericea* (Huds.) Kütz, accounting for approximately 1% of the average phytomass of the cenosis and 92% of the total phytomass of all green algae in this section. Among brown algae, *Ericaria crinita* (Duby) Molinari et Guiry (63%) takes the most active part in the productional process. *Vertebrata subulifera* (C. Agardh) Kuntze and *Phyllophora crispa* (Huds.) P.S. Dixon are the main producers among red algae (about 70% of the average phytomass in this section). *Palisada perforata* (Bory) K.W. Nam dominate solely at a depth of 0.5 m (Table 2).

According to De Vries, the frequency of dominance for *Ericaria crinita* is 67%, for *Phyllophora crispa* and *Vertebrata subulifera* – 17%. All key producers belong to the group of oligosaprobes - indicators of clean waters. Subdominants in this section are represented by 8 species with a predominance of red algae, primarily the species *Ceramium* Roth. At shallow depths, the richest floristic composition of the subdominant group includes a representative of green algae. In contrast to the dominant complex of producers, the subdominant one consists of both oligosaprobes and species indicators of medium and high trophicity, as well as the marine environment desalination.

Values of the Shannon index vary greatly demonstrating their maximum and minimum at 0.5 and 15 m, respectively. At a depth of 0.5 m, the habitat conditions of algae are diverse and highly dynamic that contributes to the polydominant phytocenoses formation here. More uniform habitat conditions at greater depths provide the development of a limited number of species. The average index of H (1.5) is evidence of a transitional (poly- and monodominant) type of the study community. The Pielou index makes up 0.3. Values of both indices illustrate the heterogeneity of the bottom cenosis in terms of phytomass.

The system of productional dominance, based on the relative phytomass data, includes the species of all categories, except for the dominants. The first position is occupied by the species of little (by phytomass) significance, every fifth is a secondary species (Table 3).

Section II (center of the NM)

In section II, the absolute phytomass of MPB varies widely. Its lowest values are recorded for large depths; in the rest part of the phytal zone it is 5–7 times greater. Het species dominate at depths from 0.5 to 5 m, while Rh at 10 and 15 m. Green algae are noted at 0.5, 1 and 5 m, where they are in the second (0.5 m) and third place (1 and 5 m) by productional activity. The absolute biomass of the phytocenosis and Het demonstrate the same trend in spatial changes (Fig. 2). Dynamics of the analyzed indicator for Rh and cenosis is also similar, but only below a 5 m horizon. According to the values of C_v, the divisions and cenosis are located as follows: Ch> Het > Rh > cenosis. By depth, the distribution of the absolute and relative phytomass of divisions corresponds to each other. Dynamics of the relative phytomass of Rh is directly dependent on habitat depths. For Het, this indicator increases with depth from 0.5 to 1 m and then their relationship becomes inverse. Oscillating variations in the absolute phytomass are characteristic of the cenosis.

Table 1. Parameters of spatial phytomass variability in the divisions and cenosis of sections. X_{avr} is the average, Δ – the confidence interval, $x_{min} - x_{max}$ are minimum and maximum values, C_v,% – the variation coefficient.

Section	Parameters and level of variability of the phytomass (B, $g \cdot m^{-2}$)					
	$x_{avr} \pm \Delta$	$x_{min} - x_{max}$	range of values	$C_{v,\%}$	level	depth
			Chlorophyta			
I	51.4 ± 98.4	0.004–302.5	302.4	239	abnormally high	0.5 m
II	44.9 ± 707.7	0.1–2205.3	2205.2	213	abnormally high	0.5 m
III	23.4 ± 23.3	0.004–68.8	6883.6	124	abnormally high	10 m
			Heterokontophyta			
I	3110.1 ± 2294.4	110.2–6100.0	5989.8	92	large	1 m, 3 m
II	3441.8 ± 2084.7	49.2–6271.6	6222.4	76	large	1 m
III	3714.0 ± 2972.0	12.6–6621.9	6609.3	72	large	5 m
			Rhodophyta			
I	1577.1 ± 568.2	838.56–2854.4	2015.8	45	significant	5 m
II	1823.3 ± 962.0	552.7–4009.0	3456.3	66	significant	5 m
III	1964.4 ± 957.7	901.2–4051.3	3150.1	61	significant	5 m
			phytocenosis			
I	4738.6 ± 2487.5	1312.7–7773.5	6460.9	66	significant	1 m, 3 m, 5 m
II	5680.1 ± 2608.5	1370.3–9098.7	7728.4	57	significant	5 m
III	5707.3 ± 2713.5	1967.6–10673.3	8705.4	59	significant	5 m

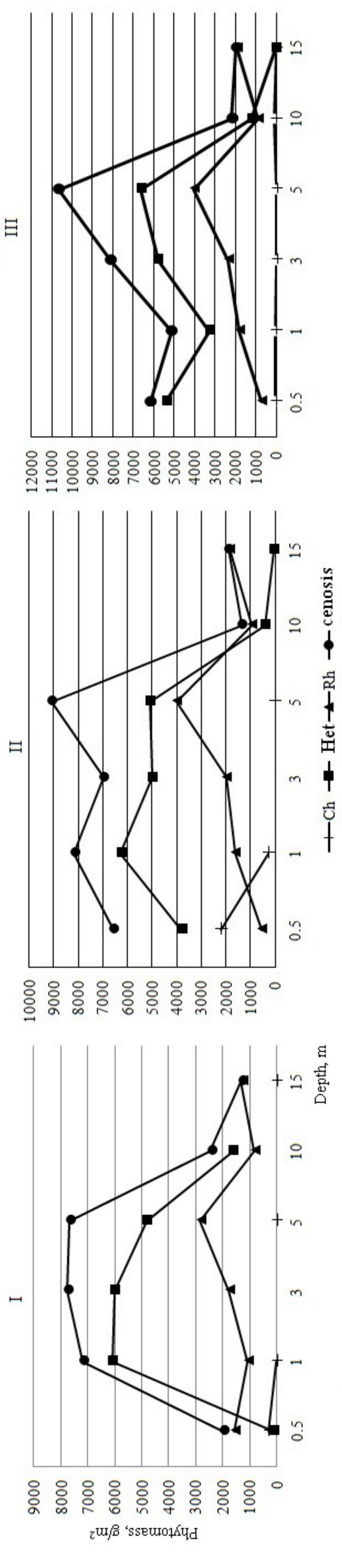

Fig. 2. Bathymetric changes of the absolute phytomass in CAC at Cape Sarych. I, II, III – section numbers; Ch – Chlorophyta, Het – Heterokontophyta, Rh – Rhodophyta.

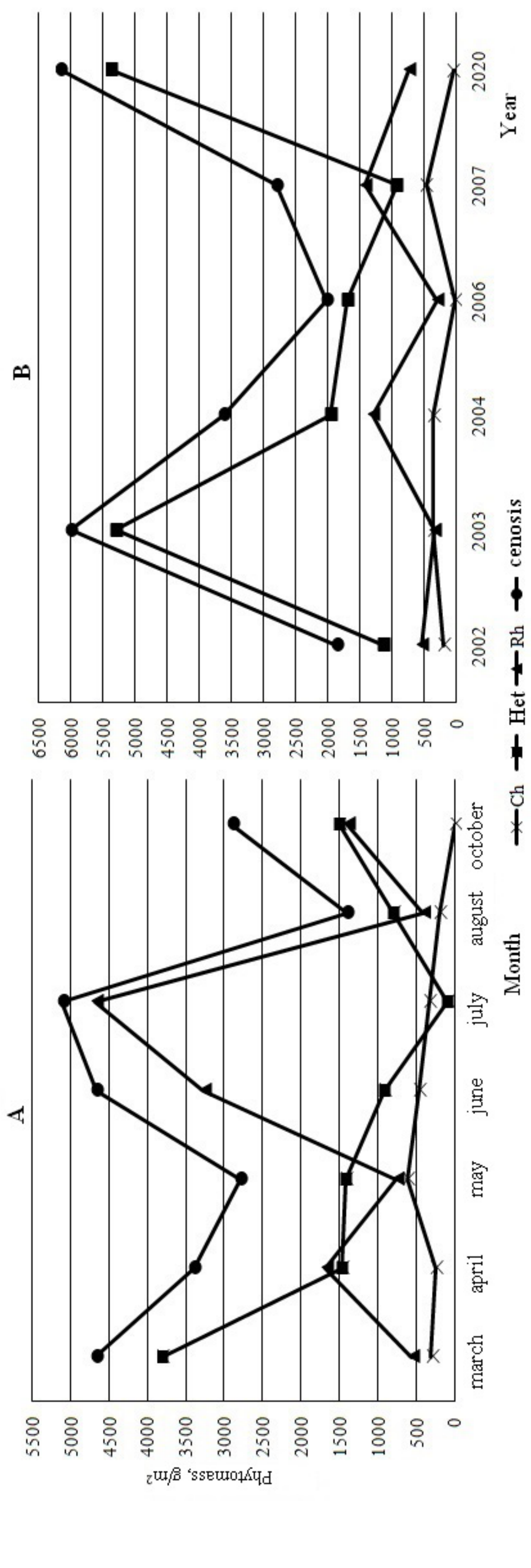

Fig. 3. Intra- (**A**) and interannual (**B**) variability of the absolute phytomass of macroalgae in CAC.

Table 2. The species composition of the dominant MPB complex in CAC.

Depth, m	Section	Dominant species (share of the phytomass, %)	Subdominant species	Shannon index
0.5	I	*Palisada perforata* (31)	*Cladophora sericea*, *Ceramium virgatum* Roth, *Ceramium diaphanum* (Lightf.) Roth, *Ceramium ciliatum* (Ell.) Ducl., *Corallina officinalis* L.	2.8
	II	*Gongolaria barbata* (Stackhouse) Kuntze (33), *Ulva rigida* C. Agardh (28)	Ericaria crinita	3.8
	III	*Gongolaria barbata* (72)	Ericaria crinita	1.7
1	I	*Ericaria crinita* (81)	–	1.1
	II	*Ericaria crinita* (60)	*Gongolaria barbata*, *Vertebrata subulifera*	2.3
	III	*Ericaria crinita* (48)	*Gongolaria barbata*, *Vertebrata subulifera*, *Carradoriella elongata* (Huds.) Savoie et G.W. Saunders	2.3
3	I	*Ericaria crinita* (76)	*Vertebrata subulifera*	1.0
	II	*Ericaria crinita* (68)	*Vertebrata subulifera*	1.6
	III	*Ericaria crinita* (60)	*Vertebrata subulifera*, *Gongolaria barbata*	1.7
5	I	*Ericaria crinita* (59)	*Vertebrata subulifera*, *Phyllophora crispa*	1.8
	II	*Ericaria crinita* (53)	*Vertebrata subulifera*, *Phyllophora crispa*	1.7
	III	*Ericaria crinita* (62)	*Vertebrata subulifera*, *Phyllophora crispa*	1.5
10	I	*Ericaria crinita* (66)	*Phyllophora crispa*	1.5
	II	*Phyllophora crispa* (52)	*Ericaria crinita*, *Spermothamnion strictum* (C. Agardh)	1.5
	III	*Ericaria crinita* (44)	*Phyllophora crispa*	1.9
15	I	*Phyllophora crispa* (77)	*Spermothamnion strictum*	0.8
	II	*Phyllophora crispa* (86)	*Spermothamnion strictum*	0.7
	III	*Phyllophora crispa* (87)	–	0.6

Table 3. Groups of productional dominance of species in three sections. N is the absolute number of species, % – the share of the total number.

Group	Section I			Section II			Section III		
	N	%	Species	N	%	Species	N	%	Species
minor	39	73	–	51	86	–	39	80	–
secondary	11	21	–	4	7	–	6	12	–
subdominant	2	4	*Vertebrata subulifera Phyllophora crispa*	3	5	*Vertebrata subulifera Phyllophora crispa Gongolaria barbata*	3	6	*Vertebrata subulifera Phyllophora crispa Gongolaria barbata*
dominant	–	–	–	1	2	*Ericaria crinita*	1	2	*Ericaria crinita*
absolute dominant	1	2	*Ericaria crinita*	0	0	–	–	–	–

Most phytomass of Ch is produced by *Ulva rigida*, the contribution of which to the average phytomass of MPB and the division phytomass is 6 and 78%, respectively. In this section, the productional dominant among Het species and in the entire community is *Ericaria crinita*. It accounts for almost half of the cenosis phytomass and 86% of brown algae from the central section of NM. Among Rh, only two species (*Carradoriella denudata* (Dillwyn) Savoie et G.W. Saunders, *Phyllophora crispa*) form 28% of MPB phytomass and 86% of red algae. *Ericaria crinita* dominates at depths from 1 to 5 m; its dominance frequency reaches 50%. *Gongolaria barbata* prevails at a depth of 0.5 m and *Phyllophora crispa* at 10, 15 m (Table 2).

In the system of productional dominance, the "absolutely dominant" species are absent, whereas the minor ones prevail (Table 3).

The lowest H index falls on a depth of 15 m and the highest on 0.5 m. In contrast to diverse and dynamic conditions of algae habitat near land, the environment in the distance from the coast at a depth of 15 m is characterized by a certain homogeneity. In section II, low average values of H index (1.9) and a large deviation of the Pielou index from 1 (0.19) indicate the MPB heterogeneity by phytomass.

Section III (Mayak)

The cenosis phytomass in this section of NM varies greatly; its extreme values differ by an order of magnitude (Table 1). Het species make the main contribution to the total phytomass at depths up to 10 m, while Rh at 15 m. In other cases, red algae are in the second and green in the third place. The average absolute phytomass of Het is twice as high as for Rh and two times higher than that of Ch. The curves of bathymetric changes in the phytomass and phytocenosis of Het are similar. The same is true for Rh, but for depths from 1 to 10 m (Fig. 2). The largest phytomass of the cenosis, Het and Rh are observed at the same depth (5 m). As in other sections of NM, the by-depth distribution of the absolute phytomass of divisions in the Mayak area directly depends on light transmission in water and light-sensitive pigments in the representatives of each division. Taking into consideration the coefficient of the absolute phytomass variation, the divisions and cenosis are arranged as follows: Ch > Het > Rh > cenosis.

In the phytal zone, limited by depths of 0.5 and 10 m, Het dominates by the relative phytomass and only at a 15-m depth it is replaced by Rh. The average relative phytomass of Ch is tenfold less. Almost half of the green algae phytomass is accounted for by *Codium vermilara* (Olivi) Delle Chiaje. Among brown algae, the phytomass of *Gongolaria barbata* and *Ericaria crinita* reaches 63% of the average in MPB and 97% in Het. In Rh, the main producers are *Vertebrata subulifera* and *Phyllophora crispa*.

There are no absolute dominants in the community; minor species have the greatest diversity followed by the secondary ones (Table 3). The group of species with a high dominance consists of the subdominants *Gongolaria barbata*, *Vertebrata subulifera*, *Phyllophora crispa* and the dominant *Ericaria crinita.* The latter prevails in the community at depths of 1, 3, 5 and 10 m, *Gongolaria barbata* at 0.5 m, and *Phyllophora crispa* at 15 m. The frequency of *Ericaria* dominance is 67%, *Gongolaria* and *Phyllophora* – 17% each.

The Shannon index ranges as 0.6–2.3. The most noticeable structural “skew” is characteristic of the community at 15 m, the least pronounced – at shallow depths. The Pielou index is low and equals 0.3 (Table 2).

Comparative characteristics of the productional potential of MPB in different sections of NP in 2020

Analysis of the results presented in Table 1 shows that the average phytomass of Ch in section I is half that in other parts of NM. The phytomass maximum of green algae is detected at shallow depths of sections I and II, as well as on 10 m of section III. In all sections, Het dominates by the average phytomass. This indicator for Rh and, in most cases, for the phytocenosis, is the highest at the same depth of 5 m. The phytomass and phytocenosis of Rh vary slightly in all parts, while in Ch it is subject to significant spatial variations (“anomalously” high). The arrangement of sections and cenosis (by bathymetric phytomass variability) in sections II and III is similar, but differs from section I by the smallest indicator for the cenosis, not for Rh (Table 1).

In sections, the similarity of the productional dominance is manifested in the prevalence of minor species with a very small relative phytomass, the second position of secondary elements and the obligatory presence of *Vertebrata subulifera* and *Phyllophora crispa* among subdominants (Table 3). At the same time, MPB in sections I and III includes an equal number of minor species. In sections II and III, we recorded similar species composition and contribution to the general structure of subdominants and dominants, as well as the absence of species of the category "absolute dominant". In section I, the absolute and relative number of secondary algae species is higher than in other sites of NM. Only here *Ericaria crinita* functions as an absolute dominant, being a dominant in other cases.

The general composition of the dominant and subdominant groups, identified by the relative phytomass without regard for gradation proposed by E.L. Lyubarsky, includes 13 species: by two species of Ch and Het, the rest fall on Rh. Of these, 5 species are dominants and 11 subdominants. Such species as *Gongolaria barbata*, *Phyllophora crispa* and *Ericaria crinita* combine both functions and are considered to be facultative dominants. *Palisada perforata* behaves as a dominant solely at a depth of 0.5 m of section I. Here, *Cladophora sericea*, *Ceramium virgatum*, *Ceramium diaphanum*, *Ceramium ciliatum* and *Corallina* officinalis form a group of subdominants only once. At a 1-m depth of the Mayak water area, *Carradoriella elongata* is a subdominant, along with *Gongolaria barbata* and *Vertebrata subulifera*.

The central part of NM is distinguished by the greatest variation and the highest average value of the Shannon index.

Intra- and interannual variability of MPB taxonomic composition in NM

The species composition and structure of macrophyte communities experience seasonal and annual changes induced by hydrological and hydrochemical conditions varying throughout the year and for several years. Among them, the most important are solar radiation, temperature regime and water pollution (Kalugina-Gutnik, 1973). Figure 3 presents the data illustrating the features of the intra-annual phytomass variability of the cenosis and divisions. The largest absolute phytomass of Ch and Het falls on spring months (March and May), while for Rh and the cenosis on summer (June, July). The phytomass of MPB is close to its maximum in March when a noticeable rise in water temperature is absent, but active spore germination occurs. In April, the water warms up to +15 °C that is accompanied

Table 4. Variability of the absolute (**A** – intra-, **B** – interannual) and relative (**C** – intra-, **D** – interannual) phytomass of the cenosis-forming species.

Group	Month													
	March		April		May		June		July		August		October	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
minor	15	52	13	39	10	56	10	38	5	26	7	33	–	–
secondary	11	38	15	45	3	17	12	46	11	58	10	48	2	33.3
subdominant	1	3	4	12	4	22	3	12	2	11	3	14	2	33.3
dominant	2	7	1	3	1	6	1	4	0	0	1	5	2	33.3
absolute dominant	–	–	–	–	–	–	–	–	1	5	–	–	–	–

by rapid growth of macrophytes. The lowest absolute phytomass of the cenosis, Rh and Ch is recorded in October, and Het – in July. By production, intra-annual phytocenosis heterogeneity is associated with both ontogenetic features of the species and the seasonal distribution of abiotic environmental factors. Monthly dynamics of the total phytomass of benthic and green algae (in particular, by the degree of manifestation according to the G.N. Zaitsev scale) is considered "significant". For other divisions, the intra-annual variability of the analyzed indicator is characterized by greater intensity (C_v = 81–87%). Fluctuations in the absolute phytomass of MPB, Het and Rh are synchronous, starting from April for the first. Divisions dominated in the absolute and relative phytomass from March to October are replaced as follows: Het → Rh → Het → Rh → Rh → Het → Het + Rh.

The system of productional dominance undergoes the year-round transformations relating to the list and quantitative representation of all categories of species involved, including the taxonomic affiliation of key producers. For example, the group of "absolute dominants" in the dominance system is represented by *Phyllophora crispa* only in July. In the rest months, it is replaced by the species of the "dominant" category. The complex of "dominants" consists of three Het species and two Rh species (Table 4). *Scytosiphon lomentaria* (Lyngb.) L., a typical winter species, included in the simple monodominant winter phytocenoses of the homonymous association, appears among the dominants in March. Earlier studies report that the association reaches its greatest development just in March (Kalugina-Gutnik, 1975). During the period of maturation and release of spores, the cells of Scytosiphon thallus gradually deteriorate and by May this association is replaced by the spring-summer communities. From April to May, the bulk of the phytomass is formed by individual species of brown algae, in June and July – by red algae. In August, the dominant producer is the brown alga *Gongolaria barbata* and in October – both Het and Rh species. The subdominant group is taxonomically more diverse than the dominant one. In addition to Het and Rh, it includes Ch species in April, May and August. In April and May, most phytomass is formed by Ulvacean algae together with brown algae and at the end of summer – by Cladophorales. In summer, strong warming of bay waters is responsible for oxygen deficiency and mass death of algae under the Ulva canopy. Abundant unattached Cladophora is located above other species assemblages, outside the zone of suffocation.

Every month, except for October, the composition of MPB is dominated by minor species (26–56% of the total number of species). In October, their share is 13%, two times less than that of the secondary, subdominant and dominant species. Annual reduction in minor species number is gradual, while for the

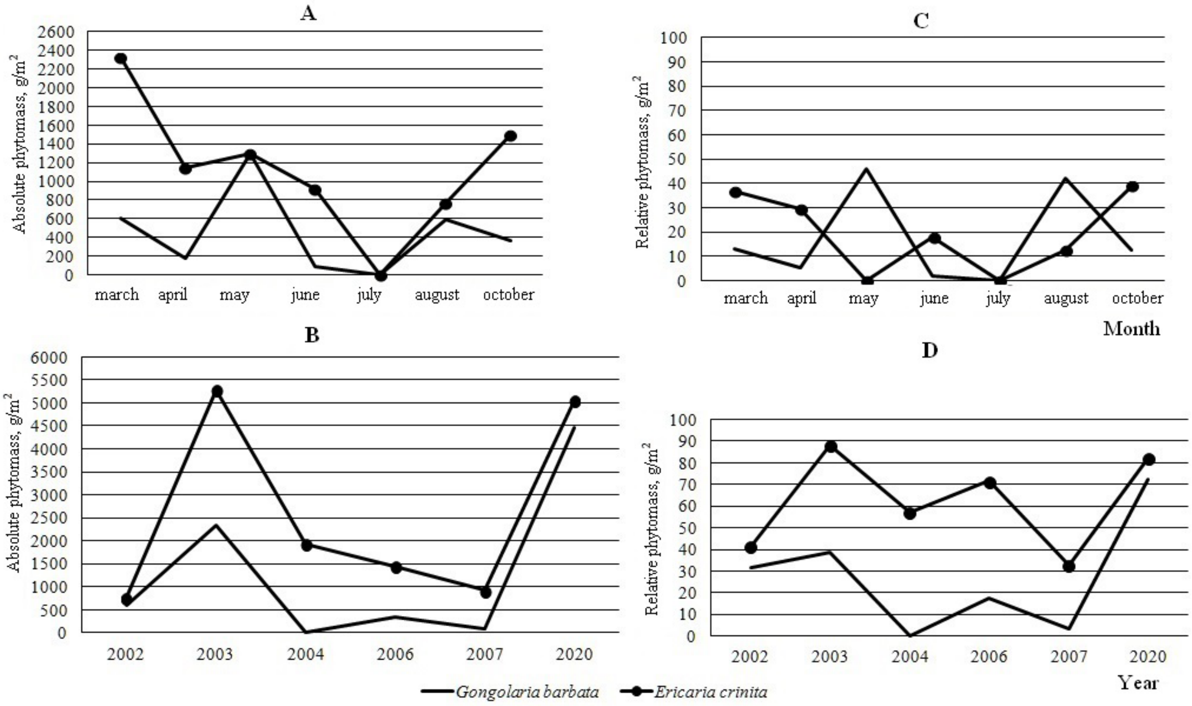

Fig. 4. Variability of the absolute (**A** – intra-, **B** – interannual) and relative (**C** – intra-, **D** – interannual) phytomass of the cenosis-forming species.

secondary elements this dynamics is oscillatory. The greatest number of subdominant species is noted in April–May, the lowest – in March when diversity of dominants is minimal.

Fig. 4 shows the trend in dynamics of the absolute and relative phytomass of two cenosis-forming Black Sea species *Gongolaria barbata* and *Ericaria crinita.* The intra-annual dynamics of the absolute phytomass of both species is practically identical. From mid-spring, the curves of relative phytomass variations become inverse; the next peak in the productive contribution of one species is accompanied by its decline in the other. Such intra-annual fluctuations in the absolute and relative phytomass of key species can be considered compensatory, ensuring the sustainable development of the entire cenosis in the study area.

Monthly variations of the Shannon index make up 2.05 in October and up to 4.05 in April (C_v = 24%). The Pielou index reaches 0.51, thereby clearly indicating that the level of the community heterogeneity (by phytomass) in different months and at the same depth is lower than at different depths.

The total phytomass of the cenosis (2002–2020) varied widely with a range of 4299 g/m^2. For almost two decades, the phytomass of the community has tripled. Its level mutually comparable only for the years 2002 and 2006 (Fig. 3). The greatest contribution to the average phytomass of the cenosis is made by brown algae (73% the average for the community). Red algae produced the fifth of the total average phytomass; the proportion of green algae (9%) was insignificant. For most of the analyzed period, Het quantitatively dominated in the community, giving way to Rh only in 2007 when the absolute and relative phytomass of Ch reached the maximum. Interannual dynamics of the absolute phytomass of the divisions and cenosis did not always coincide. According to the G.N. Zaitsev scale, for Ch and Het it was “large” (C_v = 75%), while for others “significant” (C_v < 64%). The trends in long-term dynamics of the absolute and relative phytomass of basic producers *Gongolaria barbata* and *Ericaria crinita* demonstrated strong similarity.

In 2003–2007, the Shannon index gradually increased and then decreased. The community was characterized by the greatest diversity of productional subdominants-producers in the beginning of observations when the proportion of the dominant *Gongolaria barbata* was almost a third of the cenosis phytomass (32%). In subsequent years, the dominance of one or two species in the community was growing. For example, in 2003, 88% of the total biomass was formed by *Gongolaria barbata* and *Ericaria crinita*. In the last year of observations, the phytomass of *Gongolaria barbata* alone reached 72%.

According to the scale of E.L Lyubarsky, *Gongolaria barbata* and *Ericaria crinita* most of time replaced each other in the positions of dominant and absolute dominant, except for the last year of observations when *Ericaria crinita* acquired the subdominant status. Despite different relative and absolute phytomass abundance, their interannual dynamics was unidirectional for both species. For instance, we recorded a sharp increase in 2002–2003, followed by a decrease by 2007, and another rise in 2020 (Fig. 4).

Floristic composition, productional features and distribution of indicator groups of halobity and saprobity (2020)

The research has found that marine and oligosaprobic species dominate in each CAC site. They account for more than half of the species in the phytocenosis. In all sites, the composition of Ch includes the equal number of oligosaprobic species. Representatives of the brackish-marine and polysaprobic ecogroups are not typical for Het. There are no brackish-water species among Rh, the absolute number of meso- and polysaprobic species is comparable.

The algae complex in the Tunnel Rock water area is characterized by the absence of brackish-water species, the prevalence of brackish-water-marine species among green algae, approximately equal number of species in the meso- and oligosaprobic groups, and the qualitatively homogeneous Het composition. In the central section of CAC, where the city beach operates and sewage waters are periodically discharged, the indicator groups, i.e. brackish-water (strong desalination of the marine environment), poly- and mesosaprobic (high and medium degree of eutrophication) ones are most common in all sections. In the Mayak area, species indicators of medium desalination of the marine environment also predominate; oligo- and mesosaprobes are represented approximately equally.

Oligosaprobes and the marine group dominate not only in species number, but also in phytomass. Their contribution to the total phytomass of the entire community reaches 91–98%. The share of mesosaprobic and brackish-water-marine species makes up 1.5–8% of the total phytomass; for polysaprobionts and brackish-water plants it is even less.

Conclusions

1. The study allowed to obtain the information on the productional potential of macrophytobenthos and determine the role of species and their ecological groups in biomass formation in different sections of CAC.

2. Heterokontophyta appeared to be the key benthic producer in the protected water area, with Rhodophyta and Chlorophyta occupying the second and third positions. The species with categories of high dominance include *Vertebrata subulifera*, *Ericaria crinita*, *Gongolaria barbata*, and *Phyllophora crispa*.

3. The absolute phytomass of MPB in all sites of CAC fluctuated widely, showing its minimum at large depths and being several times greater in the rest part of the phytal zone. The curves of bathymetric changes in the Het phytomass and phytocenosis are identical.

4. The productional dominance in the sections was characterized by the prevalence of minor species, the second position of the secondary elements and the obligatory presence of *Vertebrata subulifera* and Phyllophora *crispa* among subdominants.

5. The intra-annual phytomass variability is distinguished by its spring maximum in Chlorophyta and Heterokontophyta, summer peak in Rhodophyta and the entire phytocenosis, as well as a high degree of its manifestation ("significant" – "anomalously" high).

6. The long-term observations demonstrate wide annual variations in the benthic phytomass and a threefold (for almost 20 years) increase due to intensive development of Heterokontophyta.

7. The productional heterogeneity of the community, estimated using the Shannon and Pielou indices, was lower in time than at different depths.

8. By response to halobity and saprobity of the environment, marine and oligosaprobic ecogroups were in the lead by phytomass and species diversity; brackish-water, poly- and mesosaprobic species develop en masse in the areas with high anthropogenic pressure.

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