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Article

The taxonomic diversity and prognostic assessment of the benthic algoflora species richness in the upper sublittoral of the Crimean Black Sea coast

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Abstract. By the results of algological surveys conducted in 2017–2024 in 43 sublittoral sites along the Crimean Black Sea coast, 140 species, including Rhodophyta (72 species), Chlorophyta (40) and Heterokontophyta (28), have been identified. The highest proportion of the flora (4 species/order) is inherent to the phytocenoses in the pristine areas, while the lowest ratio (less than 3 species/order) is recorded in waters with anthropogenic impact. Analysis of taxonomic distinctness indices (AvTD and VarTD) shown that in ecologically undisturbed waters of the southeastern Crimea, the hierarchical structure of communities does exceed the expected average level for the sublittoral algoflora. The taxonomic structure is predominated by mono- and oligospecific branches converging at family or order levels. Phytocenoses of the southwestern Crimea characterized by negative deviations of AvTD values from the expected average; the hierarchical tree is formed mainly by polyspecific branches joining at genus level. The species with the highest taxonomic exclusiveness (*A. arcta*, *Z. typus*, *C. savianum*, *G. longissima* and *P. dubyi*) have been identified; such species form separated monophyletic branch up to order level. The predictive assessment of expected species richness has evidenced that Chao-2 estimator gives the closest results to the actual macrophytobenthos inventory (166 species). It is shown, that in a single randomly taken sample about 26%, and in 11 samples up to 75% of sublittoral algal flora can be revealed.

Keywords: macroalgae, hierarchical diversity, taxonomic distinctness indices, AvTD, VarTD, expected species richness, species accumulation curves, estimators, Black Sea

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Научная статья

Таксономическое разнообразие и прогностическая оценка видового богатства бентосной альгофлоры верхней сублиторали черноморского побережья Крыма

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Аннотация. В период полевых сборов с 2017 по 2024 гг. на 43 участках сублиторали черноморского побережья Крыма обнаружено 140 видов альгофлоры из отделов Rhodophyta (72), Chlorophyta (40) и Heterokontophyta (28). В зонах ООПТ таксономическая структура альгоценозов характеризуется наибольшей видовой насыщенностью (более 4 видов/порядок), а в районах с высокой антропогенной нагрузкой – минимальной (менее 3 видов/порядок). Расчет индексов таксономического разнообразия (AvTD и VarTD) показал, что только в районе побережья Феодосийского залива, включая антропогенно ненарушенную акваторию б. Двукорная, иерархическая структура альгоценоза выше среднеожидаемого уровня для альгофлоры сублиторали Крыма, а в архитектонике таксономического древа преобладают моно- и олиговидовые ветви, соединяющиеся в общий узел на уровне семейства или порядка. На юго-западном побережье Крыма для альгоценозов характерны отрицательные отклонения индекса AvTD от ожидаемого уровня. Видовое богатство сформировано филогенетически близкими видами, смыкающимися на уровне рода. Выделены виды с наивысшей таксономической исключительностью (*Acrosiphonia arcta*, *Zanardinia typus*, *Colaconema savianum*, *Gracilariopsis longissima* и *Peyssonnelia dubyi*), в случае элиминации которых исчезает монотаксонная ветвь, включающая несколько таксономических уровней. Результаты прогностической оценки видового богатства показали, что эстиматор Чжао-2 дает наиболее близкие значения относительно мастера-листа макрофитобентоса прибрежной зоны Крыма (166 видов). Рассчитано, что в одной пробе может быть в среднем выявлено около 26% видового состава альгофлоры сублиторали Крыма, в 4 пробах – не менее 50%, а в 11 пробах – до 75% видового богатства.

Ключевые слова: макроводоросли, иерархическое разнообразие, индексы таксономической отличительности, AvTD, VarTD, ожидаемое видовое богатство, кривые накопления видов, эстиматоры, Черное море

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Introduction

The sublittoral zone of a sea is the most ecologically dynamic and directly affected by a set of environmental factors influencing the taxonomic composition and structure of its phyto- and zoobenthic communities. As a result of anthropogenic impact on the coastal waters caused by the recreational and technogenic transformation of the Crimean Black Sea coast, hydrobiological studies on assessing the structure and state of sublittoral phytocenoses are highly relevant for protection and maintenance of their biological diversity, self-purification, and bioresource potential (Pascual et al., 2016). Furthermore, obtaining the detailed information on the species composition of macroalgae is an important step in developing the scientifically based approaches to the rational nature management in the Crimea, including waters of specially protected natural areas (SPNAs) (Evstigneeva and Tankovskaya, 2020a, b, 2024, 2025; Kostenko et al., 2018; Milchakova et al., 2015; Sadogursky et al., 2022).

The structural and functional organization of macroalgal communities is quite sensitive to changing environmental conditions (Minicheva et al., 2020; Mouliott et al., 2005). Therefore, a comparative assessment of their floristic composition may serve as a good monitoring tool, especially in the man-transformed western and southern coastal areas of the Crimea.

To study various aspects of the algal flora biodiversity with further development of recommendations on the individual macroalgal taxa conservation under current marine management conditions, it is necessary to analyze the entire taxonomic structure of phytocenoses using both traditional floristic studies and biodiversity indicators, as well as modern formalized methods. These include, in particular, a comparative quantitative evaluation of taxonomic (hierarchical) diversity of the community structure based on taxonomic distinctiveness indices (TaxDI) (Warwick and Clarke, 1998, 2001).

From the aforesaid, the main objective of the study is to identify the features of the taxonomic structure of the algal flora in various water areas of the Crimean Black Sea coast under current recreational and economic development of the coastal zone.

Objectives of this study include:

- 1) comparison of sublittoral water areas along the Crimean coast in terms of the macrophytobenthos species composition;
- 2) analysis of the taxonomic structure and diversity of macroalgal communities in the study areas;
- 3) predictive assessment of expected species richness of the algal flora in the upper sublittoral zone based on extrapolation algorithms.

Materials and methods

Algological studies were conducted in different sites of the Black Sea coast of the Crimea from 2010 to 2023, primarily in summer (July–August) during mass vegetation of the majority of algal species. In the algae collection period, temperature and salinity in the study areas varied slightly, ranging from 21–24 °C and 16.8–17.5‰, respectively. Sampling of macrophytes from hard substrates in the upper sublittoral was carried out in quadruplicate at depth range of 0.5–1 m using 25×25 cm rectangular sampling frames. Samples were collected in 43 sites, which were subsequently grouped into 12 nearshore regions based on the spatial arrangement and similarity of landscape-environmental conditions (Goryachkin and Dolotov, 2019). These regions are located along the Crimean coast from Feodossia Gulf to Cape Tarkhankut and Bakalskaya Spit (Karkinitzky Gulf) (Fig. 1).

We collected a total of 160 macrophytobenthos samples, the species composition of which was determined in the laboratory using an Armed XS-90 microscope. Species were identified in accordance with the taxonomical manual for algae identification by A.D. Zinova (1967) and with regard for the latest nomenclature revisions (Guiry and Guiry, 2025)¹.

Prognostic calculations and construction of the model curves for species richness extrapolation were performed from the results of identification of macroalgae species composition by summation of data on total samples collected in each site. The combination of 3–5 adjacent sites in each of the 12 regions provided the best accounting of the macroflora taxonomic composition.

Description of regions

The total length of the surveyed section of the Crimean southern and western coasts is approximately 350 km. Of this, 200 km from Feodossia to Cape Sarych are referred to the southern coast of the Crimea, 75 km from Laspi Bay to Cape Lukull (including Balaklavskaya and Sevastopolskaya Bays) to the southwestern Crimea, and approximately 70 km from Cape Tarkhankut to Cape Bakalskaya Spit are situated within Karkinitzky Bay. Most of the explored coastline is slightly indented, being disrupted in places of large capes' formation (Kiik-Atlama, Plaka, Martyan, Fiolent, Chersoneses, etc.). In waters around the capes, i.e., from the sea surface to depths of 10–30 meters, landscape features of seabed in the form of small rocky ridges, piles of boulder heaps, boulders, and slabs composed of coarse-grained material (basically limestone) covered with macroalgae are often noted. Between the capes, gravel and pebble beaches, gravel landslide "tongues" and terraces emerge at depths of 10–15 meters. In the open gently sloping terrains of the southern and western Crimea, the coastline is predominantly of the landslide type, characterized by highly dynamic abrasion and landslide processes. In many places, the coast is composed of limestone, partially overlain by alluvial clay-pebble and sandy deposits, and reddish-brown clays. Topography and dynamics of the coastline in numerous parts of the western coast are determined by the along shore wind-and-wave driven removal of coastal marine sediments (Goryachkin and Dolotov, 2019).

Statistical data processing

Algorithms of multivariate statistical analysis (PRIMER® 6.1.2 statistical package) were employed to evaluate a similarity of nearshore regions by macroalgae species composition, to analyze the hierarchical structure of taxonomic trees of phytocenoses, and to predict the expected species richness (Clarke and Gorley, 2006). Floristic similarity of sampling sites was assessed by means of hierarchical clustering and n-MDS ordination methods based on the present/absent data matrix of species composition through applying the Bray-Curtis similarity coefficient and group-average linkage calculation (CLUSTER and MDS programs). Statistical reliability of the revealed differences between the algological complexes corresponding to each cluster, was estimated via using the pairwise comparison of variability of rank similarity (R-statistics) (one-way ANOSIM test) (Clarke and Gorley, 2006).

Taxonomic (hierarchical) diversity of the community structure was defined using taxonomic distinctness indices (TaxDI), which enabled studying diversity aspects with consideration for the architecture of the community's hierarchical tree (Warwick and Clarke, 1998, 2001). Such indices are

¹ Guiry, M.D., Guiry, G.M., 2025. AlgaeBase. Web page. URL: <http://www.algaebase.org> (accessed: 24.04.2025).

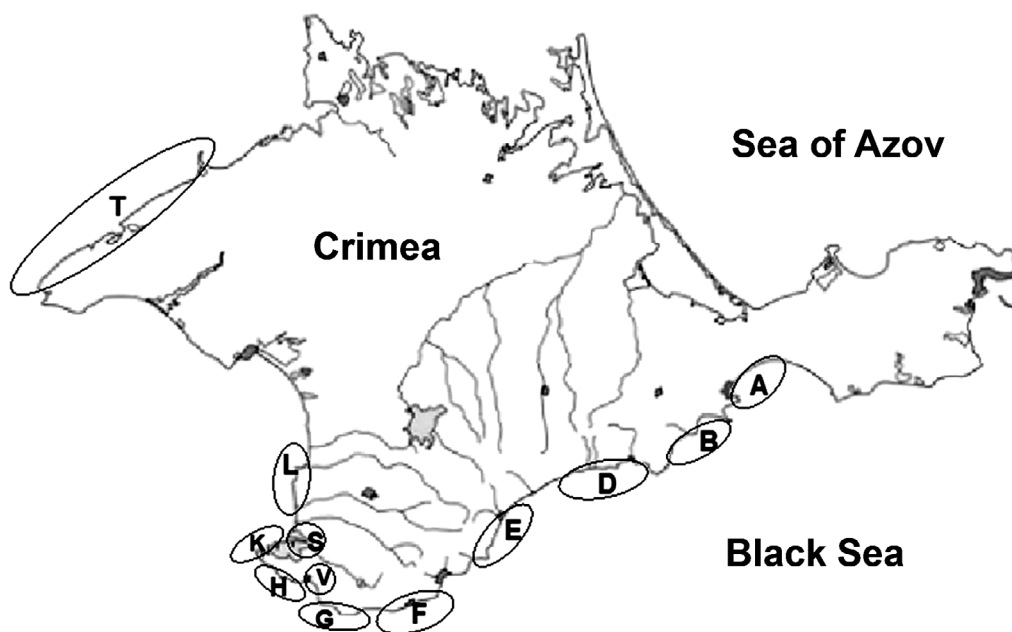


Fig. 1. Schematic map of 12 sublittoral sampling areas (43 locations) along to Crimean coast of the Black Sea. The designation of the districts herein after (see fig. 2 and 3, tables 1, 2, 3): A – Primorskoye – Feodosiya – Dvuyakornaya Bay (4 sampling locations); B – cape Kiyk-Atlama – Kurortnoye (4); D – Sudak–Malorechenskoye (4); E – Alushta–cape Martyan (4); F – Miskhor–Foros (4); G – cape Sarych–Bathyliman (5); H – cape Aya – cape Fiolent (2); V – Balaklava Bay (2); K – cape Chersones – Streletskaia bay (4); S – Sevastopol Bay (2); L – Lyubimovka – cape Lukull (5); T – cape Tarkhankut – Bakalskaya spit (3).

almost independent from the number of identified species and sampling efforts. This allows to assess local differences in the taxonomic structure of communities relatively to the expected average level for the whole region, in our case the Crimea, through applying the datasets obtained from known-different number of samples and/or represented solely by species lists.

The average taxonomic distinctiveness index Δ^+ characterizes a vertical hierarchical evenness of a community tree, i.e., the proportionality of the ratio of taxa number at the preceding and subsequent tree levels. This index is calculated as the average conditional "path length" between each pair of species i and j , randomly withdrawn 1000 times from the master list up to phylogenetically common node on the hierarchical tree of phytocenosis:

$$\Delta^+ = \frac{\sum \sum_{i < j} \omega_{ij}}{S(S-1)/2},$$

where ω_{ij} is the taxonomic "path length" between species i and j ; S – the number of species in the phytocenosis.

The variability index Λ^+ characterizes the horizontal asymmetry of the taxonomic tree relative to the expected average level derived from the entire regional list of algal species. In fact, this index shows a different representation of lower taxa in higher ones within individual tree branches converging at various hierarchical levels (families, orders, etc.) (Nevrova et al., 2015; Warwick and Clarke, 1998). This indicator is calculated as the variance of all pairwise "path lengths" (ω_{ij}) between pairs of species i and j relative to their mean value (Δ^+):

$$\Lambda^+ = \frac{\sum \sum_{i < j} \omega_{ij}^2}{S(S-1)/2} - (\Delta^+)^2$$

Predictive estimates of expected species richness for macroalgal communities are obtained using nonparametric extrapolation algorithms (hereinafter referred to as estimators) from Chao, jack-knife, and bootstrap groups (Clarke and Gorley, 2006; Shitikov et al., 2010). These estimators calculate average expected number of species in the each set with a different number of samples, and based on randomization/permutation method applied for 5000-fold resampling (Foggo et al., 2003; Shitikov, 2012; Ugland et al., 2003). These assessment algorithms yield satisfactory results when dealing with a small number of samples. Previously, the algorithms were successfully applied in predictive analysis of data on the species composition of Black Sea zoo- and microphytobenthos (Petrov, 2025; Petrov and Nevrova, 2012, 2016).

Results and discussion

Using the results of processing the algological samples collected in the upper sublittoral zone of the Crimea coast, a matrix of 140 macroalgae species, including Chlorophyta (40 species), Heterokontophyta (28), and Rhodophyta (72), was compiled. In each region, the taxonomic structure of algal communities had a specific ratio of taxa of different ranks (flora proportions) that can serve as an additional structural characteristics of the algal flora diversity in different coastal areas of the Crimea. Quantitative data for taxonomic categories of macroalgae (from species to orders) and a taxa ratio are presented in Table 1.

In regions K, E, T, B, and G, algal communities of coastal waters, primarily around capes and in SPNAs, show the highest ratio of species richness (4 or more species per 1 order). On the contrary, regions A and V subject to severe anthropogenic impact, are characterized by the lowest ratio of richness (less than 3 species per 1 order). By species composition, the findings of hierarchical clustering and multivariate ordination routine suggest the grouping of 12 regions into four main clusters with a similarity level of 67% (Fig. 2).

Heavily technogenically impacted regions are included in cluster I (waters near Feodosia, the port, and Balaklava Bay) and cluster II (Main Sevastopol Bay, the water area between Kruglaya Bay to Cape Chersoneses, as well as the recreationally transformed part of the Alushta coastline) (Fig. 2A). Cluster III covers the regions of the eastern and southern coasts of the Crimea: from Dvuyakornaya Bay to Karadag; from villages Novy Svet to Malorechenskoye and from settlement Miskhor to Foros; from Cape Sarych to Batiliman nearshore area. Cluster IV includes southwestern sites of the peninsula from Cape Aya to Cape Fiolent and the open coast of the western Crimea from Lyubimovka settlement to Cape Lukull. Meanwhile, the part of the northwestern coast of the Crimea from Cape Tarkhankut to Cape Bakalskaya Spit (T) noticeably differs from other areas (with similarity cut-off level less than 50%).

Multivariate ordination results also confirm the spatial similarity in the mutual arrangement of the studied regions on the 2-D plot, estimated from the macroalgae composition (Fig. 2B). It should be noted that the rather low stress value (0.13) derived from the Shepard diagram denotes well-pronounced correspondence between visual proximity of the relative position of groups of regions on the ordination plot and their actual similarity in terms of algal composition.

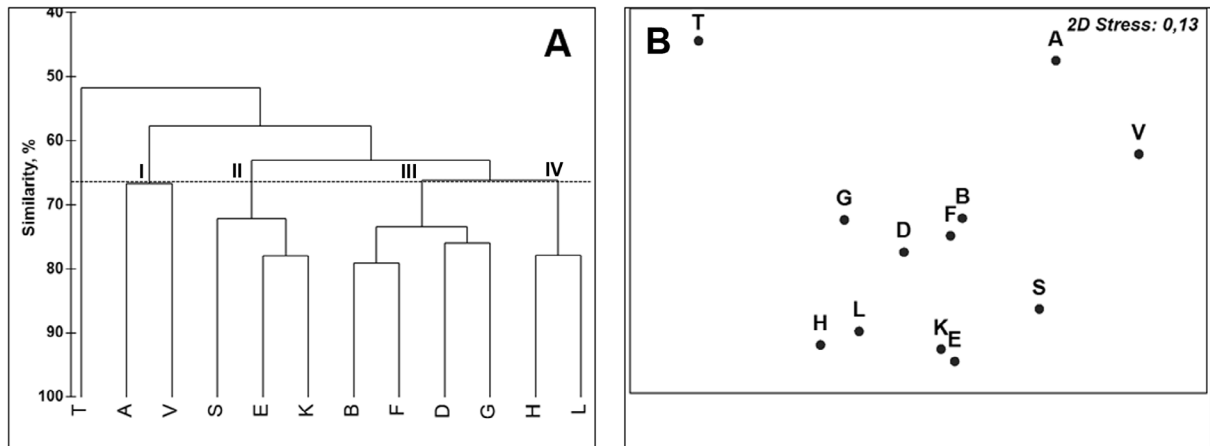
Inter-regional pairwise comparison the degree of similarity in the algal species composition (according to the Bray-Curtis coefficient) varies from 63% (clusters I and IV) to 76% (clusters II and III). Regions of clusters I–IV display the lowest similarity (52–56%) unlike region T (the Crimean coast of Karkinitzky Bay). Among other regions being compared, the latter differs significantly in temperature and salinity, which may affect the specific features of the macroalgae species composition (Pukhtyar et al., 2003).

Differences in the species composition between macroalgae taxonomic complexes in each cluster are statistically significant. For instance, the estimates of the rank similarity variability with account for all clusters give the parameter $R_{\text{global}} = 0.84$ (at a significance level of $P < 0.001$). Results of pairwise comparison of clusters return R_{pairwise} values ranging from 0.80 to 0.99 ($P < 0.03 \dots 0.1$) (ANOSIM test). This confirms that macroalgal communities with a specific taxonomic structure and species composition are formed within each of the studied regions of the Crimean sublittoral. Differences in the algal composition across regions may be related to substrate type, bottom illumination with a varying transparency in the water column, and the degree of eutrophication and anthropogenic pollution of water masses in the sublittoral zone (Evstigneeva and Tankovskaya, 2020b, 2025; Minicheva et al., 2020; Nevrova and Petrov, 2019; Nevrova et al., 2015).

Since in our study the initial taxonomic data were presented as the simple list of species without account of biomass or abundance, the traditional diversity indices (Shannon, Margalef, Pielou, etc.) for assessing the algal diversity can not be applied. In addition, the comparative evaluation results of taxonomic diversity may be incorrect in case of sizeable variations in sampling efforts in different areas, or when comparing the communities with similar species richness, but including both phylogenetically

Table 1. The total number of taxa and its ratio at different hierarchical levels of the algological communities for 12 regions of the Crimean coast.

Region	Number of taxa				Proportions of flora in relation to number of orders			
	Species	Genus	Family	Order	Taxa			
					Order	Family	Genus	Species
A	41	28	20	16	1	1.3	1.8	2.6
B	67	48	28	16	1	1.8	3.0	4.2
D	61	41	26	16	1	1.6	2.6	3.8
E	77	52	29	18	1	1.6	2.9	4.3
F	67	45	28	19	1	1.5	2.4	3.5
G	68	42	25	17	1	1.5	2.5	4.0
H	57	39	24	16	1	1.5	2.4	3.6
V	43	28	20	15	1	1.3	1.9	2.9
K	77	48	29	17	1	1.7	2.8	4.5
S	70	44	31	19	1	1.6	2.3	3.7
L	56	37	24	17	1	1.4	2.2	3.3
T	71	41	26	17	1	1.5	2.4	4.2

**Fig. 2.** Grouping of sublittoral coastal regions of the Crimea based on species richness similarity of macrophytes. Dotted line indicates integration level of regions (67%) into the clusters (I–IV) on dendrogram (A) and into corresponding compact groups of points on the ordination plot (B).

close species (referred to the same genus) and those belonging to different families, orders, and classes. In such cases, the taxonomic (hierarchical) aspects of diversity may not coincide even when comparing two communities having the same number of species. Moreover, a community consisting of predominantly closely related species is less taxonomically diverse than that containing the same number of species but phylogenetically more distant (Nevrova et al., 2015; Warwick and Clarke, 1998).

Subject to the above-mentioned limitations, a comparative analysis of taxonomic diversity of the algal flora in sublittoral waters of the Crimea was performed using TaxD indices: average taxonomic distinctness (AvTD, Δ^+) and variability of TD (VarTD, Λ^+) (Warwick and Clarke, 2001). The master-list of macroalgae of the Crimean Black Sea coast, which was compiled from our own data and scientific reviews prepared by other authors, totally comprises 164 species (Evstigneeva and Tankovskaya, 2020a, b, 2024, 2025; Kalugina-Gutnik, 1975; Minicheva et al., 2020) being aggregated into six hierarchical levels (from species to division). It was used to plot the 95% "probability funnel" for individual Δ^+ and Λ^+ values, based on 1000-fold random combinations for subsets with a different number of species (Fig. 3).

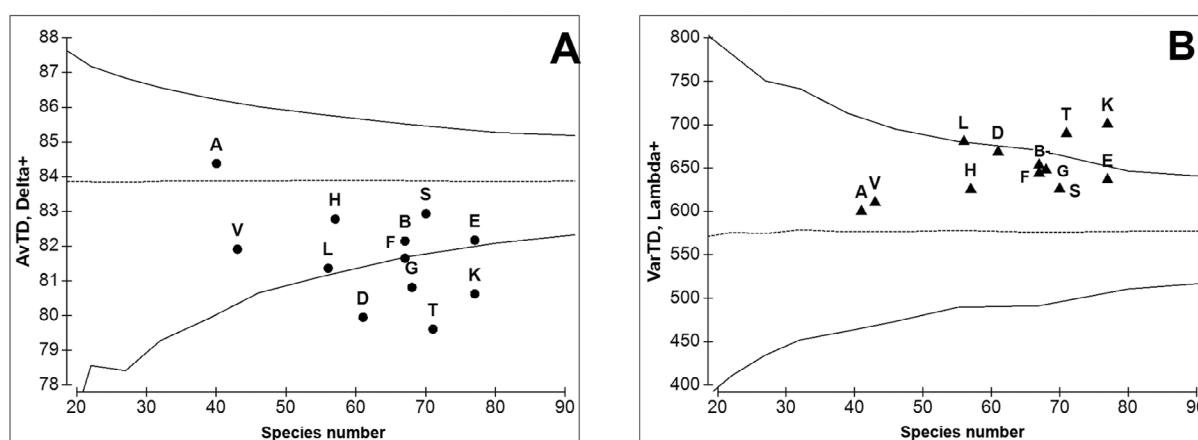


Fig. 3. Taxonomic distinctness indices points AvTD (**A**) and VarTD (**B**) superimposed on 95% «probability funnels», corresponding to taxonomic diversity of macrophytes in each sublittoral region of Crimean coast. Dotted line indicates the average expected levels of AvTD (83.9) and VarTD (577), calculated from a master-list of the Crimean coastal algoflora (164 species).

In Fig. 3A, points on the "probability funnel" plot represent the average values of AvTD, i.e. the degree of taxa distribution evenness along the ascending levels of the algal flora hierarchical tree for each region. Fig. 3B illustrates the horizontal variability (VarTD) of the hierarchical structure of the phytocommunity in each region relative to the expected average level (dotted line) calculated from the list of total macroalgal species of the Crimean Black Sea coast.

On the AvTD plot, only the point corresponding to region A (4 locations on the Feodosia Gulf coast, including Dvuyakornaya Bay waters not subject to anthropogenic influence) is above the average expected level of hierarchical diversity for the whole algal flora of the Crimean sublittoral (Fig. 3A). This is indicative of a relative predominance of mono- and oligospecific branches in the regional taxonomic tree architecture, composed of rare and non-cenosis-forming species that hierarchically converge into a common node at the family or even order levels. It is noteworthy that for the macroalgal community of region A, the ratios species/genus and species/family are minimal: 1.45 and 2.05, respectively. These data imply that, in fact, every three species are aggregated into two genera, while four species into two families. For communities of the rest sublittoral regions, the AvTD points are positioned on the plot below the expected average level (Fig. 3A), thus showing a probable reduction in vertical evenness and hierarchical structure of taxonomic trees. The 95% probability "funnel" for AvTD in regions H, S and V is indicative of the hierarchically simplified taxonomic macroalgae structure, as compared to the total algal flora of the Crimea coast. For algal communities of these regions, the average taxa ratios make up species/genus = 1.53 and species/family = 2.29.

The greatest negative deviations of AvTD values from the expected average are observed in regions D, G, K, and T. On the plot, the corresponding points are below the lower contour of the 95% probability

funnel (Fig. 3A). For these regions, taxa ratios are the highest: species/genus = 1.66; species/family = 2.71. This demonstrates that the species richness of the algal flora is largely formed by phylogenetically related species, which in the hierarchical structure of the taxonomic tree are converged on a common generic node. At the same time, the proportion of species forming distinct monospecific branches down to the family or order level is relatively small: it implies that changes in the community's species composition occur generally through the appearance or disappearance of closely related species.

It should be noted that despite the nearly twofold increase in absolute species richness in regions G, T, and K (compared to region A), the hierarchical diversity of algal flora here is reduced, with the community tree architecture being formed mainly by closely related species aggregated at the genus level. At the same time, taxa aggregation from the family level upwards is almost non-pronounced. Thus, in region A, 41 species of the community are grouped into 16 orders and 4 classes, while in regions G, T and K, 68–77 species at total, are grouped into 17 orders and 4 classes. Hence, changes in species richness and taxonomic (hierarchical) diversity of the algocenosis are not unidirectional and reflect different structural aspects of diversity.

When dealing with VarTD (Λ^+), its values were plotted above the expected average level for the whole Crimean algal flora, but remained within the 95% contour of the probability funnel (Fig. 3B) in the majority of the studied areas except for T and K. High variability of the hierarchical algocenosis structure can be determined by the increased taxonomic diversity in ecologically undisturbed habitats. In such locations, the tree structure equally includes both monospecific and polyspecific taxonomic branches merging at the genus level (Evstigneeva and Tankovskaya, 2025; Heino et al., 2007; Nevrova and Petrov, 2019). However, increased variability (Λ^+) along with reduced Δ^+ values can also characterize the depressed status of the communities living under permanent and profound anthropogenic impact (e.g., region K) (Evstigneeva and Tankovskaya, 2020a; Nevrova et al., 2015; Petrov et al., 2010). In environmentally unfavorable conditions, some species can be eliminated from polyspecific taxa that lead to altering in the ratio of mono- and polyspecific branches in the community tree structure and increasing VarTD index (Ceschia et al., 2007; Leonard et al., 2006; Mouliott et al., 2005; Xu et al., 2012).

To study the taxonomic diversity and architecture of hierarchical trees of algocenoses existing in different ecological conditions, the assessment of the taxonomic exclusiveness rank of encountered species is crucial (Nevrova et al., 2015). If branches of genera, each comprising a large number of species, aggregate with other similar branches at the family or order level, then species belonging to such multispecific genera will be phylogenetically close. When habitat conditions change, the possible elimination of one or more species does not bring to removal from the algocenosis tree of the entire taxonomic branch, including the genus, family, etc. levels. For all that values of Δ^+ and Λ^+ vary insignificantly, however the overall species richness of the regional algal flora may decrease due to elimination a large number of species. Species with a *low rank* of taxonomic exclusiveness predominate in the species composition of almost any phytocenosis.

In turn, species that form a monotaxon lineage up to the family (or even order) level are characterized by a *high (highest) rank* of taxonomic exclusiveness (Tables 2, 3). If one or more such species are eliminated from the community, the entire taxonomic branch (species – genus – family, etc.) disappears that seriously transforms the hierarchical structure of the algal tree in a given region and, accordingly, changes AvTD and VarTD indices as well. Among the species that form such monotaxon branches, rare species are of particular importance (Table 2). Removal of these species can lead to changes not only in the hierarchical structure of the algal community in a particular region, but also in the tree architecture of the total algal flora of the Crimea. Such representatives of the algal flora require enhanced protection, chiefly, the preservation of their biotopes.

Among the 12 species with the highest rank of taxonomic exclusiveness, the rare species *Acrosiphonia arcta*, *Zanardinia typus*, *Colaonema savianum*, *Gracilariopsis longissima*, and *Peyssonnelia dubyi* are particularly noteworthy. They were found solely in one or two localities of the studied Crimean coast.

Thus, taxonomic distinctiveness indices (TaxDI) enable assessing the previously overlooked hierarchical aspects of algal community diversity, which cannot be described using traditional quantitative diversity indices. For instance, we have identified species with the highest rank of taxonomic exclusiveness, which form mono- and oligotaxon branches on the algal community hierarchical tree reaching a high level of aggregation (order). The conservation of such species, especially registered only in specific biotopes, is critical for maintaining the genetic pool of the benthic algal flora within the SPNAs or in strongly impacted coastal water areas.

Table 2. Species of macroalgae of the Crimean sublittoral with high rank of taxonomic exclusivity, forming monospecific taxonomic branches up to the family level.

Species	Order	Class	Region
<i>Blidingia minima</i> (Näg. ex Kütz.) Kylin	Ulvales	Ulvophyceae	S
<i>Phaeophila dendroides</i> (P. Crouan et H. Crouan) Batters			T
<i>Codium vermilara</i> (Olivi) Delle Chiaje	Bryopsidales		B, D
<i>Cladostephus spongiosus</i> (Huds.) C. Agardh			All regions, excepting V
<i>Halopteris scoparia</i> (L.) Sauvageau	Sphacelariales	Phaeophyceae	E, H, K
<i>Sphacelaria cirrosa</i> (Roth) C. Agardh			Bce
<i>Scytosiphon lomentaria</i> (Lyngb.) Link	Ectocarpales		B, E, G, K, S
<i>Pterocladia capillacea</i> (S.G. Gmelin) Santelices et Hommersand	Gelidiales		B
<i>Lithophyllum cystoseirae</i> (Hauck) Heydrich	Corallinales	Florideophyceae	D
<i>Rhodochorton purpureum</i> (Light.) Rosenv.	Acrochaetiales		E, K, S
<i>Spermothamnion strictum</i> (C. Agardh) Ardiss.	Ceramiales		All regions, excepting A

Table 3. Species of macroalgae of the Crimean sublittoral with the highest rank of taxonomic exclusivity, forming monospecific taxonomic branches up to the order level.

Species	Class	Region
<i>Acrosiphonia arcta</i> (Dillw.) Gain	Ulvophyceae	A, F
<i>Ulothrix implexa</i> (Kütz.) Kütz.		E, H, K, S, L
<i>Nereia filiformis</i> (J. Agardh) Zanard.	Phaeophyceae	B, E, F, S, L
<i>Zanardinia typus</i> (Nardo) P.C. Silva		S; L
<i>Colaconema savianum</i> (Menegh.) R. Nielsen		G, T
<i>Dermocorynus dichotomus</i> (J. Agardh) Gargiulo, M. Morabito et Manghisi		B, D, F, G, V, K, S, L
<i>Gracilariopsis longissima</i> (S.G. Gmelin) Steentoft, L.M. Irvine et Farnham		D, K
<i>Lomentaria clavellosa</i> P.H. Crouan	Florideophyceae	A, E, F, H, V, K, S
<i>Nemalion elminthoides</i> (Vellay) Batters		B, E, F, G
<i>Peyssonnelia dubyi</i> P.H. Crouan		G, T
<i>Phyllophora crispa</i> (Huds.) P.S. Dixon		A, B, D, E, F, G, H, L, T
<i>Erythrotrichia carnea</i> (Dillw.) J. Agardh	Compsopogonophyceae	A, B, D, E, F, G, H, V, K, S, L

Predictive assessment of macroalgal species richness in the sublittoral zone of the Crimean coast

When studying a regional diversity of the algal flora and assessing the gained taxonomic knowledge, determination of complete species richness is one of the main tasks. However, in most studies, conclusions about species number and phytocenoses diversity are often made based on the collection and processing of a relatively small number of samples (usually less than 10–20) (Bevilacqua et al., 2018; Minicheva et al., 2020; Ugland et al., 2003). With limited sampling efforts, it is hardly possible to identify species composition in full. Therefore, the expected species richness S_{exp} is often estimated with the use of predictive extrapolation algorithms (estimators) from Chao, jackknife, bootstrap, and other groups. These algorithms are based on determining the expected average number of species by generating a large number of pseudo-samples from different amount of samples (randomization method) (Bevilacqua et al., 2018; Petrov and Nevrova, 2012; Shitikov, 2012; Shitikov et al., 2010). Moreover, the calculation results of S_{exp} may differ by 20–40% depending on the estimator used (Beguinot, 2016; Cam et al., 2002; Foggo et al., 2003; Petrov and Nevrova, 2016).

Based on the total samples collected from 43 coastal locations, the cumulative curve, describing recorded species (S_{obs}) increment with increasing number of sampling efforts, was constructed (Fig. 4). It can be seen that even when accounting all detected species (S_{obs}), the empirical accumulation curve does not reach a horizontal asymptote corresponding to the complete species richness of algae in the region. Besides, with the increasing number of randomly collected samples, a variability range for a detected species amount decreases relative to the mean value. In such studies, determination of the % share of revealed species from the entire list of flora, has obtained under different sampling efforts, is an important methodological outcome. For example, in our study, with random selection of one sample, the proportion of the detected species constitutes approximately 26% macroalgae species richness registered for all 43 locations. At the same time, variability coefficient (cV) of this indicator is quite high (cV = 38%). In fact, this means that 23–50 species (an average of 37 ± 14) can be recorded in a single random sample. Four random samples may account for approximately 50% of the identified species richness (an average of 72 ± 12 species), while 10–11 samplings can represent about 75% of the regional macrophytobenthos species richness (Table 4).

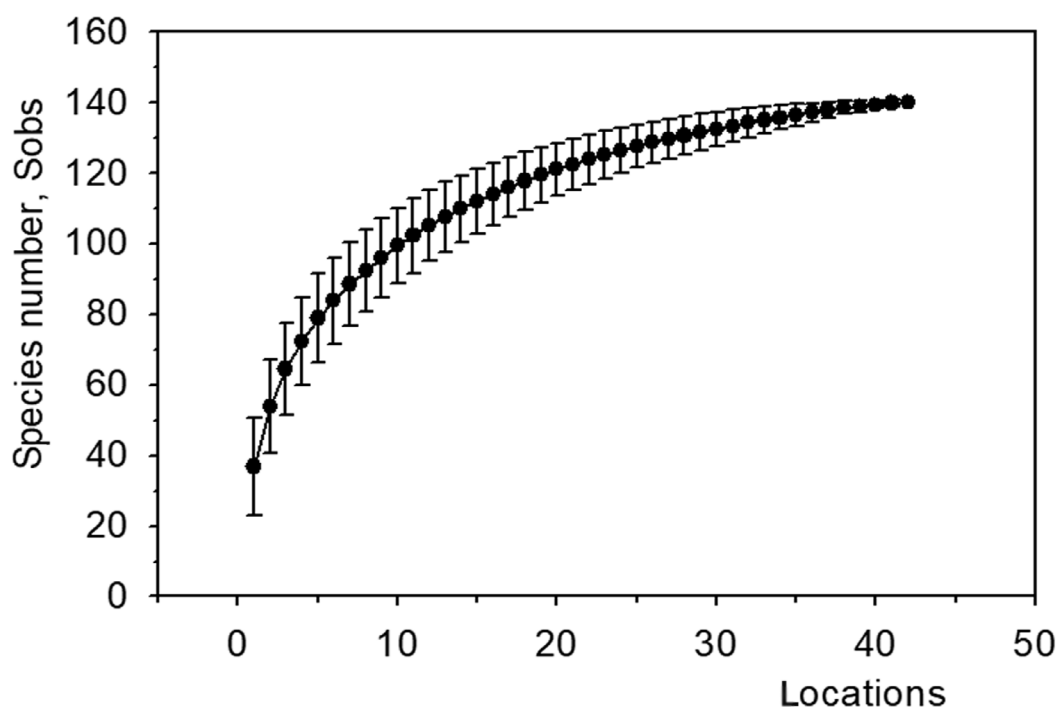
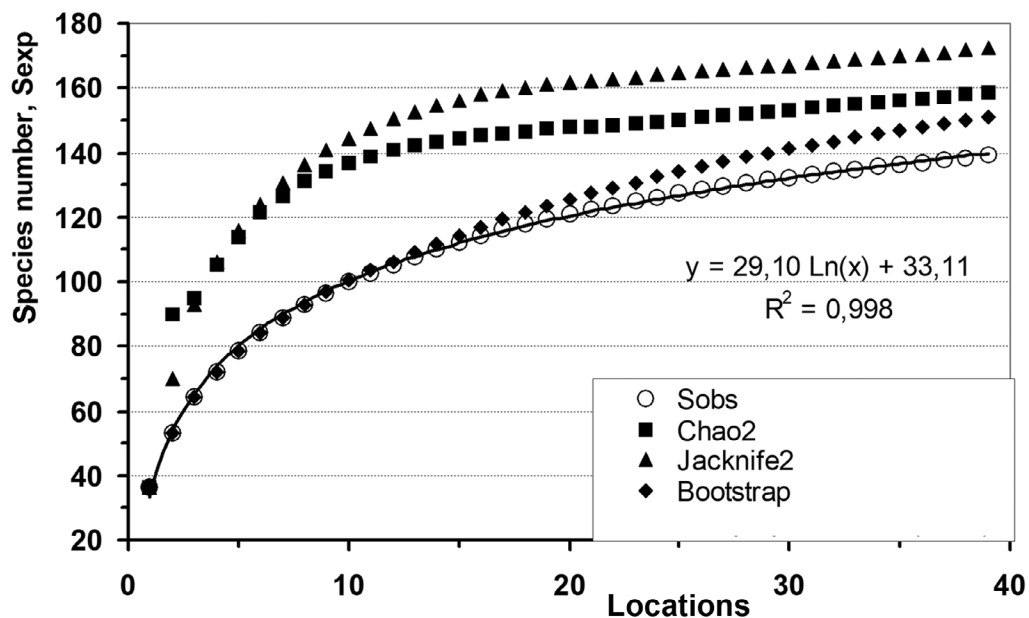


Fig. 4. Cumulative log-curve ($S_{obs} = 29.10 \cdot \ln(N) + 33.11$; $R^2 = 0.999$) of the dependence in the number of observed species (S_{obs}) with increasing in the number of samples (N) taken in 43 locations along the Crimean coast. Confidence intervals (p-values = 0.05) the median values of species richness are indicated.

Table 4. Average estimated number of species (S_{obs}) identified with different randomized sampling efforts and changes in the relative number of species (in % of the regional algal flora species richness).

Location number	Average species number, $S_{obs} \pm \sigma_x$	Variation coefficient C_v , %	Share of species, % of S_{obs}
1	37 ± 14	38	26
3	64 ± 13	20	46
4	72 ± 12	17	52
5	79 ± 11	15	56
7	89 ± 11	13	64
10	100 ± 10	10	72
12	106 ± 10	9	76
15	112 ± 9	8	80
20	121 ± 7	6	87
30	133 ± 4	3	95
40	139 ± 1	<1	99
43	140 ± 1	<1	100

**Fig. 5.** Accumulation curves of the expected number (S_{exp}) of macrophytes species richness in sublittoral zone of the Crimea, obtained for 3 estimators (Chao-2, jackknife-2 and bootstrap). The accumulation curve of the observed species number (S_{obs}) registered in 43 locations is also shown.

Calculations based on the cumulative curve equation (Fig. 4) show that for 50 samples richness is about 147 species, for 70 samples – 157 species, and around 164 species for 90 or more randomly taken samples. In the latter case, species richness most closely corresponds to the master list of 165 species compiled owing to a large amount of our own and other authors' datasets (Evstigneeva and Tankovskaya, 2020a, b, 2024, 2025; Kalugina-Gutnik, 1975; Minicheva et al., 2020). Clearly, such a high number of samples is hardly possible to collect and process in practice. Meanwhile, the level of species richness of the benthic flora (140 species) identified in our research reaches 86% of the complete regional species list.

When considering at least 40 samples, the jackknife-2 estimator produces the most overestimated results for S_{exp} (approximately 173 species), whereas bootstrap (152 species) and Chao-2 (159 species) underestimated ones, as compared to the master list (Fig. 5). It is evidenced from the calculations of the expected macroalgae species richness S_{exp} for the sublittoral zone of the Crimea using several extrapolation algorithms. The cumulative curves corresponding to Chao-2 and jackknife-2 estimators demonstrate a slight increase in the upper part of the randomized series of the number of sampling efforts, approaching horizontal asymptotes at the level of 160–170 species. Hence, the number of algal species actually discovered in the sublittoral zone of the Crimea (165) and included in the master list is close to the theoretically expected upper limit of species richness derived from the extrapolative calculations. Nevertheless, according to the bootstrap estimator, the curve S_{exp} does not approach the horizontal asymptote that may point to underestimated composition of the macroalgae species given the low occurrence of the rarest species.

It is worthy of note that the presented results assume a theoretically equal probability of occurrence of any species in each sample (the Holdridge model). Census of common species can be actually performed based on the analysis of a smaller number of samples than expected in predictive calculations. However, in order to reveal rare and unique species observed only in single samples, the total number of sampling efforts must be much greater than estimated, since the value S_{exp} is calculated by permutation of random pseudo-samples and simulating the cumulative losses followed by sequential removal of unique species from the lists (Shitikov et al., 2010). With a high share of rare species in the community and increasing sampling efforts, steep rise jackknife estimator curve can imply a higher level of S_{exp} (Beguinet, 2016; Bevilacqua et al., 2018; Cam et al., 2002; Zou and Axmacher, 2021).

Thus, the results of prognostic assessment ensure the estimation of the expected richness of the algal flora species at different number of samples, and also optimization of sampling efforts during hydrobotanical surveys when under limited number of samples the highest proportion of the macroalgae species richness can be revealed.

Conclusion

As a result of algological studies, totally 140 macroalgae species (Rhodophyta (72), Chlorophyta (40 species), and Heterokontophyta (28) from 43 sites of the upper sublittoral zone in 12 regions of the Crimean Black Sea coast were identified. Species richness in each region ranged from 41 to 77 species, and the taxonomic structure of algal communities was characterized by a specific ratio of taxa of different ranks. The highest species richness (more than 4 species per 1 order) was recorded in the communities from coastal waters located around capes and in SPNAs, while the lowest (less than 3 species per 1 order) was detected primarily in sites with high anthropogenic pressure (bays, port water areas, and open coastal areas with intensive recreational and industrial development).

A comparative analysis of indicators of taxonomic (hierarchical) diversity (AvTD and VarTD) revealed that only in the coastal area nearby Feodosia and waters of Dvuyakornaya Bay not affected by technogenic impact for decades (region A), the hierarchical diversity of algal communities exceeded the expected average level for the sublittoral algal flora of the Crimea coast (AvTD index). The taxonomic architecture was dominated by mono- and oligospecific branches converging into a common node at the family or order level, resulting in the lowest ratios of species/genus (1.45) and species/family (2.05). At the same time, regions D, G, T, and K exhibited the largest negative deviations of AvTD values from the expected average for the Crimean algal flora. In these regions, the ratios species/genus and species/family made up 1.66 and 2.71, respectively. Species richness of algal communities was formed primarily due to phylogenetically close macroalgal species converging into a common genus node.

Owing to branching of taxonomic trees of algal communities from different coastal regions of the Crimea, the species with the highest rank of taxonomic exclusiveness were marked. Elimination of such species leads to exclusion of an entire monotoxon branch from the taxonomic structure of the community,

encompassing several levels (genus, family, order). Such changes in the community structure may cause the transformation of the architecture of the entire taxonomic tree of the Crimean algal flora that necessitates the enhanced protection of species encountered only in specific biotopes.

When considering samples from 40–43 locations, a prognostic estimation of the expected species richness (S_{exp}) for the regional macroalgae turns out to be the highest (173 species) when applying jackknife-2 and the lowest (152 species) for bootstrap estimator. Chao-2 yields approximately 159 species demonstrating close similarity with the actual species richness (165–166 species) of macrophytobenthos in the coastal zone of the Crimea.

From the estimates based on an empirical log-model of species increment with increasing number of sampling efforts, it follows that a single randomly collected sample can represent approximately 26% of the macroalgae species richness determined from at least 40 analyzed samples (assuming equal probability of occurrence of any species in a sample). A random selection of four samples gives at least 50% of the species richness (72 species). Randomized 10–11 samples may contain up to 105 species, representing approximately 75% of the macroalgae species richness in the upper sublittoral zone of the Crimea.

These results can be applied for determining the taxonomic capacity of environmentally different water areas (including SPNAs), as well as for predictive assessment the species richness in algal communities during hydrobotanical surveys, taking into account optimization of sampling efforts routine and possible underestimation of rare species.

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