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1 **Distribution and abundance of phytobenthic communities, and implication for connectivity**
2 **and ecosystem functioning in a Marine Protected Area in the SW Black Sea**

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11 **Keywords:** Phyllophora crispa; primary production; dissolved organic matter; species distribution
12 model, cells of ecosystem functioning;

13 **Abstract**

14 In this study, we mapped and quantified the distribution and abundance of macroalgal communities
15 in an MPA along the Bulgarian Black Sea coast, with particular focus on the previously unstudied
16 *P. crispa* lower-infralittoral communities on *Ostrea edulis* biogenic reefs. Data from high
17 resolution geophysical substrate mapping was combined with benthic community observations
18 from georeferenced benthic photo surveys and sampling. Multivariate analysis identified four
19 distinct assemblages of lower-infralittoral macroalgal communities at depths between 10 and 17
20 m, dominated by *P. crispa*, *Apoglossum ruscifolium*, *Zanardinia typus* and *Gelidium* spp. Maxent
21 analysis showed distinct preferences of the identified communities to areas with specific ranges of
22 depth, inclination and curvature, with *P. crispa* more frequently occurring on vertical oyster
23 biogenic reef structures. By combining production rates from literature, biomass measurements
24 and the produced habitat maps, we found that the highest proportion of primary production and
25 DOC release was provided by the upper infralittoral *Cystoseira barbata* and *Cystoseira*
26 *bosporica*, followed by the production of the lower-infralittoral macroalgae. We related the
27 observed distribution of *P. crispa* within the studied MPA to the network of Natura 2000 maritime
28 MPAs along the Bulgarian Black Sea coast, and discussed whether the connectivity of the
29 populations of the species within the established network is sufficient within this cell of ecosystem
30 functioning.

31 **1. INTRODUCTION**

32 Coastal marine ecosystems are essential components of the marine environment. They are
33 hotspots of biodiversity, major participants in the food webs, matter and energy cycles, as well as
34 important sources of commodities and ecosystem services for human populations. Marine
35 macroalgae inhabit hard substrates in the euphotic zone, form some of the most diverse and
36 productive marine ecosystems (Greze, 1979; Ballesteros, 1991; Alongi, 1998; Wada and Hama,
37 2013), and provide food and living environment for a diversity of marine invertebrates (Christie et
38 al., 1998, 2003) and fish species (Norderhaug et al., 2005; Cheminée et al., 2013). Key services
39 provided by marine ecosystems, such as primary production, nutrient cycling and fisheries, depend
40 on the abundance, spatial distribution and structure of macroalgal communities (Loreau, 2000;
41 Scherer-Lorentzen, 2005). Located at the interface between land and open seas, the distribution
42 and structure of macroalgal communities is shaped by a complex interaction of various
43 environmental factors such as latitude, involving gradients in irradiance, day length and
44 temperature (Rinde and Sjøtun, 2005; Wernberg et al., 2010, 2013; Sales et al., 2012; Tuya et al.,
45 2012; Vergés et al., 2014;), wave exposure (Eriksson and Bergstrom, 2005; Sala et al., 2012;
46 Spatharis et al., 2011), as well as eutrophication and pollution gradients (Panayotidis et al., 2004;
47 Kraufvelin et al., 2006; Arevalo et al., 2007; Ballesteros et al., 2007; Krause-Jensen et al., 2007b;
48 ; Orfanidis et al., 2011; Thibaut et al., 2014; Blanfuné et al., 2016a, 2016b, 2017,). Increased
49 pressures from human activities in the coastal zones worldwide in recent decades, including
50 pollution, eutrophication and extraction of marine living resources, has had negative influence on
51 the distribution and functioning of marine macroalgal communities (Milchakova and Petrov, 2003;
52 Thibaut et al., 2005, 2016a, 2016b; Blanfuné et al., 2016). The abrupt changes in the ecosystem
53 functioning of the Black Sea in the 1970s and 1980s caused by a combination of elevated nutrient
54 loading, overexploitation of fish stocks, invasive species and climate anomalies (Zaitsev, 1992;
55 Daskalov, 2002) had a significant effect on pelagic (Hiebaum and Karamfilov, 2005; Yunev et al.,
56 2007) and phytobenthic (Minicheva et al., 2008) ecosystems. These negative changes were most
57 pronounced in the coastal zone in the western parts of the basin where large-scale reduction of
58 spatial distribution of macroalgal communities was observed (Mee, 1992; Zaitsev, 1992;
59 Milchakova and Petrov, 2003; Bologna and Sava, 2006; Berov et al., 2012).

60 The present day Black Sea macroalgal flora consists of approx. 325 species (80
61 Chlorophyta, 76 Ochrophyta, 169 Rhodophyta) with mostly Mediterranean and Atlantic origin
62 (Kalugina-Gutnik, 1975; Dimitrova-Konaklieva, 2000; Milchakova, 2003, 2002). In the upper
63 infralittoral, between depths of 1 and 10-15 m, the dominant habitat-forming species are the
64 perennial brown macroalgae *Cystoseira bosporica* Sauv. (= *Cystoseira crinita* f. *bosporica*
65 (Sauvageau) A.D.Zinova & Kalugina, see Berov et al., (2015)) and *Cystoseira barbata*
66 (Stackhouse) C.Agardh. In the 1970s the total biomass of these two species was estimated to be
67 approximately $2 \cdot 10^6$ tonnes for the whole Black Sea, with the majority of biomass found along
68 the Caucasus coast of Russia and Georgia (Greze, 1979).

69 At depths below 10-15 m, the most typical macroalgal communities are those formed by
70 the red sciaphylic low-light adapted *Phyllophora crispa* (Hudson) P.S.Dixon (Zinova, 1967;
71 Kalugina-Gutnik, 1975; Dimitrova-Konaklieva, 2000; Minicheva et al., 2008) . The species has an
72 attached form, growing on hard substrates, and an unattached form, growing on sandy and shelly
73 sediments. *Phyllophora crispa*, growing on sediments (Associations *P. nervosa* subf. *intermedia*
74 and *P. nervosa* subf. *latifolia*, (Kalugina-Gutnik, 1975)), forms a unique phytobenthic ecosystem
75 in the NW shelf of the Black Sea, the Zernov's Phyllophora field, which in the 1950s had an area
76 of approx. 11 000 km² and a total biomass between 5 and $10 \cdot 10^6$ tonnes (Greze, 1979; Zaitsev,
77 2008). During the period of increased eutrophication impacts in the NW Black Sea shelf in the
78 1980s, the biomass of the Zernov's Phyllophora field decreased by more than one order of
79 magnitude, with *P. crispa* gradually being replaced by filamentous red macroalgae (Kostylev et
80 al., 2010). In recent years a process of slow recovery of the species in the area was noted, which is
81 curbed by secondary eutrophication resulting from leaching of nutrients from the bottom sediments
82 (Minicheva et al., 2013).

83 The *Phyllophora crispa* form growing on hard substrates forms the plant association
84 *Phyllophora nervosa* f. *longiarticulata* (Kalugina-Gutnik, 1975; Minicheva et al., 2008; Simakova,
85 2011). It is widespread throughout the Black Sea and is typical for the Caucasus coast of Russia
86 and Ukraine, Bulgaria (Dimitrova-Konaklieva, 2000), as well as Turkey (Aysel et al., 2004). In the
87 1970s, the species occurred at depths down to 30 m along the Russian coast, with maximum
88 development in the range 24-26 m (Kalugina-Gutnik, 1975). In the early 2000s the lower depth
89 range of the species in the same area had decreased to 15-23 m, with maximum biomass found

90 between 12 and 15 m depth (Simakova, 2011). The overall biomass of this form of *P. crispa* along
91 the Russian, Georgian and Ukrainian coasts in the 1970s was estimated to be up to $5 \cdot 10^4$ tonnes (
92 Kalugina-Gutnik, 1975; Greze, 1979). No published data on the biomass and depth distribution of
93 the species is available for the rest of the Black sea, including the Bulgarian coastline.

94 Recently, a unique habitat of the attached form of *Phyllophora crispa* growing on biogenic
95 *Ostrea edulis* oyster reefs was described along the Southern Bulgarian Black Sea coast within the
96 Natura 2000 site Ropotamo (Todorova et al., 2009). The taxonomy and structure of this unique
97 algal community has not been described in details by now. The *O. edulis* biogenic reefs are a red
98 listed habitat in Bulgaria and are considered as priority habitat under the EU Habitats Directive
99 (92/43/EEC) and the EU Marine Strategy Framework Directive (2008/56/EC). The area of main
100 occurrence of this habitat, the Natura 2000 site Ropotamo, is categorized as an area with ‘medium
101 conservational priority’ for the Mediterranean and the Black Seas (Boero et al., 2016).

102 The dispersal ranges of red macroalgal species is not well-studied (Kain and Norton, 1990;
103 Lindstrom, 2001; Lester et al., 2007). In principle, the dispersal of macroalgal propagules and
104 spores is rather limited and is greatly influenced by the hydrographic conditions at the time of
105 propagule release and their physical and morphological properties (Santelices, 1990; Norton,
106 1992). The attached form of *Phyllophora crispa* predominantly reproduces sexually by producing
107 tetrasporangia and releasing them in the water column in the cold season between December and
108 March (Kalugina-Gutnik, 1975). Laboratory experiments with the unattached form of *P. crispa*
109 have shown that it has the ability to form a thick protective cuticle, then pause its development
110 for a period of up to two years, for later to resume growth once it settles in waters with optimal
111 light and temperature (Kalugina-Gutnik, 1975). This indicates the possibility for large distance
112 dispersal through drifting plants. The actual drift range of the attached form of *P. crispa* has not
113 been studied and the dispersal range of the species remains unknown.

114 Traditionally, Marine Protected Areas (MPAs) are established to protect unique features of
115 the coastal environment, and are isolated ‘reserves’ protecting local biodiversity. This concept
116 gradually evolved with the implementation of the Habitats Directive (Council Directive
117 92/43/EEC, 1992) and the creation of a EU-wide marine Natura 2000 network that offers protection
118 of important marine habitats. More recently, the concept of conserving the natural functional and
119 spatial units that form a functional marine ecosystem, the so called Cells of Ecosystem Functioning

120 (CEF), was proposed (Boero, 2015). In order for an operational network of MPAs to be established
121 within a given CEF, it needs to include all typical and important habitats within that area, preserve
122 the physical and genetic connectivity within the populations of species present, and have a
123 management and monitoring system that ensures maintenance of Good Environmental Status
124 (GES) of the ecosystem, following the principles of the EU Marine Strategy Framework Directive
125 (Council Directive 2008/56/EC, 2008) (Boero, 2015; Boero et al., 2016). Preliminary
126 investigations of the CEFs within the Western Black Sea coastal area, identified all Natura 2000
127 Special Areas of Conservation (SAC) along the Southern Bulgarian Black Sea coast and the W
128 Black Sea coastal zone of Turkey to be part of the same CEF (Boero et al., 2016). The effectiveness
129 of this network of MPAs in light of this new conservational concept has not been evaluated so far.

130 The aims of this work were 1) to identify and map infralittoral phytobenthic communities,
131 their distribution and abundance within a MPA along the Bulgarian Black Sea coast and to integrate
132 them in an web GIS platform accessible for management purposes, 2) to estimate the relative
133 contribution of these macroalgal communities to the coastal food web based on primary production
134 rates, and 3) to relate the observed spatial distribution and functioning of these habitats to the
135 proposed principles of the CEF-based MPA design and to explore the effectiveness of protection
136 of these communities, and in particular *Phyllophora crispa* -dominated communities, within the
137 network of MPAs along the SW coast of the Black Sea.

138 2. MATERIALS AND METHODS

139 2.1 Study area

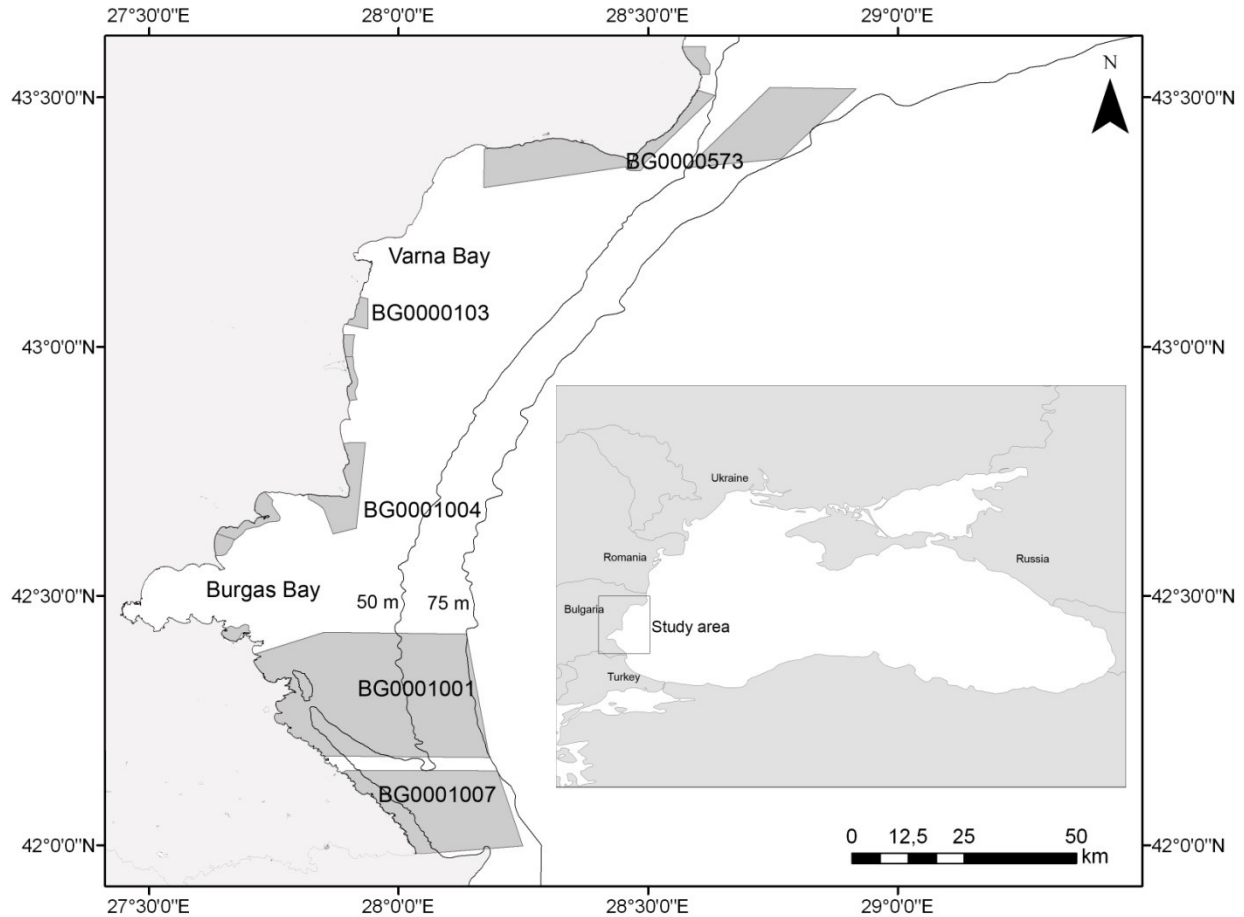
140 The study area is a Special Area of Conservation (SAC) designated under the EC Habitats
141 Directive (Ropotamo BG0001001) and is located in the southern section of the Bulgarian Black
142 Sea coast, south of the Bay of Burgas, between Cape Agalina to the north and the town of Tsarevo
143 to the south (Fig. 1, Figure 2). It covers a marine area of 881.91 km² and is the largest marine
144 protected area within the Bulgarian Black Sea Natura 2000 ecological network. Water depths are
145 down to 75 m, with the deepest areas at the eastern part of the site. The area comprises a variety of
146 marine habitats of national and European conservation importance including sandbanks, rocky
147 reefs, seagrass meadows and biogenic reefs. SAC Ropotamo includes the largest part of the national
148 area of the Habitats Directive Annex I listed habitat types 1170 'Reefs' and 1110 'Sandbanks which
149 are slightly covered by sea water all the time', with 15 % and 13 % of their total area in the

150 Bulgarian national waters respectively. This ranks the area as the most important site for
151 maintenance and restoration of favourable conservation status of those habitat types (see Todorova
152 et al., (2015) for details on habitat type 1110 mapping results).

153 **2.2 Bathymetric and terrain data sampling**

154 Bathymetry was recorded using 100 kHz multi-beam sonar system SeaBat 7111 and two
155 digital terrain models (DTM) were created, one for the open sea (from 30 to 55 m), with a resolution
156 of 3 m, and one for the coastal area (from 7-10 to 30 m), with a resolution of 2 m. In addition, a
157 DTM based on airborne LiDAR, with a resolution of 3 m and covering the shallowest areas of SAC
158 Ropotamo, was provided by the Centre of Underwater Archaeology (CUA). The DTMs were
159 combined to a single raster that was used to develop a detailed bathymetric chart with contour lines
160 with 1 m depth interval.

161 Based on the combined DTM raster, we calculated the following terrain characteristics; the
162 slope (in degrees) and the plan curvature for each cell/pixel using the ArcGIS Spatial Analyst
163 toolbar, and a 3 by 3 pixel calculation window.



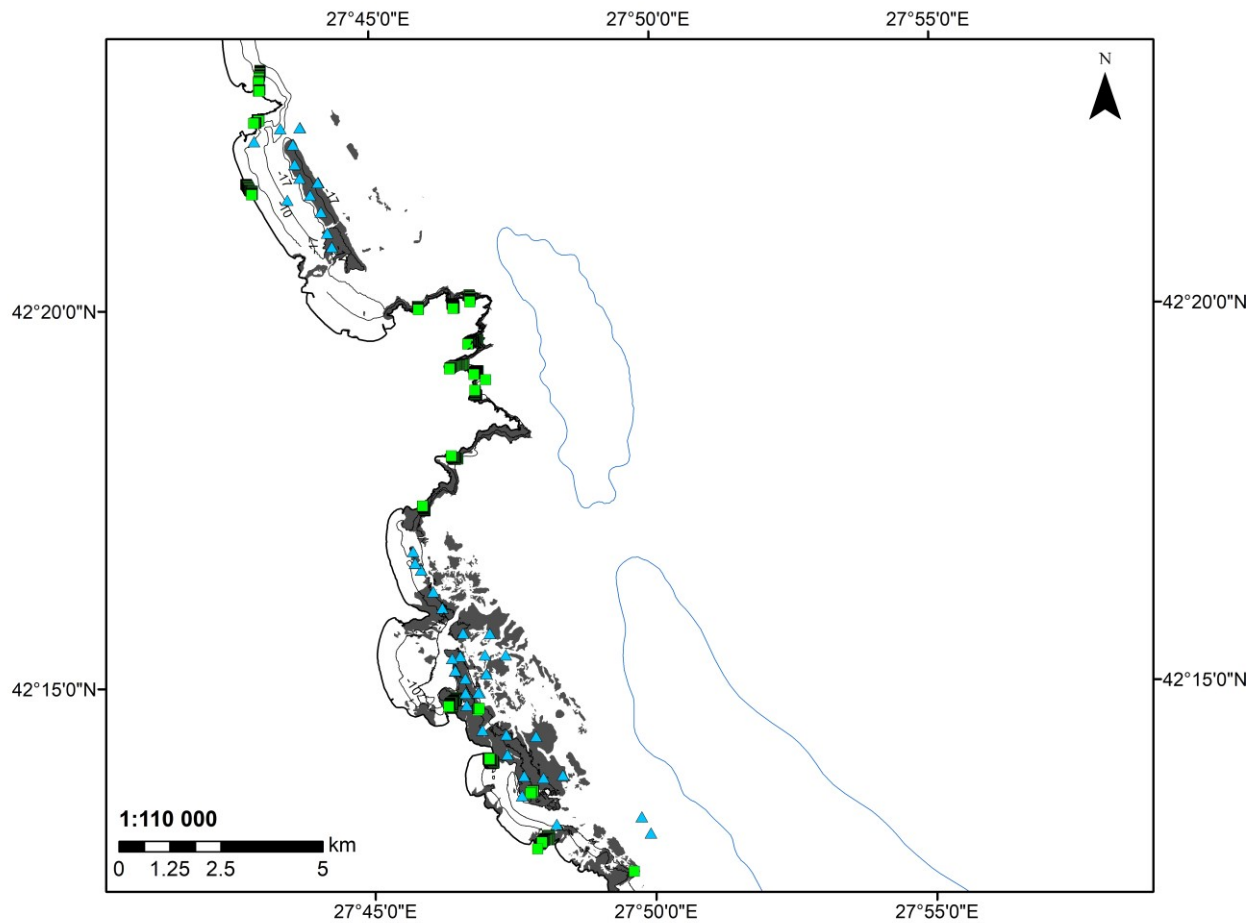
164

165 **Fig. 1** Natura 2000 Marine protected areas (MPAs) along the Bulgarian Black Sea coast. Dark grey areas represent
 166 spatial extent of the MPAs, including the pilot study area Ropotamo labelled as BG0001001. Kaliakra - BG0000573,
 167 Rodni Balkani - BG0000103, Emine- BG0001004, Strandja- BG001007. Small maritime Natura 2000 areas are not
 168 labelled with codes.

169 **2.3 Seabed sediment mapping**

170 Data on physical characteristics of seabed sediment (i.e. backscatter strength) was collected
 171 using the sonar function of the SeaBat 7111 multi-beam, processed with SonarWiz Map software.
 172 To achieve more detailed data, a mosaic of backscatter strength was also created using “snippets”
 173 of the sonar system in a 16-Bit grey colour scheme. Multibeam system co-registered water depth
 174 and reflectivity at the same time, thus the two types of data were geographically referenced
 175 together, ensuring that extracted backscatter data were correctly situated on the seafloor. A high
 176 resolution sonar mosaic in a 16-Bit rusty colour scheme of the shallow most area south of the town
 177 Kiten (provided by the CUA) was also used and combined with the other data. Areas with similar

178 backscatter characteristics were delineated in a GIS (Geographical Informations System,
179 ArcGIS®) to identify acoustic characteristics that presumably represent different lithological
180 substrate types of seabed sediments. For verification and assigning a lithological substrate types to
181 each area with similar backscatter characteristics, over 100 sediment samples taken by Van Veen
182 grab were analysed.



183
184 **Figure 2** Map of the spatial extent of the surveyed coastal zone of the pilot study area Ropotamo (BG0001001).
185 Contour lines indicate isobaths (10, 17 and 50 m depth). Rocky substrates are colored in black, blue triangles represent
186 drop camera survey points, green rectangles - scuba divers transect locations.

187 **2.4 Benthic communities mapping**

188 Georeferenced digital photographs were used to collect spatial data on the presence and
189 abundance of the dominant benthic communities, using the methodological guidelines of
190 Roelfsema and Phinn (2009) and the survey methods by Berov (2013) and Berov et al. (2016).

191 Coastal rocky reefs down to ~20 m were surveyed by scuba divers along depth transects covering
192 the whole depth range of distribution of macroalgae (Figure 2). The transects were placed based
193 on previous data and local knowledge of the presence of rocky substrates in the area (Todorova et
194 al., 2012). In order to achieve a uniform coverage of all rocky shores within the study area, transects
195 were placed at approximately 500 m distances from each other in areas with coastal reefs. At each
196 transect site scuba divers started at the deeper end of the rocky reefs (usually at around 15-18 m)
197 and moved along the bottom towards the coast, taking photographs every 2-5 m.

198 Photographs were taken with a 14.7 MP Canon G10 camera in a Ikelite box equipped with an
199 Ikelite DS-160 strobe and a WD-4 wide angle lens convertor, mounted on a PVC frame (designed
200 by Preskitt et al. 2004) or on a monopod. Images were taken from a distance of 90 cm and covered,
201 due to the wide angle (equivalent focal distance of 6,1 mm), a 0.623 m² of the substrate with a
202 resolution of 2321.5 pixels per cm², giving sufficient details for identification of typical benthic
203 species (Berov et al., 2016). Images were georeferenced with the GPS Photo Link (GeoSpatial
204 Experts, Inc), using time stamp synchronization with the GPS track of a Garmin GPS 76 CS
205 mounted on a surface buoy attached with a rope to the camera. The buoy was positioned as
206 vertically as possible above the dive team, minimizing the inaccuracy of the coordinates of the
207 bottom position. The depth of each photo sample was determined based on the depth profile log of
208 the diving computer of the diver taking the photos (Aladin Prime, Suunto Vyper) using an MS
209 Excel algorithm for matching diving computer log data with photo samples. The offshore infra-
210 and circalittoral reefs within the study area were surveyed using a drop camera. A grid of 500 by
211 500 meters was established for the reef areas, and at least one photo sample per quadrant was taken
212 with a 14 megapixel GoPro HD2 digital photo camera mounted on a PVC frame and equipped with
213 underwater lightning system and a depth gauge. These photos were georeferenced with GPS Photo
214 Link software, using time stamp synchronization with the GPS track of the survey vessel.
215 Additional scuba dives were performed in areas where phytobenthic communities of interest were
216 identified with the drop camera.

217 Representative samples for taxonomical analysis and biomass estimation of the present
218 macroalgal species were also taken. Quadrants (size 20 by 20 cm) were used to collect typical
219 phytobenthic communities from representative macroalgal assemblages along the study transects.
220 Samples were placed in labelled and sealed plastic bags, stored in a cooler box and transported to

221 the lab for further analysis. Macroalgal species were identified to species level using regional
222 species identification guides (Dimitrova-Konaklieva, 2000; Zinova, 1967). Members of the
223 Cladophora and Ulva genera were identified following Brodie et al. (2007). The latest species
224 names and classification were checked in Algaebase (Guiry and Guiry, 2017). The biomass and
225 projected cover of species was measured.

226 Two sampling campaigns were carried out - in June-July 2013 and June-July 2014. The
227 northern section of the study area was surveyed in 2013, while the area south of Cape Maslen Nos
228 was surveyed in 2014. During the surveys a total of 19 dive transects were performed, sampling
229 in total 1440 photos and 22 macroalgal samples, in addition to 74 photo samples collected during
230 4 drop camera surveys.

231 **2.5 Benthic community analysis**

232 The images were analysed with the CPCE 3.6 software using the point intercept method
233 (Kohler and Gill, 2006). On each image the presence or absence of the dominant macroalgal and
234 zoobenthic species was determined for 100 points, selected randomly using a random stratified
235 distribution within a 10 by 10 grid (Berov et al., 2016). The dominant species, the type of substrate,
236 and the presence of typical topographical features in each photo were observed and recorded. The
237 presence of phytobenthic habitats in each photo was also categorized, based on the presence of
238 dominant and habitat-specific species in each photo, and data from the macroalgal samples.

239 Data on coverage and grouping of the benthic species was analysed using multivariate
240 methods in Primer 6.0 (Anderson et al., 2008). The grouping of samples was analysed and
241 visualized in MDS plots based on the Bray-Curtis similarity matrix of the data using data on
242 substrate type, substrate characteristics and depth. Contributions of macroalgal species to the
243 differences between the outlined communities were determined using one-level SIMPER analysis
244 and a 20% similarity cut-off from the Bray-Curtis analysis as a factor.

245 Macroalgal samples collected during scuba diving (this survey and Berov, 2013) were used
246 to calculate the average dry biomass (g. m² D.W.) of typical macroalgal species and communities.
247 The overall biomass of the phytobenthic habitats was calculated from the estimated area of
248 distribution of these habitats. Estimations of macroalgal communities primary production were

249 based on Greze (1979). Dissolved organic matter release estimations were based on data published
250 by Khailov and Burlakova (1969).

251 **2.6 Geographical Information System work and species distribution modelling**

252 Georeferenced data from each photo sample was integrated into ArcGIS together with data on
253 depth, dominant species, habitat types and substrate types (from the geophysical mapping). The
254 substrate and depth preferences of the identified macroalgal communities based on the multivariate
255 analysis were used to create of polygons of the communities' distribution within the area. For that
256 purpose, polygons of hard substrates delineated from the seabed sediment mapping, were cut along
257 isobaths lines, thus creating polygons of the observed depth range of distribution of these identified
258 communities. The generated shapefiles were formatted and labelled following the hierarchical
259 scheme of organization of georeferenced data of Grande et al. (2015), and were then included in
260 the WEB-GIS portal of the Coconet project (<http://coconetgis.ismar.cnr.it>).

261 Despite the availability of detailed description of the seafloor morphology preferences of
262 the studied macroalgal species, the lack of spatial data on presence of vertical outcrops and of
263 *Ostrea edulis* biogenic reefs, the only feasible way to map the distribution of the lower-infralittoral
264 macroalgal communities was to group all the identified lower-infralittoral macroalgal assemblages
265 as one community. Example maps of the resulting habitat distribution within the study area, of both
266 the upper and lower infralittoral zone as well as the circalittoral zone, based on the identified depth
267 zonation preferences, is outlined in the supplementary material. Interactive maps of the results of
268 this mapping can also be explored in the in the GIS data base of the Coconet project (available at
269 <http://gismarblack.bo.ismar.cnr.it:8080/cocowebpp.html>).

270 The relationship between geomorphology and species occurrence was analyzed by applying
271 the Species Distribution Modelling tool (SDM) Maxent 3.3 software package (Phillips et al., 2006)
272 using presence data of the identified dominant macroalgal communities and of lower-infralittoral
273 species of conservational importance (*Phyllophora crispa* (Hudson) P.S.Dixon, *Zanardinia typus*
274 (Nardo) G. Furnari, *Apoglossum ruscifolium* (Turner) J. Ag.). The predictor variables were depth
275 (2 m resolution), seabed substrate type (2 m resolution, categorical variable – hard or soft bottom),
276 terrain slope, and terrain curvature (the two latter with a 6 m resolution). Modelling accuracy was

277 evaluated using the receiver operating characteristic (ROC) area under the curve (AUC) measure
278 (Phillips et al., 2006; Reiss et al., 2011).

279 **3. RESULTS**

280 **3.1 Substrate types and geology**

281 The geophysical mapping showed that the seafloor within the study area has a rather
282 complex and distinct morphology. Within the coastal area down to water depths of 30-35 m, the
283 seafloor is dominated by scattered rocky reefs built up by volcanic rocks. The reefs have a general
284 orientation in NW-SE direction eastward and at depths deeper than 30-35 m the reefs are buried by
285 soft sediments. A deep coastal depression valley is situated seaward of the reef structures. Its
286 midstream is well delineated by the 50 m isobath and is oriented in NNW-SEE direction along the
287 general trend of the coastline. The valley shallows and widens northward of Cape Korakya. Further
288 offshore it follows the accumulative plain of the central shelf where the tongue-like end of the so-
289 called Emine accumulative bar occurs. The bar has steep Western and a gentle Eastern board
290 spreading down to 60-65 m water depth with crests as shallow as 37 m. A specific
291 geomorphological feature of the rocky reefs that were surveyed was the presence of vertical
292 outcrops on both the biogenic type substrates and on the bedrock types (see supplementary material
293 for photos). These vertical outcrops are of height between 10-20 and 50 cm and were found
294 throughout the whole study area.

295 **3.2 Macroalgal species diversity and vertical zonation**

296 In total 18 species of macroalgae were identified in the samples from the lower infralittoral
297 rocky bottoms in the area (Table 1) i.e. at depth below the lower distribution of *Cystoseira barbata*
298 (see Berov et al.(2012) for detailed species list of *Cystoseira*-dominated communities in the same
299 area). Rhodophyta dominates with a total of 11 species, followed by Chlorophyta with 5 species
300 and Ochrophyta with just 2 species.

301 In terms of morphology and habitat preferences, the sampled *Phyllophora crispa*
302 corresponded to the *Phyllophora nervosa* var. *nervosa* f. *breviarticulata* Kalugina as described by
303 Kalugina-Gutnik (1975). In NW Black Sea this variety and form of the species is typically attached
304 to hard substrates at depths between 7 and 25 m, has a bushy, branching morphology reaching sizes
305 up to 10-15 cm.

306 **Table 1** Macroalgal species from the lower infralittoral samples collected in the Ropotamo (BG0001001) study area
307 in June-July 2013 and 2014

Rhodophyta

Gelidium crinale (Hare ex Turner) Gaillon
Gelidium spinosum (Gmelin) Silva
Parviphycus antipai (Celan) Santelices
Phyllophora crispa (Hudson) P.S.Dixon
Lomentaria clavellosa (Lightfoot exTurner) Gaillon
Callithamnion corymbosum (Smith) Lyngbye
Ceramium pedicellatum C. Agardh
Ceramium diaphanum (Lightfoot) Roth
Apoglossum ruscifolium (Turner) J. Agardh
Polysiphonia subulifera (C. Agardh) Harvey
Polysiphonia elongata (Hudon) Sprengel

Ochrophyta

Zanardinia typus (Nardo) P.C.Silva
Cladostephus spongiosum (Hudson) C.Agardh

Chlorophyta

Chaetomorpha aerea (Dillwyn) Kützing
Chaetomorpha linum (O. F. Müller) Kützing
Cladophora albida (Nees) Kützing
Cladophora coelothrix Kützing
Ulva rigida C. Agardh

308 The upper infralittoral belt of the study area (0.5-1 m depth) was populated by *Mytilus*
309 *galloprovincialis* and/or bare rocks, overgrown by *Ceramium virgatum*, *Gelidium spinosum* and
310 *Gelidium crinale*, with small patches of *Corallina mediterranea*, *Ulva linza*, *U. intestinalis* and
311 *Chaetomorpha aerea* in more sheltered S-SW facing coast. At depths between 1 and 3-4 m the
312 upper-infralittoral was dominated by *Cystoseira bosphorica* Sauv. communities, followed by
313 *Cystoseira barbata* Bory communities at depths between 3-5 and 7-10 m. The latter had a
314 shallower upper limit of 1 m S-SW facing sheltered coastlines (See Berov (2013) for details). A
315 transitional zone with presence of both *C. barbata* and lower infralittoral macroalgal assemblages
316 of red and brown macroalgae was observed in the depth range between 7 and 10 m. This low depth
317 limit of distribution of the perennial *C. barbata* marked the depth limit between the upper and
318 lower infralittoral, as defined by Peres and Picard (1964).

319 Rocky reefs below the lower depth limit of distribution of *Cystoseira barbata* were
320 dominated by a mixture of macroalgal assemblages, with abundant presence of the sciaphylic red
321 and brown macroalgae - *Phyllophora crispa*, *Zanardinia typus*, *Apoglossum ruscifolium* as well as
322 the widely adaptive turf-forming green macroalgae *Cladophora albida* and *Cladophora coelothrix*,
323 and the red macroalgae *Gelidium spinosum*, and *Gelidium crinale*. The depth limit of the lower
324 infralittoral rocky bottom zone formed by these assemblages was observed to be 15-18 m,
325 depending on local conditions and substrate availability. Below 15-18 m, which marked the upper
326 depth limit of the circalittoral, the only prominent macroalgal species was the red *Antithamnion*
327 *cruciatum*. The described upper-lower infralittoral and lower infralittoral-circalittoral depth limits
328 are significantly shallower than those noted during the ‘pre-eutrophication’ period in the Black Sea
329 in the 1960s and the 1970s, when *Cystoseira barbata* reached down to 20-25 m along the Bulgarian
330 coast, and *Phyllophora crispa* on rocky reefs – reached 25-30 m (Dimitrova-Konaklieva, 2000;
331 Kalugina-Gutnik, 1975).

332 The black mussel *Mytilus galloprovincialis* was the most typical hard-bottom
333 macrozoobenthic species in the study area. It was found growing on hard substrates at all depths,
334 with preferences for vertical rocks on exposed coasts. The whack snail *Rapana venosa*
335 (Valenciennes) that preys preferentially on *M. galloprovincialis* was also abundant throughout the
336 study area, creating some local zones with no black mussels present (‘barrens’). No live *Ostrea*
337 *edulis* oysters were found within the surveyed area, confirming the observations of Todorova et al.
338 (2009) of a complete disappearance of live specimens of the species from this area of the Black
339 Sea coast.

340 **3.3 Community structure**

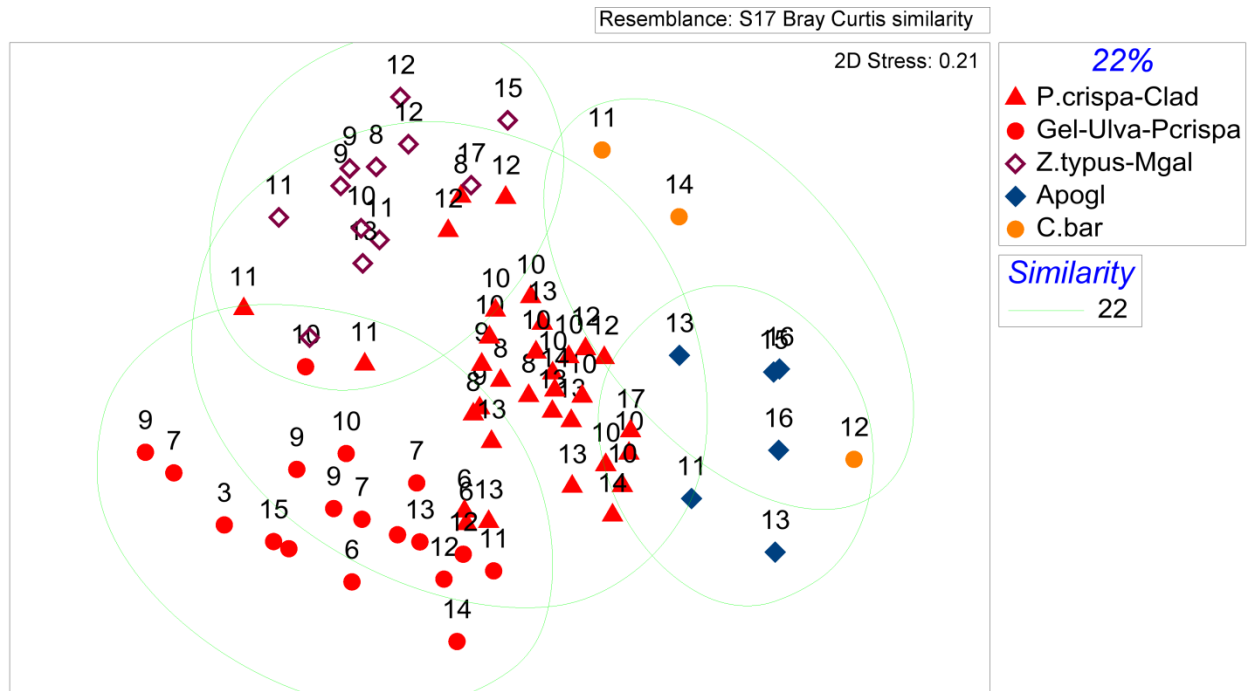
341 Several lower infralittoral benthic communities were outlined in the MDS plot based on the
342 photo samples (Fig. 3, Fig. 4, Fig. 5). Five typical groupings of species were determined (22%
343 similarity factor, SIMPER analysis, Table 2). These included one assemblage dominated by 1)
344 *Phyllophora crispa* with presence of *Cladophora albida*, *Z. typus*, *A. ruscifolium*, 2) an assemblage
345 dominated by *Z. typus*, 3) monospecific communities of *A. ruscifolium*, 4) as well as a *Gelidium*
346 spp. – *Ulva rigida* assemblage with occasional presence of *P. crispa* and *P. elongata.*, and 5) single
347 *C. barbata* individuals with epiphytes. Despite the relatively high 2D stress in the MDS plots
348 (0.21), the observed grouping of samples is relevant for the evaluation of the community structure,

349 as the distinct groups are also outlined as separate clusters in the cladogram of the same similarity
 350 matrix (visible as outlines in the MDS plots) (Clarke and Warwick, 2001).

351 Table 2 SIMPER analysis of benthic communities identified by multivariate analysis of the species coverage in photo
 352 samples within the SAC Ropotamo in the Black Sea, Bulgaria, with values of the species average coverage (av. abund),
 353 average similarity (av.sim) and cumulative percentage contribution to the community group is provided (cum.%).

Species	av.abund	av.sim	cum.%
Group <i>P. crispa</i>-Clad Average similarity: 46.23			
<i>Phyllophora crispa</i>	22.34	27.06	58.54
<i>Cladophora</i> spp.	12.19	10.85	82
<i>Zanardinia typus</i>	6.84	5.2	93.24
<i>Apoglossum ruscifolium</i>	3.58	1.44	96.36
Group <i>Z. typus</i>-Mgal Average similarity: 48.10			
<i>Zanardinia typus</i>	34.32	43.3	90.03
<i>Mytilus galloprovincialis</i>	9.46	2.09	94.37
<i>Polysiphonia elongata</i>	2.54	0.82	96.07
Group Gel-Ulva-<i>P. crispa</i> Average similarity: 46.61			
<i>Gelidium</i> spp.	26.38	27.14	58.23
<i>Ulva rigida</i>	18.24	13.66	87.54
<i>Phyllophora crispa</i>	4.7	2.47	92.85
<i>Polysiphonia elongata</i>	4.61	1.34	95.73
Group Apogl Average similarity: 64.12			
<i>Apoglossum ruscifolium</i>	36.98	61.58	96.04
Group Cbar Average similarity: 70.40			
<i>Cystoseira barbata</i>	51.34	68.17	96.83

354



355
 356 **Fig. 3** MDS plot of the Bray-Curtis similarity matrix of the species community structure of typical phytobenthic
 357 communities (22% similarity) within the infralittoral zone in an MPA in the Black Sea, Bulgaria, based on photo
 358 sample analysis. The samples are labelled by the sampling depth. The used acronyms are described in Table 2.

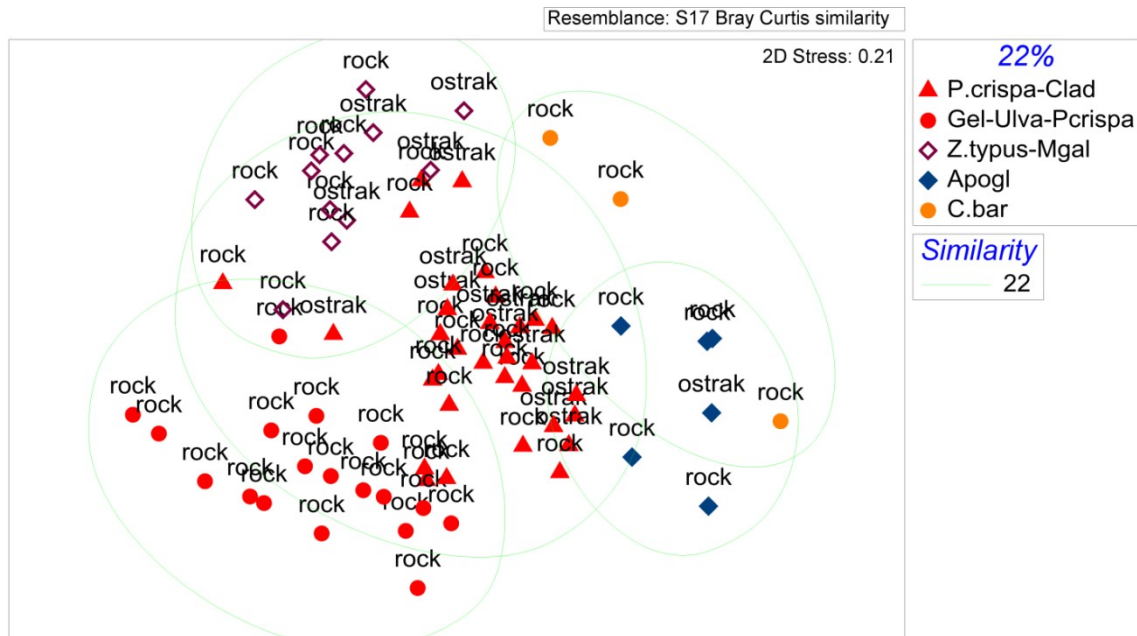
359
 360
 361 The *P. crispera*-Clad. macroalgal assemblage has some of the elements of the association
 362 ‘(*Cystoseira barbata*)- *Phyllophora nervosa*- *Cladophora dalmatica*’ described along the N coast
 363 of the Black Sea in Russia and Ukraine by Kalugina-Gutnik (1975), but with the notable absence
 364 of many of the typical macroalgal species for this association such as *Nereia filiformis*, *Codium*
 365 *vermiliaria*, *Asperococcus bullosus*, *Nitohyllum punctatum*, *Jania rubens* and others. It could be
 366 considered a new, previously undescribed plant association, typical for the SW Black Sea.

368 3.4 Lower infralittoral phytobenthic habitats preferences for substrate types

369 The combination of data from geological mapping and classification of substrates in major
 370 categories with biological sampling did not show any visible patterns of association of the

371 identified macroalgal communities with specific hard-bottom types. All distinct groups of
372 infralittoral macroalgae were found on the substrate types ‘coastal bedrock’ and ‘reef’. The MDS
373 grouping of samples and the visual description of substrate types from the photo samples showed
374 a certain preference of *Phyllophora crispa* towards biogenic reefs –‘ostrak’, but also with presence
375 on other types of hard substrates (Fig. 4, Fig. 5). The other identified lower infralittoral macroalgal
376 communities were found on both biogenic reefs and bedrocks, with no apparent preference. Within
377 these substrates, *P. crispa* preferentially occurred at sites where vertical outcrops were present (Fig.
378 5). Indeed, within the app. 1 m² of the seafloor that was photographed for each photo sample, *P.*
379 *crispa* typically occurred on the edges of these outcrops or on their vertical surface (see
380 supplementary materials). The species was rarely found on the flat horizontal areas of the rocks,
381 which were typically colonized by *Zanardinia typus*, *Cladophora* spp, *Gelidium spinosum* and
382 *Apoglossum ruscifolium*.

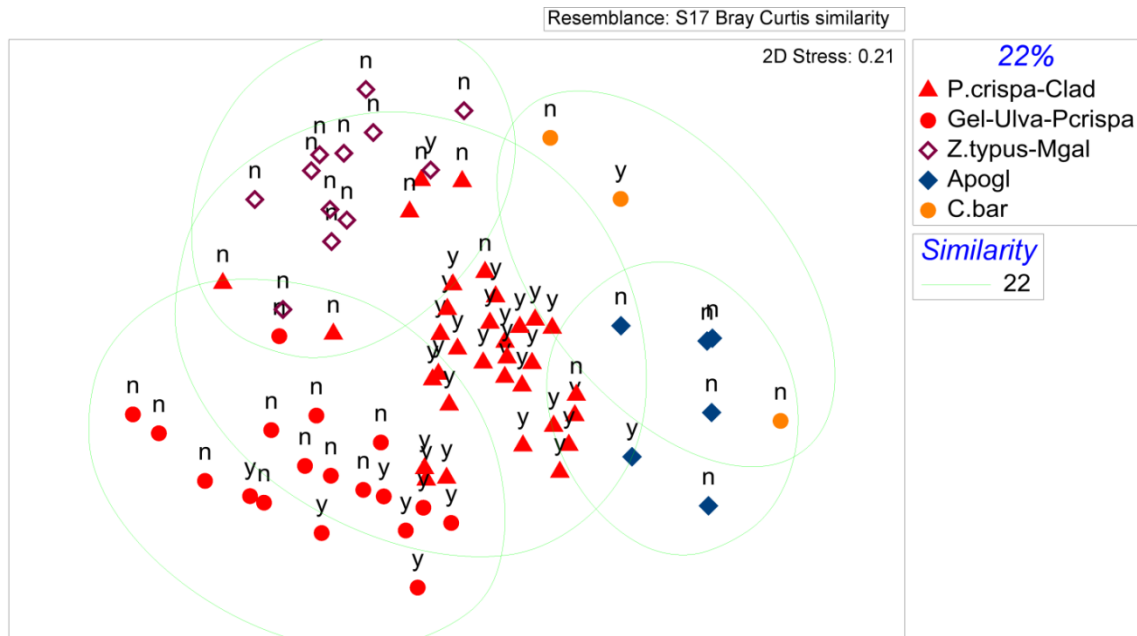
383 *Z. typus* was present in higher quantities in zones without vertical outcrops, and often on
384 ‘ostrak’ biogenic reefs (Fig. 4, Fig. 5). It formed densely covered patches, often overgrowing the
385 shells of *M. galloprovincialis* mussels. In sites where it was not the dominant algal species, it was
386 often present as a secondary species, in particular in *P. crispa* dominated areas. *A. ruscifolium* was
387 present in both zones with and without vertical outcrops, most often in association with *P. crispa*.
388 The *Gelidium – Ulva - P. crispa* community occurred throughout the area on different substrate
389 types and consisted of dense patches of the two former species interspersed with some *P. crispa* in
390 sites where vertical outcrops were available.



391
 392 **Fig. 4** MDS plot of the Bray-Curtis similarity matrix of the species community structure of typical phytobenthic
 393 communities (22% similarity) within the infralittoral zone in an MPA in the Black Sea, Bulgaria, based on photo
 394 sample analysis. The substrate type is also marked - rock; ostrak- *Ostrea edulis* biogenic reefs. The used acronyms
 395 are described in Table 2.

396 Summary statistics of the habitat preferences of the four typical lower infralittoral
 397 macroalgal communities outlined in the MDS analysis is presented in the supplementary materials.

398



399
 400 **Fig. 5** MDS plot of the Bray-Curtis similarity matrix of the species community structure of typical phytobenthic
 401 communities (22% similarity) within the infralittoral zone in an MPA in the Black Sea, Bulgaria, based on photo
 402 sample analysis. The presence (y=yes) and absence (n=no) of vertical rocky outcrops is also marked. The used acronyms
 403 are described in Table 2.

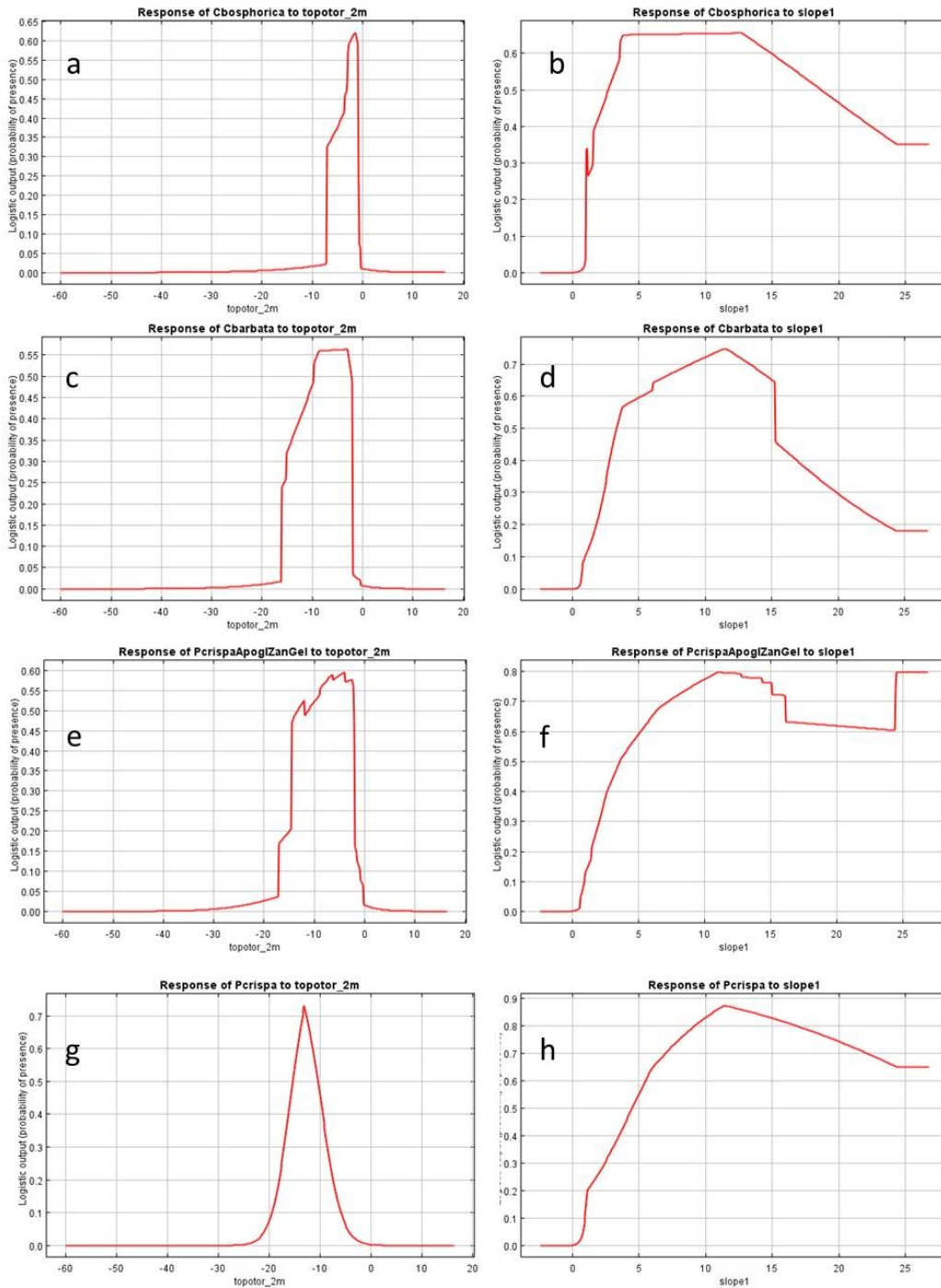
404 The Maxent distribution models of the macroalgal communities identified by the SIMPER
 405 analysis of the photo surveys data (Table 2) and of the three lower-infralittoral macroalgae of
 406 conservational interest had excellent predictive accuracy (AUC between 0.973 and 0.992, Table
 407 3). The Species Distribution Model (SDM) confirmed a higher probability of observing the
 408 macroalgal communities and species on rocky reefs with distinct and different slope, substrate type
 409 and curvature (Table 3, Fig. 6, Fig. 7). Considering the relative percentage contribution of the
 410 modelled environmental variables to the probability for their presence, the substrate slope was the
 411 most important structuring factor (36.2 – 61.6 % contribution), followed by depth (23.5 – 34.4 %
 412 contribution) and substrate type (11.2- 28.2 % contribution). The terrain curvature, at the used
 413 spatial scale (6x6 m), had a minor contribution (0.2 – 2.2 %).

414 The Maxent results suggest that the current realised niche of the macroalgal communities
 415 within the depth ranges identified in the multivariate analysis of the sample data differ with respect
 416 to substrate type and terrain slope. The upper infralittoral *Cystoseira bosphorica* communities
 417 were most likely to occur at depths between 0-3 m (probability of occurrence >0.5), whereas those
 418 of *Cystoseira barbata* communities – in a slightly wider depth range – between 1 and 10 m (Fig.

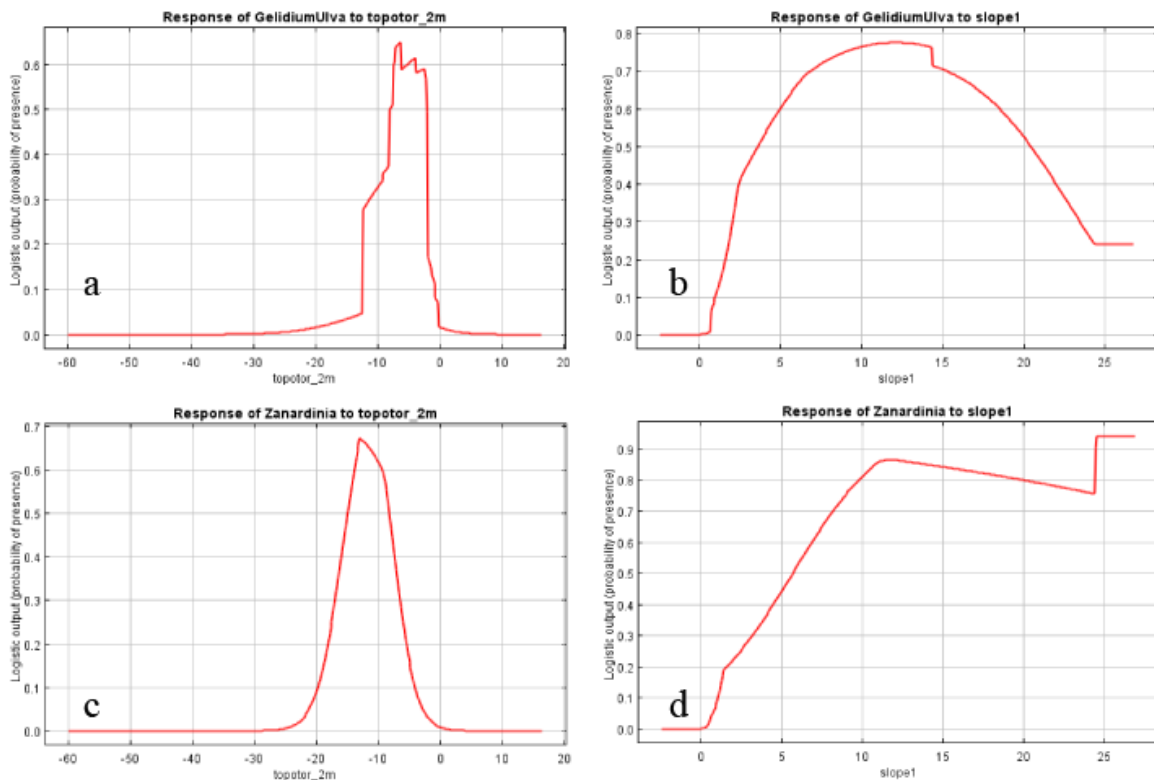
419 6). Both *Cystoseira* communities were most likely to occur on sloping terrain between 3 and 18
 420 degrees (probability of occurrence >0.5), which is similar to previous findings of the these species
 421 on terrain with steepness less than 15-20 degrees, Berov (2013). The Maxent model results also
 422 indicate differences in the realized niches of the lower-infralittoral communities in terms of depth
 423 and slope. The *Gelidium* spp. - *Ulva rigida* assemblage occurred mostly in the 2-10 m range, while
 424 *Phyllophora crispa* and *Zanardinia typus* were more likely to occur at depths below 10 m (10-15
 425 m for *P. crispa*, 8-15 m for *Z. typus*, probability of occurrence >0.5). There were also some
 426 differences in slope preferences ,with the assemblage *Gelidium* spp. -*U. rigida* preferably
 427 occupying substrates with 3-20 degrees slope, and the species *P. crispa* and *Z. typus* both found on
 428 terrains with slope between 5-28 degrees (probability of occurrence >0.5) (Fig. 7). Given the
 429 resolution of the slope raster (6 by 6 m), the higher probability of occurrence of *Z. typus* and *P.*
 430 *crispa* on substrates with higher slope is an additional confirmation of their apparent preference for
 431 ‘ostrak’ biogenic reefs. These structures were typically elevated above the surrounding terrain and
 432 have vertical walls. This was further confirmed by the higher probability of occurrence of the two
 433 species in cells with highly negative curvature values (-7 to -1 for *P. crispa* and -6 to -1 for *Z. typus*,
 434 not shown).

435 Table 3 Estimates of modelling accuracy (Area Under the Curve – AUC), and relative percentage contributions of the
 436 environmental variables in the Maxent models of selected macroalgal habitats and species. Terrain slope and curvature
 437 are calculated from a DTM with 2 m resolution.

Community / Species	Presence records	AUC	Slope	Depth	Substrate type	Curvature
<i>Cystoseira bosporica</i>	149	0.987	36.7	34.4	28.7	0.2
<i>Cystoseira barbata</i>	314	0.973	61.9	26.2	10.9	1
<i>Phyllophora crispa</i> , <i>Apoglossum ruscifolium</i> , <i>Gelidium spinosum</i> , <i>Zanardinia typus</i>	185	0.975	57.8	24.8	16.6	0.8
<i>Gelidium</i> spp. - <i>Ulva rigida</i>	139	0.984	56.5	30.6	11.2	1.7
<i>Phyllophora crispa</i>	16	0.993	49.4	29.5	18.9	2.2
<i>Zanardinia typus</i>	34	0.987	59	23.5	17.2	0.2



439
 440 **Fig. 6** The individual response curves of the environmental variables depth (left column) and slope (right column) in
 441 the Maxent models of presence of selected macroalgal associations and species (a, b –*Cystoseira bosporica*
 442 community; c, d *Cystoseira barbata* f. *hoppii* community; e, f - *Phyllophora crispa*, *Apoglossum ruscifolium*, *Gelidium*
 443 *spinosum*, *Zanardinia typus* mixed assemblages g, h - *Phyllophora crispa* individual species



444
 445 **Fig. 7** The individual response curves of the environmental variables depth (left column) and slope (right column) in
 446 the Maxent models of presence of selected macroalgal associations and species (a, b – *Gelidium* spp. - *Ulva rigida*
 447 assemblage; c, d – *Zanardinia typus* individual species)

448 **3.5 Habitat area, total biomass, productivity and DOM release**

449 Based on literature data, the biomass samples and the produced habitat maps, the different
 450 habitats area, total biomass, and total primary production and DOM release were estimated (Table
 451 4). In terms of area coverage, the infralittoral area of the study zone was dominated by the lower
 452 infralittoral macroalgal communities (367.8 ha), followed by the upper infralittoral communities
 453 of *C. bosporica* and those of *C. barbata*. *C. bosporica* communities were calculated to have the
 454 highest standing biomass, followed by *C. barbata*, and the lower infralittoral communities (one
 455 order of magnitude lower biomass). The overall biomass of macroalgae in the study area was app.
 456 $5.62 \cdot 10^9$ g DW, with a calculated total primary productivity of $4.87 \cdot 10^{10}$ g.yr⁻¹, responsible for a
 457 release of over $1.86 \cdot 10^{10}$ g.yr⁻¹ DOM. *C. barbata* communities had the highest share of the
 458 estimated primary production and DOM release, followed by *C. bosporica*, and the lower
 459 infralittoral macroalgal communities.

460 **Table 4** Total area coverage, standing and total biomass, primary production rate and estimated total primary
 461 production, and total DOM release by macroalgal communities in the study area BG0001001 Ropotamo-Kiten

Macroalgal community	Area [m ²]	Standing biomass [g . m ² DW]	Total biomass [g DW]	Primary Production rate [g.m ² .yr ⁻¹] (Greze, 1979)	Total primary production rate [g.yr ⁻¹]	total DOM release [g.yr ⁻¹] (Khailov,1977)
<i>Cystoseira bosporica</i>	1 928 000	1158.03	2.23*10 ⁹	8.00*10 ³	1.54*10 ¹⁰	5.89*10 ⁹
<i>Cystoseira barbata</i>	1 553 000	659.86	1.02*10 ⁹	2.00*10 ⁴	3.11*10 ¹⁰	1.19*10 ¹⁰
<i>Cystoseira barbata</i> and <i>Phyllophora crispa</i> , <i>Apoglossum ruscifolium</i> , <i>Gelidium spinosum</i> , <i>Zanardinia typus</i> mixed assemblage	1 700 000	75.94	1.29*10 ⁸	8.00*10 ²	1.36*10 ⁹	5.20*10 ⁸
<i>Phyllophora crispa</i> , <i>Apoglossum ruscifolium</i> , <i>Gelidium spinosum</i> , <i>Zanardinia typus</i> mixed assemblage	3 678 000	138.40	1.29*10 ⁸	6.10*10 ²	8.48*10 ⁸	3.24*10 ⁸
Circalittoral rocks and other hard substrates	6 475 000	-	-	-	-	-
Total	15 334 000	-	5.62*10⁹	-	4.87*10¹⁰	1.86*10¹⁰

462

463 It should be noted that the biomass estimates are based on summer samples(June-July),
 464 collected in the period of seasonally high biomass of macroalgal communities in the Black Sea
 465 (Kalugina-Gutnik, 1975). Seasonal studies of the dynamics of the *Cystoseira bosporica* upper
 466 infralittoral communities show a 30-77% decrease of biomass between the season of maximum
 467 (May) and minimum (September) development (Kalugina-Gutnik, 1975; Berov, 2013;). This
 468 decrease should result in a corresponding change in primary production and DOM release
 469 estimates, and total annual production estimates. Nevertheless, these estimates give a good first
 470 impression of the importance of the studied phytobenthic communities with respect to productivity,
 471 influence to food webs and ecosystem services within the coastal zone in the Black Sea.

472 4. Discussion

473 4.1 Structuring factors

474 The descriptive multivariate statistical analysis and the SDM revealed similar depth ranges
475 of the identified macroalgal communities. However, the Maxent models indicated a more detailed
476 response of the involved species to variation in slope and substrate type and different realized
477 niches of these communities within the same depth ranges. The SDM showed that *Phyllophora*
478 *crispa* and *Zanardinia typus* in the lower infralittoral zone have a higher probability of occurrence
479 on steeper slopes than *Gelidium* spp. and *Ulva rigida*. This response can be attributed to various
480 biological properties, such as the possible preference of the propagules of *P. crispa* and *Z. typus* to
481 settle on steep terrain with rough textures such as the ‘ostrak’ biogenic reefs and their vertical
482 outcrops. Similar observations are presented by Simakova (2011, 2009) who in a survey of the
483 structure of phytobenthic communities in the infralittoral of the Caucasian coast of the Black Sea
484 found *P. crispa* growing predominantly on top of ridges and their vertical walls. The absence of
485 sediment cover on these inclined and vertical substrates can also play a role in forming these
486 realized niches, as many species of macroalgae are unable to settle on substrates covered with
487 sediments (Airoldi, 2003; Airoldi and Cinelli, 1997; Irving et al., 2009). Contrary to what Bonifazi
488 et al. (2017) observed in the Central Mediterranean, the *P. crispa* algal turfs in our study area do
489 not accumulate sediments within their branches.

490 The relatively high importance of depth as a structuring factor in the SDM can be attributed
491 to the change in light quantities with depth and the adaptation of macroalgae to different light
492 environments (Ballesteros, 1991; Krause-Jensen et al., 2008, 2007; Markager and Sand-Jensen,
493 1992). *Cystoseira barbata* is highly adaptive to different levels of illumination, as it occurs as
494 shallow as 1 m, where the average yearly PAR is between 60 and 70% of the surface PAR, down
495 to 10 m, which has an average seasonal 10% PAR_{surf}. (Berov, 2013). *Phyllophora crispa* on the
496 other hand, is adapted to low-light conditions and occurs in a much narrower range of average
497 yearly PAR_{surf}. (between 10 and 7 %). As *P. crispa* is the deepest occurring perennial macroalgae
498 in this area of the Black Sea, this lower depth limit of distribution can be considered as the border
499 between the lower infralittoral- and the circalittoral in the area.

500 Depth can also be considered as an indirect indication of the strength of physical impacts
501 from wave action, which play an essential structuring role in infralittoral macroalgal communities

502 in temperate seas (Hurd et al., 1996; Kiirikki, 1996; Graham, 1997; Bäck and Ruuskanen, 2000;
503 Eriksson and Bergstrom, 2005; Bekkby et al., 2009; Spatharis et al., 2011; Rinde et al., 2014). The
504 degree of wave exposure is the main factor determining the upper distribution limit of the two
505 dominant brown macroalgal species along the Black Sea coast (Kalugina-Gutnik, 1975). The
506 dominant presence of *Cystoseira bosphorica* in the shallow areas of the upper infralittoral (1-4 m
507 depths), especially in the most exposed and open coastal zones, can be explained by the adaptation
508 of the species to resist direct wave impact by having a very robust and flexible thalli and being
509 strongly attached to the substrate by the basal discs (Kalugina-Gutnik, 1975). The upper
510 distribution limit of *Phyllophora crispa* in the area can also be related to the depth with optimal
511 and maximum sea water temperatures for its growth and survival, as described by Minicheva et al.
512 (2013) in the NW Black Sea, where the species preferentially grows at depths below the seasonal
513 summer thermocline.

514 **4.2 Long-term change in distribution**

515 The *Phyllophora crispa* community in our study area had a depth distribution similar to that in
516 the lower infralittoral communities in the N Black Sea (Simakova, 2011), unfortunately no
517 historical data exist on the distribution of this community along the SW Black Sea coast during the
518 ‘pre-eutrophication’ period before the 1980s. Considering the recent significant reduction in the
519 lower depth distribution of the *Cystoseira* communities along the S Bulgarian Black Sea coast –
520 from 20-25 m in the 1970s to 10-12 m (Dimitrova-Konaklieva, 2000; Berov et al., 2012), it is
521 likely that a similar change may have occurred with the *P. crispa* lower-infralittoral communities.
522 Such a change implies a significant loss of macroalgae covered area, and a corresponding loss of
523 biomass, primary production and ecosystem functions. Similar reduction in distribution, biomass
524 and primary production have also occurred within the upper infralittoral *Cystoseira barbata* and
525 *Cystoseira bosphorica* habitats (Milchakova and Petrov, 2003; Minicheva et al., 2008; Berov et
526 al., 2010), resulting in a drastic change in the overall functioning of the shallow-water coastal
527 ecosystem in the SW Black Sea, contributing to changes in functioning of the basin’s benthic and
528 pelagic trophic cascades and regime shifts in the basin’s ecosystem functioning (Daskalov, 2002;
529 Daskalov et al., 2007, 2016; Oguz and Gilbert, 2007). Similar long-term loss of diversity and
530 spatial distribution of *Cystoseira* species due to various human-induced pressures has also been

531 observed in recent decades across the Mediterranean (Cormaci and Furnari, 1999; Thibaut et al.,
532 2005; Serio et al., 2006; Bianchi et al., 2014)

533 The possible impact of trophic interactions and herbivory on the occurrence of *Phyllophora*
534 *crispa* in the study area, which is a major factor contributing to the change in distribution of
535 keystone macroalgal species in the Mediterranean (Hereu et al., 2008; Coma et al., 2011; Giakoumi
536 et al., 2011;; Tsiamis et al., 2013) and the N Atlantic (Bekkby et al., 2009; Rinde et al., 2014), has
537 not been investigated so far in the Black Sea. Due to the absence of herbivorous echinoideans and
538 large herbivorous fish species feeding on perennial macroalgae in the Black Sea, such pressures
539 habitat-forming perennial macroalgal assemblages is non-existent, or at least no obvious impacts
540 related to these pressures have been observed in recent field studies and monitoring campaigns
541 (authors' personal observations). Given the large-scale changes in the trophic cascades of pelagic
542 ecosystems in the Black Sea, the possible influence of herbivory on macroalgal communities
543 should be further investigated with in-situ exclusion experiments, as well as in-situ and laboratory
544 studies of the diets of major invertebrate and fish species inhabiting the coastal zone of the Black
545 Sea.

546 **4.3 Dispersal range and connectivity**

547 Considering the current distributional range *Phyllophora crispa* along the Bulgarian Black
548 Sea coast, it is likely that the SAC Ropotamo is the northernmost zone where the species has a
549 well-established population. South of Ropotamo, *P. crispa* is found within the Natura 2000 zone
550 Strandja 3 km from Ropotamo, see Fig. 1, which offers suitable environmental conditions and
551 habitats for the species. The Burgas Bay, located 20 km to the north, is highly impacted by
552 anthropogenic eutrophication and pollution and has suffered a significant loss of macroalgal
553 communities (Berov et al., 2012), probably serves as a dispersal barrier preventing the spread of the
554 species propagules to areas with suitable environmental conditions, such as the SCI Cape Emine-
555 Irakli (30 km north from Ropotamo) and Galata (70 km north from Ropotamo), where recent
556 surveys showed that the species is not present (Berov, unpublished). Further north, beyond Varna
557 Bay there are some observations (Todorova, unpublished) of *P. crispa* within the Natura 2000 site
558 Kaliakra (120 km from Ropotamo). Additionally, the eutrophicated and polluted waters of Varna
559 Bay probably also serve as a dispersal barrier, preventing any connectivity with populations of the
560 species in the south. Given the short dispersal range of *P. crispa* and the probable barrier effect of

561 the Burgas and Varna Bays, the current network of MPAs along the Bulgarian Black Sea coast
562 does not seem to provide sufficient connectivity of the populations of the species within the
563 identified CEF, mostly because of the severe anthropogenic impact resulting in unsuitable
564 conditions for growth and reproduction of eutrophication-sensitive macroalgal species.

565 The absence of *Phyllophora crispa* from the Romanian coast (Bologa and Sava, 2006;
566 Marin et al., 2013), means that its populations in SW Black sea are isolated from those along the
567 coast of Ukraine and Russia. The distribution of *P. crispa* along the European coast of Turkey,
568 which falls within the same CEF as the Southern Bulgarian Black Sea coast (Boero et al., 2016),
569 is not well studied, however the species is found East of the Bosphorus channel in the vicinity of
570 Sinop (Aysel et al., 2004). Given the presence of suitable habitats along the Turkish coast north
571 of the Bosphorus, it is probable that *P. crispa* has well-established populations in this coastal area,
572 possibly connected with that in the SCI Strandja (BG0001007) in Bulgaria. Currently no
573 functioning network of MPAs exists along the W Black Sea coast of Turkey that would ensure
574 conservation and connectivity of the populations of *P. crispa* with the Bulgarian Black Sea coast.
575 Further studies using genetic methods and simulations of propagule drift of keystone macroalgal
576 species (e.g. Jahnke et al., 2016; Thibaut et al., 2016) are needed in order to better understand the
577 distribution and state of the species along the Black Sea and to take appropriate conservational
578 measures in the identified CEFs in the basin.

579

580 **5. Conclusions**

581 Our study demonstrates the efficiency of using multidisciplinary approaches in studying
582 the structure and distribution of infralittoral habitats. The combination of geophysical substrate
583 mapping with georeferenced in-situ biological sampling allows data integration and analysis of
584 habitat preferences of species with statistical and habitat modelling tools. The approach proved to
585 be an efficient method for mapping habitat distribution and to estimate biological functions and
586 ecosystem services that can be used for MPA management purposes in the context of the CEF
587 concept. Our results show that the current Natura 2000 network along the SW Black Sea coast
588 does not provide sufficient connectivity between individual zones that would ensure the long-term

589 preservation of the conservationally important lower-infralittoral communities of *Phyllophora*
590 *crispa*.

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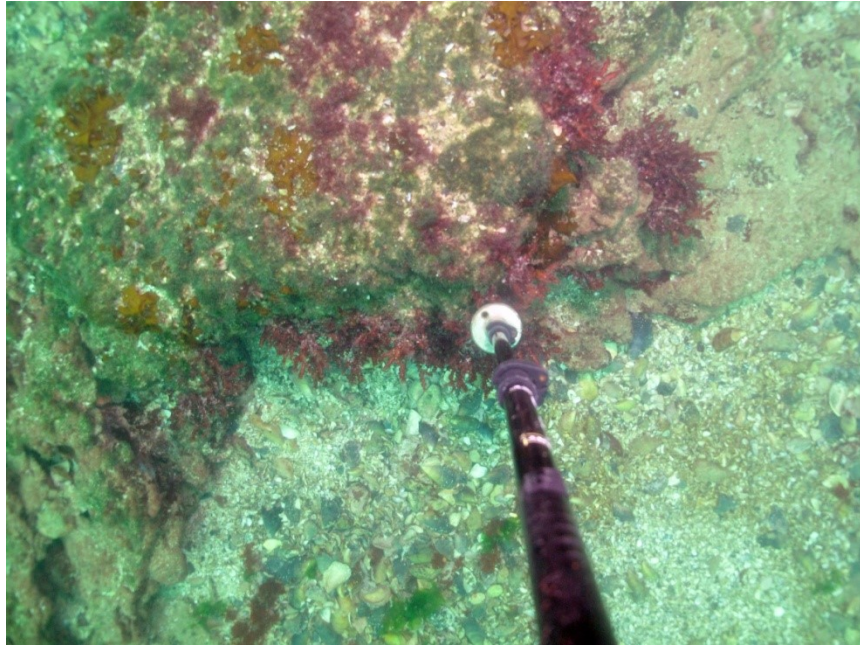
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Supplementary material



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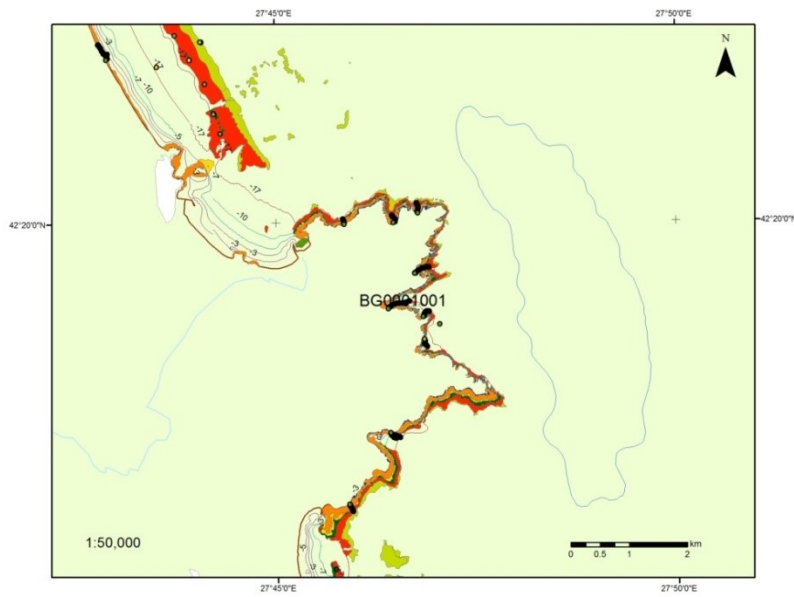
920 Typical 'vertical outcrop' feature colonized by *Phyllophora crispera*, and adjacent flat hard surface dominated by
921 *Gelidium* spp. and *Zanardinia typus* (photo 1 – sideways view, photo 2 – planimetric view from top). Photos taken in
922 July 2014 at ~ 10 m depth, at N 42.247 E 027.774

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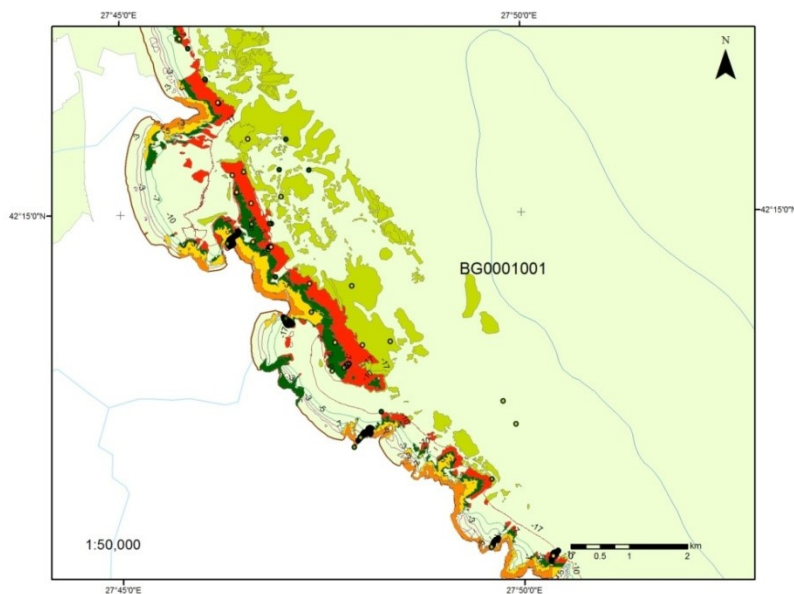


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925 'Ostrak' biogenic reef overgrown by *Mytilus galloprovincialis* and *Zanardinia typus*. Photo taken in July 2013 at 11
926 m depth at N 42.289 E 027.765

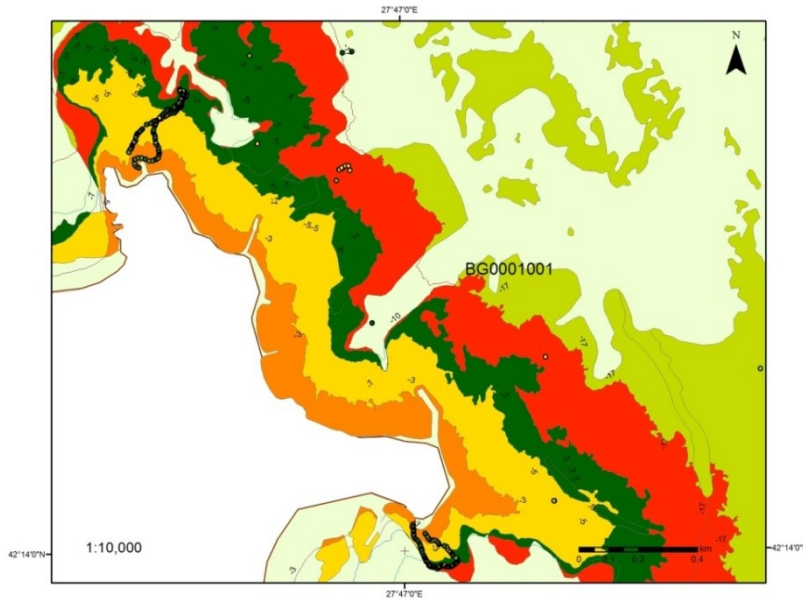


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928 A 1:50 000 map of distribution of infra- and circalittoral phytobenthic habitats in the northern section of pilot study
929 area ('BG0001001- MPA Ropotamo'). Orange – *Cystoseira bosporica* communities, yellow – *Cystoseira barbata*
930 communities, green- *Cystoseira barbata*-lower infralittoral transitional zone, red – lower infralittoral mixed
931 *Phyllophora crisper*-*Apoglossum ruscifolium* *Gelidium spinosum*-*Zanardinia typus* mixed assemblages, light green –
932 circalittoral)



933

934 A 1:50 000 map of distribution of infra- and circalittoral phytobenthic habitats in the S section of pilot study area (
 935 Kiten Reef area of 'BG0001001- Ropotamo'). Orange – *Cystoseira bosporica* communities, yellow – *Cystoseira*
 936 *barbata* communities, green- *Cystoseira barbata*-lower infralittoral transitional zone, red – lower infralittoral mixed
 937 *Phyllophora crista*-*Apoglossum ruscifolium* *Gelidium spinosum*-*Zanardinia typus* mixed assemblages, light green –
 938 circalittoral)



939
 940 A 1:10 000 map of distribution of infra- and circalittoral phytobenthic habitats in the coastal area of Kiten
 941 ('BG0001001- Ropotamo'). Orange – *Cystoseira bosporica* communities, yellow – *Cystoseira barbata* communities,
 942 green- *Cystoseira barbata*-lower infralittoral transitional zone, red – lower infralittoral mixed *Phyllophora crista*-
 943 *Apoglossum ruscifolium* *Gelidium spinosum*-*Zanardinia typus* mixed assemblages, light green – circalittoral)

944
 945 **Supplementary table** Summary of the observed preferences of the identified macroalgal communities with respect
 946 to depth and PAR range, geomorphological feature, substrate type and presence on vertical outcrop or not.

Macroalgal community	depth range	PAR range	Geomorphological feature	substrate type (visual description)	vertical outcrops
<i>Phyllophora crista</i> (<i>P. crista</i> -Clad group)	8-17 m	7-10%	coastal bedrock	'ostrak' biogenic reef; rocks	yes
<i>Zanardinia typus</i>	8-17 m	7-10%	coastal bedrock; reef	'ostrak' biogenic reef; rocks	no

<i>(Z. typus-Mgal group)</i>					
<i>Gelidium spp. - Ulva rigida</i> <i>(Gel-Ulva-P. crispa group)</i>	7-16 m	7-10%	coastal bedrock	rocks	no
<i>Apoglossum ruscifolium</i> <i>(Apogl group)</i>	10-17 m	7-10%	coastal bedrock; reef	'ostrak' biogenic reef; rocks	no
<i>Cystoseira bosporica</i>	1-4 m	40-70%	coastal bedrock; reef	rocks	no
<i>Cystoseira barbata</i>	1-10 m	10-70%	coastal bedrock; reef	rocks	no