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Unveiling the diversity of benthic habitats of the Romanian Black Sea coast: New records and an updated checklist

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ABSTRACT

This study presents a comprehensive ecological assessment of the benthic habitats along the Romanian Black Sea coast, with a central focus on the rediscovery and population analysis of the rare burrowing bivalve *Barnea candida*. Reported for the first time in over six decades, the species was identified in marl soft-rock outcrops stations at two stations located in shallow areas, making it a significant conservation milestone. Detailed morphometric measurements were used to evaluate population structure and growth patterns. Our results revealed the presence of both mature and juvenile individuals, indicating successful local recruitment and habitat resilience. Thirteen stations corresponding to distinct benthic habitats (marl outcrops, biogenic reefs, photophilic algae beds, seagrass meadows, and deep rock substrata) have been analyzed in terms of species richness and community structure using both density and biomass data and integrated with substrate. The faunal associations included *Brachynotus sexdentatus* and *Pholas dactylus* with marl beds, *Molgula manhattensis* on shallow rock with photophilic algae, *Mytilus* and *Mytilaster* on exposed biogenic reefs, and *Petricola lithophaga* in deep rocky areas. A new record of *Zostera marina* and the reappearance of the red alga *Dasya pedicellata* were also documented, further highlighting the ecological value and recovery potential of these coastal systems. Overall, this study provides the first integrated ecological and population-level analysis of *Barnea candida* in the region, highlighting marl beds as keystone microhabitats for its conservation. The findings aim to support monitoring, habitat protection, and benthic biodiversity management in the Romanian Black Sea coastal waters.

1. Introduction

Coastal zones include a variety of habitats and numerous biodiversity components, which provide important ecosystem functions (Levin et al., 2001; Gammal et al., 2025). These environments play a crucial role in biogeochemical processes, including nutrient cycling, and provide essential food sources and physical structure that support a vast array of marine life, thereby significantly contributing to overall marine biodiversity (Levin et al., 2001; Snelgrove et al., 2014). Coastal benthic communities are highly vulnerable to a wide range of natural and human-caused disturbances acting at both regional and global scales. Regional impacts include overfishing, introduced species and coastal development, while global impacts involve climate change and sea level rise. These factors can significantly alter the structure and function of coastal ecosystems, impacting biodiversity, fisheries, and other ecosystem

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services (Louzao et al., 2010).

The Romanian Black Sea coast represents a unique and ecologically significant region where a variety of benthic habitats exist, each with its own distinct characteristics and ecological value (Bacescu et al., 1971; Surugiu et al., 2021; Begun et al., 2022; Marin et al., 2024). One of the habitats with significant ecological value is soft-rock habitats because they provide a rare and distinct environment that differs markedly from both hard-rock and soft-sediment habitats. Their intermediate nature offers a mosaic of microhabitats-crevices, tunnels, and cavities-that are colonized by a variety of organisms adapted to these conditions. Among the most notable inhabitants are Pholadidae mollusks, a family of bivalves known for their ability to bore into and inhabit these soft-rock substrates. These mollusks play a crucial role in bioerosion processes, shaping the physical structure of the habitat and influencing sediment dynamics (Morton, 1981; Taylor and Glover, 2010).

Since the 1960s, researchers have conducted extensive studies on benthic communities along the Romanian coast, during a time when the Black Sea ecosystems were generally regarded as stable (Bacescu et al., 1971). Findings from this period revealed a diverse marine biota that continued to grow as new species were identified and documented. From the early observations of diverse benthic fauna and flora, research expanded in scope and precision, incorporating quantitative sampling and ecological indices to assess habitat health. More generally, macrozoobenthic communities on the Romanian shelf encompass approximately 340 taxa (Bacescu et al., 1971). However, in the northern Constanta region, only one detailed investigation (Gomoiu and Müller, 1962) has been conducted on benthic diversity, documenting over 45 macrozoobenthic species across sedimentary habitats and underscoring the complexity and richness of these benthic assemblages. Between the 1970s and 1990s, the region experienced significant ecological shifts due to eutrophication and increasing hypoxia in the bottom water layer. These changes led to a decrease in species diversity, alterations in dominant community structures, and a shift of macrophytobenthos habitats to shallower depths (Gomoiu, 1998). Notable for its high endemism (Bacescu et al., 1971), the Romanian Black Sea coast confronts growing pressures from human activities like overfishing, habitat destruction, pollution (chemical and noise), eutrophication, and climate change. Studies highlight the ecological importance of habitats like eelgrass beds, which act as biodiversity hotspots despite being exposed to stressors (Surugiu et al., 2021). Additionally, marine protected areas (MPAs) have been established to mitigate these impacts (Zaharia et al., 2012; Begun et al., 2018, 2022). However, challenges persist due to invasive species and anthropogenic pressures like industrial pollution and eutrophication. Although these pressures have decreased along the Romanian Black Sea Coast (Teaca et al., 2020; Begun et al., 2022; Lazar et al., 2024), they continue to pose significant threats, a problem exacerbated by non-EU countries not bounded by agreements like the Water Framework Directive (WFD) or the Marine Strategy Framework Directive (MSFD). Furthermore, other human activities such as beam-trawling and coastal protection works are also important threats in the area and they are the main responsible of the decline of the soft rock habitat with Pholadidae (Lopez et al., 2021). These activities lead to habitat destruction, smothering, and increased siltation, which significantly degrade these ecosystems. Beam-trawling disrupts the seabed (Teaca et al., 2019; Mureșan et al., 2019; Nenciu et al., 2023; Nita et al., 2025), while coastal protection measures often alter natural sedimentation processes, exacerbating habitat loss (Airoldi and Bulleri, 2011). These pressures highlight the vulnerability of soft rock habitats to anthropogenic impacts.

Barnea candida (Linnaeus, 1758), commonly known as the white piddock, is a bivalve mollusc belonging to family Pholadidae, which includes bivalves with unique adaptations for burrowing into soft rock or wood. *B. candida* is found from Norway to the Mediterranean and West Africa, typically inhabiting the midlittoral and shallow sublittoral zones of soft rock coasts (Mordukhay-Boltovskoy, 1972; Poppe and Goto, 1993; Ballerstedt, 2006). The Black Sea holds to four rock-boring mollusc species: *Pholas dactylus* (Linnaeus, 1758), *B. candida* (Linnaeus, 1758), *Rocellaria dubia* (Pennant, 1777), and *Petricola lithophaga* (Retzius, 1788). These bivalves burrow into the substrate, and this cryptic behavior may explain the limited knowledge about these species. Despite early naturalists' fascination with their luminescent properties and burrowing abilities, interest in them has remained relatively scarce.

The presence of *B. candida* in the Black Sea was documented by early Russian researchers such as Middendorf, Bichwald, and Ostroumov (Gomoiu and Müller, 1962). Zernov (1913) was the first to find large quantities of *Barnea* by examining stones submerged in the Gulf of Sebastopol. Milashevich (1916) continued these studies, compiling all available data on *Barnea* in the Black Sea and establishing a new subspecies, *Barnea candida var. pontica*. Bekmah (1940) discovered *Barnea* colonies on hard clay at Karadag, while Nikitin (1951) conducted a quantitative assessment of its occurrence along the Caucasian coast. The presence of *Barnea* off the Romanian coast was first noted by Zernov (1913) near the Danube River mouths. Later, researchers such as Borcea (1936), Carausu (1957) and Grossu (1962) also reported its presence. Gomoiu and Müller (1962) describe the benthic community dominated by *B. candida* in the Mamaia South – Constanta North zone. For over 60 years, *B. candida* had not been reported again, until October 2016, when 1–2 valves were found in the Ukrainian part of the Danube Delta (Alexandrov, 2017). Despite being a rare species, even threatened in the Black Sea, *B. candida* has not been included in the Black Sea Red Data Book (1999), the Red Book of the Invertebrates from Romania (Murariu and Maican, 2021), or the Red Data Book of Ukraine (2021).

B. candida, as a member of the benthic filter-feeding community, plays a vital role in maintaining the ecological balance of the Black Sea's shallow waters. Protecting the health of these species is crucial, as they help enhance the overall well-being of the ecosystem. By ensuring the survival and prosperity of filter-feeding species and focusing on the restoration and management of benthic environments, we can strengthen the Black Sea's ecological resilience in the face of climate change, pollution, and human activity. Currently, various conservation initiatives are underway to improve the Black Sea's ecosystem. These efforts include pollution reduction measures,

habitat restoration, and international collaboration among Black Sea countries (Bulgaria, Romania, Turkey, Ukraine and Georgia), aimed at sustainable fishing practices, endangered species protection, and overall ecosystem health.

At present, of the four rock-boring mollusc species, only *P. dactylus* is officially protected under the Bern Convention (Appendix II) and the Barcelona Convention (Appendix II) throughout the Mediterranean (SoHelME et al., 2005). Micu (2007) proposed the regional IUCN status of Critically Endangered CR A2abce + 3de; B1ac(i–iv) + 2ac(i–iv) for *P. dactylus* in the Romanian Black Sea. Later, both *P. dactylus* and *P. lithophaga* were listed in the List of Endangered Marine Species from the Romanian Black Sea coast for their protection and conservation, as approved by Order No. 488/2020. *B. candida* is classified as Data Deficient on the IUCN Red List, and it does not have an official protection in the Black Sea. Hence, is crucial to gather more scientific evidence to support the development of effective measures and conservation policies for the sustainable management of this species.

In recent years, a critical challenge has emerged concerning the significant gaps in our understanding of the state of benthic populations from the Romanian Black Sea coast. This deficiency in knowledge is particularly concerning given the profound ecological changes observed in the Black Sea. From this perspective, dedicated studies of marine habitats are urgently needed. Such research is essential not only to accurately estimate the anthropogenic impact on the marine environment but also to provide crucial information and tools that can effectively support environmental management applications. These studies would help fill existing knowledge gaps, enabling a more comprehensive understanding of ecosystem health and informing targeted recovery and conservation measures.

Within this framework, a primary objective was to establish baseline data on benthic biodiversity from the Romanian Black Sea Coast. Such baseline information is indispensable for accurately assessing the current state of ecosystems, understanding long-term trends, and quantifying the impact of anthropogenic activities. Specifically, efforts focused on identifying and characterizing macrozoobenthic communities within a shallow bay located north of Constanța. This involved detailed assessment of species composition, abundance, and distribution within these communities, recognizing that their taxonomic and functional diversity is fundamental to overall ecosystem functioning. Furthermore, the paper aimed to comprehensively map coastal benthic habitats, providing a detailed overview of their status, with particular attention given to soft-rock environments inhabited by Pholadidae mollusks, which represent a unique and ecologically significant habitat type along this coast.

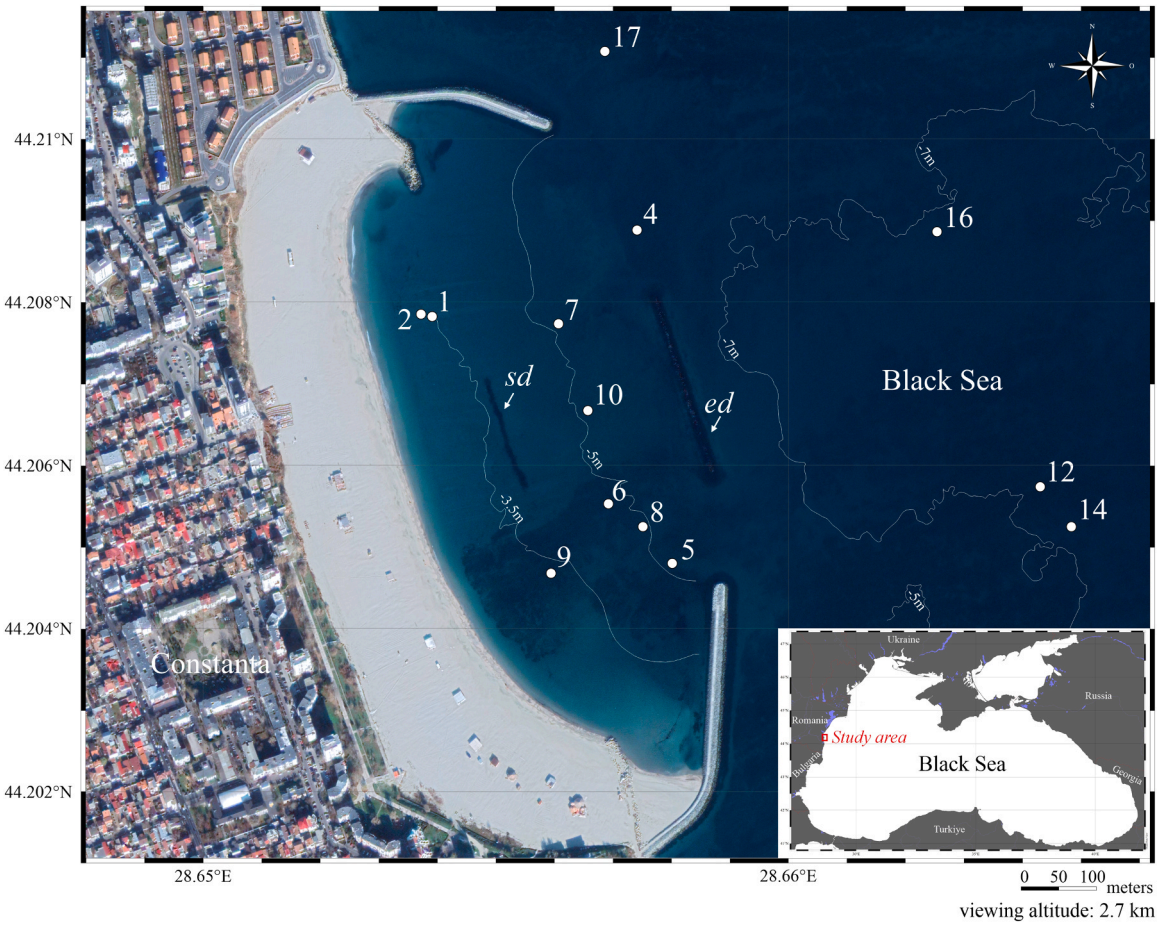

Fig. 1. Sampling stations map in the study area (Constanta, Romania). Source of map: Google Earth (date of image acquisition: 25.01.2020) and ODV. Legend: *sd* – submerged dyke, *ed* – emersed dyke.

2. Material and methods

2.1. Study site

2.1.1. Study area and geophysical survey

The study area is located in a shallow bay north of Constanța, Romania (Black Sea), which underwent beach nourishment in 2015 as a coastal erosion mitigation measure. Interventions included the construction of submerged dike (located 400 m offshore), north and south embankments, and extensive sand replenishment using coarse, shell-rich sediments. These modifications resulted in a beach advancement of approximately 100–130 m and altered local sediment transport and hydrodynamic regimes. Geologically, the area lies within the stable South Dobrogea tectonic unit (part of the Moesian Platform), with nearshore substrates composed of Sarmatian limestones and loess deposits. A detailed geological and hydrological background is provided by Popa et al. (2024).

A field campaign was conducted in August 2020 and included two major components: (i) a geophysical survey, and (ii) biological sampling and visual habitat assessment. The geophysical survey, carried out between 11 and 14 August, utilized a multibeam echosounder (MBES), single-beam echosounder (SBES), and side-scan sonar (SSS) to characterize the seabed. These tools provided high-resolution bathymetric data and acoustic backscatter imagery used for substrate classification and habitat delineation (Popa et al., 2024).

2.1.2. Biological sampling strategy

Biological sampling was conducted from 18 to 21 August 2020 at 13 sampling stations, which were selected to represent the diversity of benthic substrates identified through geophysical mapping (STable 1 and Fig. 1). Sampled and observed habitat types include: Infralittoral sand, Coarse biogenic sediments, Marl soft-rock outcrops, Infralittoral rock with photophilic algae, exposed biogenic reefs and Infralittoral rock colonized by burrowing bivalves.

During the field survey, stations St. 04, St.12, and St.16, characterized by limestone substrates colonized by the burrowing bivalve *Petricola lithophaga*, were visually inspected for habitat validation using *in situ* methods (Fig. 1). Stations St. 09 and St.17, representing rocky habitats with photophilic algae (St. 09) and exposed biogenic reefs dominated by Mytilidae (St. 17), were sampled in two replicates each to account for natural heterogeneity and species patchiness.

Samples were collected following habitats typology by using a combination of Van Veen grab (0.04 m^2), SCUBA diving and free diving along with *visual census* techniques, hand corer (20 × 20 cm) and surface scraping (20 × 20 cm). A *visual census* was conducted to confidently identify and classify encountered benthic habitats, with sampling collections where necessary. Scraping was applied in rocky habitats, while marl outcrops were sampled using hand corer for extraction of piddocks bivalve. Due to the method's invasiveness, only two marl samples were taken. Visual inspections were used in seagrass habitats (free diving) to identify the main floristic community structure. No sampling was performed in seagrass habitats, which will be the subject of a future study.

2.1.3. Sample processing, laboratory and statistical analyses

All sediment samples were sieved onboard through a 0.5 mm mesh. Retained material was preserved in formalin and later transferred to 70 % ethanol. Hard-bottom organisms were similarly preserved following preliminary field sorting.

Taxonomic identification was carried out using Zeiss SteREO Discovery.V8 and AxioLab.A1 microscopes, and species names were validated using the World Register of Marine Species (WoRMS). Macrozoobenthic species were determined to the lowest possible taxonomic level (except Oligochaeta). Abundance and wet weight biomass were standardized per square meter (indv·m^{-2}, g·m^{-2}). For *Barnea* individuals, morphometric measurements (length, width, height) were recorded, excluding damaged specimens, and width-to-length ratios were calculated for condition index assessment.

Statistical analyses were conducted using PRIMER v7 and PERMANOVA+. Species richness, diversity indices (Shannon diversity H', Simpson and Pielou evenness J'), and ordination methods were applied to explore community structure across habitats and stations.

Abundance data (transformed with log (x + 1) function) were used to create a similarity matrix based on the Bray-Curtis similarity index. The matrices were used to perform hierarchical cluster analysis (CLUSTER) and nonmetric multidimensional scaling ordination (MDS), in order to evaluate similarities between samples (grouped by stations). To evaluate the contribution of the species that determined the differences between the groups created by the cluster analysis, the similarity percentages were calculated (SIMPER analysis). We used one-way analysis of similarity (ANOSIM) to test the null hypothesis of no indices differences among all sampling sites. The R-value (ranging from 0 to 1) highlights variables discriminating between the sites, and the p-values assess the statistical significance of these relationships. We also applied one-way ANOVA to Bray-Curtis dissimilarities to test for significant differences among benthic habitats. To identify significantly differences among the benthic habitats, the non-parametric Kruskal–Wallis test was also used.

2.1.4. Habitat classification and mapping

Substrate classification followed the 5/7 Folk sediment scheme, with integration of EMODnet Seabed Habitats protocols and national guidelines (Populus et al., 2017; Vasquez et al., 2020). Spatial analysis and map production were performed using Ocean Data View (ODV, Schlitzer, 2025), Google Earth Pro (v7.3.6), and ArcMap (ESRI). Coastal line in 1961 where prepared according to the terrestrial maps scale 1:50,000, 1972 editions and according to the hydrographic works from 1959 to 1962, 1974 to 1975. Map base - geodetic coordinates system year 1942 (Black Sea coast of Romania: From the Tuzla cape to Mamaia, 050-2). The 1961 coastline was reconstructed using terrestrial maps at a 1:50,000 scale (1972 editions) and hydrographic surveys conducted between 1959–1962 and

1974–1975. The map base used was in the 1942 geodetic coordinate system, covering the Romanian Black Sea coast from Cape Tuzla to Mamaia (sheet 050-2). The coastline reconstruction was carried out through manual georeferencing and digitization using Global Mapper software. Visuals were edited in CorelDRAW 2023.

2.1.5. Morphometric and growth analysis

Shell morphometric analysis was conducted on individuals of the *Barnea* piddock collected at two stations. For each individual, shell length (maximum anterior - posterior distance), height (dorsal–ventral axis), width (lateral thickness), and wet weight were recorded using digital callipers (± 0.1 mm) and a precision balance (± 0.001 g). Damaged specimens were excluded from the analysis.

The Condition Index (CI) was calculated as an indicator of body condition using the formula:

$$CI = (Weight/(Length \times Height \times Width)) \times 100$$

To assess long-term growth dynamics and age structure, shell lengths were modelled using the inverse von Bertalanffy Growth Function (VBGF):

$$L_t = L_\infty (1 - e^{-k(t-t0)})$$

where L_t is length at age t, L_∞ is the theoretical maximum shell length, k is the growth rate coefficient, and t_o is the hypothetical age at zero length. The model used the following reference parameters derived from Pinn et al. (2005):

$L\infty = 29.6$ mm, $k = 1.17$ year^{-1}, $t_o = -0.62$ years.

Each individual's estimated age was derived from shell length using the inverse of the VBGF. Age classes were grouped into 1-year intervals to assess population structure. Residuals between observed and predicted lengths were used to evaluate model fit. Station-wise comparisons of age distribution and condition index were performed using Student's t-tests. These analyses were conducted in R.

2.1.6. Historical comparison

Historical data from 1961 were used for comparative analysis (Gomoiu and Müller, 1962). To assess long-term trends in shell size, a historical dataset from 1961 was used, comprising shell length, height, and weight data from the same region. These measurements were compared to present-day stations using the same statistical procedures. Distribution patterns were visualized via histograms, and t-tests were applied to detect significant changes over time.

2.1.7. Molecular identification – Molgula manhattensis

Total genomic DNA was extracted from two individuals of *M. manhattensis* using the DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany), following an optimized protocol that included an initial stage of cell disruption (Iancu et al., 2015), and further processed according to the manufacturer's instructions. A partial region of the mitochondrial COI gene was amplified using metazoan universal primers (CO1490 (5′-GGTCAACAAATCAAA-GATATTGG-3′) and HCO2198 (5′-TAAACTTCAGGGTGAC-CAAAAAATCA-3′) (Folmer et al., 1994). PCR amplification, electrophoresis, purification of amplicons, sequencing and sequence analysis were performed according to the protocols described by Menabit et al., (2022). Molecular identification was based on sequence identity using a 97 % threshold for BLAST screening of the NCBI GenBank database (Hebert et al., 2003). The COI sequences were deposited in GenBank under the following accession numbers: [OK272500]; [PV439837].

3. Results

3.1. Species composition

A total of 76 macrozoobenthic taxa belonging to 17 major taxonomic groups have been identified (STable 2). These taxa include Cnidaria (1), Platyhelminthes (2), Nemertea (4), Polychaeta (26), Oligochaeta, Polyplacophora (1), Gastropoda (4), Bivalvia (11), Phoronida (1), Bryozoa (2), Cirripedia (1), Amphipoda (11), Isopoda (1), Cumacea (3), Mysida (1), Decapoda (4) and Tunicata (1). Among the collected species, *Irus irus* (Linnaeus, 1758), *Pholas dactylus* Linnaeus, 1758 and *Petricola lithophaga* (Retzius, 1788) are currently listed in the Order No. 488/2020, which outlines the list of endangered marine species of the Romanian Black Sea coast to aid in their protection and conservation. In addition, six invasive species established in the Black Sea were identified: the mollusks *Rapana venosa* (Valenciennes, 1846) and *Anadara kagoshimensis* (Tokunaga, 1906); the polychaetes *Alitta succinea* (Leuckart, 1847) and *Polydora cornuta* Bosc, 1802; the crustacean *Amphibalanus improvisus* (Darwin, 1854); and the tunicate *Molgula manhattensis* (De Kay, 1843).

Taxonomic richness ranged from 9 taxa (Stations 8 and 9) to 40 taxa (Station 9_2). The most widespread species, occurring at over 50 % of the sampling sites, included *Capitella* sp., *Mysta picta*, *Heteromastus filiformis*, *Platynereis dumerilii*, *Lepidochitona cinerea*, *Microdeutopus gryllotalpa*, *Dynamene bidentata*, and *Brachynotus sexdentatus*.

3.2. Benthic habitat and their communities

Seven benthic habitats were delineated using a broad manual mapping approach based on a geophysical measurement (Popa et al., 2024), sampling point grid, considering community structure, the presence and coverage of ecosystem engineers' species, substrate

type and visual census. Four habitats were defined based on a combination of all these factors, two were defined using geophysical investigations and visual census alone, and one was defined solely based on visual census.

The analysis of macrozoobenthic community structure across sampled stations revealed clear patterns related to substratum type. According to the cluster analysis result, the macrozoobenthic community was divided into four clusters: the first group - **rock** (St. 17_1, St. 17_2, St.09_1 and St. 09_2) represents the infralittoral exposed biogenic reefs with mytilidae habitat, the second group – **marl** (St. 01 and St. 02) – infralittoral soft-rock outcrops (marlstone) with Pholadidae (*B. candida* and *Ph. dactylus*), the third group – **sand** (St. 07, St. 08 and St. 10) – infralittoral sand sediments with varied infauna and the fourth group - **coarse** (St. 05, St. 06, St. 14) – infralittoral biogenic coarse sediments with varied infauna (STable 3, Figs. 2 and 3). Moreover, the nMDS further confirmed the result of the cluster analysis, and the stress value was 0.08. This observation was statistically supported by a one-way ANOVA on Bray-Curtis dissimilarities, which revealed significant differences among substratum types ($F = 3.81$, $p = 0.0099$). These results confirm the substratum heterogeneity as a major determinant of faunal distribution. Thus, the more complex substrates such as rock and marl supporting the more structured and consistent assemblages were observed. The two infralittoral rock habitats, one with photophilic algae, mytilidae mollusks and molgulidae (*M. manhattensis*) and the other with endolithobiont mollusks (*P. lithophaga*) were delineated based on a geophysical measurement and visual census, while the exposed upper infralittoral clean sands habitat located further south of the investigated area was identified by visual census only (Fig. 3).

The ANOSIM analysis revealed significant dissimilarities between stations ($R = 0.948$, $p = 0.001$ %). Pairwise comparisons revealed notable dissimilarities between the Coarse and Rock groups ($R = 0.815$, $p = 0.029$ %) as well as between the Sand and Rock groups ($R = 1$, $p = 0.029$ %). Several species contributed substantially to these differences, with *Mytilaster minimus* accounting for 17.49 % and *Dynamene bidentata* for 5.37 % in the Coarse and Rock groups. Additionally, 18 other species collectively contributed up to 71 %, with individual contributions ranging from 4.51 % to 1.35 %. When comparing group Sand to group Rock, the average dissimilarity was found to be 92.1 %. The key species contributing to this difference was *M. minimus*, which accounted for 17.5 % of the variation.

The comparison between group Marl and group Rock showed an average dissimilarity of 89.02 %. *M minimus* contributed 16.45 % to this dissimilarity, followed by *Barnea candida* at 11.1 %. Groups Sand & Marl and Groups Coarse & Marl exhibit substantial dissimilarities, with differences of 87.04 % and 86.30 %, respectively. In both cases, *B. candida* significantly contributed to the overall dissimilarity, accounting for 32.62 % and 24.43 % of the differences, respectively.

Significant contributors to similarity were identified in each group, characterized by distinct species (Fig. 4). In group Marl, with an average similarity of 52.5 %, the major contributors were *B. candida* (57.7 %) and *Microdeutopus gryllotalpa* (10.3 %). Group Rock, with an average similarity of 50.89 %, are key contributions from *M. minimus* (21.9 %), *Platynereis dumerilii* (8.8 %), and *Amphibalanus improvisus* (8.4 %). In group Sand, characterized by an average similarity of 50.82 %, the main contributors were *Capitella sp.* (43.4 %), *Mysta picta* (22.1 %), and *Micronephthys longicornis* (13 %). Group Coarse, with an average similarity 28.19 %, are major contributors from *Heteromastus filiformis* (19.1 %), *Prionospio maciolekae* (14.7 %), *Cumella limicola* (13.6 %) and *Lepidochitona cinerea* (13.2 %).

Of the 75 taxa identified in the quantitative samples, 54 were recorded in the infralittoral exposed biogenic reefs with Mytilidae habitat, 40 in infralittoral biogenic coarse sediments with varied infauna, 19 in infralittoral soft-rock outcrops (marlstone) with Pholadidae (*B. candida* and *Ph. dactylus*), and also infralittoral sand sediments with varied infauna. The diversity metrics showed moderate-to-high variability across stations, with Shannon index values ranging from 0.88 (St. 17_1) to 2.65 (St. 05), and species

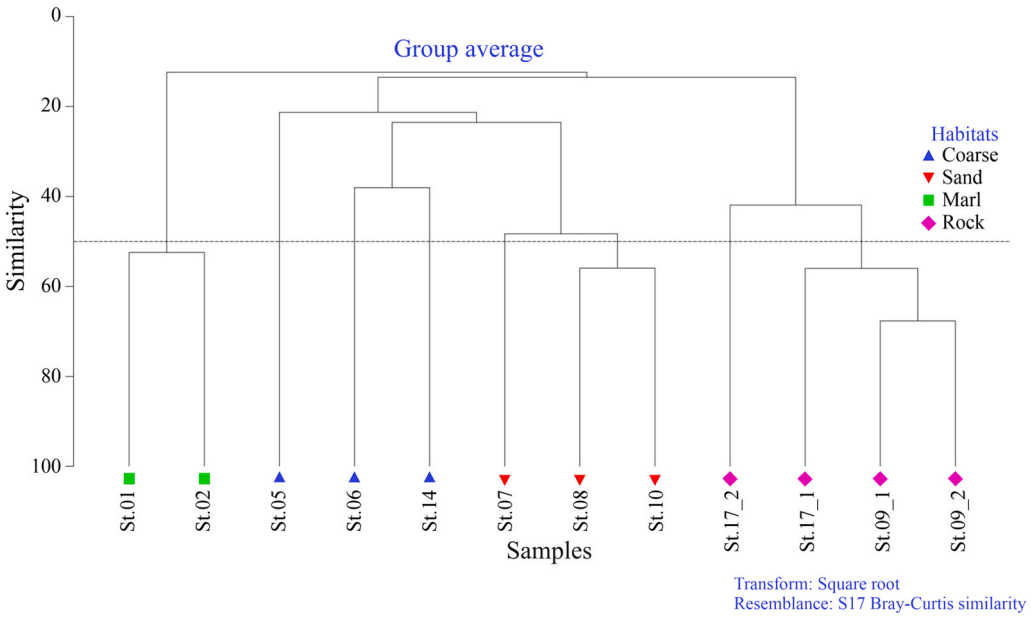

Fig. 2. Dendrogram for hierarchical clustering of stations (group average of Bray-Curtis similarities on log (x + 1) transformed abundance).

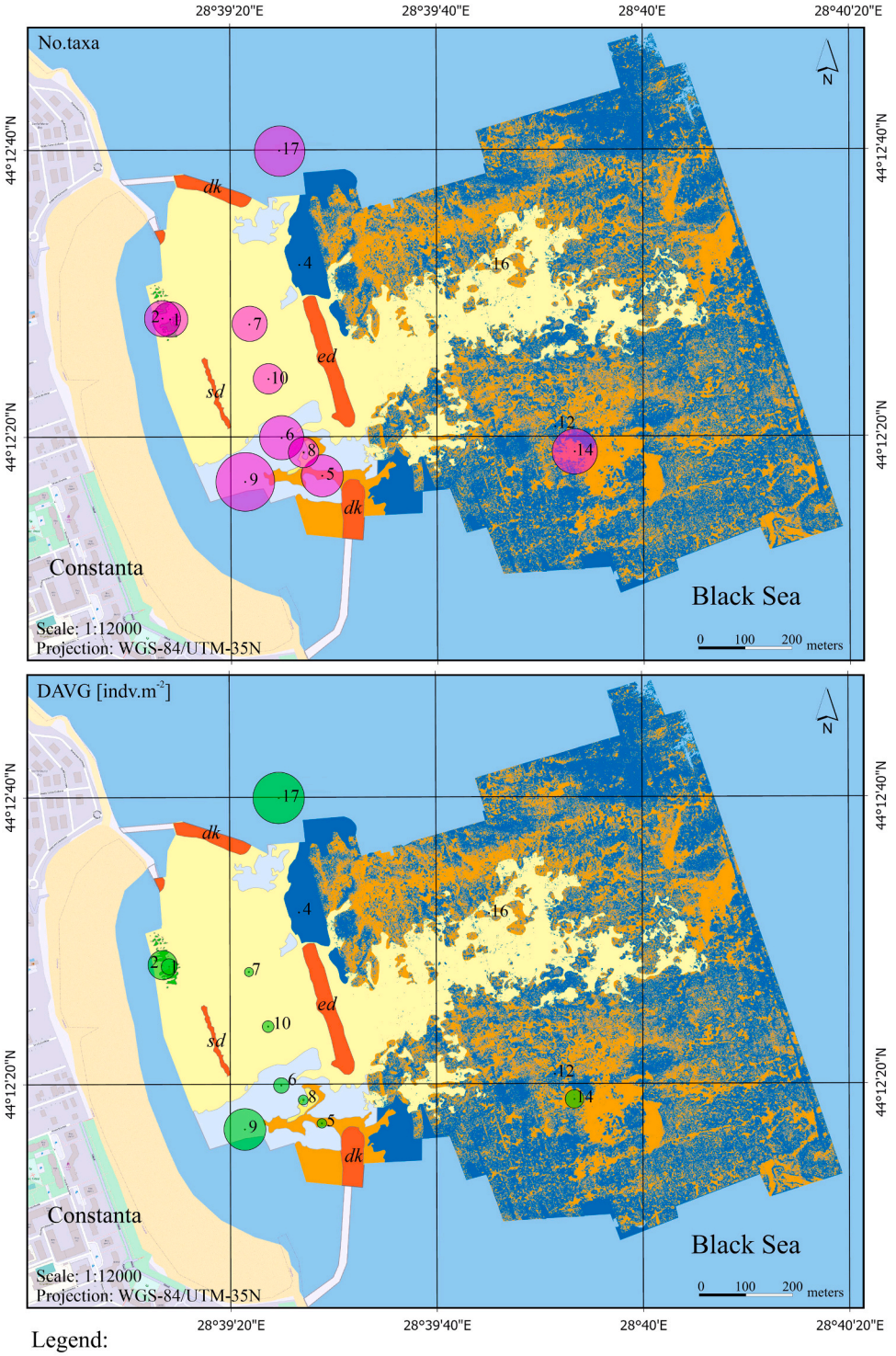

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Fig. 3. Benthic habitats and spatial distribution of number of taxa (No.taxa) and average density of macrozoobenthos in the study area (Davg indv.m^{-2}).

richness ranging from 9 (St. 08 and St. 10) to 40 (St. 09_2) taxa per station. These results reflect the influence of natural gradients such as depth, and sediment heterogeneity in shaping benthic communities across the area. Results indicated that infralittoral exposed biogenic reefs with Mytilidae habitat and infralittoral biogenic coarse sediments with varied infauna had higher biodiversity. However, statistical analysis revealed that only species richness varied significantly across different habitats. The Kruskal-Wallis test showed a significant effect of substratum type on species richness ($H = 10.16$, $p = 0.04$), with the highest values observed in rocky and coarse habitats. In contrast, differences in Shannon ($p = 0.15$), Simpson ($p = 0.25$), and Pielou ($p = 0.22$) indices were not statistically significant, although these metrics consistently suggested that structurally complex substrata supported higher biodiversity (Fig. 5), which reflects the ecological heterogeneity of the coastal ecosystem. The combination of sandy areas, consolidated marl, and hard rocky substrates creates a mosaic of ecological niches that support a rich and structured benthic community.

Similar to diversity, both the numerical abundance (density, indiv.m^{-2}) and biomass (g.m^{-2}) of macrozoobenthos varied significantly across stations, as evidenced by the population similarity indices and the station clustering dendrogram (Figs. 2 and 4). On average, the macrozoobenthic density in this area was approximately 7757 indiv.m^{-2}, with an average biomass of about 459 g.m^{-2}. The highest average density was observed in the infralittoral exposed biogenic reefs with Mytilidae habitats (18,990 indv.m^{-2}), dominated by over 70 % of *M. minimus, D. bidentata, C. limicola,* and *P. dumerilii*. This substantial density underscores the capacity of these biogenic structures to support a large number of organisms, likely due to the physical complexity and provision of resources and shelter within the habitat. In contrast, the lowest density was recorded in infralittoral sand sediments with varied infauna habitats (850 indv.m^{-2}). This value is substantially lower than that observed in the infralittoral exposed biogenic reefs with Mytilidae habitat.

Regarding biomass, the infralittoral soft-rock outcrops with Pholadidae habitats exhibited the highest values (1400 g.m^{-2}). This high biomass, despite potentially not corresponding to the highest individual density, suggests the dominance of relatively large and/or heavy organisms within this environment, such as *B. candida* which represents in our study over 96 % of the total biomass. This could imply a potential vulnerability of the habitat to factors specifically affecting this dominant species. Despite the infralittoral exposed biogenic reefs with Mytilidae habitat exhibiting the highest density, their recorded biomass was 2.3 times lower than that of infralittoral soft-rock outcrops with Pholadidae. Comparatively, the biomass in these biogenic reefs with Mytilidae habitat was 99 times greater than infralittoral sand sediments with varied infauna, and 8 times higher than infralittoral biogenic coarse sediments with varied infauna.

3.3. In situ visual census of benthic habitats and detection of overlooked taxa

Two sampling stations were located within marl soft-rock outcrops: Stations St.01 at 3.3 m depth and St. 02 at 2.7 m depth. These outcrops, representing one of the rarest and most dynamic benthic habitats along the Romanian Black Sea coast, occur close to shore, at an average depth of 3 m, covering an area of approximately 0.002 km^2, with a length of 108 m (parallel to the shoreline) and an average width of 20 m. The marl layer reaches a maximum thickness of 70 cm above the underlying sand, with an average thickness of 35 cm (Fig. 6a- e). The landscape corresponds to the description provided by Gomoiu and Müller (1962): the seabed consists of compact sandy-clay rock, likely formed by the interaction between loess and seawater. It marks the transition zone between the offshore sandy sublittoral and the nearshore rocky bottom composed of Sarmatian limestone, and supports dense *Mytilus* beds and macroalgal assemblages (e.g., *Cystoseira, Cladophora, Enteromorpha*). In contrast, the clay outcrops are barren, lacking vegetation, and are heavily perforated by burrows and galleries, giving them a sponge-like appearance. The surrounding is dominated by well-preserved shells of *B. candida* (Fig. 7).

Two distinct marl bed outcrops were identified: one nearshore site (SFig. 1 - Mr1), characterized by intense burrowing activity from bivalve species, and a deeper one (~ 5 m depth) (SFig. 1 - Mr2), located near St. 06, with no boreholes. This deeper marl bed exhibits a dome-like ridge structure, oriented perpendicular to the coastline, and is colonized by red annual macroalgae, such *Callithamnion sp.* and *Dasya pedicellata* (C.Agardh) C.Agardh, 1824 (Fig. 8e, f).

In contrast, the shallow marl outcrop is partially colonized by green macroalgae (*Enteromorpha, Cladophora, Ulva*) (Fig. 6a). These beds support a diverse cryptobenthic community, with common inhabitants as *Brachynotus sexdentatus* (Fig. 6h).

Due to its location in a high-energy coastal zone, parts of the marl bed are actively eroded and fragmented by wave action, likely playing a critical role in modulating benthic colonization and community turnover. Since its discovery in 2018 (Teaca pers. comm.), the habitat is in a continuous transformation, the marl outcrops being periodically either exposed and buried beneath shifting sands. This accounts for the interannual variability in the spatial extent of the marl beds (SFig. 1).

In contrast, the innermost sheltered coastal zone supports a dense seagrass meadow dominated by *Zannichellia palustris* L., extending over an area of 2000 m^2 (SFig. 1 - Gr). This stable, low-energy habitat supports a distinctive associated fauna, particularly epifaunal gastropods and infaunal polychaetes (which will be the subject of future studies) (SFig. 1).

Of particular significance, this study confirms the existence of *Zostera marina* Linnaeus, 1753 in the research area in association with *Z. palustris* (Fig. 8c, d). The initial findings were observed in 2019, forming small patches with an average diameter of 1 m and leaf lengths reaching 90 cm. These patches have since shown continuous expansion, reaching diameters exceeding 1.7 m and leaf lengths over 120 cm by 2023.

Molgula manhattensis (De Kay, 1843), another often-overlooked taxon, was identified in this study using morphological analysis and genetic approaches (GenBank accession numbers: [OK272500]; [PV439837]). The species was recorded at St. 09, in infralittoral rock

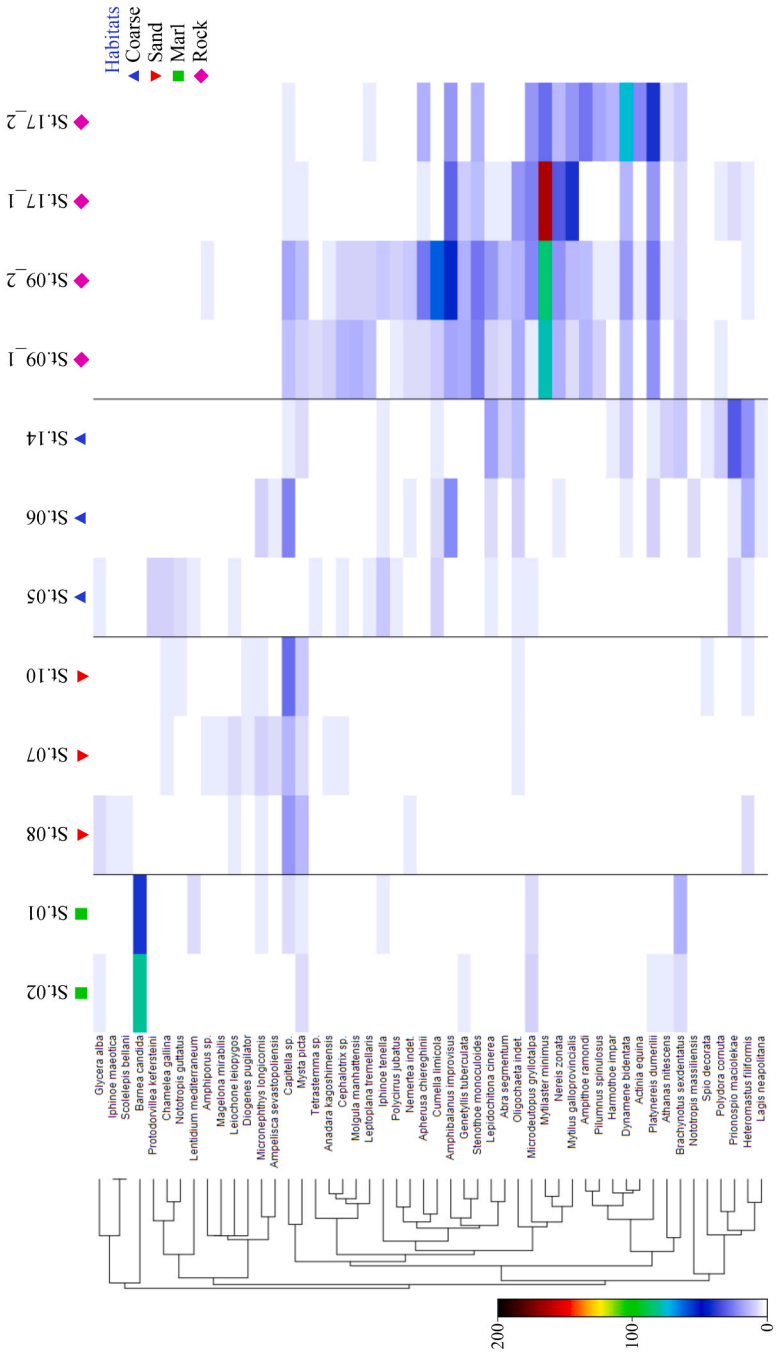

Fig. 4. Shade plot of species square root transformed abundance at stations arranged by habitat. The species list is reduced to 50 most important taxa. Species clustering based on index of association.

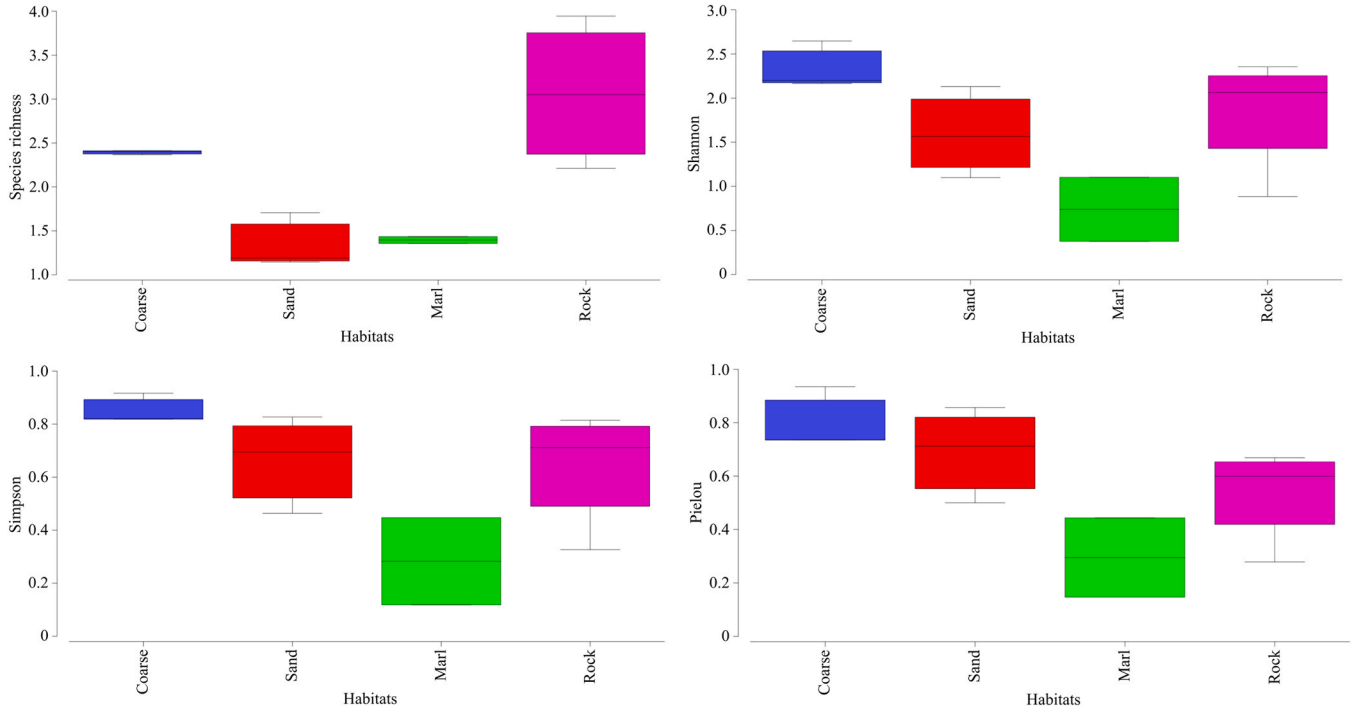

Fig. 5. Univariate characteristics of identified habitats expressed in standard box plots. Values of Species richness, Shannon-Wiener, Simpson and Pielou evenness index are shown.

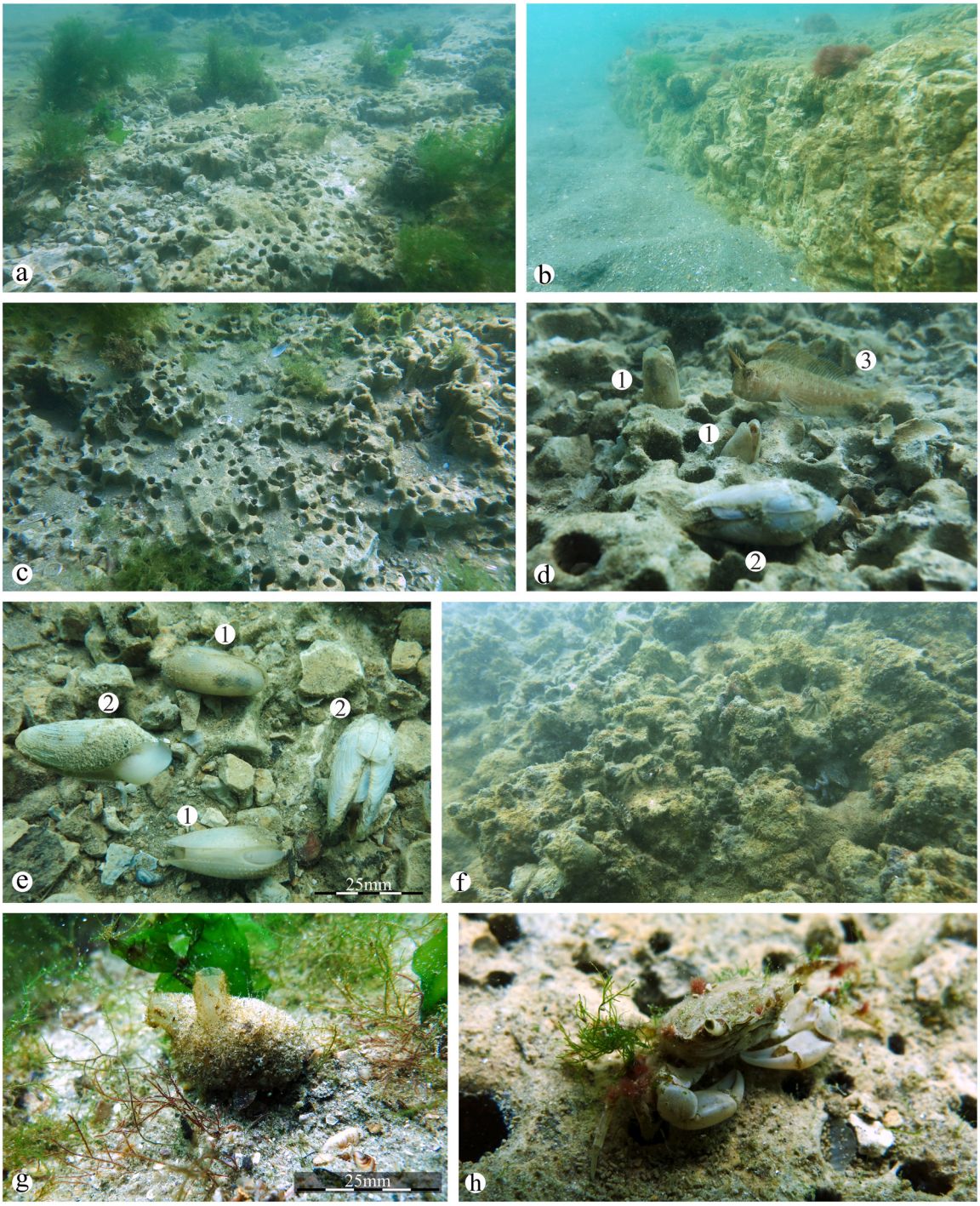

Fig. 6. Underwater seascape of infralittoral benthic habitats. Marl beds with Pholadidae (a-e); Limestone rock with endolithic bivalve (*Petricola lithophaga* (Retzius, 1788)) (f); Rock with photophilic algae and *Molgula manhattensis* (De Kay, 1843) (g); *Brachynotus sexdentatus* (Risso, 1827) on marl outcrops (h). 1 – *Barnea candida* (Linnaeus, 1758), 2 – *Pholas dactylus* Linnaeus, 1758, 3 – *Parablennius tentacularis* (Brünnich, 1768). Images taken between 18 and 21.08.2020 (photo: Adrian Teaca).

habitats with photophilic algae (Fig. 6g and SFig. 2B). The taxonomic ambiguity within this group arises from the morphological resemblance between *M. manhattensis, M. appendiculata*, and *M. euprocta* - all of which being reported in the Black Sea and exhibit overlapping habitat preferences.

The deeper part of the study area (6–7 m depth) consists primarily of bare limestone which supports populations of the burrowing bivalve *Petricola lithophaga* (Retzius, 1788) (Fig. 6f and SFig. 2A). This species contributes to habitat modification through bioerosion,

Fig. 7. *Barnea candida* (Linnaeus, 1758). Lateral left side (A), dorsal view showing protoplax ancillary plate (B), ventral side and foot opening (C), anterior view (D). Arrows indicate protoplax. Scale bar: 5 mm (photo: Adrian Teaca).

enhancing microhabitat complexity and local biodiversity.

3.4. Morphometric structure and population composition of Barnea candida

3.4.1. Morphometric structure and historical comparison

Analysis of 195 *B. candida* specimens collected from two sampling sites (St. 01 and St. 02) showed shell lengths ranging from 10.8 to 33.5 mm and weights between 0.08 and 1.52 g. St. 01 individuals were significantly larger (mean length: 25.3 mm) and heavier (mean weight: 0.75 g) compared to St. 02 (mean length: 17.4 mm, mean weight: 0.29 g). Shell length distributions indicated distinct population structures, with St. 01 showing a wider range and higher frequencies of larger individuals, suggesting a mature, mixed-age community (Fig. 9). Morphometric data from 1961 showed predominance of larger individuals, with lengths commonly exceeding 35 mm. No significant difference was found between historical data and St. 01 ($t = -0.11$, $p = 0.92$). However, St. 02 individuals were significantly smaller than those from 1961 ($t = 3.52$, $p = 0.004$), indicating a possible decline in growth potential or age structure, likely due to environmental pressures or recruitment shifts (Fig. 9).

Despite smaller shell sizes, the St. 02 had calculated a slightly higher mean Condition Index (CI) indicating a greater soft tissue mass in younger individuals. This is due to early growth strategies and enhanced feeding efficiency within the younger cohort.

3.4.2. Growth dynamics and age structure

Estimated ages have been obtained using the inverse VBGF, based on reference parameters from Pinn et al. (2005) ($L\infty = 29.6$ mm, $k = 1.17$ year^{-1}, $t_0 = -0.62$ years) and length measurements obtained in this study. The resulting plot demonstrates a strong alignment between observed data and the theoretical growth curve, particularly for individuals whose shell lengths fall within the expected range defined by the reference model. To maintain the integrity of the Pinn derived parameters, only individuals with shell lengths less than 29.6 mm were included in the VBGF fit and visualization. Hence, six individuals exceeding 29.6 mm, with maximum lengths reaching 33.5 mm at St. 01 were excluded (SFig. 3). These larger individuals fall outside the asymptotic length defined by the Pinn model, suggesting that the Romanian population of *B. candida* may either exhibit different growth patterns, potentially due to local environmental or genetic factors.

The estimated ages ranged from 0.1 to 3 years. At St. 01, the population showed a wide age distribution with a mean age of 1.2 years, indicating a stable and established population. In contrast, St. 02 was dominated by younger individuals aged 0–1 years (mean age: 0.6 years), suggesting recent recruitment.

4. Discussions

This study offers comprehensive data on the species diversity, distribution, and abundance of macrozoobenthos in the northern Constanta region of the Black Sea. A total of 76 taxa were identified during the research, which exceeds the number (31) reported by Marin et al. (2018).

Our study revealed the existence of five distinct infralittoral habitats, as follows: exposed biogenic reefs with mytilidae, soft-rock outcrops with Pholadidae (*B. candida* and *Ph. dactylus*), sandy sediments with varied infauna and biogenic coarse sediments with

varied infauna. These habitats show a distinct diversity and community, which suggests with implications in different ecosystem functioning.

Diversity indices exhibited significant variation in the area, highlighting the influence of habitat heterogeneity on benthic community structure. Shannon and Simpson indices were consistently higher in rocky and coarse substrates, indicating communities that were both more diverse and compositionally balanced. Species richness followed the same trend, with marl and rocky habitats supporting the greatest number of taxa. In contrast, sandy and marl sediments exhibited lower richness and diversity, likely due to reduced habitat complexity and higher environmental variability. The species richness significantly increased with increasing depth and changing the type of substrate, which is in line with the results reported for the Romanian Black Sea coast (Teaca et al., 2010; Begun et al., 2018, 2022; Marin et al., 2018; Tănase et al., 2022; Popa et al., 2024). These patterns highlight the ecological value of stable, complex habitats in supporting diverse and functionally rich benthic assemblages in shallow marine environments.

In line with findings from previous studies (Begun et al., 2006, 2022; Teaca et al., 2006, 2010; Marin et al., 2018; Abaza et al., 2019; Tănase et al., 2022), our research identified polychaetes (26 species), crustaceans (21 species), and mollusks (16 species) as the dominant macrozoobenthic groups inhabiting the shallow coastal zone. Within sandy bottom habitats, polychaete species such as *Heteromastus filiformis, Prionospio maciolekae, Mysta picta* and *Nephtys hombergii* are frequently abundant (Begun et al., 2006; Marin et al., 2018; Abaza et al., 2019). In contrast, our study found that *Capitella sp.* and *Mysta picta* were the dominant polychaete species, with *Capitella sp.* often associated with organically enriched environments. *Capitella sp.* is known for rapidly colonizing disturbed habitats or areas with high organic input, which may result from natural enrichment or anthropogenic activities. In our study area, this habitat overlapped with reefs, where organic enrichment might originate from pseudofecal produced by mussels. Such enrichment likely creates favorable conditions for high densities of *Capitella* species. The prevalence of different dominant species across studies highlights the dynamic nature of benthic communities and their sensitivity to local environmental variations.

Conversely, in biogenic reef habitats, mollusk abundance was dominated by *M. minimus*, while crustaceans such as *D. bidentata* and *C. limicola*, along with the polychaete *P. dumerilii*, were most prevalent. These species assemblages are typical of hard substrate environments like biogenic reefs, where mollusks can attach and filter feed, crustaceans utilize crevices for refuge, and polychaetes exploit a range of feeding niches. The observed taxonomic dominance reflects the functional roles and ecological opportunities shaped by the structural complexity of biogenic reefs (Teaca et al., 2006, 2010).

According to our results, the soft-rock outcrops with Pholadidae (*B. candida* and *Ph. dactylus*) habitat, was dominated by *B. candida*. This species was reported for the first time in over six decades. The first and only documented occurrence of a *B. candida* - dominated benthic assemblage along the Romanian Black Sea coast was provided by Gomoiu and Müller (1962), based on observations performed near Constanța at depths of 1–4 m. Conducted in 1961, the study represents one of the earliest which utilized direct underwater observation (visual census) for benthic research in the region. The unique habitat was associated with compact sandy-clay (marl) outcrops, where *B. candida* exhibited densities of over 4000 indiv.m^{-2} and biomass levels exceeding 3300 g.m^{-2} comparable only to Mytilus-dominated reefs. The community display high structural and taxonomic complexity, with more than 50 associated taxa, including *Monocorophium insidiosum, Parablennius tentacularis*, and *Brachynotus sexdentatus*. The authors defined this as a distinct "*Barnea* biocoenosis of clay grounds", highlighting its specificity to compact, vegetation-poor substrata and its role as a biodiversity hotspot and habitat modifier.

In contrast to the dense, extensive *Barnea* aggregations described in 1961, our observations indicate a more fragmented and spatially limited distribution of *B. candida*, on the same geologic features - marl soft-rock outcrops at depths of 2–5 m. While current densities are notably lower, the species (*B. candida*) still acts as a key habitat engineer, supporting specialized burrowing and cryptic fauna such as *Brachynotus sexdentatus* and *Pholas dactylus*. The dominance of *Barnea* and the rich associated fauna described by Gomoiu and Müller appear to have diminished or shifted, likely due to habitat loss, sedimentation, and hydrodynamic changes. Nevertheless, the reappearance of living *Barnea* after more than six decades suggests the persistence of relict habitats and highlights the importance of conserving these rare biotopes (SFig. 4).

The marl outcrops seem to belong to the same assemblage of sparsely distributed soft-clay beds described by Gomoiu and Müller (1962) in the Cap Singol area (Constanța Nord). Parts of these compact sandy-clay outcrops are now buried under extensive anthropogenic dumping waste and hydrotechnical defense, which has altered the shoreline and gradually extended it by over 100 m in the `80–`90 (Stanica et al., 2012) (SFig. 4).

The current study area underwent large-scale beach nourishment in 2015, involving substantial sand deposition (SFig. 1, SFig. 4). This intervention may have buried other similar marl formations situated nearshore.

Dasya pedicellata long considered rare or extincted from the Romanian coast since the 1970s, was recently rediscovered near Constanța in 2019 (Dumitrescu (Marin), 2021). Our observations confirm the presence of *D. pedicellata* in the study area since 2018 (Teaca pers. comm.), once pholadidae active marl beds were documented.

This study marks the first confirmed record of *Z. marina* in Romanian Black Sea waters. The Black Sea supports several species of seagrasses, most notably *Z. marina* and *Zostera noltei* (Berov et al., 2022; Surugiu et al., 2021; Milchakova and Phillips, 2003). Early studies of the marine flora along the Romanian Black Sea coast documented the widespread presence of both *Z. marina* (common eelgrass) and *Z. noltei* (dwarf eelgrass) (Grinţescu aet al., 1966; Skolka, 1977). These species were reported to form extensive underwater meadows, particularly in the sheltered, brackish waters of lagoons such as Sinoie, Zmeica, and Goloviţa (Teodorescu-Leonte et al., 1956), Cape Midia, Eforie South, Tuzla, Comorova, Costinești, and the Port of Mangalia (Bacescu et al., 1971). Sparse populations of *Z. marina* were observed in the shallow waters near Agigea (0.8–1 m depth), with more robust patches reported in the vicinity of Cape Midia.

Although earlier reports sometimes referred generically to "*Zostera sp.*" without species-level identification, more recent investigations at these same sites have consistently confirmed the species present as *Z. noltei* (Surugiu, 2008). This suggests that earlier

references may have involved misidentifications or that *Z. noltei* has become the more resilient and ecologically dominant species in these habitats. However, in recent decades, *Z. marina* has not been confirmed along the Romanian Black Sea coast, while *Z. noltei* continues to be regularly observed. Recent scientific literature provides no evidence regarding the presence of *Z. marina* in the area (Surugiu et al., 2021). Most recent research has focused on *Z. noltei* meadows, particularly those in the southern coastal zone near Mangalia (Marin et al., 2024).

Our study demonstrated the presence of *Z. marina* in the Constanța area, although it has not been reported in recent biodiversity surveys (Marin et al., 2018, 2024; Surugiu et al., 2021). These findings suggest that the species may persist in small populations within sheltered areas along the Romanian Black Sea coast.

The deeper part of the study area (6–7 m depth) consists primarily of bare limestone which supports populations of the burrowing bivalve *Petricola lithophaga* (Fig. 6f). This species contributes to habitat modification through bioerosion, enhancing microhabitat complexity and local biodiversity. *P. lithophaga* lives in calcareous rock, which probably excavated by acid secretion, like the related *P. lapicida* (Gmelin, 1791) (Morton and Scott, 1988). This species is mentioned only in general lists of benthic animals (Zernov, 1913; Milashevich, 1916; Kaneva-Abadjieva, 1960; Bacescu et al., 1963; Zenetos et al., 2005; De Smit and Bába, 2001; Sen et al., 2010; Crocetta et al., 2013; Ricci et al., 2015). *P. lithophaga* was reported as abundant in the rocky habitats near Agigea, Black Sea (Bacescu et al., 1963). Currently, *P. lithophaga* occurs along the entire southern Romanian coast (Teaca, pers. comm.), but it's rarely detected due to lack of targeted sampling methods for rock-boring bivalves.

In the present study we used a combination of approaches to confirm the presence of *M. manhattensis*. The taxonomy of molgulid ascidians in the Black Sea has been subject to debate in the past (Borcea, 1930; Bacescu et al., 1971). The representative of molgulids genus was first recorded on the Romanian coast by Borcea (1930) as *Caesira (Molgula) impura* Heller, 1877, and later identified by Băcescu et al. (1971) as *Molgula manhattensis* De Kay, 1843 (syn. *Molgula impura* auct.). Borcea documented this species in circa- and offshore circalittoral sedimentary habitats (Borcea, 1930).

Haydar et al. (2011) confirm the genetic identity of *M. manhattensis* at the Bulgarian Black Sea Coast. Haydar et al. (2011) showed that introduced populations in San Francisco Bay, the Black Sea, and Osaka Bay (Japan) displayed unique haplotype diversity, with some harbouring multiple haplotypes, including those common to the Northwest Atlantic. Medium- to high-frequency NW Atlantic haplotypes were present in Japan and the Black Sea but notably absent in Europe. Both Europe and North America also contained private haplotypes not shared with other regions. These findings reinforce the species' native status in the Northwest Atlantic and its introduced status in the Black Sea, Japan, and San Francisco Bay.

In this study, VBGF parameters were estimated for *B. candida* populations from soft-rock outcrops with Pholadidae (*B. candida* and *Ph. dactylus*) habitat. Results suggesting that individuals at St. 01 attain larger sizes more slowly. This pattern is consistent with earlier

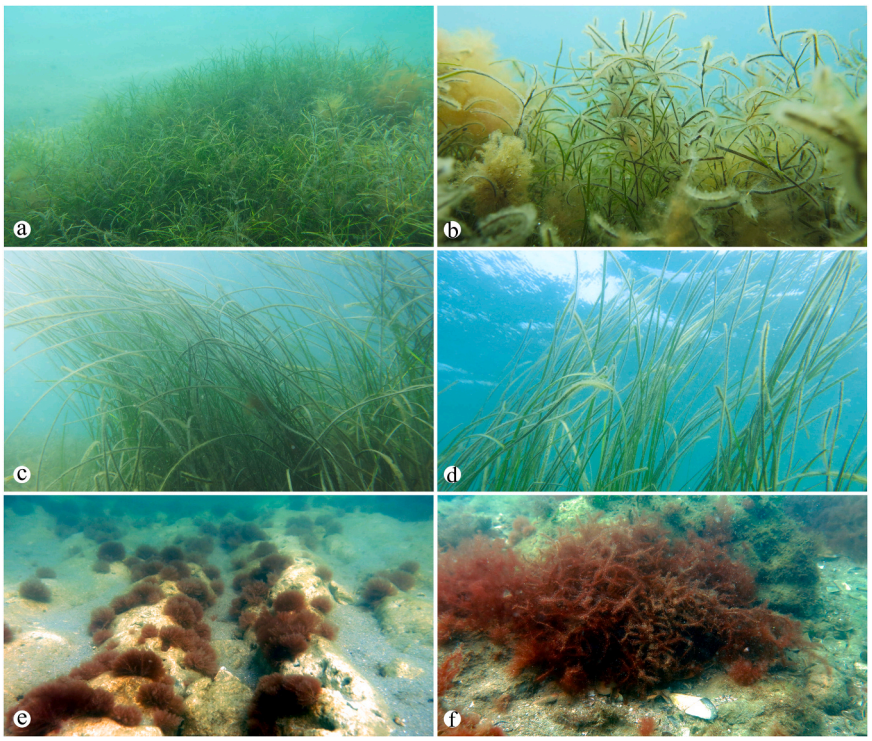

Fig. 8. Underwater seascape of seagrass meadows of *Zannichellia palustris* L. (a, b) and *Zostera marina* Linnaeus, 1753 (c, d) in the study area (Gr site indicative on SFig. 1). *Callithamnion sp.* (e) and *Dasya pedicellata* (C.Agardh) C.Agardh, 1824 (f) on deep dome-like ridge marl outcrops (Mr2 site indicative on SFig. 1). Images taken on: A-D - 25.09.2022; e, f – 21.08.2020 (photo: Adrian Teaca).

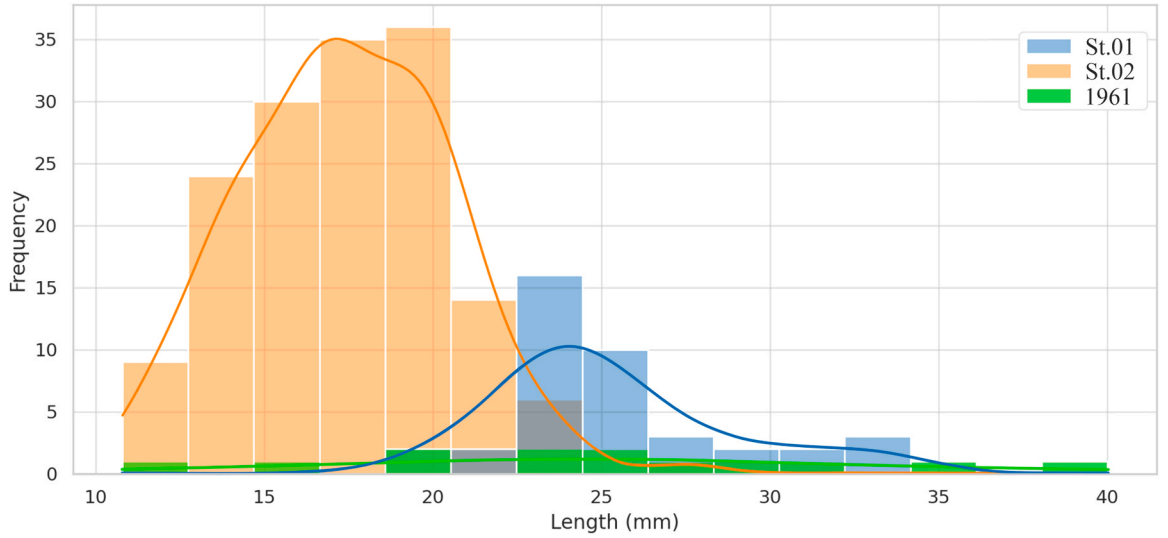

Fig. 9. Shell length histogram of *B. candida* individuals from St. 01, St. 02 and historical 1961 data. St. 01 exhibits a broader, right-skewed distribution with a higher frequency of larger individuals. The size structure of St. 02 significantly diverges from the 1961 population.

findings in other pholadid bivalves, were local environmental conditions and resource availability shape growth trajectories (Pinn et al., 2005; Bagur et al., 2013). Age-frequency histograms support the VBGF results: *B. candida* from St.01 displays a broader age structure with a higher proportion of older individuals, indicating a stable, long-established population. St. 02, in contrast, is dominated by younger individuals, suggesting recent recruitment and a less developed demographic structure. Such patterns have been widely observed in growth studies of boring and sediment-dwelling bivalves (Lomovasky et al., 2002).

Understanding the growth and demographic structure of *B. candida* supports habitat-specific conservation strategies. The presence of older individuals and wider size classes at St. 01 highlights its ecological importance as a stable, high-quality habitat. Meanwhile, St. 02 may represent a recently colonized or more dynamic environment, where population may be more vulnerable to disturbance. These insights emphasize the importance of site-level monitoring and adaptive management.

B. candida is susceptible to various environmental factors. Its sensitivity to pollution, especially eutrophication, is well documented (Alexandrov, 2017). Also, sediment modifications, such as siltation caused by excessive deposition of fine particles, could affect the species' ability to drill and feed (Alexandrov, 2017). Fishing activities, especially those involving the use of trawls, can have a negative impact on its habitat and associated populations. Therefore, human activities leading to pollution and physical habitat modifications represent significant threats to the survival of *B. candida* populations on the Romanian Black Sea coast.

Despite the national and international legislative framework for the protection of the marine environment and designation of marine protected areas, the effective implementation of protection and mitigation measures requires sustained and coordinated efforts. Within this context we propose the regional IUCN status of Critically Endangered CR A2abc + 3bc; B1ac(i–iv) + 2ac(i–iv); C2a(i) for *B. candida* in the Romanian Black Sea, in accordance with the IUCN Red List Categories and Criteria: Version 3.1 (IUCN, 2012).

Considering the environmental importance of this rare ecosystem, characterized by valuable species and habitats, specific conservation strategies should be adopted in the area. Finally, the habitat mapping that combine seafloor features and key benthic communities are valuable tools for managing ecosystems. Our dataset provides a valuable snapshot of present-day biodiversity conditions and offers a baseline for future monitoring and conservation efforts.

CRediT authorship contribution statement

Adrian Teacă: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Tatiana Begun:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Mureșan Mihaela:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis. **Selma Menabit:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis. **Adrian Popa:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis. **Ana Bianca Pavel:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03885.

Data availability

Data will be made available on request.

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