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Article

Spatio-temporal changes in the macrophytobenthos of the western coast of Sevastopol

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Abstract. Based on long-term research (1964, 2009, and 2020), three phytocenoses are recognized in the coastal waters off the western coast of Sevastopol, showing significant changes in their composition and structure. The study has recorded significant shifts in the quantitative indicators of dominant macrophyte species and their spatial distribution, likely driven by the combined effects of natural processes and intense human activity along the coast. It is shown that over a period of more than 50 years, algal species adapted to high-nutrient, eutrophic conditions emerged within what had previously been more diverse phytocenoses. In the *Ericaria crinita* + *Gongolaria barbata* phytocenosis, recorded at a depth of 0.5(1)–5 m, an increase in its biomass (1.3–2.9 times) was recorded, mainly due to the appearance of **associated** and epiphytic algal species, while the proportion of dominant macrophytes significantly decreased (from 91–100 to 36–95%), and the contribution of epiphytes increased (from 0–7 to 4–17% of the total macrophyte biomass). The (*Gongolaria barbata*) – *Phyllophora crispa* phytocenosis, recorded at a depth of 5–10(15) m, experienced a significant decline in quantitative indicators. The proportion of the dominant species in the first tier decreased slightly from 54–88% to 21–80%, while that in the second tier increased slightly (5–43% and 1–54%, respectively), while the contribution of epiphytes increased (from 1–6% to 7–15% of the total macrophyte biomass). The *Phyllophora crispa* phytocenosis, first described in 2020 at a depth of 10–15 m, was dominated by its edifier (82–90% of the total macrophyte biomass).

Keywords: *Ericaria crinita*, *Gongolaria barbata*, *Phyllophora crispa*, phytocenosis, epiphyte, coastal waters, Black Sea

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Научная статья

Пространственно-временные изменения макрофитобентоса у западного побережья г. Севастополя

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Аннотация. На основе многолетних исследований (1964, 2009 и 2020 гг.) в акватории западного побережья г. Севастополя было выделено три фитоценоза, в составе и структуре которых обнаружена существенная перестройка. Изменения отмечены в количественных показателях доминирующих видов макрофитов и в их пространственном распределении, что, вероятно, связано с комплексным воздействием природных факторов, так и возросшей хозяйственной деятельностью на побережье. Показано, что за более чем 50-летний период в составе изученных фитоценозов появились виды водорослей, обитающие в среде с повышенным уровнем эвтрофирования. В фитоценозе *Ericaria crinita* + *Gongolaria barbata*, зарегистрированном на глубине 0.5(1)–5 м, отмечено увеличение его биомассы (в 1.3–2.9 раза) в основном за счет появления сопутствующих и эпифитирующих видов водорослей, при этом доля доминирующих макрофитов существенно снизилась (с 91–100 до 36–95%), а вклад эпифитов возрос (с 0–7 до 4–17% общей биомассы макрофитов). В фитоценозе (*Gongolaria barbata*) – *Phyllophora crispa*, зафиксированном на глубине 5–10(15) м, выявлено снижение его количественных показателей. Доля доминирующего вида 1-го яруса несколько снизилась с 54–88 до 21–80%, а 2-го яруса – незначительно повысилась (5–43 и 1–54% соответственно), при этом возрос вклад эпифитов (с 1–6 до 7–15% общей биомассы макрофитов). Фитоценоз *Phyllophora crispa*, впервые описанный в 2020 г. на глубине 10–15 м, характеризовался господством его эдификатора (82–90% общей биомассы макрофитов).

Ключевые слова: *Ericaria crinita*, *Gongolaria barbata*, *Phyllophora crispa*, фитоценоз, эпифит, прибрежная зона, Черное море

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Introduction

Benthic vegetation, acting as a primary producer and a foundational component of the trophic chain, is crucial for maintaining the ecological balance of coastal ecosystems (de la Torre-Castro et al., 2014; Orth et al., 2006). The increased intensification of coastal development in the Black Sea in recent decades has significantly elevated anthropogenic pressure on the marine biota including plants. Research has confirmed that perennial phytocenoses of macrophytobenthos are highly vulnerable, and this vulnerability is expressed primarily in a change in the diversity of macroalgae, a decline in their quantitative indicators; in addition, perennial dominant species are being replaced by associated short-lived epiphyte species (Fourqurean et al., 2001; Milchakova et al., 2011). Monitoring the state of bottom vegetation (or benthic vegetation/macrophytes) is a critical part of environmental assessment.

Until recently, the macrophytobenthos of the western coast of Sevastopol remained poorly studied. Two phytal biocenoses – *Cystoseira* and *Phyllophora* – were first identified in the coastal zone of this area by E.B. Makkaveeva in 1964 (1964). A.A. Kalugina-Gutnik and N.M. Kulikova (1974) published a more detailed study of the structure of phytocenoses and determination of the biomass of common macrophyte species. More than half a century later (2020), E.K. Evstigneeva and I.N. Tankovskaya (2021, 2022, 2023) documented transformation of phytocenoses (plant communities) in coastal areas, specifically marked by an increase in the species richness of green and red algae, characteristic of areas with aquatic pollution, which indicated a deterioration in the environmental situation in this water area.

The purpose of this study was to compare and analyze spatiotemporal changes in the composition, structure and quantitative characteristics of macrophytobenthos off the western coast of Sevastopol for the period from 1964 to 2020.

Material and methods

The studied coastal area is located in the western part of the federal city of Sevastopol and extends from Cape Tyubek to the mouth of Nemetskaya Balka (Fig. 1). The underwater slope is shallow, composed primarily of sandy sediments, with bedrock outcrops (Goryachkin and Dolotov, 2019). A gravel-pebble-block bench is observed over most of the studied coastal area. The water area contains a concentrated accumulation of conglomerate slabs and blocks, which form bottom protrusions and isolated patches (banks) down to a depth of 10 m (Pankeeva and Mironova, 2021). Changes in the lithological composition of the coastal zone are largely due to the longshore transport of coastal marine sediments. The direction and intensity of longshore currents are determined by the characteristics of the wind-wave regime in the adjacent water area. The primary factors for sediment movement are storm waves coming from the south-northwest sector (Osobo okhranyaemye..., 2020).

Hydrobotanical studies were conducted in the summer of 2020, using lightweight diving equipment and small vessels. To study the composition of macrophytobenthos, three profiles were measured, and samples were collected using standard methods (Fig. 1, Table 1) (Kalugina-Gutnik, 1969). At depths of 0.5, 1, 3, 5, 10 and 15 m, four survey plots measuring 25×25 cm were sampled. A total of 72 quantitative samples were collected. The phytocenoses were identified according to the dominant classification by A.A. Kalugina-Gutnik (1975). The Shannon species diversity index (H) was used to analyze the structure of phytocenoses. To outline the boundaries of phytocenoses in the western coastal waters, additional studies were conducted at six profiles. At standard sampling points (0.5, 1, 3, 5, 10, and 15 m isobaths), a scuba diver took photographs and video, recording the dominant algal species. A

combined analysis of bathymorphic and lithological maps, as well as underwater survey data, allowed for the integrating of multiple data sources and extrapolating the results to unmapped bottom areas with similar parameters. These data formed the basis for mapping the habitats of phytocenoses. Tiers in the communities were distinguished by aspective species, taking into account the biomass of macrophytes. Algae were identified using Zinova's (1967) guide, taking into account the most recent nomenclatural changes (AlgaeBase¹).

Hydrobotanical surveys for 1964 and 2009 were conducted during the summer in the same areas using a similar methodology, allowing for a comparative analysis of long-term changes in the composition and structure of the macrophytobenthos. Data for 1964 were taken from the archives of the Institute of Biology of the Southern Seas, while data for 2009 were obtained by one of the authors who participated in sample collection and processing. Published data were also used (Kalugina-Gutnik and Kulikova, 1974).

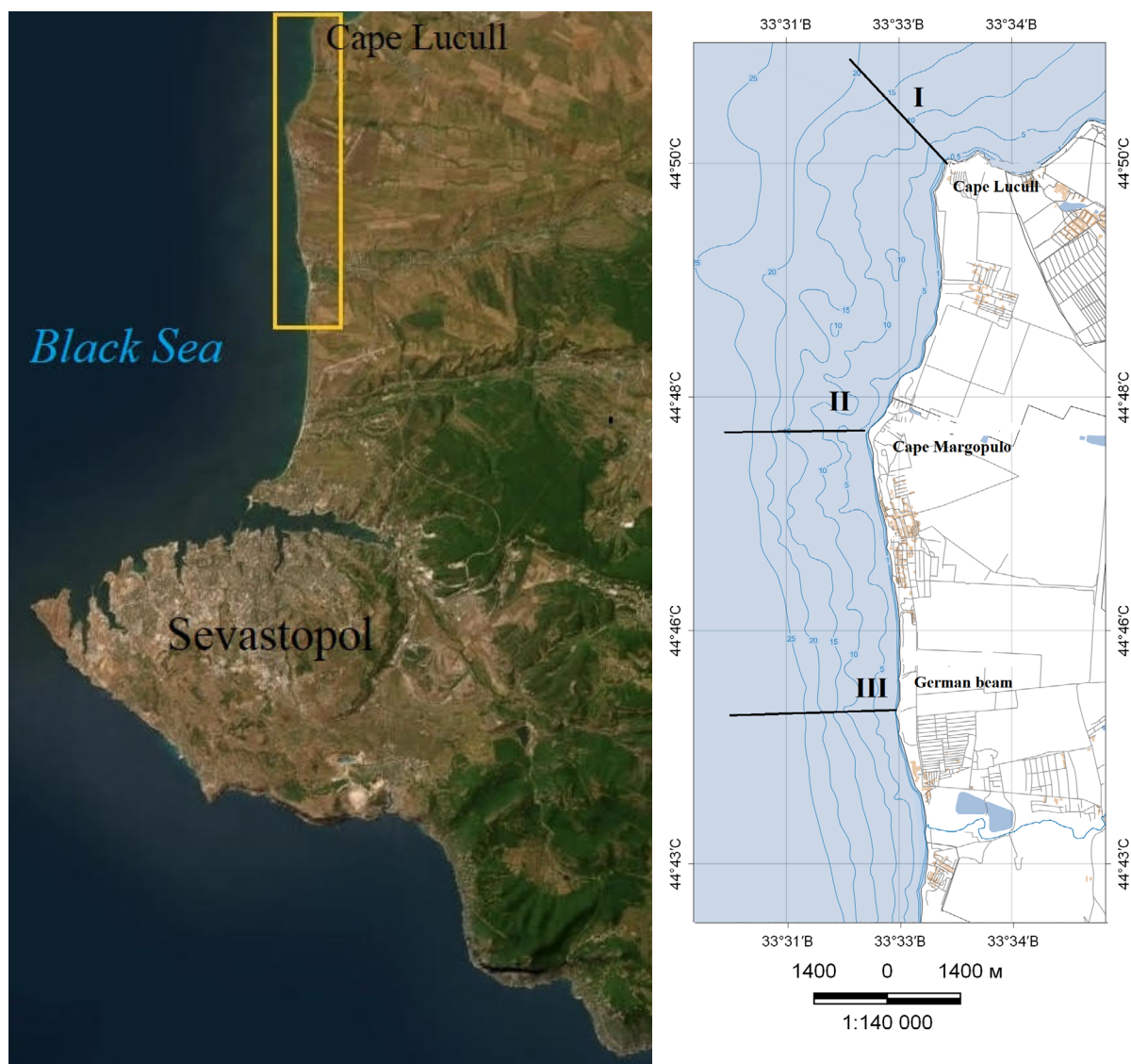


Fig. 1. Schematic map of the location of hydrobotanical profiles in the western coastal area of the city of Sevastopol. Roman numerals stand for profiles: I – cape Lucull; II – cape Margopulo; III – cape at the German beam. Boundaries of the study area are marked with a rectangular.

¹ AlgaeBase, World-wide electronic publication, National University of Ireland, Ireland. Web page URL: <http://www.algaebase.org> (accessed: 15.12.2024).

Table 1. Characteristics of the profiles of the western coast of Sevastopol in 2020.

Profile	Coordinates		Depth range, m	Width of the phytal, m
	North latitude	East longitude		
I	44°50.411'	33°33.274'	0.5–10	850
II	44°47.383'	33°32.115'	0.5–15	1450
III	44°45.225'	33°32.758'	05–15	950

Results and discussion

Based on long-term research in the waters of the western coast of Sevastopol, three phytocenoses were identified, the composition, structure, quantitative indicators and spatial distribution of which changed over the period from 1964 to 2020.

Ericaria crinita + *Gongolaria barbata* phytocenosis

More than half a century ago, in 1964, this phytocenosis was recorded in profiles I and II at a depth of 1–5 m (Fig. 2). Its biomass increased slightly with increasing depth, while the proportion of dominant species was high (Table 2). The community showed an insignificant contribution of epiphytic synusia represented by *Vertebrata subulifera* (C. Ag.) Kuntz. (2–6%) and species of the genus *Ceramium* (1–5% of the total macrophyte biomass). It is characteristic that in profile III the same phytocenosis was described at a depth of 3–10 m. Its biomass increased by 1.3 times with an increase in depth from 3 to 5 m and reached a maximum, then decreased by approximately half. The proportion of dominant species was also high; practically “pure” thickets of *Ericaria crinita* (Duby) Molinari & Guiry (= *Cystoseira crinita*) and *Gongolaria barbata* (Stackhouse) Kuntze (= *Cystoseira barbata*) were recorded. Relatively low values of the species diversity index (H) indicate a homogeneous structure of the phytocenosis with a predominance of dominant species (Table 3).

Forty-five years later, in 2009, the *Ericaria crinita* + *Gongolaria barbata* phytocenosis was described in profiles I and III within a depth range of 0.5–5 m, while in profile II its range had expanded to occupy depths of 0.5–10 m (Fig. 2). Significantly, the phytocenosis biomass varied differently with increasing depth across different profiles. Thus, in profile I, with an increase in depth from 0.5 to 5 m, quantitative indicators decreased by 1.2 times, and the contribution of dominant species almost halved (Table 2). It is characteristic that in this profile, in the studied depth range, the values of the phytocenosis biomass were comparable, while the proportion of its edifiers was lower, especially at the lower boundary of the community, compared with similar indicators recorded in 1964. The phytocenosis included representatives of the genus *Gelidium* (1–6%), *Cladostephus spongiosus* (Huds.) C. Ag. (1–7%), and *Ulva intestinalis* L. (1% of the total macrophyte biomass). In 2009, records at profile I showed a sharp increase in epiphytes, primarily at the lower boundary of the phytocenosis, where the epiphytic synusia was dominated by *Vertebrata subulifera* (1–24%), *Ceramium virgatum* Roth (4–6%), and *Laurencia* species (1–8% of the total macrophyte biomass).

In profile II in 2009, with an increase in depth from 0.5 to 10 m, the total biomass of macrophytes decreased to a nineteenth of its former level, while the contribution of dominant species varied within a narrow range (Table 2). Over the period from 1964 to 2009, a sharp decrease in the biomass of the phytocenosis was recorded at its lower boundary, while at the upper boundary the values were comparable, with the proportion of *Ericaria crinita* and *Gongolaria barbata* decreasing significantly. Species of the genus *Ulva* were abundant in the macroalgae community at a depth of 0.5–3 m; their contribution decreased with depth from 13 to 1%; at a depth of 5–10 m, *Cladostephus spongiosus* (5–22%) and *Phyllophora crispa* (Huds.) P.S. Dixon (1–5% of the total macrophyte biomass) were recorded. The proportion of epiphytic algae increased by more than an order of magnitude compared to similar values recorded in 1964. *Ceramium virgatum* was predominant among the representatives of the epiphytic synusium (4–8%); *Vertebrata subulifera* (1–8%) and *Stilophora tenella* (Esper) P.C. Silva (1–2% of the total macrophyte biomass) were also present. In 2009, the lower boundary of the macrophytobenthos growth was recorded at a depth of 10 m in this profile.

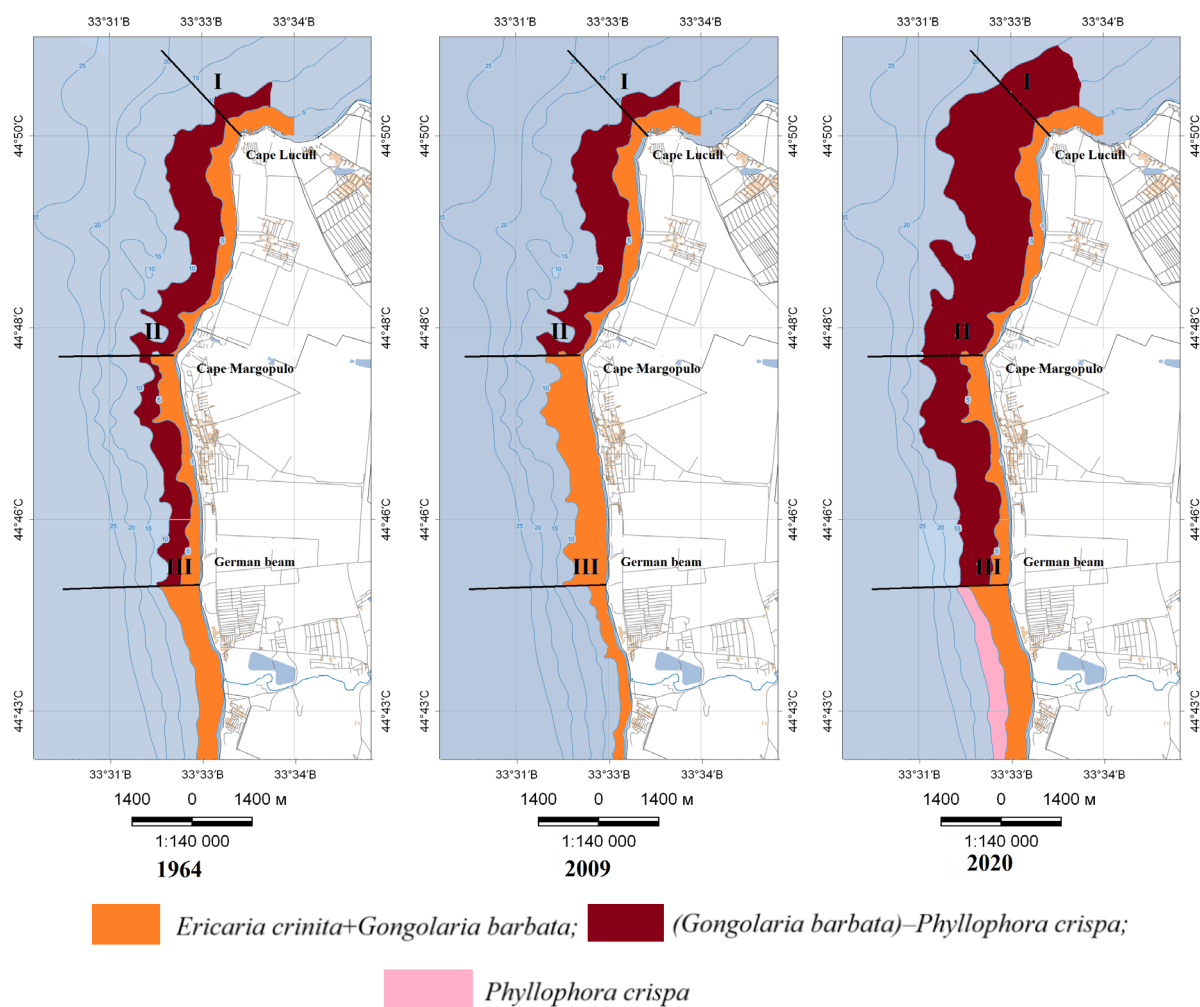


Fig. 2. Schematic map of distribution of phytocenoses *Ericaria crinita* + *Gongolaria barbata*, (*Gongolaria barbata*) – *Phyllophora crispa* and *Phyllophora crispa* on the western coast of Sevastopol in various depths and years.

In profile III in 2009, at a depth of 0.5–1 m, the biomass of the *Ericaria crinita* + *Gongolaria barbata* phytocenosis was low (623.2 ± 92.6 – 618.0 ± 184.2 g m⁻²). These indicators increased almost threefold with an increase in depth from 1 to 3 m, then decreased again to less than half (Table 2). A comparative analysis of the values showed that the biomass of the phytocenosis at all studied depths became significantly lower than that in 1964. The proportion of dominant algal species at a depth of 0.5–1 m was high (97–85%), while at a depth of 3–5 m their contribution was more than two times lower (40–44% of the total macrophyte biomass). The macrophytobenthos included species of the genus *Ulva* (1%), *Cladostephus spongiosus* (1–3%), and *Gelidium crinale* (Hare ex Turner) Gaillon. (1–6% of the total macrophyte biomass). *Phyllophora crispa* was abundant at depths greater than 5 m. In 2009, a significant increase in the contribution of epiphytic synusia was noted with increasing depth, with its proportion being an order of magnitude higher than that in 1964. Representatives of the genus *Cladophora* (1%) predominated among epiphytes at shallow depths, while at depths of 3–5 m, *Vertebrata subulifera* (10–29%), *Ceramium virgatum* (2–6%), and species of the genus *Laurencia* (5–7% of the total macrophyte biomass) predominated. The values of the Shannon species diversity index (H) indicate a polydominant structure of the phytocenosis and a significant contribution of epiphytic algae species (Table 3).

In 2020, in profiles I and II, the phytocenosis *Ericaria crinita* + *Gongolaria barbata* was described at a depth of 0.5–5 m, while in profile III this community occupied depths of 0.5–10 m (Fig. 2). Its biomass in the first two profile with an increase in depth from 0.5 to 1 m increased by 1.2 and 2 times, respectively, and in profile III – by 8 times (Table 2). With further increase in depth, these values decreased by approximately 30% in all profiles. Comparative analysis showed that in profiles I–III, both at the upper

Table 2. Changes in macrophytobenthos parameters in profiles of the western coast of Sevastopol with increasing depth over the years.

Phytocenosis	Depth, m	Year	Total biomass of macrophytes, g·m ⁻²	Proportions, %		
				<i>Ericaria crinita</i> , <i>Gongolaria barbata</i>	<i>Phyllophora</i> <i>crispa</i>	Epiphytes
I paspez						
<i>Ericaria crinita</i> + <i>Gongolaria barbata</i>		1964	3953.7 ± 294.9–4290.0 ± 683.9	94–91	0–2	6–7
	0.5(1)–5	2009	4589.6 ± 508.6–3902.5 ± 650.6	78–44	0	9–47
		2020	6013.6 ± 561.5–5495.8 ± 634.8–	76–82	0–1	16–17
<i>(Gongolaria barbata) – Phyllophora crispa</i>		1964	2485.0 ± 399.9–2599.0 ± 254.0	88–72	5–24	6–4
	5–10	2009	3408.2 ± 544.2–920.2 ± 149.7	61–55	0–21	36–19
		2020	3997.4 ± 501.3–3591.0 ± 311.2	59–61	1–24	38–13
II paspez						
<i>Ericaria crinita</i> + <i>Gongolaria barbata</i>		1964	4030.0 ± 366.5–4717.0 ± 504.4	100–99	0	0–1
	0.5(1)–5(10)	2009	4263.4 ± 898.3–222.6 ± 86.1	78–65	0–5	20–12
		2020	5484.1 ± 747.3–8504.4 ± 457.2	82–95	0	5–4
<i>(Gongolaria barbata) – Phyllophora crispa</i>		1964	5375.0 ± 467.4–4249.0 ± 167.5	86–54	8–43	6–1
	5–10					
	5–15	2020	3722.4 ± 294.6–1730.4 ± 201.1	80–21	6–54	7–15
III paspez						
<i>Ericaria crinita</i> + <i>Gongolaria barbata</i>		1964	2820.0 ± 123.3–1915.0 ± 107.6	100–97	0–2	0–1
	0.5(3)–5(10)	2009	623.2 ± 155.2–784.4 ± 133.6	97–44	0–22	1–30
		2020	1049.3 ± 106.3–7170.7 ± 401.9	36–77	0–4	11–15
<i>Phyllophora crispa</i>	10–15	2020	2951.0 ± 289.5–1965.7 ± 186.5	10–3	82–90	5–4
Bottom vegetation is absent	5–10	2009	62.7 ± 5.4	32	14	24

Table 3. Changes in the Shannon species diversity index (H) on the western coast of Sevastopol by depth and year. Dashes indicate no data.

Profile	Year	Depth, m					
		0.5	1	3	5	10	15
I	1964	–	1.30	1.33	1.55	1.75	–
	2009	1.47	1.90	2.44	2.13	2.74	–
	2020	2.16	1.31	1.88	1.74	2.02	–
II	1964	–	0.33	0.63	1.34	1.72	–
	2009	1.85	1.74	1.43	2.52	1.98	–
	2020	1.38	1.16	1.18	2.00	1.63	1.83
III	1964	–	–	0	0.70	1.20	–
	2009	0.45	1.81	2.46	2.50	3.13	–
	2020	2.96	1.83	1.95	2.28	1.07	0.66

and lower boundaries of the studied phytocenosis, the biomass was 1.3–1.7, 1.8–4.9, and 1.8–3.1, 1.3–1.8 times higher, respectively, than these figures in 2009 and 1964. The contribution of dominant species in 2020 in profiles I and II was high and ranged within 76–95%, while in profile III it was somewhat lower and ranged from 36 to 84% of the total macrophyte biomass (Table 2). In 2009, the proportion of *Ericaria crinita* and *Gongolaria barbata* in all profiles with increasing depth ranged from 78–97 to 44–65%, and in 1964 – from 94–100 to 91–99% of the total macrophyte biomass (Table 2). In the composition of the macrophytobenthos in all profiles at a depth of 0.5– m among the thickets of *Ericaria crinita* and *Gongolaria barbata*, green species of algae and lithophytic forms of representatives of the genus *Ceramium* were abundant. The proportion of species of the genus *Ulva* varied significantly in different profiles: in profile I, the contribution of representatives of this genus was 2–6%, in profile II – 3–12%, and in profile III – 23% of the total macrophyte biomass. In the structure of the phytocenosis at a depth of 3–5 m, *Cladostephus spongiosus* (1–4%) and *Phyllophora crispa* (1–4% of the total macrophyte biomass) were recorded. The proportion of epiphytic algae in the profiles varied widely (Table 2). In profile I at a depth of 0.5–1 m, the following epiphytes were found: *Polysiphonia opaca* (C. Ag.) Moris et De Notaris (1–4%), *Cladophora albida* (Nees) Kütz. (1–4%), *Vertebrata subulifera* (1–2%) and species of the genus *Ceramium* (1–2% of the total macrophyte biomass), and at a depth of 3– m, species of the genus *Laurencia* (2–3%) and *Sphacelaria cirrhosa* (Roth) C. Ag. (1–2%), while the role of *Vertebrata subulifera* increased significantly (up to 10% of the total macrophyte biomass). In profile II, epiphytes were poorly represented, with *Cladophora albida* accounting for the largest contribution (1–4% of the total macrophyte biomass). In profile III, the proportion of epiphytic synusia was quite high, with the highest values observed at a depth of 1 m and the lowest at depths of 0.5 and 3 m. The epiphytes at a depth of 0.5 m included species of the genera *Cladophora* (7%) and *Polysiphonia* (2%), with few *Callithamnion corymbosum* (Smith) Lyngb. recorded. At a depth of 1 m, species of the genus *Ceramium* were abundant (24%), and deeper – *Laurencia obtusa* (Huds.) J. V. (2–4%), *Vertebrata subulifera* (2–3% of the total macrophyte biomass). At all profiles, the proportion of epiphytic synusia was significantly higher than in 1964, but significantly lower than in 2009 (Table 2). The species diversity index values in 2020 indicate a complex polydominant structure of the phytocenosis, with a high contribution of associated macrophyte species and epiphytic algae (Table 3).

Thus, between 1964 and 2020, the composition, structure, and quantitative parameters of the *Ericaria crinita* + *Gongolaria barbata* phytocenosis in the waters off the western coast of Sevastopol have changed. The spatial distribution of the community has also changed. While this phytocenosis, recorded in profiles I and II, has remained virtually unchanged for over half a century, the same community in profile III, which occupied depths of 3 to 10 m in 1964, was described at depths of 0.5–5 (10) m in subsequent years (Table 2). The appearance of macrophytobenthos in this area at depths of up to 3 m is likely related to longshore drift. This hypothesis is supported by T.V. Efremova and Yu.N. Goryachkin (2022), who indicated that the greatest influence on changes in the lithodynamics of Western Crimea is exerted by hydraulic engineering construction and the reduction of river runoff (Belbek, Kacha, and Alma) resulting from river channel regulation. It is known that prior to human intervention, the lithodynamics from Yevpatoria to Sevastopol featured a nearly uniform longshore drift. However, due to the construction of transverse beach retention structures, this sediment transport has now been effectively fragmented into a series of separate lithodynamic cells with virtually no sediment exchange (Efremova and Goryachkin, 2022). Currently, the waterfront zone of this area shows a sharp increase in the content of large pebbles and boulders due to the reduction in the thickness of sand deposits, facilitating the formation of a substrate for benthic vegetation, beginning at a depth of 0.5 m.

It is characteristic that in this coastal area, the structure of a typical four-tiered phytocoenosis (*Ericaria crinita* + *Gongolaria barbata* – *Cladostephus spongiosus* – *Ellisolandia elongata*) is characterized by a reduction in the lower tiers. This is due to the fact that the lower parts of the *Ericaria crinita* and *Gongolaria barbata* thalli, as well as the macrophytes of the second through fourth tiers, are often buried by sandy bottom sediments, characteristic of the studied coastal zone. The algae die when exposed to sand for long periods, and the phytocoenosis acquires a simple oligodominant structure. Similar communities have been described for the Caucasian and Crimean coasts (Kalugina-Gutnik, 1975).

The *Ericaria crinita* + *Gongolaria barbata* phytocenosis, occupying depths of 0.5(1)–5(10) m and recorded on an underwater slope in boulder-block sediments, was observed at all profiles throughout the study period. In 1964, macrophytes comprising the second and third tiers of the phytocenosis were not encountered at depths of 0.5–3 m, whereas in 2009 and 2020, representatives of the genus *Ulva* were recorded, indicating increasing eutrophication of the aquatic environment. Significantly, species of this genus are most abundantly recorded in profiles II and III. Since the 2000s, profile II has been the site of discharge from wastewater treatment facilities belonging to military units and the northern part of the city, while profile III is the site of the most active coastal development (planned construction of a cottage community site) (Gruzinov et al., 2019). At the same time, the saprobiont composition of the bottom vegetation in profile I is likely to be positively influenced by the hydrological natural monument "Coastal aquatic complex near Cape Lukull" located here (Evstigneeva and Tankovskaya, 2023; Pankeeva et al., 2021). Under the canopy of edificers of Tier 1 at a depth of over 3 m, *Cladostephus spongiosus* and low-growing algae forming dense turfs (*Gelidium spinosum* (S.G. Gmel.) P.C. Silva, *G. crinale*, *Ellisolandia elongata* (J. Ellis & Solander) K.R. Hind & G.W. Saunders, *Cladophoropsis membranacea* (Hofm. Bang ex C. Ag.) Børgesen) were recorded. In 1964, epiphytic synusia on the thalli of *Ericaria crinita* and *Gongolaria barbata* were poorly represented, whereas in 2009 and 2020 the proportion of epiphytes increased significantly (Table 2). Among the epiphytic algae, *Vertebrata subulifera* and species of the genus *Ceramium* (*Ceramium virgatum*, *C. ciliatum* (Ell.) Ducl., *C. diaphanum* (Lightf.) Roth) dominated; *Sphacelaria cirrhosa*, *Laurencia coronopus* J. Ag., *L. obtusa*, *Osmundea pinnatifida* (Huds.) Stackhouse, *Polysiphonia opaca*, *Antithamnion cruciatum* (C. Ag.) Nägeli, *Apoglossum ruscifolium* (Turner) J. Ag., *Chondria dasyphylla* (Woodw.) C. Ag., *Ch. capillaris* (Huds.) M.J. Wynne, *Stilophora tenella* and species of the genera *Cladophora* and *Chaetomorpha* were also present. In 2020, epiphytic synusia was most abundant in the waters of profile III, where intensive economic activity occurred along the coast (Table 2). In addition to algae of the genus *Ulva*, it began to include *Callithamnion corymbosum*, a species found in heavily polluted waters.

In 1964, the biomass of the *Ericaria crinita* + *Gongolaria barbata* phytocenosis in the studied depth range was generally comparable across all three profiles, as anthropogenic pressure was virtually absent in the coastal zone of Sevastopol's western coast in the mid-1960s. The waters were in a natural or near-natural state, and the phytocenoses were very well preserved (Kalugina-Gutnik, 1975; Kalugina-Gutnik and Kulikova, 1974).

A comparative analysis of the phytocenosis biomass in 2009 showed that in profile I the differences were minor and generally comparable, whereas in profiles II and III a sharp decrease in biomass was noted at the lower boundary of the community compared to similar values in 1964. Over a 45-year period, the contribution of dominant species decreased in all profiles, while the proportion of epiphytic synusia increased significantly. It is well known that the mass development of epiphytes, which suppress dominant species, is characteristic of areas subject to anthropogenic impact, where the volume of domestic wastewater has increased significantly (Kalugina-Gutnik, 1975; Milchakova et al., 2011).

In 2020 the biomass of macrophytobenthos increased significantly (by 2–4 times) along the entire western coast of Sevastopol, at depths of 0.5–3 m, primarily due to the appearance of associated and epiphytic algae, while the proportion of dominant species decreased. It is known that since the end of the last century, in many areas of the Crimean shelf where increasing levels of water eutrophication have been recorded, an increase in the density of macrophyte growths, including *Ericaria crinita* and *Gongolaria barbata*, has been observed in the upper sublittoral zone. This is likely due to decreased water transparency (Milchakova et al., 2011). In recent decades, the amount of pollutants entering the waters of this coastal region via river and domestic wastewater has increased significantly, inevitably impacting the plant component of biocenoses (Gruzinov et al., 2019; Ovsyanny et al., 2001). Currently, the macrophytobenthos along the western coast of Sevastopol is characterized by a widespread dominance of oligosaprobe species, a large number of mesosaprobies, and the presence of polysaprobions, allowing the coastal waters of this area to be characterized as mesotrophic (Evstigneeva and Tankovskaya, 2023).

(*Gongolaria barbata*) – *Phyllophora crispa* phytocenosis

In 1964, this phytocenosis was described only in profiles I and II at depths of 5–10 m. Its biomass varied insignificantly within these depths (Table 2). The contribution of the dominant species of the 1st tier ranged from 17 to 46%, and that of the 2nd tier ranged from 5 to 43% of the total macrophyte biomass. A high proportion of *Ericaria crinita* was noted in the community (25–69% of the total macrophyte biomass). Epiphytic algae were poorly represented. Among them, only *Vertebrata subulifera* was found (1–6% of the total macrophyte biomass). Relatively high Shannon index values indicate a more complex structure of the phytocenosis, compared to the community at shallower depths (Table 3).

In 2009, the phytocenosis (*Gongolaria barbata*) – *Phyllophora crispa*, which was recorded in 1964, was registered only in profile I at a depth of 5–10 m (Table 2). Its biomass decreased to a quarter with increasing depth, while it was 1.4 times higher at the upper boundary and almost three times less at the lower boundary than in 1964. The contribution of the edifier of the 1st tier was 32–57% of the total biomass of macrophytes, which was generally slightly higher than the values in 1964. The share of the representative of the 2nd tier varied within the range of 1–21% of the total biomass of macrophytes and was approximately half as low as the figures in 1964. *Cladostephus spongiosus* was occasionally found in the phytocenosis (1–2%), while the role of *Ericaria crinita* (4–23% of the total biomass of macrophytes) decreased compared to the figures in 1964. Over the past period, the proportion of epiphytic algae has significantly increased. The most abundant species were *Vertebrata subulifera* (5–7%), *Ceramium virgatum* (1–5%), and *Ectocarpus siliculosus* (Dillwyn) Lyngb. (1–5% of the total macrophyte biomass). The species diversity index values indicate a polydominant structure of the phytocoenosis, with a high contribution of associated and epiphytic algal species (Table 3).

In 2009, at profiles II and III at a depth of 10 m, bottom vegetation was practically absent. The biomass of the highly degraded, sparse macrophyte community was very low. A few occurrences of *Ericaria crinita*, *Gongolaria barbata*, *Cladostephus spongiosus*, *Phyllophora crispa*, *Chondria dasyphylla*, *Ch. capillaris*, *Cladophoropsis membranacea* are recorded. The epiphytic synusia included *Cladophora dalmatica* Kütz., *Vertebrata subulifera*, *Ceramium virgatum*, and *Laurencia obtusa*.

In 2020, the phytocoenosis (*Gongolaria barbata*) – *Phyllophora crispa* was described only in profiles I (depth 5–10 m) and II (depth 5–15 m). Its biomass in profile I fluctuated within a narrow range. Values of this parameter at the upper boundary of the community were approximately twice as high and comparable to those in 1964 and 2009 (Table 2). The most significant difference in phytocoenosis biomass values was observed at the lower boundary of benthic vegetation habitat, where these values were 1.4 and 4 times higher than those in 1964 and 2009, respectively.

In 2020, in the depth range of 5–10 m, the total biomass of macrophytobenthos in profile II changed insignificantly and decreased almost twice with an increase in depth from 10 to 15 m (Table 2). In the phytocenosis composition in both profiles, the edificator of the 1st tier (*Gongolaria barbata*) accounted for 21–57%, and the edifier of the 2nd tier (*Phyllophora crispa*) accounted for 1–54% of the total macrophyte biomass. In profiles I and II, *Ericaria crinita* was noted in the community (1–47% of the total macrophyte biomass). However, if the phytocenosis in profile I included *Cladostephus spongiosus* (2–3%), then in profile II it included *Nereia filiformis* (J. Ag.) Zanard. (1–8%) and *Zanardinia typus* (Nardo) P.C. Silva (2–6% of the total macrophyte biomass). Epiphytes in these profiles at a depth of 5–10 m are mainly represented by *Vertebrata subulifera* (5–30%) and *Laurencia obtusa* (1–4%), while in profile II at a depth of 10–15 m, *Spermothamnion strictum* (C. Ag.) s predominated (6–15% of the total macrophyte biomass). The species diversity index values indicate a polydominant phytocoenosis structure and a high contribution of epiphytic algal species (Table 3).

The phytocenosis (*Gongolaria barbata*) – *Phyllophora crispa*, found at depths of 5–10(15) m and recorded on an underwater slope on blocky-boulder deposits with a mosaic of pebble-gravel sediments with broken shells, was described in profile I throughout the study period and in profile II in 1964 and 2020. In addition to its edifier, *Ericaria crinita* was found in the first tier. The second tier is represented by *Phyllophora crispa*, a species primarily associated with sandy shell rock with admixture of gravel and pebbles, but also growing on coarse-grained substrate. In 1964, only *Cladostephus spongiosus* was recorded in the structure of the phytocenosis; in 2009, it included all of the above-mentioned species noted in the phytocenosis *Ericaria crinita* + *Gongolaria barbata*, while in 2020, occurrences of typical deep-sea species of algal flora (*Nereia filiformis* and *Zanardinia typus*) began at a depth of 10–15 m.

In the 1960s and 1970s, *Zanardinia typus* and *Nereia filiformis* were recorded at depths exceeding 25 m along the Black Sea coast of Crimea (Kalugina-Gutnik, 1975). Currently, these sciaphilous (shade-loving) species are found at shallower depths in the study area, indicating a vertical shift in their habitat depths, likely related to reduced water transparency due to increased eutrophication.

The biomass of the phytocenosis (*Gongolaria barbata*) – *Phyllophora crispa* in 1964 varied within the range of 2485.0 ± 399.9 – 5375.0 ± 467.4 g m⁻², while in 2009 and 2020, with increasing depth, its values decreased respectively to a quarter, and a half (Table 2). Thus, the most significant negative changes in the quantitative indicators of the phytocenosis were identified at its lower boundary. Our research coincides with the results of a long-term study of bottom vegetation off the coast of Crimea, where in recent decades, especially in the lower sublittoral zone (depth 5–15 m), significant structural changes in phytocenoses, their transformation and a decrease in production characteristics have been noted (Milchakova et al., 2011; Pankeeva and Mironova, 2019).

***Phyllophora crispa* phytocenosis**

This phytocenosis was recorded only in 2020 at profile III at a depth of 10–15 m. Its biomass, with increasing depth, declined to two-thirds of its original level (Table 2). At a depth of 10–15 m, a high proportion of the community edifier was detected, while the contribution of *Ericaria crinita* and *Gongolaria barbata* to less than a third with increasing depth. The phytocenosis also included *Nereia filiformis* (2–3%) and *Zanardinia typus* (1% of the total macrophyte biomass). The epiphytic synusia is represented mainly by *Spermothamnion strictum* (4–5% of the total macrophyte biomass). The simplification of the phytocenosis structure with increasing depth is reflected in the values of the species diversity index, the indicators of which decreased to less than a third (Table 3).

The *Phyllophora crispa* phytocoenosis is widespread on a gently sloping plain, on gravelly-sandy sediments with broken shells. In addition to edificator, its community included *Nereia filiformis* and *Zanardinia typus* on hard inclusions, as well as *Ericaria crinita*, *Gongolaria barbata*, *Cladostephus spongiosus*, and *Gelidium crinale*. *Spermothamnion strictum* predominated in the epiphytic synusium, with occasional occurrences of *Vertebrata subulifera* and *Cladophora dalmatica*.

According to A.A. Kalugina-Gutnik (1975), the lower limit of *Ericaria crinita* and *Gongolaria barbata* growth was recorded off the coast of Crimea in the 1960s and 1970s at a depth of 18–20 m, while the ecological optimum of *Phyllophora crispa* was located at a depth of 18–25 m. Currently, accumulations of *Phyllophora* mats have been found at a shallower depth (10–15 m), probably due to reduced water transparency.

Conclusions

1. Long-term research on phytocenoses in the waters off the western coast of Sevastopol has shown significant changes in their composition, structure, quantitative indicators, and spatial distribution between 1964 and 2020. This is likely due to the combined impact of both natural factors and increased human (anthropogenic) activity on the coast.

2. On the studied coastline, in profiles I–III (Cape Lukull – Cape near the Nemetskaya Balka ravine), three phytocenoses were described: *Ericaria crinita* + *Gongolaria barbata*, (*Gongolaria barbata*) – *Phyllophora crispa* and *Phyllophora crispa*. The phytocenosis contain species of algae adapted to increased eutrophication.

3. In the phytocenosis *Ericaria crinita* + *Gongolaria barbata*, recorded at a depth of 0.5(1)–5 m, an increase in its biomass (by 1.3–2.9 times) was recorded for the period from 1964 to 2020, mainly due to the appearance of associated and epiphytic algae species, while the proportion of dominant macrophytes decreased significantly (from 91–100 to 36–95%), and the contribution of epiphytes increased (from 0–7 to 4–17% of the total macrophyte biomass).

4. In the phytocenosis (*Gongolaria barbata*) – *Phyllophora crispa*, recorded at a depth of 5–10(15) m, a decrease in its quantitative indicators was recorded from 1964 to 2020. Across all profiles in this depth range, the proportion of the dominant species of the 1st tier decreased slightly from 54–88 to 21–80%, while that of the 2nd tier increased slightly (5–43 and 1–54%, respectively), while the contribution of epiphytes increased (from 1–6 to 7–15% of the total macrophyte biomass).

5. The *Phyllophora crispa* phytocenosis, first described in 2020 at a depth of 10–15 m, was characterized by high biomass values, dominated by the dominant species (82–90% of the total macrophyte biomass), while the proportion of epiphytic algae was low and varied slightly (4–5% of the total macrophyte biomass).

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