1871
ИнБЮМ – IBSS

Морской биологический журнал
Marine Biological Journal
2025, vol. 10, no. 2, pp. 67–86
https://marine-biology.ru

UDC 581.526.323(262.5.04)

COMPOSITION AND STRUCTURE OF MACROPHYTOBENTHOS OFF THE COAST OF THE NATURAL MONUMENT KUCHUK-LAMBAT STONE CHAOS (CRIMEA, BLACK SEA)

© 2025 **S. Sadogurskiy, T. Belich, and S. Sadogurskaya**

Nikitsky Botanical Gardens – National Scientific Center of RAS, Yalta, Russian Federation
E-mail: *ssadogurskij@yandex.ru*

Received by the Editor 29.01.2024; after reviewing 13.03.2024;
accepted for publication 20.03.2025.

The southern coast of the Crimea (SCC) is characterized by a high level of anthropogenic transformation; therefore, the areas preserved in a natural or quasi-natural state are of a certain nature conservation value. Those include the territorial-aquatic complex uniting the geological natural monument Kuchuk-Lambat Stone Chaos and the adjacent coastal waters of the Black Sea. The water area has never been studied from the hydrobotanical point of view and is not included in any list of protected natural sites. Considering this, the research was carried out based on data of 2015 and 2022; it was aimed at characterizing species composition, biomass, and spatial structure of macrophytobenthos to clarify information on distribution and dynamics of the benthic vegetation cover off the SCC and in relation with the prospect for conservation of this area. Macroscopic vegetation was found to develop on hard and soft substrata which determines its general nature. In total, 63 species of macrophytes were recorded: Chlorophyta, 14 (22.2%); Ochrophyta, 9 (14.3%); Rhodophyta, 39 (62.0%); and Tracheophyta, 1 (1.6%). The total number of species (NS) and the ratio of systematic groups by NS in both years are similar. However, the composition of the flora and the biomass (BM) ratio of dominant species and ecological-floristic groups changed significantly at minimum and maximum depths, and this governed the transformation of the vegetation cover. In the shallows, their dynamics has a fluctuating character, and it is driven by local disturbance and subsequent recovery of macrophytobenthos after a mudflow. At depth, the changes are caused by the invasion of the transformer species *Bonnemaisonia hamifera* into natural communities. These changes seem to have a long-term character. To reveal their degree and reversibility, it is necessary to monitor the distribution of the invasive species off the SCC and within the boundaries of the Sea of Azov–Black Sea region in general. Currently, along the surveyed shore, macrophytes form five belt-like communities with BM 0.2–6.0 kg·m^{-2} and NS 14–27. The extreme values of these indicators are registered in the sublittoral zone: maximum ones, on hard substrata in the upper and central spots of a *Cystoseira* belt (*Cystoseira* s. l. species), and minimum ones, on soft substrata in the deepest seagrass community (*Nanozostera noltei*). In general, perennial macrophytes dominate in the BM, and short-vegetating macrophytes prevail in the NS. Phytobenthos has a pronounced oligosaprobic marine warm-water character. The vegetation cover of the water area shows a high degree of preservation; its spatial distribution, composition, and structure (except for changes caused by biological invasion) are typical for the Black Sea hydrobotanical region "SCC." The rare species fraction of the flora covers 12 taxa; biotopes formed by macrophyte communities are listed in Directive 92/43/EEC. It is expedient to form a complex territorial-aquatic nature reservation which will unite the existing natural monument and the adjacent water area.

Keywords: Black Sea, southern coast of the Crimea, Kuchuk-Lambat, macrophytobenthos, species composition, biomass, spatial structure

Due to its unique geographical location and favorable combination of natural and climatic conditions, the Crimean Peninsula is one of European centers of biological diversity; at the same time, it is characterized by a significant level of anthropogenic transformation [Johnson, 1995; Sovremennoe sostoyanie, 2015]. This applies in full to the southern coast of Crimea (hereinafter SCC): a narrow strip stretching between the Main Ridge of the Crimean Mountains and the Black Sea. Recreational development of this area began 1.5 centuries ago and acquired an industrial scale by the second half of the XX century. By now, the shore is much reinforced with concrete hydraulic structures and is occupied by recreational and tourist infrastructure; importantly, its density is continuously increasing. However, some of its spots, usually confined to inconvenient areas, escaped a similar fate and now are of great conservation importance [Sadogurskiy et al., 2017]. Thus, near the settlement of Utes, where a village of Kuchuk-Lambat was located, the marine area and the adjacent section of the shore have been preserved almost in their natural state, unlike the surrounding sites. This is governed by the active dynamics of the gravitational relief of the coastal zone formed by the Kuchuk-Lambat Stone Chaos. It is a picturesque pile of rock debris extending for 1 km along the coast and 1.5 km up the slope to a height of 0–235 m above sea level [Vakhrushev, Amelichev, 2000]. More than 50 years ago, part of this tract with a total area of 5 hectares (protected zone of 7.1 hectares) received the status of a geological natural monument (by decision of the Regional Executive Committee No. 19/8-67, 30.01.1969). Later, it was highlighted that its territory is also of high botanical value, and this made it possible to raise an issue of transferring the object to the category of complex natural monuments [Ryff, 2013; Vakhrushev, Amelichev, 2000]. The water area at the foot of the tract does not have a nature conservation status; it remained unexplored until recently. Previously, we noted as follows: given the inextricable structural and functional relationship between territorial and aquatic components of integral territorial-aquatic ecosystems mediated by material and energy flows, it is advisable to form territorial-aquatic protected objects and elements of econetworks in the marine coastal zone that will be common in terms of area and management [Sadogurskiy et al., 2017; Sadogursky et al., 2009, 2013]. In this regard, a hydrobotanical study of this water area was initiated, and preliminary data were provided on phytobenthos of its supra- and pseudolittoral, where a direct contact between land and sea occurs [Belich et al., 2020].

The aim of this work is to characterize species composition, biomass, and spatial structure of macrophytobenthos of the marine water area at the foot of the natural monument Kuchuk-Lambat Stone Chaos in order to clarify the ideas about the distribution and dynamics of the benthal vegetation cover off the SCC, with the prospect of conservation taken into account.

RESEARCH AREA, OBJECTS, AND METHODS

The surveyed area is a 300-m site of the natural coast of the Black Sea located between two recreational complexes (Fig. 1a). Along the site, there is a boulder-block beach (sometimes boulder one), up to 10–15 m wide (Fig. 1b). Within the boundaries of the natural monument (I), above the beach, there are block heaps of stone chaos composed in the coastal part mainly of Upper Jurassic limestones and cemented breccias of the Massandra suite (see Fig. 1a, b). In the protected zone of the monument (II), steep coastal slopes are composed of terrigenous flysch of the Tauride series consisting of alternating folded layers of argillites, siltstones, and sandstones. Along the boundary between the territory and the protected zone of the monument, there is a small watercourse into the sea. Its surface runoff is extremely variable: in summer, it disappears for 1–2 months; after heavy rains, it can increase and even form mudflows with a velocity of 1–4 $m \cdot s^{-1}$ and a detrital material content of 100–500 $kg \cdot m^{-3}$ [Vakhrushev, Amelichev, 2000]. The adjacent water area is located within the boundaries of the hydrobotanical region "SCC" [Kalugina-Gutnik, 1975]. The seabed is deep; in pseudolittoral and sublittoral, to a depth of 5–6 m, block and block-boulder heap (hereinafter heap) dominates sometimes alternating with pebble areas. Sands with a slight admixture of shells extend beyond the lower boundary of hard substrata.

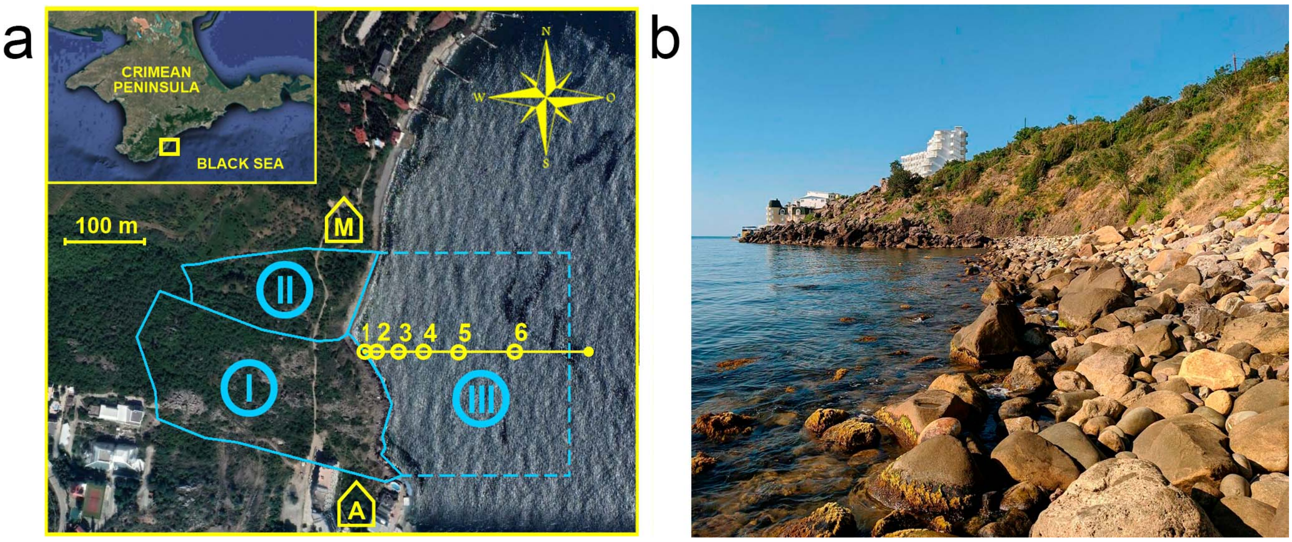

Fig. 1. Research area: a, map of the surveyed area of the coastal zone; 1–6, numbers and location of stations along the hydrobotanical profile (44°36′06.3″N, 34°22′19.9″E at the point of intersection with the water's edge); I, the territory of the geological natural monument Kuchuk-Lambat Stone Chaos; II, the protected zone of the natural monument [Pasport pamyatnika prirody, 2021]; III, the water area recommended to be included in the proposed complex territorial and aquatic reservation; recreational complexes (M, a tourist center Mayak; A, a hotel Arkadia); b, the natural shore of the surveyed area (north to south view), 27.07.2022

Off the SCC, the direction of the coastal current usually coincides with the direction of the Rim Current; the current is directed to the southwest, usually with a speed up to 10 cm·s^{-1}, although with a tailwind, in 5% of cases, a speed exceeds 30 cm·s^{-1} [Belokopytov et al., 2003]. The highest frequency of storm waves is observed from eastern and southeastern directions [Gidrometeorologiya i gidrokhimiya morei SSSR, 1991; Goryachkin, Repetin, 2009]. Off the SCC, fluctuations in sea level of any nature (*inter alia* surges) are insignificant; those are overlapped by surf and wave activity [Gidrometeorologiya i gidrokhimiya morei SSSR, 1991]. The mean temperature of the surface water layer there (according to data for the city of Alushta) varies from +7.4 °C in February–March to +23.3 °C in August. Interestingly, during summer upwellings, the amplitude of temperature fluctuations can exceed 15 °C. The mean annual salinity varies within 17.0–18.2‰, with a minimum in April–May.

The water area was surveyed twice, on 07.08.2015 and 27.07.2022, during independent scuba dives by the generally accepted method [Kalugina, 1969; Kalugina-Gutnik, 1975]. In the central part of the analyzed site of the natural shore, there was a hydrobotanical profile with coordinates 44°36′06.3″N, 34°22′19.9″E at the point of intersection of the water's edge (see Fig. 1a). Sampling was carried out along this profile in a depth interval of 0–8.0 m: at each station, 10 quantitative samples were taken with a frame of 0.01 m^2 in pseudolittoral, and 5 samples were taken with a frame of 0.04 m^2 in sublittoral (the key parameters of stations are provided in Table 1). Visual observations covered all the surveyed water area down to a depth of 10–12 m.

The object of the study is benthic macrophytes. The nomenclature of Chlorophyta, Ochrophyta (class Phaeophyceae), Rhodophyta, and Tracheophyta representatives is given according to AlgaeBase [2024]; surnames of the authors of taxa are provided in the standard abbreviation, as recommended by IPNI [2024]. The identification guide of A. Zinova [1967] is used as a basic one for identifying macroalgae. Ecological-floristic characteristics are given according to A. Kalugina-Gutnik [1975]; saprobiological and halobic ones are based on unpublished data of A. Kalugina-Gutnik and T. Eremenko. The projective cover (hereinafter PC) was determined visually; the mean biomass (hereinafter BM) was established for each species separately: $\bar{x} \pm S_{\bar{x}}$ (wet weight). Layers in communities were identified by aspective species taking into account BM; the vegetation height (hereinafter VH) was given by mean values of the length of thalli (shoots) of dominants in the upper layer. Underwater pictures were taken with an Olympus TG-835 digital camera. Temporary preparations of algae were studied by light microscopy under a Leica DM2500 microscope.

Table 1. Characteristics of sampling stations (No. 1–6) and benthic vegetation cover in the coastal-marine water area off the coast of the Kuchuk-Lambat tract

07.08.2015						
Parameter	PSL*	SBL				
	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6
Depth, m**	±0.25	–0.5	–1.0	–3.0	–5.0	–8.0
Distance from the shore, m	0	3–5	30	60–70	110–120	170–200
Plant community	*Ulva intestinalis* + *Ulva kylinii*	*Ericaria bosphorica* – *Padina pavonica* + *Dictyota fasciola*	*Ericaria bosphorica* + *Gongolaria barbata* + *Vertebrata subulifera* – *Cladostephus hirsutus*			*Nanozostera noltei*
Projective cover, %	85–90	55–60	60–65	95–100	85–90	25–30
Vegetation height, cm	7.41	8.17	17.41	27.02	29.08	22.89
27.07.2022						
Plant community	*Ceramium ciliatum*	*Ericaria bosphorica* + *Gongolaria barbata* – *Padina pavonica* + *Dictyota fasciola*	*Ericaria bosphorica* + *Gongolaria barbata* + *Vertebrata subulifera* – *Cladostephus hirsutus*	*Ericaria bosphorica* + *Gongolaria barbata* + *Vertebrata subulifera* – *Bonnemaisonia hamifera*		*Nanozostera noltei*
Projective cover, %	85–90	70–75	95–100	95–100	85–90	25–30
Vegetation height, cm	6.22	12.32	28.60	34.27	32.33	21.67

Note: hereinafter, PSL, pseudolittoral zone; SBL, sublittoral zone (*). For the pseudolittoral zone, indicator is provided within the vertical range of surge fluctuations in water level (**).

RESULTS AND DISCUSSION

Results of the survey of the coastal water area at the foot of the Kuchuk-Lambat Stone Chaos are as follows (the species list and BM values of macrophytes are provided in Table 2).

Table 2. The species list and biomass value ($g \cdot m^{-2}$) of macrophytes off the coast of the Kuchuk-Lambat tract (stations No. 1–6)

Species	2015						2022					
	PSL	SBL					PSL	SBL				
	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6
CHLOROPHYTA Rchb.												
Chaetomorpha aerea (Dillwyn) Kütz.	0.10	m	m	m	6.67			m	m	m	m	
Chaetomorpha gracilis Kütz.	m						m					
Cladophora albida (Nees) Kütz.	106.00			0.42		m	13.70	m	0.83 ± 0.81			
Cladophora sericea (Huds.) Kütz.			0.83	0.41	m		3.10	m	0.67			
Cladophora vadorum (Aresch.) Kütz. ✱	119.30											
Cladophoropsis membranacea (Bang ex C. Agardh) Børgesen ✱	m		23.00 ± 14.89	35.42	10.42	m						m
Ulothrix flacca (Dillwyn) Thur.						m						
Ulva intestinalis L.	541.80						8.20					
Ulva kylinii (Bliding) H. S. Hayden, Blomster, Maggs, P. C. Silva, Stanhope et Waaland	584.60						47.20					
Ulva rigida C. Agardh					2.08							
Ulvella lens P. Crouan et H. Crouan												m
Ulvella leptochaete (Huber) R. Nielsen, O'Kelly et B. Wysor		m	m	m	m		m	m	m	m	m	m
Ulvella scutata (Reinke) R. Nielsen, O'Kelly et B. Wysor											m	m
Ulvella viridis (Reinke) R. Nielsen, O'Kelly et B. Wysor			m	m					m	m	m	

Continued on the next page…

Species	2015						2022					
	PSL	SBL					PSL	SBL				
	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6
OCHROPHYTA Caval.-Sm.												
Cladostephus hirsutus (L.) Boudour. et M. Perret ex Heesch et al. ✱		4.75	192.58 ± 105.7	895.83 ± 318.06	371.67 ± 137.93	32.50		10.08	832.50 ± 31.45	203.25	29.92 ± 9.07	
Dictyota fasciola (Roth) J. V. Lamour.		118.08 ± 49.16	120.42 ± 20.63				47.30	55.67 ± 31.69	0.83			
Ericaria bosphorica (Sauv.) D. Serio et G. Furnari ★○▲		348.75 ± 109.68	590.83	2,157.92 ± 1,898.27	1,904.17 ± 1,524.67		23.30	467.92	2,572.50 ± 51.98	2,245.00	1,713.58 ± 777.40	
Eudesme virescens (Carmich. ex Berk.) J. Agardh							11.20					
Gongolaria barbata (Stackh.) Kuntze ★○▲			604.17 ± 569.55	1,046.25	832.92			186.42 ± 75.43	629.17	1,924.58	1,554.92 ± 754.90	
Myriactula rivulariae (Suhr ex Aresch.) Feldmann	m							m	m	m		
Padina pavonica (L.) Thivy □		246.83 ± 33.12	29.25 ± 21.46				19.10	308.75 ± 39.03	10.55			
Scytosiphon lomentaria (Lyngb.) Link, nom. cons.	1.70											
Sphacelaria cirrosa (Roth) C. Agardh	m	m	m	m	m	m		m	m	m	m	
RHODOPHYTA Wettst.												
Acrochaetium parvulum (Kylin) Hoyt				m								
Acrochaetium secundatum (Lyngb.) Nägeli	m		m									
Antithamnion cruciatum (C. Agardh) Nägeli									m	m	m	
Apoglossum ruscifolium (Turner) J. Agardh					6.83 ± 6.33					2.08	0.75	
Bonnemaisonia hamifera Har.							m	m	10.00	409.17 ± 110.79	593.00 ± 98.14	0.33 ± 0.14
Carradoriella denudata (Dillwyn) Savoie et G. W. Saunders	1.50			5.00	0.42		49.00	m				
Ceramium ciliatum (J. Ellis) Ducluz.	69.0	1.25		m		m	390.70 ± 357.65					
Ceramium diaphanum (Lightf.) Roth	m	0.75				m						0.25

Continued on the next page…

Species	2015						2022					
	PSL	SBL					PSL	SBL				
	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6
Ceramium siliquosum var. *elegans* (Roth) G. Furnari			m									
Ceramium virgatum Roth	7.20	0.50	1.42	1.67	4.83 ± 4.23	m	27.50	m	1.92 ± 0.63	0.42	0.08	
Chondria capillaris (Huds.) M. J. Wynne		2.50					50.90	0.08	18.92 ± 17.77			1.17
Chondria dasyphylla (Woodw.) C. Agardh			7.92	10.83	2.08	9.17				18.92 ± 10.96		m
Choreonema thuretii (Bornet) F. Schmitz									m	m		
Chroodactylon ornatum (C. Agardh) Basson ✱						m						
Chylocladia verticillata (Lightf.) Bliding				15.0 ± 13.52								
Colaconema daviesii (Dillwyn) Stegenga	m											m
Dasya baillouviana (S. G. Gmel.) Mont.								21.75 ± 16.84				
Gelidium crinale (Hare ex Turner) Gaillon	0.50	18.83	m					m	m	0.58		
Gelidium spinosum (S. G. Gmel.) P. C. Silva			4.33		4.58 ± 4.00	0.83						
Grania efflorescens (J. Agardh) Kylin					m	m						
Jania rubens (L.) J. V. Lamour.			1.01	34.51 ± 20.48	27.13 ± 25.56				69.33 ± 45.79	16.25		
Jania virgata (Zanardini) Mont.	1.5	0.92	2.32 ± 2.15	145.49 ± 43.23	80.95 ± 74.43	1.83 ± 1.61			99.42 ± 83.46	10.92 ± 9.36	2.25	
Laurencia coronopus J. Agardh ✱▲									153.50 ± 134.80	22.58 ± 16.38	1.75	
Laurencia obtusa (Huds.) J. V. Lamour.		1.25			37.50 ± 33.07				13.42	164.17 ± 86.30	26.67 ± 14.34	
Leptosiphonia brodiei (Dillwyn) Savoie et G. W. Saunders					1.67 ± 1.44							
Lithophyllum cystoseirae (Hauck) Heydr.									m	m	m	

Continued on the next page…

Species	2015						2022					
	PSL	SBL					PSL	SBL				
	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6
Lomentaria compressa (Kütz.) Kylin ✚▲			4.33		8.75				m	m	m	
Lophosiphonia obscura (C. Agardh) Falkenb.	3.00						64.20	m			m	
Palisada perforata (Bory) K. W. Nam			13.33				90.60					
Palisada thuyoides (Kütz.) Cassano, Sentíes, Gil-Rodríguez et M. T. Fujii									0.42			
Peyssonnelia rubra (Grev.) J. Agardh						m						
Phyllophora crispa (Huds.) P. S. Dixon ★✚▲											28.25	
Pneophyllum confervicola (Kütz.) Y. M. Chamb.		m	m	m	m	m	m	m	m	m	m	m
Pneophyllum fragile Kütz.						m						m
Polysiphonia opaca (C. Agardh) Moris et De Not.								0.67 ± 0.52				
Pterothamnion plumula (J. Ellis) Nägeli	1.50											
Stylonema alsidii (Zanardini) K. M. Drew ✱		m	m	m		m		m				m
Vertebrata fucoides (Huds.) Kuntze							0.50					
Vertebrata subulifera (C. Agardh) Kuntze		14.25	77.92	213.33	282.08 ± 69.42	22.08 ± 16.65		4.92 ± 3.17	889.17 ± 545.64	827.42 ± 666.64	389.08 ± 99.72	0.67
TRACHEOPHYTA Sinnott ex Caval.-Sm.												
Nanozostera noltei (Hornem.) Toml. et Posl. ★▲❖						203.42 ± 20.45						193.70 ± 8.76

Note: cells are empty if a species is absent from samples. The error of the mean (± $S_{\bar{x}}$) is given for cases where the coefficient of variation *v* < 100%. Hereinafter, m is minor quantity (less than 0.01 g in a sample). Conservation status of taxa: ○, Convention for the Protection of the Mediterranean Sea Against Pollution (Barcelona Convention, 1976) [2009]; ✱, Red Data Book of Ukraine [2009]; ✚, Red Book of the Russian Federation [2008]; □, Red Data Book of the Republic of Bulgaria [2015a; 2015b]; ★, Black Sea Red Data Book [1999]; ▲, Red Book of the Republic of Crimea [2015]; ❖, Red Data Book of Priazovsky Region [2012].

Results of 2015. In **pseudolittoral** (PSL) on the heap (sta. No. 1), the vegetation cover was a well-separated belt, not divided into subzones and layers, 0.25–0.45 m wide. It was formed by the community *Ulva intestinalis* + *Ulva kylinii* (see Table 1). BM was 1,438 g·m^{-2}; PC, 85–90%; VH, 7.4 cm; and the number of species (hereinafter NS), 20 (Tables 3, 4).

Table 3. The number of species of macrophytes in ecological-floristic groups (GR) off the coast of the Kuchuk-Lambat tract

GR	Number of species / % (stations No. 1–6)													
	2015							2022						
	PSL	SBL					Total	PSL	SBL					Total
	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6		No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	
Ch	7 / 35.00	1 / 6.25	5 / 20.83	6 / 28.57	5 / 22.72	3 / 15.79	12 / 24.00	6 / 31.58	4 / 18.18	5 / 18.52	3 / 13.04	4 / 19.05	4 / 28.57	11 / 22.45
Oh	3 / 15.00	5 / 31.25	6 / 25.00	4 / 19.05	4 / 18.18	2 / 10.53	8 / 16.00	4 / 21.05	7 / 31.82	7 / 25.93	5 / 21.74	4 / 19.05	0 / 0	8 / 16.33
Rh	10 / 50.00	10 / 62.50	13 / 54.17	11 / 52.38	13 / 59.09	13 / 68.42	29 / 58.00	9 / 47.37	11 / 50.00	15 / 55.56	15 / 65.22	13 / 61.90	9 / 64.29	29 / 59.18
Th	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 5.26	1 / 2.00	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 7.14	1 / 2.04
Os	7 / 35.00	12 / 75.00	18 / 75.00	15 / 71.43	16 / 72.73	9 / 47.37	26 / 52.00	10 / 52.63	13 / 59.09	21 / 77.78	19 / 82.61	16 / 76.19	8 / 57.14	32 / 65.31
Ms	9 / 45.00	2 / 12.50	5 / 20.83	5 / 23.81	5 / 22.73	7 / 36.84	19 / 38.00	6 / 31.58	8 / 36.36	5 / 18.52	3 / 13.04	3 / 14.29	4 / 28.57	12 / 24.49
Ps	3 / 15.00	2 / 12.50	1 / 4.17	1 / 4.76	1 / 45.55	3 / 15.79	4 / 8.00	2 / 10.53	1 / 4.55	1 / 3.70	1 / 4.35	2 / 9.52	2 / 14.29	4 / 8.16
?	1 / 5.00	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 2.00	1 / 5.26	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 2.04
An	13 / 65.00	6 / 37.50	10 / 41.67	12 / 57.14	11 / 50.00	9 / 47.37	27 / 54.00	13 / 68.42	10 / 45.45	11 / 40.74	9 / 39.13	10 / 47.62	10 / 71.43	24 / 48.98
Ss	3 / 15.00	4 / 25.00	5 / 20.83	3 / 14.29	1 / 4.55	4 / 21.05	8 / 16.00	3 / 15.79	5 / 22.73	3 / 11.11	1 / 4.35	0 / 0	2 / 14.29	7 / 14.29
Sw	1 / 5.00	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 2.00	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Pr	3 / 15.00	6 / 37.50	9 / 37.90	6 / 29.57	10 / 45.45	6 / 31.58	14 / 28.00	2 / 10.53	6 / 27.27	11 / 40.74	11 / 47.83	10 / 47.62	1 / 7.14	16 / 32.65
?	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 5.26	1 / 4.55	2 / 7.41	2 / 8.70	1 / 4.76	1 / 7.14	2 / 4.08
Mr	10 / 50.00	12 / 75.00	18 / 75.00	14 / 66.67	17 / 77.27	14 / 73.68	34 / 68.00	11 / 57.89	14 / 63.64	20 / 74.07	18 / 78.26	16 / 76.19	10 / 71.43	37 / 75.51
Bm	9 / 45.00	4 / 25.00	6 / 25.00	7 / 33.33	5 / 22.72	5 / 26.32	14 / 28.00	7 / 36.84	8 / 36.36	7 / 25.93	5 / 21.74	5 / 23.81	4 / 28.57	11 / 22.45
Bw	1 / 5.00	0 / 0	0 / 0	0 / 0	0 / 0	1 / 5.26	2 / 4.00	1 / 5.26	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 2.04
Ww	9 / 45.00	12 / 75.00	16 / 66.67	12 / 57.14	13 / 59.09	12 / 63.16	29 / 58.00	9 / 47.37	13 / 59.09	15 / 55.56	12 / 52.17	11 / 52.38	10 / 71.43	31 / 63.27
Cw	9 / 45.00	3 / 18.75	6 / 25.00	7 / 33.33	8 / 36.36	6 / 31.58	18 / 36.00	7 / 36.84	7 / 31.82	8 / 29.63	7 / 30.43	6 / 28.57	3 / 21.43	13 / 26.53
Cp	2 / 10.00	1 / 6.25	2 / 8.33	2 / 9.52	1 / 4.55	1 / 5.26	3 / 6.00	3 / 15.79	2 / 9.09	3 / 11.11	3 / 13.04	3 / 14.29	1 / 7.14	4 / 8.16
En	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 3.70	1 / 4.35	1 / 4.76	0 / 0	1 / 2.04
Σ	20 / 100	16 / 100	24 / 100	21 / 100	22 / 100	19 / 100	50 / 100	19 / 100	22 / 100	27 / 100	23 / 100	21 / 100	14 / 100	49 / 100

Note. Hereinafter, systematic groups: Ch, Chlorophyta; Oh, Ochrophyta (class Phaeophyceae); Rh, Rhodophyta; Th, Tracheophyta. Saprobiological groups: Os, oligosaprobes; Ms, mesosaprobes; Ps, polysaprobes. By the duration of the vegetation period: An, annuals; Ss, seasonal summer; Sw, seasonal winter; Pr, perennials. In relation to halobility: Mr, marine; Bm, brackish–marine; Bw, brackish. Phytogeographical groups: Ww, warm-water; Cw, cold-water; Cp, cosmopolitan; En, endemic. ?, no data available.

In **sublittoral** (SBL), all hard substrata were occupied by communities of a so-called *Cystoseira* belt (with the dominance of *Cystoseira* s. l. representatives).

In the shallowest spots, the community *Ericaria bosphorica* – *Padina pavonica* + *Dictyota fasciola* developed (see Table 1). At sta. No. 2, BM was 758 $g \cdot m^{-2}$; PC, 55–60%; VH, 8.2 cm; and NS, 16 (see Tables 3, 4).

Table 4. The biomass of macrophytes in ecological-floristic groups (GR) off the coast of the Kuchuk-Lambat tract

GR	Biomass, g·m^{-2} / % (stations No. 1–6)													
	2015							2022						
	PSL	SBL					Mean	PSL	SBL					Mean
	1	2	3	4	5	6		1	2	3	4	5	6	
Ch	1,351.80 / 94.02	m / 0	23.83 / 1.42	36.25 / 0.80	19.17 / 0.54	0 / 0	238.51 / 11.74	72.20 / 8.53	m / 0	1.50 / 0.02	m / 0	m / 0	m / 0	12.28 / 0.42
Oh	1.70 / 0.12	718.41 / 94.69	1,537.25 / 91.85	4,100.00 / 89.87	3,108.76 / 86.72	32.50 / 10.95	1,583.11 / 77.12	100.90 / 11.92	1,028.84 / 97.40	4,045.55 / 76.29	4,372.83 / 74.81	3,298.42 / 76.00	m / 0	2,141.10 / 73.04
Rh	84.20 / 5.86	40.25 / 5.31	112.58 / 6.73	425.83 / 9.33	456.82 / 12.74	33.91 / 11.42	192.26 / 9.47	673.40 / 79.55	27.42 / 2.60	1,256.10 / 23.69	1,472.51 / 25.19	1,041.83 / 24.00	2.42 / 1.23	745.61 / 25.44
Th	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	203.42 / 68.53	33.90 / 1.67	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	193.70 / 98.77	32.28 / 1.10
Os	70.60 / 4.91	738.58 / 97.35	1,667.08 / 99.61	4,554.58 / 99.83	3,572.84 / 99.67	65.58 / 24.30	1,778.21 / 86.84	633.60 / 74.85	1,055.59 / 99.94	5,289.73 / 99.74	5,435.17 / 92.98	3,747.17 / 86.34	1.84 / 0.94	2,693.85 / 91.90
Ms	233.50 / 16.24	18.83 / 2.48	5.16 / 0.31	5.83 / 0.13	7.08 / 0.20	204.25 / 75.70	79.11 / 3.86	130.00 / 15.35	0.67 / 0.06	11.50 / 0.22	409.75 / 7.01	593.00 / 13.66	194.03 / 98.93	223.16 / 7.61
Ps	549.00 / 38.19	1.25 / 0.16	1.42 / 0.08	1.67 / 0.04	4.83 / 0.13	m / 0	93.03 / 4.54	35.70 / 4.22	m / 0	1.92 / 0.04	0.42 / 0.01	0.08 / 0.002	0.25 / 0.13	6.40 / 0.22
?	584.6 / 40.66	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	97.43 / 4.76	47.20 / 5.58	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	7.86 / 0.27
An	1,365.00 / 94.94	18.00 / 2.37	92.42 / 5.52	246.66 / 5.41	306.50 / 8.55	31.25 / 11.58	343.31 / 16.77	275.50 / 32.55	5.00 / 0.47	911.51 / 17.19	827.84 / 14.16	389.16 / 8.96	2.09 / 1.06	401.85 / 13.71
Ss	69.00 / 4.80	366.16 / 48.26	172.67 / 10.32	35.42 / 0.78	10.42 / 0.29	m / 0	108.94 / 5.32	457.10 / 53.99	386.17 / 36.56	11.38 / 0.21	m / 0	m / 0	m / 0	142.44 / 4.86
Sw	1.70 / 0.12	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0.28 / 0.01	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Pr	2.00 / 0.14	374.5 / 49.36	1,408.57 / 84.16	4,280.00 / 93.82	3,267.83 / 91.16	238.58 / 88.42	1,595.25 / 77.90	113.90 / 13.46	665.09 / 62.97	4,370.26 / 82.41	4,608.33 / 78.84	3,358.09 / 77.37	193.70 / 98.77	2,218.23 / 75.67
?	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	m / 0	m / 0	10.00 / 0.19	409.17 / 7.00	593.00 / 13.67	0.33 / 0.17	168.75 / 5.76
Mr	658.60 / 45.81	757.41 / 99.84	1,671.41 / 99.87	4,554.58 / 99.83	3,572.83 / 99.67	269.83 / 100.00	1,914.11 / 93.47	745.00 / 88.01	1,056.26 / 100.00	5,289.73 / 99.75	5,435.75 / 92.99	3,747.17 / 86.34	195.54 / 99.70	2,744.91 / 93.64
Mb	237.30 / 16.51	1.25 / 0.16	2.25 / 0.13	7.50 / 0.16	11.92 / 0.33	m / 0	43.37 / 2.12	93.30 / 11.02	m / 0	13.42 / 0.25	409.59 / 7.01	593.08 / 13.66	0.58 / 0.30	185.00 / 6.31
Bw	541.80 / 37.69	0 / 0	0 / 0	0 / 0	0 / 0	m / 0	90.30 / 4.41	8.2 / 0.97	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1.36 / 0.05
Ww	75.60 / 5.26	753.41 / 99.31	1,478.83 / 88.36	3,663.75 / 80.31	3,199.75 / 89.26	237.33 / 87.96	1,568.11 / 76.57	735.10 / 86.84	1,046.18 / 99.05	4,303.73 / 81.15	5,207.84 / 89.09	3,714.75 / 85.59	195.79 / 99.83	2,533.90 / 86.44
Cw	813.10 / 56.56	4.75 / 0.63	193.41 / 11.55	896.66 / 19.65	380.17 / 10.61	32.50 / 12.04	386.77 / 18.89	75.70 / 8.94	10.08 / 0.95	834.00 / 15.73	205.33 / 3.51	30.67 / 0.71	m / 0	192.63 / 6.57
Cp	549.00 / 38.19	0.50 / 0.06	1.42 / 0.08	1.67 / 0.04	4.83 / 0.13	m / 0	92.90 / 4.54	35.70 / 4.22	m / 0	11.92 / 0.22	409.59 / 7.01	593.08 / 13.66	0.33 / 0.17	175.10 / 5.98
En	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	153.50 / 2.90	22.58 / 0.39	1.75 / 0.04	0 / 0	29.64 / 1.01
Σ	1,437.70 / 100	758.66 / 100	1,673.66 / 100	4,562.08 / 100	3,584.75 / 100	269.83 / 100	2,047.78 / 100	846.50 / 100	1,056.26 / 100	5,303.15 / 100	5,845.34 / 100	4,340.25 / 100	196.12 / 100	2,931.27 / 100

In a depth range of 1–5 m, right up to the boundary with sand, the community *Ericaria bosphorica + Gongolaria barbata + Vertebrata subulifera – Cladostephus hirsutus* was recorded (see Table 1). The vegetation cover was fairly uniform, but the ratio of the key quantitative indicators varied with depth. At sta. No. 3–5, BM was 1,674–4,562 g·m^{-2}; PC, from 60–65 to 95–100%; VH, 17.4–29.1 cm; and NS, 22–24 (see Tables 3, 4).

Soft substrata from the boundary with hard substrata to the isobath of 7–7.5 m were devoid of permanent macroscopic vegetation. However, from this mark and down to 8.5–9 m, those were occupied by the community of *Nanozostera noltei* (see Table 1). At sta. No. 6, BM was 270 g·m^{-2}; PC, 25–30%, VH, 22.9 cm; and NS, 19 (see Tables 3, 4)[1] . Several *N. noltei* clumps, 1–3 m in diameter and 1–5 m apart (sometimes up to 10 m), were formed by vegetative shoots alone. Deeper than 9 m, no permanent vegetation cover was revealed.

In 2015, 50 macrophyte species were registered in the surveyed area: Chlorophyta, 12 (24.0%), Ochrophyta, 8 (16.0%), Rhodophyta, 29 (58.0%), and Tracheophyta, 1 (2.0%) (see Table 3). The minimum species diversity was noted for a depth of 0.5 m (16 species), and the maximum one, for 1 m (24 species); in other cases, NS distribution along the profile was relatively uniform (19–22 species). With the dominance by NS of short-vegetating (annual, seasonal winter, and seasonal summer) species (86.0%), the flora of the water area in general had an oligosaprobic (52.0%) marine (68.0%) warm-water (58.0%) character. In SBL, with increasing depth, there was no clear trend in the shift in the ratio of ecological-floristic groups. However, macrophytobenthos of PSL had a pronounced specificity in NS distribution by ecological-floristic groups, even more evident when analyzing BM. Thus, its overwhelming majority was formed by short-vegetating (99.7%), mainly annual Chlorophyta (94.0%), while proportions of marine (45.8%) oligosaprobic (4.9%) warm-water (5.3%) species were minimal for the surveyed area (see Table 4). At the same time, in SBL on hard substrata, Ochrophyta dominated (86.7–94.7%), while macroalgae species were chiefly oligosaprobic (97.4–99.8%) marine (99.7–99.9%) perennial (49.3–93.8%) warm-water (88.0–99.3%) ones (importantly, with increasing depth, there were no clear trends in the shift in the ratio of BM of these groups). On soft substrata, BM was formed mostly by mesosaprobic (79.1%) Tracheophyta (68.5%); the values of other indicators were close to those on hard substrata.

Results of 2022. The second survey showed that the vegetation belt of **PSL**, not divided into subzones and 25–45 cm wide, is formed by the community of *Ceramium ciliatum* (see Table 1). At sta. No. 1, BM was 847 g·m^{-2}; PC, 85–90%; VH, 6.2 cm; and NS, 19 (see Tables 3, 4).

Soft substrata of **SBL** are occupied by communities of the *Cystoseira* belt.

In the shallowest areas, the community *Ericaria bosphorica* + *Gongolaria barbata* – *Padina pavonica* + *Dictyota fasciola* develops. At sta. No. 2, BM was 1,056 g·m^{-2}; PC, 70–75%; VH, 12.3 cm; and NS, 22 (see Tables 1–4).

A depth of 1 m is still occupied by the community *Ericaria bosphorica* + *Gongolaria barbata* + *Vertebrata subulifera* – *Cladostephus hirsutus* (see Table 1). At sta. No. 3, BM was 5,303 g·m^{-2}; PC, 95–100%; VH, 28.6 cm; and NS, 27 (see Tables 3, 4). In a depth range of 3–5 m, *Bonnemaisonia hamifera* became one of the dominants of the second layer; as a result, the community *Ericaria bosphorica* + *Gongolaria barbata* + *Vertebrata subulifera* – *Bonnemaisonia hamifera* was formed (see Table 1). At sta. No. 4–5, BM was 4,340–5,845 g·m^{-2}; PC, from 85–90 to 95–100%; VH, 32.3–34.3 cm; and NS, 21–23 (see Tables 1–4).

The general character and vegetation distribution on soft substrata did not change. In a depth range from 7–7.5 to 8.5–9 m, the community of *Nanozostera noltei* was recorded (see Table 1). At sta. No. 6, BM was 196 g·m^{-2}; PC, 25–30%; VH, 21.7 cm; and NS, 14 (see Tables 3, 4). However, among vegetative shoots determining VH, a few generative ones were registered; those had a mean length of 13.6 cm and constituted less than 3% of the aboveground BM of *N. noltei*.

[1]For *Nanozostera noltei*, only the biomass (BM) of the aboveground part is given. BM of the underground part (rhizomes and roots) was not taken into account when calculating the total BM of the community and individual ecological-floristic groups.

In 2022, 49 macrophyte species were recorded in the surveyed area: Chlorophyta, 11 (22.5%), Ochrophyta, 8 (16.3%), Rhodophyta, 29 (59.2%), and Tracheophyta, 1 (2.0%) (see Table 3). The minimum species diversity was noted for soft substrata at a depth of 8 m (14 species), and the maximum one, at a depth of 1 m (27 species); in other cases, NS distribution along the profile remained quite stable (19–23 species). By NS, short-vegetating species predominate (63.3%); in general, the flora of the water area has an oligosaprobic (65.3%), marine (75.5%) warm-water (63.3) character. The same as earlier, macrophytobenthos of PSL differs from SBL one by these indicators; the analysis of the ratio of BM of ecological-floristic groups evidences for it even more clearly. However, in 2022, BM in PSL was chiefly formed by Rhodophyta (79.6%) represented mainly by short-vegetating (86.5%) seasonal summer and annual species (see Table 4). At the same time, proportions of most ecological-floristic groups in the total BM were slightly different from values recorded for hard substrata in SBL. It was dominated by Ochrophyta (76.0–97.4%), with high prevalence of oligosaprobic (86.3–99.9%) marine (86.3–100%) perennial (63.0–82.4%) warm-water (81.2–99.1%) species (there are no trends in the shift in the ratio of BM of the listed groups with a change in depth). On soft substrata, BM is chiefly formed by mesosaprobic (98.9%) Tracheophyta (98.8%); the values of other indicators are close to those observed for hard substrata.

As evidenced by generalization of the results obtained in 2015 and 2022, in the surveyed area, macrophytobenthos develops on different natural substrata which determines the nature of the vegetation cover on hard substrata (*Thalassophycion sclerochthonophytia*) and soft ones (*Thalassopoion malacochthonophytia*) [Kalugina-Gutnik, 1975]. In total, 63 macrophyte species were recorded at the analyzed site (see Table 2): Chlorophyta, 14 (22.2%), Ochrophyta, 9 (14.3%), Rhodophyta, 39 (62.0%), and Tracheophyta, 1 (1.6%). The comparison showed: the total NS of macrophytobenthos and the ratio of systematic groups by NS were quite close in two years. But at certain depths, the flora composition and the ratio of species (including dominant ones) and ecological-floristic groups had changed by 2022, and this determined the corresponding transformations in the vegetation cover. To date, along the surveyed shore, macrophytes form five belt-located plant communities (see Table 1). Their total BM has increased significantly on average, and the flora (NS) has acquired a more oligosaprobic marine warm-water character (see Tables 3, 4). The main qualitative and quantitative changes were recorded in the shallowest and deepest areas. Apparently, they occurred mainly for two different reasons.

In 2015, there were obvious signs of a recent mudflow both on the coast and on the seabed. Specifically, we noted fairly fresh gullies in the ravine and beach pebble deposits (sometimes mixed with unrounded rubble and clay) in a shallow area. Approximately 1–1.5 months before our survey, there were heavy rains in this area followed by significant (but not disastrous) floods into the sea. Macrophytobenthos near the water's edge was the first to be subjected to the destructive effect of the flow loaded with solid particles. The vegetation of PSL seems to have quickly recovered: due to the mass development of *Ulva* L. representatives, a community was formed there which is usually more typical of spring period (sometimes autumn) and/or eutrophic waters [Sadogurskiy et al., 2023b]. While the mechanical damage to the seabed vegetation at the ravine mouth was local and rapid, the eutrophication of waters was more large-scale and relatively long-term (due to a summer decrease in storm activity). As *Ulva intestinalis* is one of the fastest growing annual macroscopic polysaprobic species under favorable light and temperature conditions and an increased nutrient concentration [Kim et al., 2021; Parchevsky, Rabinovich, 1991], the 'off-season' transformation of the vegetation cover in the damaged area occurred. Visual observation of the adjacent areas of PSL revealed the widespread dominance of the seasonal summer oligosaprobic species *Ceramium ciliatum* during this period. And in 2022, when the above- and underwater parts of the coastal zone had no signs of recent mudflow activity, this species continued to form the basis of the vegetation cover of SBL in the entire area, including the spot at the ravine mouth. At the same time, lower values of VH and total BM (see Tables 1, 4) are mostly mediated by morphological differences between *C. ciliatum* and a larger-sized species *U. intestinalis*.

For perennial communities of the shallow part of SBL, the mudflow in 2015 had more long-term consequences. In addition to the fact that the rate of recovery of perennial macroalgae was lower, the situation was worsened by partial burial of the bottom heap by terrigenous sediments. During the initial survey, at a depth of 0.5–1 m, *Cystoseira* s. l. thalli were significantly damaged: there were broken branches, and sometimes, bases of their trunks were covered with pebble and rubble (Fig. 2a). Visual observation showed as follows: the nature of the seabed vegetation at the ravine mouth did not change compared to that of the periphery of the surveyed area and the adjacent waters, but its quantitative indicators obviously dropped. This is sure to have affected the species composition, as other algae species inhabit either *Cystoseira* epilithon or its epiphyton. Although additional sampling along the periphery of the area was not carried out that year, the second survey was planned in a year – to identify the dynamics of macrophytobenthos; however, 7 years had passed before it was carried out. So, we did not establish how long it takes for macrophytobenthos to recover, and we do not have reliable information about whether similar damage occurred during that period (probably, yes), but we know how it ends. More precisely, we can characterize the vegetation cover of this area not subjected to the recent destructive effect of the mudflow that could occur again. Thus, at a depth of 0.5 m (sta. No. 2), where in 2015 the minimum NS and total BM for hard substrata were recorded, the values of 2022 increased by 27–28% (see Tables 3, 4). At 1 m (sta. No. 3), with a three-fold rise in the total BM, the indicators reached maximum or close-to-maximum values. They became comparable with those at greater depths which did not experience such a strong effect of the mudflow in 2015.

The difference between PC and VH values established in different years within the boundaries of the *Cystoseira* belt is quite obvious (see Table 1). Thus, in 2022, compared to 2015, VH increased by depths as follows: at 0.5 m, by 33.7%; at 1 m, by 39.1%; at 3 m, by 21.2%; and at 5 m, by 10.1%. Accordingly, the further from the shore, the less pronounced these changes; this corresponds to the weakening of the mudflow intensity. Therefore, it is quite natural that the total BM of *Cystoseira* s. l. representatives forming the basis of the vegetation cover in a depth range of 3–5 m, least affected by the mudflow (sta. No. 4 and 5), has close values in two analyzed years (see Table 2). An increase in the total BM of macrophytobenthos in this depth range in 2022 was governed by the abundant growth of epiphytes, mainly *Vertebrata subulifera* and *Bonnemaisonia hamifera*.

While the first one is a typical representative of the native flora, the second is a new invasive species for the region [Sadogurskiy et al., 2023a, b]. Developing almost in epiphyton alone, thalli of *B. hamifera* sporophytes occur now in absolutely all samples taken off the SCC. The only difference is that numerous filaments are common in shallow waters, while separate spherical thalli (Ø of 2–3 cm) appear deeper; from a depth of 2.5–3 m, those merge into growths sometimes reaching an area of 1–3 m^2. As a result, to date, the invader has become one of the dominants of the deepest plant communities and even caused their local degradation; it made it possible to classify the species as a transformer one [Sadogurskiy et al., 2023a, b]. In the surveyed area, at depths of 3–5 m, *B. hamifera* forms 6.0–13.7% of the total BM of the community, as well as most of BM and an aspect of the lower layer (previously almost exclusively *Cladostephus* one) (Fig. 2b). Under a dense epiphytic cover, *Cladostephus hirsutus* thalli appear extremely depressed having lost almost all of their characteristic short branches. This is the key difference from the pattern recorded earlier in other areas off the SCC, where *B. hamifera* developed mostly on *Cystoseira* thalli [Sadogurskiy et al., 2023a, b].

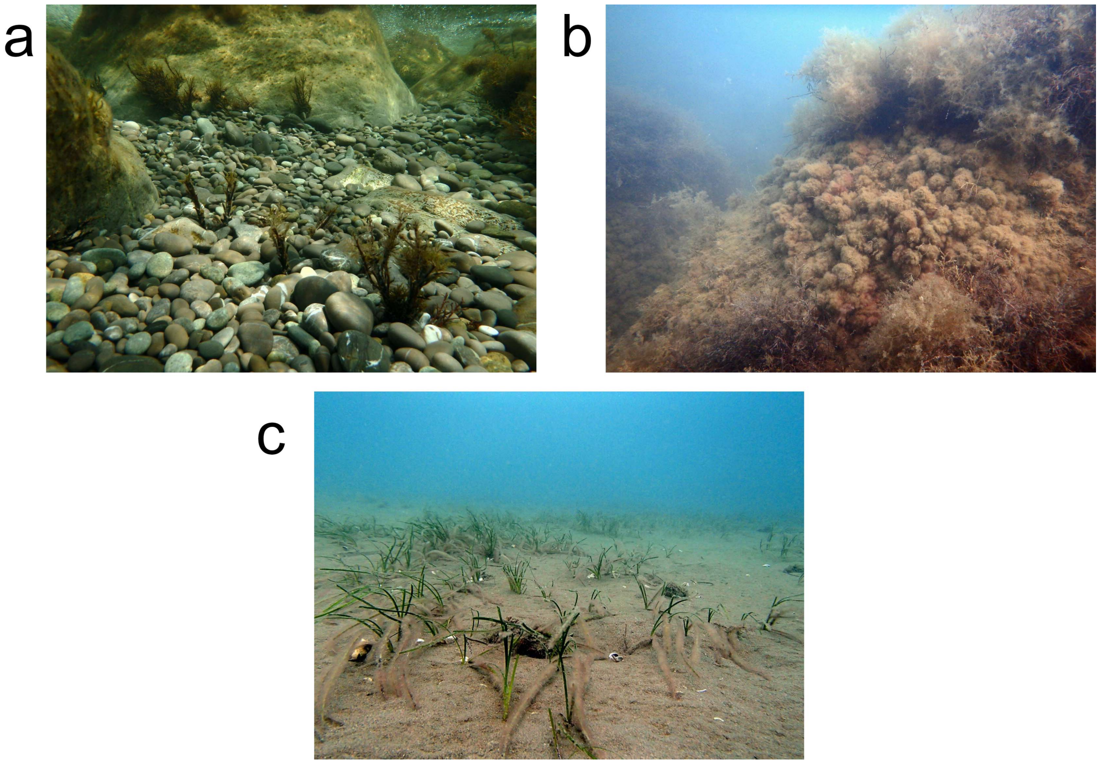

Fig. 2. Some features of macrophytobenthos off the coast of the Kuchuk-Lambat tract: a, community of the *Cystoseira* belt (*Cystoseira* s. l.) damaged by a mudflow, a depth of 0.5 m (07.08.2015); b, *Bonnemaisonia hamifera* growth in the community of the *Cystoseira* belt, a depth of 5 m (27.07.2022); c, laying of *Nanozostera noltei* leaves overgrown by *Bonnemaisonia hamifera*, a depth of 8 m (27.07.2022)

Importantly, *Ericaria bosphorica* and *Gongolaria barbata*, both *Cystoseira* s. l. representatives, used to be quite widespread off the SCC [Maslov, 2004; Maslov, Kuropatov, 1987; Pogrebnyak, Maslov, 1976]. Since about the mid-1990s, abundance and occurrence of the second species have dropped; as a result, its role in the formation of thickets has decreased for more than two decades. At some sites, the species was not registered in samples at all [Sadogursky, 2009, 2014]. Interestingly, within the last 3–5 years, a sudden recovery in quantitative indicators of *G. barbata* was observed, and it has almost returned to its dominant position, along with *E. bosphorica*. Thus, in the surveyed area, *G. barbata* was noted at 0.5 m in 2022 (it was absent there in 2015); in a depth range of 3–5 m, its BM almost doubled (see Tables 2, 4). It is hard to establish the cause for such dynamics, but we have to highlight the fact as follows. Along southern shores of the Sea of Azov, the pattern has been different all these years: most thickets were formed by *G. barbata*, while *E. bosphorica* was rare and non-abundant [Sadogurskiy et al., 2020].

Off the SCC, in the area of capes, mobile soft substrata are usually devoid of permanent macroscopic vegetation. Seagrass communities (with the dominance of *Zostera* L. and *Nanozostera* Toml. et Posl. representatives) develop fragmentarily at significant depths at sites with a concave coastline [Sadogurskiy et al., 2022]. The surveyed area is one of such sites. Seagrasses, unlike *Cystoseira*, belong to a different saprobiological group. Moreover, their thickets have a poorly represented dense substrata suitable for the attachment of large-thallus species; that is why epiphytic macroalgae settle mostly on leaves. Only some of them develop on a few mollusc shells (scattered over the substrata surface) and less often on rhizomes of seagrasses (if those are exposed from the substrata). Therefore, in seagrass thickets off the SCC, NS and total BM are lower (the second one, by an order of magnitude) than in the *Cystoseira* belt; ecological-floristic indicators also differ much. The mudflow of 2015 did not affect the deep-water community of *N. noltei*; consequently, in both years, BM of the dominant and VH were almost the same (see Tables 1, 4). However, in 2022, NS and BM of epiphytic macroalgae decreased by 26.3–27.3%. The reason was that epiphytic filaments of *B. hamifera* densely covered *N. noltei* shoots; moreover, the oldest leaves were wrapped in continuous fleecy covers and, accordingly, were lying on the seabed (Fig. 2c). This directly reduces the area of substrata available to other epiphytes. In addition, their colonization is hindered by secondary metabolites of *B. hamifera*: according to several studies, they not only have a strong inhibitory allelopathic effect on the native phytobiota, but also definitely repel phytophages [Enge et al., 2012; Svensson et al., 2013]. As a result, due to its morphological plasticity, high stenobiontism, and the formation of a specific phytogenic field, *B. hamifera* successfully competes with native macrophytes. Its rapid distribution along the SCC, a part of the global expansion, poses a serious threat to natural communities and biotopes of the Sea of Azov–Black Sea region [Sadogurskiy et al., 2023a, b].

Thus, the periodic effect of the mudflow on macrophytobenthos of the surveyed area is short-term and reversible, and it weakens with increasing depth. At the same time, transformations caused by *B. hamifera* invasion become more intense with depth and are probably long-term; to date, their reversibility raises reasonable doubts. But in general, despite the close and long-term proximity to urbanized, recreational, and agricultural areas, the benthic vegetation cover shows a high degree of preservation. Its general character, as well as the flora composition and the ratio of the key ecological-floristic indicators (except for transformations mediated by the new biological invasion) are typical for the Black Sea hydrobotanical region "SCC." The rare species fraction of the flora covers 12 taxa listed in environmental documents of various ranks. Biotopes, with the basis formed by macrophyte communities, are listed in the Habitats Directive (Directive 92/43/EEC; codes 1160 and 1170) [Interpretation Manual of European Union Habitats, 2013]. Thus, both the water area and the coast certainly have obvious sozological value. Taking into account the approach proposed earlier [Sadogurskiy et al., 2017; Sadogursky et al., 2009, 2013], we consider it appropriate to establish on their basis a single territorial-aquatic nature reservation. It should unite the existing geological natural monument Kuchuk-Lambat Stone Chaos and its adjacent coastal and marine area of the Black Sea with a length of 300–350 m along the shore to a depth of at least 10 m, at a distance of at least 250–300 m from the water's edge (see Fig. 1a). To a certain extent, the official nature reserve status will protect this territorial-aquatic complex from direct anthropogenic transformation due to gradual absorption by adjacent recreational complexes. Such a nature reserve will not interfere with their functioning; on the contrary, it will increase their tourist attractiveness. Off the SCC, natural and slightly transformed areas have still been preserved, most often confined to hard-to-reach rocky capes and other inconvenient areas (as in the case analyzed). Establishing of small but relatively numerous territorial-aquatic protected areas (cores) on their basis, united into the structure of the ecological network by territorial-aquatic connecting elements (ecocorridors), will allow for the formation of a certain environmental protection framework off the SCC. At the same time, further study of *B. hamifera* invasion is required: this will reveal its dynamics and help in assessing environmental and possible social and economic consequences for the region.

Conclusion. Based on results of the hydrobotanical study carried out in 2015 and 2022, it was established as follows: in the coastal-marine water area adjacent to the geological natural monument Kuchuk-Lambat Stone Chaos, macrophytobenthos develops on natural hard and soft substrata which determines its general character. In total, 63 macrophyte species were recorded: Chlorophyta, 14 (22.2%); Ochrophyta, 9 (14.3%); Rhodophyta, 39 (62.0%); and Tracheophyta, 1 (1.6%). The total number of species and the ratio of systematic groups by the number of species are close for two years. However, the flora composition and the ratio of dominant species and ecological-floristic groups by biomass changed significantly at minimum and maximum depths. This caused a transformation of the vegetation cover. In shallow areas, its dynamics is mediated by local disturbance and subsequent recovery of macrophytobenthos after a mudflow and has a fluctuating character. At depth, the shifts are governed by the invasion of the transformer species *Bonnemaisonia hamifera* into natural communities. These shifts are likely to be of a long-term nature; to uncover their degree and reversibility, it is necessary to monitor the distribution of the invader off the southern coast of Crimea and within the boundaries of the Sea of Azov–Black Sea region in general. At present, along the surveyed coast, macrophytes form five belt-located plant communities. Macrophytobenthos demonstrates a high degree of preservation. Its spatial distribution, composition, and structure (except for changes caused by biological invasion) are typical for the Black Sea hydrobotanical region "Southern Coast of Crimea." Taxa and biotopes subjected to special protection within the framework of regional and international legislation are recorded. To prevent anthropogenic transformation, it is reasonable to form a comprehensive territorial-aquatic nature reserve that will unite the existing geological natural monument and adjacent coastal waters of the Black Sea.

The work was carried out within the framework of NBG–NSC state research assignment No. 122041900097-3.

REFERENCES

1. Belich T. V., Sadogurskaya S. A., Sadogurskiy S. Ye. To the question of species diversity of coastal-marine areas of the south coast of Crimea. *Trudy Karadagskoi nauchnoi stantsii im. T. I. Vyazemskogo – prirodnogo zapovednika RAN*, 2020, no. 4 (16), pp. 3–12. (in Russ.). https://doi.org/10.21072/eco.2021.16.01
2. Belokopytov V. N., Sarkisov A. A., Shchurov S. V. Currents near the part of the Crimean coast from the Sarych Cape to Katsiveli. *Ekologicheskaya bezopasnost' pribrezhnoi i shel'fovoi zon i kompleksnoe ispol'zovanie resursov shel'fa*, 2003, iss. 8, pp. 64–68. (in Russ.). https://elibrary.ru/zaqmqx
3. Vakhrushev B. A., Amelichev G. N. Geologicheskii pamyatnik prirody – Kuchuk-Lambatskii kamennyi khaos – kak element opolznevoi, seismogravitatsionnoi i karstovoi morfoskul'ptury rel'efa Yuzhnogo berega Kryma. *Kul'tura narodov Prichernomor'ya*, 2000, no. 15, pp. 12–17. (in Russ.). https://elibrary.ru/hurprb
4. Goryachkin Yu. N., Repetin L. N. Storm wind and wave regime near the Black Sea coast of Crimea. *Ekologicheskaya bezopasnost' pribrezhnoi i shel'fovoi zon i kompleksnoe ispol'zovanie resursov shel'fa*, 2009, iss. 19, pp. 56–69. (in Russ.). https://elibrary.ru/yktsvr
5. *Gidrometeorologiya i gidrokhimiya morei SSSR.* Vol. 4. *Chernoe more.* Iss. 1. *Gidrometeorologicheskie usloviya* / A. I. Simonov,

E. N. Altman (Eds). Saint Petersburg : Gidrometeoizdat, 1991, 426 p. (in Russ.)
6. Zinova A. D. *Opredelitel' zelenykh, burykh i krasnykh vodoroslei yuzhnykh morei SSSR*. Moscow ; Leningrad : Nauka, 1967, 400 p. (in Russ.)
7. Kalugina A. A. Issledovanie donnoi rastitel'nosti Chernogo morya s primeneniem legkovodolaznoi tekhniki. In: *Morskie podvodnye issledovaniya*. Moscow : Nauka, 1969, pp. 105–113. (in Russ.)
8. Kalugina-Gutnik A. A. *Fitobentos Chernogo morya.* Kyiv : Naukova dumka, 1975, 248 p. (in Russ.). https://repository.marine-research.ru/handle/299011/5645
9. *Red Data Book of Priazovsky Region. Vascular Plants* / V. M. Ostapko, V. P. Kolomiychuk (Eds). Kyiv : Alterpres, 2012, 280 p. (in Russ.). https://elibrary.ru/yhslft
10. *Red Book of the Republic of Crimea. Plants, Algae, and Fungi* / A. V. Yena, A. V. Fateryga (Eds). Simferopol : ARIAL, 2015, 480 p. (in Russ.). https://elibrary.ru/wxeqef
11. *Krasnaya kniga Rossiiskoi Federatsii* (rasteniya i griby). Moscow : Tov-vo nauch. izd. KMK, 2008, 885 p. (in Russ.). https://elibrary.ru/tcnfxr
12. Maslov I. I. *Morskoi fitobentos krymskogo poberezh'ya.* [dissertation]. Yalta, 2004, 358 p. (in Russ.)
13. Maslov I. I., Kuropatov L. A. K detal'nomu opisaniyu biotsenoza tsistoziry zapovednika "Mys Mart'yan". *Byulleten' Gosudarstvennogo Nikitskogo botanicheskogo sada*, 1987, iss. 63, pp. 13–17. (in Russ.). https://elibrary.ru/zwxmst
14. Parchevsky V. P., Rabinovich M. A. Growth rate and harvest of the green alga *Enteromorpha intestinalis* on artificial substrates in a wastewater outfall area. *Biologiya morya*, 1991, no. 2, pp. 30–36. (in Russ.). https://repository.marine-research.ru/handle/299011/10759
15. *Pasport pamyatnika prirody regional'nogo znacheniya "Kuchuk-Lambatskii kamennyi khaos"* : utverzhden prikazom Ministerstva ekologii i prirodnykh resursov Respubliki Krym ot 29.04.2021 no. 523. Simferopol : [s. n.], 2021, 13 p. (in Russ.)
16. Pogrebnyak I. I., Maslov I. I. K izucheniyu donnoi rastitel'nosti raiona mysa Mart'yan. *Byulleten' Gosudarstvennogo Nikitskogo botanicheskogo sada*, 1976, vol. 70, pp. 105–113. (in Russ.). https://elibrary.ru/yoflcx
17. Ryff L. E. Flora of the nature monument "Kuchuk-Lambat stone chaos" (south coast of the Crimea). *Geopolitika i ekogeodinamika regionov*, 2013, vol. 9, no. 2-2, pp. 65–72. (in Russ.). https://elibrary.ru/vmbfup
18. Sadogursky S. Ye. Macrophytobenthos near the coast of the botanical reserve "Kanaka": Its modern state and the ways of preservation (Black Sea). *Zapovidna sprava v Ukraini*, 2009, vol. 15, iss. 1, pp. 31–39. (in Russ.). https://elibrary.ru/ynkixl
19. Sadogursky S. Ye. Composition and distribution of macrophytobenthos near the cape of Svyatoy Troitsy (Black Sea, Crimea, Ukraine). *Morskoj ekologicheskij zhurnal*, 2014, vol. 13, no. 1, pp. 53–62. (in Russ.). https://repository.marine-research.ru/handle/299011/1325
20. Sadogursky S. E., Belich T. V., Sadogurskaya S. A. To problem of separation of territory-aquatic elements of regional econet in Crimea. In: *The Nature Reserves of Crimea. Theory, Practice and Perspectives of Conservation Business in Black Sea Region* : materials of the 5th International scientific-practical conference (Simferopol, 22–23 October, 2009). Simferopol : [s. n.], 2009, pp. 134–139. (in Russ.). https://elibrary.ru/ynijcn
21. Sadogursky S. E., Belich T. V., Sadogurskaya S. A. Some aspects of formation

of territorial aquatic components of the regional and local ecological networks in the Crimea. In: *Priroda Vostochnogo Kryma. Otsenka bioraznoobraziya i razrabotka proekta lokal'noi ekologicheskoi seti* / S. P. Ivanov (Ed.). Kyiv : TOV "DIA", 2013, pp. 79–85. (in Russ.). https://elibrary.ru/zawrhd

22. Sadogurskiy S. Yu., Ryff L. E., Sadogurs'ka S. O., Belich T. V. To the strategy of preserving the natural phytodiversity of the coastal zone of the sea. In: *Proceedings of the 14th Congress of the Ukrainian Botanical Society*, Kyiv, 25–26 April, 2017. Kyiv, 2017, pp. 134. (in Ukr.)
23. *Sovremennoe sostoyanie beregovoi zony Kryma* / Yu. N. Goryachkin (Ed.). Sevastopol : EKOSI-Gidrofizika, 2015, 252 p. (in Russ.). https://elibrary.ru/urttzy
24. *Red Data Book of Ukraine. Flora* / Ya. P. Didukh (Ed.). Kyiv : Globalkonsalting, 2009, 912 p. (in Ukr.)
25. *AlgaeBase.* World-wide electronic publication, National University of Ireland, Galway / M. D. Guiry, G. M. Guiry (Eds) : [site], 2024. URL: http://www.algaebase.org [accessed: 17.01.2024].
26. *Black Sea Red Data Book* / H. J. Dumont (Ed.). New York : United Nations Office for Project Services, 1999, 413 p.
27. Enge S., Nylund G. M., Harder T., Pavia H. An exotic chemical weapon explains low herbivore damage in an invasive alga. *Ecology*, 2012, vol. 93, iss. 12, pp. 2736–2745. https://doi.org/10.1890/12-0143.1
28. *Interpretation Manual of European Union Habitats. EUR 28.* Brussels : European Commission, DG Environment, 2013, 144 p.
29. *International Plant Names Index (IPNI)* : [site], 2024. URL: https://www.ipni.org/ [accessed: 17.01.2024].
30. Johnson N. C. *Biodiversity in the Balance: Approaches to Setting Geographic Conservation Priorities.* Washington, DC : Biodiversity Support Program, 1995, 116 p.
31. Kim J.-H., Zhao Z. X., Kim Y. S. Variation in germling growth in the green tide-forming alga *Ulva intestinalis* (Chlorophyta) in response to gradients in salinity, temperature, light, and nutrients. *Journal of Applied Phycology*, 2021, vol. 33, iss. 6, pp. 3951–3962. https://doi.org/10.1007/s10811-021-02563-4
32. *Proposal for a Council Decision Establishing the Position to be Adopted on Behalf of the European Community with Regard to Proposals for Amending Annexes II and III to the Protocol Concerning Specially Protected Areas and Biological Diversity in the Mediterranean (SPA/BD Protocol) of the Convention for the Protection of the Marine Environment and the Coastal Region of the Mediterranean (Barcelona Convention) at the Sixteenth Meeting of the Contracting Parties.* COM (2009) 585 final. Brussels : Commission on the European Communities, 2009, 13 p. URL: http://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=CELEX:52009PC0585&from=EN [accessed: 17.01.2024].
33. *Red Data Book of the Republic of Bulgaria.* Vol. 1. *Plants and Fungi* / D. Peev, V. Vladimirov (Eds). Sofia : BAS & MoEW, 2015a, 881 p.
34. *Red Data Book of the Republic of Bulgaria.* Vol. 3. *Natural Habitats* / V. Biserkov et al. (Eds). Sofia : BAS & MoEW, 2015b, 422 p.
35. Sadogurskiy S. Ye., Belich T. V., Sadogurskaya S. A. Invasion of the alien species *Bonnemaisonia hamifera* Hariot in coastal phytocenoses near the southern coast of Crimea (the Black Sea). *Inland Water Biology*, 2023a, vol. 16, iss. 1, pp. 65–71. https://doi.org/10.1134/S1995082923010145
36. Sadogurskiy S. Ye., Belich T. V., Sadogurskaya S. A. Macrophytobenthos of the reserved and transformed coastal

marine areas at the south coast of Crimea in conditions of the new biological invasion (the Black Sea). *International Journal on Algae*, 2023b, vol. 25, iss. 4, pp. 365–382. https://doi.org/10.1615/InterJAlgae.v25.i4.50

37. Sadogurskiy S. Ye., Sadogurska S. S., Belich T. V., Sadogurska S. A. Distribution of *Cystoseira* s. l. species in the Sea of Azov. *International Journal on Algae*, 2020, vol. 22, iss. 4, pp. 327–346. https://doi.org/10.1615/InterJAlgae.v22.i4.30
38. Sadogurskiy S. Ye., Sadogurskaya S. A., Belich T. V. Eelgrass beds (gen. *Zostera* Linnaeus, 1753) and the related specific form of the bottom microrelief at the southern coast of Crimea (in the Black Sea). *Russian Journal of Marine Biology*, 2022, vol. 48, iss. 4, pp. 297–301. https://doi.org/10.1134/S1063074022040101
39. Svensson J. R., Nylund G. M., Cervin G., Toth G. B., Pavia H. Novel chemical weapon of an exotic macroalga inhibits recruitment of native competitors in the invaded range. *Journal of Ecology*, 2013, vol. 101, iss. 1, pp. 140–148. https://doi.org/10.1111/1365-2745.12028

СОСТАВ И СТРУКТУРА МАКРОФИТОБЕНТОСА У ПОБЕРЕЖЬЯ ПАМЯТНИКА ПРИРОДЫ «КУЧУК-ЛАМБАТСКИЙ КАМЕННЫЙ ХАОС» (КРЫМ, ЧЁРНОЕ МОРЕ)

С. Е. Садогурский, Т. В. Белич, С. А. Садогурская

ФГБУН «Никитский ботанический сад — Национальный научный центр РАН»,
Ялта, Российская Федерация
E-mail: *ssadogurskij@yandex.ru*

Южный берег Крыма (ЮБК) характеризуется высоким уровнем антропогенной трансформации, поэтому участки, сохранившиеся в природном или квазиприродном состоянии, имеют особую природоохранную ценность. К ним относится территориально-аквальный комплекс, объединяющий геологический памятник природы «Кучук-Ламбатский каменный хаос» и примыкающую прибрежную акваторию Чёрного моря. Акватория в гидроботаническом аспекте не изучена и в состав особо охраняемых природных объектов не включена. В связи с этим выполнено исследование, цель которого — по данным 2015 и 2022 гг. охарактеризовать видовой состав, биомассу и пространственную структуру макрофитобентоса для уточнения представлений о распределении и динамике растительного покрова бентали у ЮБК и в связи с перспективой заповедания указанной акватории. Установлено, что макроскопическая растительность развивается на твёрдых и мягких грунтах, что определяет её общий характер. Всего зарегистрировано 63 вида макрофитов: Chlorophyta — 14 (22,2 %), Ochrophyta — 9 (14,3 %), Rhodophyta — 39 (62,0 %), Tracheophyta — 1 (1,6 %). Общее количество видов (КВ) и соотношение систематических группировок по КВ в оба года близки. Однако состав флоры, а также соотношение по биомассе (БМ) доминирующих видов и эколого-флористических группировок существенно изменились на минимальных и на максимальных глубинах, что определило трансформации растительного покрова. На мелководье их динамика, обусловленная локальным нарушением и последующим восстановлением макрофитобентоса после схода селевого потока, имеет флуктуационный характер. На глубине изменения вызваны инвазией в природные сообщества вида-трансформера *Bonnemaisonia hamifera* и, вероятно, имеют долговременный характер; для выявления их степени и обратимости необходим мониторинг распространения вселенца у ЮБК и в границах Азово-Черноморского региона в целом. В настоящее время вдоль обследованного берега макрофиты формируют пять поясно расположенных растительных сообществ с БМ 0,2–6,0 кг·м$^{-2}$ и КВ 14–27. Крайние значения этих показателей зарегистрированы в сублиторали: максимальные — на твёрдых грунтах в верхней и центральной частях пояса цистозиры (виды *Cystoseira* s. l.), минимальные — на мягких грунтах в наиболее глубоководном сообществе морских трав (*Nanozostera noltei*). В целом по БМ доминируют многолетние, а по КВ — коротковегетирующие макрофиты; фитобентос имеет выраженный олигосапробный морской тепловодный характер. Растительный покров акватории демонстрирует высокую степень сохранности, его пространственное распределение, состав и структура (за исключением изменений, вызванных биологической инвазией) типичны для гидроботанического района Чёрного моря «ЮБК». Раритетная фракция флоры насчитывает 12 таксонов; биотопы, основу которых формируют сообщества макрофитов, попадают под действие документа Directive 92/43/EEC. Целесообразно создание комплексного территориально-аквального природного заказника, который объединит существующий памятник природы и прилегающую к нему акваторию.

Ключевые слова: Чёрное море, Южный берег Крыма, Кучук-Ламбат, макрофитобентос, видовой состав, биомасса, пространственная структура