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Partial recovery of macro-epibenthic assemblages on the north-west shelf of the Black Sea

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Author contribution statement

Tim Stevens conducted and analysed the video tows, performed most of the analyses, and prepared the text and figures
Laurence Mee was the cruise leader in 2006, and provided data on historical trends on the Dead Zone
Jana Friedrich was the cruise leader in 2008, and provided data on waterbody variables and sediment geochemistry
Dmity Aleynik provided data on oceanography of the Black Sea shelf
Galina Minicheva provided data and expertise on Ecology of Phyllophora and other algae in the Black Sea, and historical maps of Phyllophora distribution
All authors contributed to the editorial process.

Keywords

Macro-epibenthos, Black Sea, Phyllophora, Towed video, Dead zone, Ecosystem recovery

Abstract

Word count: 292

The north-west shelf of the Black Sea has suffered well-documented declines in biodiversity since the 1960s, and by the 1990s was considered a dead zone with virtually no sign of macroscopic epibenthic life. It was characterised by high levels of anthropogenic input, massive phytoplankton blooms, and periodically hypoxic to anoxic bottom waters. An important contributor to primary production on the northwest shelf is the red alga *Phyllophora* spp. growing in waters to 70 m depth. *Phyllophora* is a habitat forming taxon supporting complex assemblages of bivalves, sponges, and ascidians, with an associated rich fish fauna. From 1990 on, nutrient loads entering the system plummeted and the severity of algal blooms decreased. Changes to benthic communities, however, were far less rapid, and the trajectory and rate of any recovery of the dead zone, in particular Zernov's *Phyllophora* Field, is far from certain. This study used towed underwater video imagery from research cruises in summer 2006 and spring 2008 to classify and map macro-epibenthic assemblage structure, and related this to putative physical, chemical and spatial drivers. Distinct and relatively stable benthic communities were in evidence across the northwest shelf at that time. These communities were largely structured by substrate type and depth, but there is some evidence that nutrients continued to play a role. *Phyllophora* spp. was present across much, but not all, of its former range, but at far lower percent cover than previously. The pattern of abundance of *Phyllophora* in 2006-08 did not correlate with the documented pre-eutrophication pattern from 1966. There is some evidence that faster-growing opportunistic species have hindered to recovery. We conclude that while there was evidence of sustained recovery, by 2008 the macro-epibenthic communities of the northwest shelf of the Black Sea were far from their pre-eutrophication state.

Contribution to the field

Human influences have resulted in large-scale changes to the biology and ecology of the oceans. In extreme cases, these can result in "Dead Zones" - expanses of ocean floor that are devoid of macroscopic life. These can occur where high levels of pollution, including nutrients from fertilisers, industrial wastes, and excess sediment, are discharged from rivers, and can be made worse by overfishing. Even once the levels of pollution have decreased, and the fishing effort has been scaled back, recovery of these Dead Zones is not assured, and has seldom been documented. One such Dead Zone was on the north west shelf of the Black Sea, where nutrient inputs plummeted after the collapse of the centrally-planned economies of eastern Europe in 1989. This study examines the response of the organisms living on the sea floor almost 30 years later, to determine whether recovery of the Dead Zone has occurred, and if so to what extent. This is critical information to guide management of oceans impacted by human activities.

Ethics statements

(Authors are required to state the ethical considerations of their study in the manuscript, including for cases where the study was exempt from ethical approval procedures)

Does the study presented in the manuscript involve human or animal subjects: No

Data availability statement

Generated Statement: The datasets generated for this study are available on request to the corresponding author.

In review

Partial recovery of macro-epibenthic assemblages on the north-west shelf of the Black Sea

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Keywords: macro-epibenthos, Black Sea, *Phyllophora*, towed video, dead zone, ecosystem recovery

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Abstract

The north-west shelf of the Black Sea has suffered well-documented declines in biodiversity since the 1960s, and by the 1990s was considered a dead zone with virtually no sign of macroscopic epibenthic life. It was characterised by high levels of anthropogenic input, massive phytoplankton blooms, and periodically hypoxic to anoxic bottom waters. An important contributor to primary production on the northwest shelf is the red alga *Phyllophora* spp. growing in waters to 70 m depth. *Phyllophora* is a habitat forming taxon supporting complex assemblages of bivalves, sponges, and ascidians, with an associated rich fish fauna. From 1990 on, nutrient loads entering the system plummeted and the severity of algal blooms decreased. Changes to benthic communities, however, were far less rapid, and the trajectory and rate of any recovery of the dead zone, in particular Zernov's *Phyllophora* Field, is far from certain. This study used towed underwater video imagery from research cruises in summer 2006 and spring 2008 to classify and map macro-epibenthic assemblage structure, and related this to putative physical, chemical and spatial drivers. Distinct and relatively stable benthic communities were in evidence across the northwest shelf at that time. These communities were largely structured by substrate type and depth, but there is some evidence that nutrients continued to play a role. *Phyllophora* spp. was present across much, but not all, of its former range, but at far lower percent cover than previously. The pattern of abundance of *Phyllophora* in 2006-08 did not correlate with the documented pre-eutrophication pattern from 1966. There is some evidence that faster-growing opportunistic species have hindered recovery. We conclude that while there was evidence of sustained recovery, by 2008 the macro-epibenthic communities of the northwest shelf of the Black Sea were far from their pre-eutrophication state.

40 1 Introduction

41 “*The forgotten sea returns... to our consciousness, our everyday life, our politics*” (Vanessa
42 Winship, *Schwarzes Meer*, 2007 page 7)

43

44 The long-term decline in biodiversity on the northwest shelf of the Black Sea from the 1960s to
45 1990s is well documented (Mee, 1992; Zaitzev and Mamaev, 1997). The Black Sea suffers from
46 the combined effects of anthropogenic eutrophication, overfishing and climate forcing (Oguz and
47 Gilbert, 2007; Mee et al., 2005). By the early 1990s, as a result of unrestrained nutrient inputs,
48 coupled with overexploitation of fish stocks (Daskalov, 2002), habitat loss through intensive
49 near-bottom trawling (Revkov et al., 2018) and the invasion of exotic species (Shiganova, 1998;
50 Shiganova et al., 2003; Siokou-Frangou et al., 2004), this once highly productive habitat was
51 considered a dead zone (Mee, 2006; Todorova et al., 2019). It was characterised by high levels
52 of anthropogenic nutrients delivered by the Danube, Dniester and Dniepr rivers, periodic
53 massive phytoplankton blooms, and anoxic bottom waters during the growing season with
54 virtually no sign of macroscopic epibenthic life, as described elsewhere (Diaz and Rosenberg,
55 2008; Samyshev and Zolotarev, 2018). An important contributor to primary production on the
56 northwest shelf had been the red algae from the genus *Phyllophora*, growing drifting or attached
57 to shell-bed substrates, in waters to 70 m depth as first described by Zernov (1909). *Phyllophora*
58 spp. was present in very high densities over an area of more than 10,000 km², and was
59 commercially harvested for fertiliser (Schapova, 1954; Kalugina and Lachko, 1966). It was also
60 important as a habitat forming taxon and occurred in complex assemblages with high densities of
61 bivalves, sponges, and ascidians, with an associated rich fish fauna (Zaitsev, 1992; Mee, 2006).
62 Through the 1970s and 1980s, these extensive *Phyllophora* beds, growing to mesophotic depths
63 and hence at the limits of light availability, were lost from the effects of eutrophication and
64 persistent overfishing (Daskalov, 2002), leading to shading from algal blooms at the surface and
65 hypoxia at depth (Shapiro et al., 2011). This triggered in turn a trophic cascade leading to the
66 collapse of most fisheries, echoing up the food chain, with the Monk Seal *Monachus monachus*
67 populations in the Black Sea reduced to a handful of individuals by the mid-1990s (Zaitzev and
68 Mamaev, 1997).

69 With the collapse of centrally-planned economies in eastern Europe in 1989, agricultural
70 subsidies ceased, dramatically reducing fertilizer use (Mee et al., 2005). Simultaneously, more
71 stringent EU regulations reduced nutrient and other contaminant loads entering the western end
72 of the Black Sea via the Danube (Konovalov and Murray, 2001; Artioli et al., 2008). Within a
73 few years, nutrient concentrations in the waterbody plummeted, and the size, severity, frequency
74 and duration of algal blooms dramatically decreased (Mee et al., 2005; Mee, 2006). Changes to
75 benthic communities, however, have been far less rapid, and there remains uncertainty about the
76 fate of nutrients and other contaminants bound up in sediments (Friedl et al., 1998; Wijsman et
77 al., 1999; Fillmann et al., 2002; Readman et al., 2002), and rates of benthic nutrient cycling
78 (Friedrich et al., 2002; Gregoire and Friedrich, 2004). Concurrently, the Black Sea has been
79 subject to successive invasive species outbreaks, most notably by the ctenophore *Mnemiopsis*
80 *leidy*. *M.leidy* was first noted in the Black Sea in the early 1980s (Shiganova, 1998) and
81 reached peak densities in the late 1980s and early 1990s (Shiganova et al., 2001). The species
82 represented a trophic ‘dead-end’ and had well documented effects on planktonic and pelagic
83 biodiversity until it rapidly declined subsequent to the introduction of the predatory ctenophore
84 *Beroe ovata* in 1997 (Shiganova et al., 2003; Siokou-Frangou et al., 2004; Oguz and Velikova,
85 2010; Shiganova et al., 2018). Effects of these and other invasives on benthic ecosystems are,
86 however, not well understood (Akoglu et al., 2014a; Minicheva, 2015).

87 In spring and summer, the water column of northwest shelf of the Black Sea is characterised by
88 the formation of a strong thermohaline stratification, restricting mixing of bottom shelf waters
89 with the surface layers, which thereby exacerbates hypoxic conditions. In winter the shelf is
90 well-mixed (Sorokin, 2002). Isopycnic analysis of a long-term time series of temperature
91 anomaly records available since the 1950s, reveals the presence of a c.20 year cycle in Bottom
92 Shelf Water (BSW) temperature, with a warming period observed from the late 1950s to early
93 1970s followed by a cooling phase until the mid-1990s (Shapiro et al., 2010). A warming stage
94 has been in place since then. The regime shift in the Black Sea Western Shelf ecosystem,
95 including the dramatic reductions in nutrient inputs outlined above, thus coincides in time (mid
96 1990s) with the switch from cooling to warming in BSW (Oguz and Gilbert, 2007). It is
97 therefore important to examine the influence of oceanographic and water body properties on
98 observed epibenthic assemblage structure, as well as nutrients and biophysical factors.

99 Environmental conditions on the northwest shelf of the Black Sea are clearly influenced by a
100 wide range of drivers, and there remains considerable uncertainty about the rate and likely
101 trajectory of recovery of benthic communities in this region (Mee et al., 2005; Minicheva, 2007;
102 Friedrich & Janssen et al., 2014; Jessen et al., 2017). This is particularly important to understand,
103 since the emerging economies of Eastern Europe are now faced with critical societal choices
104 (Langmead et al., 2009; O'Higgins et al., 2014) about their future use of the Black Sea and its
105 catchments. Recovery is by no means assured (Oguz and Velikova, 2010), especially in the
106 context of current regional geopolitical instability (Christakis, 2015; Hansen, 2015). However,
107 there are encouraging signs of the adoption of contemporary adaptive management approaches
108 (Mee, 2005; Douvere and Ehler, 2011; Dungaciu, 2015), including the declaration of a 4,025
109 km² marine reserve within the area of the former “Zernov’s *Phyllophora* Field” (ZPF) (Kostylev
110 et al., 2010).

111 However, there remains little information about the status and trends in macro-epibenthic
112 assemblage structure and distributions at time-points through the “post-crisis” stage (Revkov et
113 al., 2018), and their relationship with documented changes in sediment, nutrient and water body
114 characteristics. This paper presents results from research cruises in the boreal summer of 2006
115 (RV Akademik) and spring of 2008 (RV Poseidon) which examined a wide range of benthic and
116 pelagic parameters in the region, as reported elsewhere (Pakhomova et al., 2008; Minicheva et
117 al., 2013; Friedrich et al., 2015a; Minicheva et al., 2018). With regard to epibenthic assemblages,
118 this study aimed to:

- 119 • Survey and classify macro-epibenthic communities across the northwest shelf of the
120 Black Sea, from inshore areas to mesophotic depths, to compare these with pre-
121 eutrophication accounts of assemblage composition.
- 122 • Quantify the relative influence of physical, chemical and spatial ecosystem drivers on
123 observed assemblage structure at that time, in the context of a recovering, highly
124 damaged ecosystem.
- 125 • Compare the 2006-2008 distribution and abundance of the key habitat-forming algae
126 from the genus *Phyllophora* to historic distributions.

127

128 **2 Methods**

129 **2.1 Study area**

130 The study was conducted on the northwest shelf of the Black Sea (Figure 1) in an area bounded
131 in the west by the coasts of Bulgaria and Romania, and in the north and east by the coast of
132 Ukraine including the Crimean Peninsula. The area extended northward to include the extent of
133 the ZPF, close to the mouths of the Dnieper and the Dniester rivers, and south to include the area
134 influenced by the outflow from Danube Delta. This encompasses a sea area of roughly 50,000
135 km², and 800 km of coastline. Benthic assemblage structure was examined at depths from 13 to
136 122 m.

137 <<Figure 1 about here>>

138 **2.2 Macro-epibenthos surveys**

139 The structure of macro-epibenthic communities was assessed using a combination of remotely
140 deployed and in-situ sampling techniques. The primary sampling technique was visual sampling
141 using video and still images from sensors mounted on a towed benthic imaging sled, a technique
142 now widely used for benthic habitat classification and mapping (Barker et al., 1999; Stevens and
143 Connolly, 2005), and for monitoring of ecosystem changes over time (Sheehan et al., 2013;
144 Stevens et al., 2014). Image-based underwater sampling has the advantage of being able to
145 sample very large areas cost-effectively (Michaelis et al., 2019), and including sites beyond the
146 practical reach of diver-based surveys (Enrichetti et al., 2019). The imagery also allows
147 examination of the relationship between structural elements of the benthos in-situ. The primary
148 disadvantage is lower taxonomic resolution, as samples are not retained for verification of
149 identification.

150 In the 2006 (July-August: summer) cruise, imagery was collected using a Sony 1/3" CCD
151 analogue video sensor in a custom underwater housing. Images were viewed at the surface in
152 real-time and recorded on a DV8 digital handycam at VGA resolution (640 x 480 pixels) for
153 later analysis. For the 2008 (March: spring) cruise, imagery was collected using a Kongsberg
154 Simrad 14-208 camera, which allows for real-time capture of video at VGA resolution, plus
155 higher resolution still images at 5-megapixels. Video was recorded on an ARCHOS AV700
156 digital video recorder as .avi files, using a DivX codec. Still images were stored in the camera
157 and downloaded after each tow. For both cruises lighting was provided by two OM1000 250w
158 underwater floodlights. Expert commentary about the imagery from the scientific staff aboard
159 was recorded as they viewed an on-deck monitor in real-time, allowing items of interest to be
160 flagged for more detailed investigation.

161 The basic sampling unit was a single (nominally) 200 m video tow at each station, located by
162 GPS. Video tows were effected by either allowing the vessel to drift with wind and tide, or by
163 steaming into the direction of drift to effect a speed over the ground of $\leq 0.25 \text{ m}\cdot\text{sec}^{-1}$; at any
164 greater speed images were blurred and not usable for data extraction. This is consistent with
165 contemporary practise for remote image-based sampling in deep water (e.g. Cánovas-Molina et
166 al., 2016; Michaelis et al., 2019).

167 The imaging sensors were mounted on the sled at an angle of 45° because previous experience
168 had shown that it is easier to recognise organisms in this orientation than looking straight down.
169 In both cruises the field of view was calibrated by tank testing both before and after sampling.

170 Quantitative data was extracted from the video stream by sub-sampling a frame every 2 to 5
171 seconds, depending on the speed of the camera over the ground, providing maximum coverage

172 without overlapping images. Some of the resultant frames were not usable due to blurring, or
173 turbidity, so 50 good quality video frames per tow were randomly selected for analysis. Taxon
174 identification was aided by samples retrieved by a small dredge, and, during the Spring 2008
175 survey, by ten 5-megapixel still images taken during each tow, giving high-resolution images of
176 taxa in-situ.

177 Video files were analysed using Quicktime Pro™ v7 software. A counting frame was
178 superimposed on the video files, representing a constant 1m² of sea floor. Since the field of view
179 was known and constant, counts of individual organisms within the 1m² frame were made and
180 average density of each species (ind.m⁻²) calculated over the number of frames (nominally 50)
181 for each tow. The counting frame also contained an array of 9 points (representing the
182 intersections of a 0.25m grid within the counting frame). Percent cover of macrophytes was
183 therefore estimated by counting the number of points falling on each taxon, in each frame.
184 The number of points for each taxon was summed over the entire tow and divided by the total
185 number of points from all the frames to give an accurate estimate of percent cover for each taxon
186 (Sheehan et al., 2010; Stevens et al., 2014). In some cases digital filters were used to improve
187 contrast and clarity of the imagery.

188 The extracted data were arranged in sites by species matrices for density of individual organisms
189 and % cover of macrophytes, respectively. These were then subjected to univariate and
190 multivariate analyses as detailed below.

191 **2.3 Possible drivers of epibenthic structure**

192 **2.3.1 CTD, water chemistry and nutrients**

193 Water samples were taken using a rosette of 12 sampling bottles mounted on a circular frame,
194 together with a Sea-Bird SBE 9 CTD equipped with Conductivity, Temperature, Pressure
195 sensors, providing a continuous profile of water body properties. Samples were taken 1 m below
196 the surface and c. 2 m above the bottom, as well as at intervals through the profile representing
197 discontinuities in the water body; however only the surface and bottom data are included in our
198 analyses. On recovery of the rosette, water subsamples were taken from each bottle, and
199 processed on board for water chemistry and nutrient concentrations using standard laboratory
200 techniques (Pakhomova et al., 2008; Friedrich et al., 2015a). In 2006, oxygen concentrations
201 were determined by Winkler titration of the water samples. Sensors for primary productivity (by
202 fluorescence: Chelsea Minisensor), and oxygen concentrations (SBE 43, in 2008 only) were also
203 deployed, either on the rosette frame or a separate array (Friedrich et al., 2015a; Friedrich et al.,
204 2015b). Hypoxia can also be detected by increased NH₄ in the water samples (Friedrich &
205 Janssen et al., 2014).

206 **2.3.2 Substrate type**

207 Substrate type was estimated from the video images in four grain size classes. Much of the
208 sediment of the north-west shelf of the Black Sea is biogenic, and this is reflected in the classes
209 used: sand/mud, shell grit, *Modiolus* shell, *Mytilus* shell. The final two classes denote
210 recognizable dead but whole or nearly whole shells of these two taxa, which in places form the
211 dominant substrate on the sea floor (Wijsman et al., 1999). For each frame, the substrate type
212 which formed at least 50% of the field of view was recorded. For each video tow, therefore, a
213 percent cover value for each substrate class was derived. In addition, for simplicity in subsequent
214 analyses, we calculated a single substrate score ranging from 1 to 4, weighted by sediment size
215 so that 1 represented 100% sand/mud, and 4 represented 100% *Mytilus* shell.

216 **2.3.3 Spatial drivers**

217 For each tow, spatial information relating to the distance from major input sources (the mouths
218 of the Danube, Dnieper and Dniester rivers), as well as the distance offshore, were derived using
219 GIS techniques in ARCGIS version 9.1. Depth at the start, mid-point and end of each tow was
220 also noted, and the mean value used in subsequent analyses.

221 **2.4 Analyses**

222 **2.4.1 Patterns in epibenthic assemblage structure**

223 Patterns of biodiversity within the macro-epibenthos were investigated using ordination analyses
224 of the sites by species matrices in PRIMER v6 (Clarke and Warwick, 2001). Data were 4th-root
225 transformed to moderate the influence of numerically dominant taxa, and similarity matrices
226 were constructed using the Bray-Curtis similarity measure. Differences between assemblage
227 groups derived from the ordination analyses were verified by one-way Permuted Multivariate
228 Analysis of Variance (PERMANOVA) within the PRIMER package (Anderson, 2001; Anderson
229 et al., 2007). Contribution of individual benthic species or bioturbation indicators to assemblage
230 group similarity was assessed using the SIMPER routine in PRIMER, which quantifies the
231 percent contribution of each variable to group similarity. This information was used to assign
232 descriptive titles to the groups and allowed comparisons of groups with similar composition
233 between the two sampling periods.

234 **2.4.2 Influence of drivers of epibenthic assemblage structure**

235 Data on putative biological and abiotic drivers were assembled into sites by indicators matrices.
236 The influence of this range of physico-chemical and spatial drivers on the derived biological
237 assemblage structure was assessed using the BIOENV routine in PRIMER, which iteratively
238 tests the correlation between matrices of abiotic similarity, derived from available combinations
239 of specified drivers, and the corresponding matrix of biological similarity. BIOENV provides a
240 Spearman's ranked correlation value (ρ) for possible drivers, both individually and in
241 combination, as a measure of their relative contribution to assemblage structure.

242 **2.4.3 Distribution and abundance of *Phyllophora* and other macroalgae**

243 Three separate analyses (presence/absence, overall abundance, distribution pattern) were
244 conducted to compare the distribution and abundance of *Phyllophora* from the 2006-08 surveys
245 with known historical values.

246 The presence or absence of *Phyllophora* spp. at detectable densities on the northwest shelf was
247 mapped for combined Summer 2006 and Spring 2008 data. Distribution of *Phyllophora* presence
248 was compared with mapped historical extents of the ZPF, derived from georeferenced and
249 digitised historical maps of *Phyllophora* spp. distribution and biomass, primarily contained in
250 Minicheva (2005) and Zaitzev and Mamaev (1997), in order to determine the relationship
251 between historical and 2006-08 range.

252 To compare overall abundance of *Phyllophora* spp. within the ZPF between 2006-08 and pre-
253 eutrophication values, the derived values for percent cover of *Phyllophora* were compared with
254 percent cover estimates from the ZPF documented in the percent cover distribution map of
255 Kalugina and Lachko (1966) reproduced in Minicheva (2005). Raw data for the 1966
256 distribution map is not available, so percent cover values for each station sampled in Summer
257 2006 and Spring 2008 were derived by superimposing the sample locations on the 1966 map,
258 and scoring the value of the polygon beneath each point. Percent cover values for the 1966 map
259 were derived from grab or dredge samples, supplemented by diver assessments (Kalugina and
260 Lachko, 1966), which are arguably less accurate than the video method used in this study, in that

261 they do not sample cover *in situ*. This is reflected in the categorical nature of the 1966 data.
262 Because the categories represent a range of values, and the ranges for each category are not
263 continuous (i.e. 10-20% then 50-70%) we conservatively assumed the lowest value in the range,
264 except for the range 0-5%, where we assumed a value of 1%, indicating presence. Only sample
265 locations within the footprint of the 1966 polygons were used. Given the categorical nature of
266 the data, and assumptions made in deriving data from the 1966 maps, the non-parametric
267 Wilcoxon's signed ranks test was then used to test for differences between mean 1966 percent
268 cover, and mean percent cover in 2006 and 2008 separately, and pooled to give additional power
269 in the analysis. Because of the possibility of bias when comparing percent cover values derived
270 using very different methods, the results of this and the following analysis are interpreted with
271 caution.

272 The distribution pattern of percent cover of *Phyllophora* within the boundaries of the ZPF at
273 1966 was compared to the 2006-08 patterns of percent cover by using correlation analyses to
274 compare the values at each sampled point. This analysis tests whether the historical patterns of
275 greater or lesser percent cover predicted post-crisis patterns.

276 In addition, twelve of the fourteen stations sampled on both cruises lay within the footprint of the
277 former ZPF, forming in effect a cross-shelf transect from near the mouth of the Dniester inlet to
278 the 50 m isobath (Figure 2). This allowed analyses of differences, especially in algal abundance
279 and depth distribution, between Summer 2006 and Spring 2008. It is not possible to properly test
280 for seasonal effects without replication across years, nevertheless the differences between these
281 two times are of interest, particularly from the point of view of the dynamics of *Phyllophora* spp.
282 growth and coverage (Minicheva et al., 2013).

283 3 Results

284 3.1 Descriptions of datasets:

285 Twenty-nine stations were successfully sampled with the video sled in Summer 2006, and 36 in
286 Spring 2008 (Table 1, Figure 2) for a total sampled distance of over 7.5 km in 2006, and over 8
287 km in 2008. While nominally 50 still frames were sampled per tow, in a few tows, especially in
288 turbid waters closer to the Danube Delta, less than 50 useable frames were available. Data
289 matrices used for analyses of assemblage structure in each year were therefore 29 stations by 14
290 taxa or indicators (burrows, tracks) for 2006, and 36 stations by 18 taxa or indicators for 2008.
291 These data have been lodged with Pangaea (<https://doi.org/10.1594/PANGAEA.902792>).

292 <<Table 1 about here>>

293 <<Figure 2 about here>>

294 3.2 Benthic assemblage structure Summer 2006

295 Three distinct groups were apparent within the benthic assemblage on the northwest shelf of the
296 Black Sea in Summer of 2006 (Figure 3a). These groups were consistent across ordination
297 techniques and data transformations; the nMDS based on 4th root transformed data is shown
298 because this has the lowest stress value. A one-way PERMANOVA test confirmed that the
299 derived groups were statistically distinct (df = 4, Pseudo-F = 20.3, all pairwise tests $p < 0.001$).
300 Group names are assigned based on the results of SIMPER analyses which show which
301 taxa/indicators are responsible for with-in group similarity. Table 2 shows the taxa contributing
302 up to 90% of within-group similarity, pooled by growth form (notionally phylum) for ease of
303 interpretation. The vectors on the nMDS (Figure 3a) illustrate the influence of these. The group
304 labelled Bioturbators is most strongly influenced by the presence of burrows, tracks, and
305 tubeworms. The other two groups Mytilus / Ascidiaceans and Mytilus / Algae are, as the names

306 suggest, both characterised by relatively high densities of living *Mytilus galloprovincialis* shell,
307 but with quite different associations of several species of colonial ascidians, on the one hand, and
308 algae (principally the Rhodophytes *Phyllophora crista* and *Polysiphonia sanguinea*) on the
309 other (Table 2). Two stations (one in Karkinit Bay, and the other in deep water off the Romanian
310 coast) were statistically distinct from these three groups, and from each other (PERMANOVA p
311 < 0.01). In both cases these stations were quite depauperate.

312 <<Figure 3 about here>>

313 <<Table 2 about here>>

314 Plotting the derived groups (Figure 3b) shows a clear spatial pattern. The Bioturbators group
315 occurs inshore, while the Mytilus dominated groups are in deeper water, further from the
316 coastline (although stations near the Dniester inlet are in < 20 m). Mytilus / Algae stations are
317 generally shallower than the Mytilus / Ascidians stations; the analysis of possible drivers (below)
318 explores this further.

319 **3.3 Benthic assemblage structure Spring 2008**

320 Similarly, there are three well defined groups apparent in benthic assemblage structure from the
321 Spring 2008 cruise data, and these are also consistent across ordination techniques and data
322 transformations (Figure 4a). The one-way PERMANOVA test confirmed that the derived groups
323 were statistically distinct ($df = 4$, Pseudo-F = 19.6, all pairwise tests $p < 0.001$). Again, group
324 names were assigned on the basis of SIMPER results (Table 2b). Symbology has been kept
325 consistent with the Summer 2006 analysis (Figure 3) since the principal contributors to within-
326 group similarity are largely the same. The exception to this is the Sponges / Ascidians group,
327 where the same symbology as the Mytilus / Ascidians group from 2006 has been used because
328 the group is also characterised by Ascidians. Again, vectors on the nMDS (Figure 4a) illustrate
329 the influence of benthic growth forms on the derived pattern. Two stations (not the same two)
330 were also found to be statistically distinct from the derived groups and each other
331 (PERMANOVA $p < 0.01$); in this case they were depauperate stations in > 100 m depth.

332 <<Figure 4 about here>>

333 Plotting the derived groups (Figure 4b) shows a notionally similar spatial pattern to the Summer
334 2006 stations, with the Bioturbator-dominated group inshore, and the Algae dominated group
335 constrained largely within the historical footprint of the ZPF off the Dniester inlet. Further
336 offshore the Sponge / Ascidian dominated group is widespread across the shelf.

337 **3.4 Abiotic drivers for patterns in assemblage structure**

338 The influence of abiotic factors on benthic assemblage structure for each sampling period was
339 determined by iterative BIOENV analyses. Abiotic data was not available for all stations, so the
340 BIOENV analyses were carried out for the subset where both biological and abiotic data was
341 available. Data on 32 environmental factors were available at 24 stations for 2006, and 27
342 stations for 2008.

343 The relative contribution of individual factors was determined (Appendix 1) prior to testing
344 combined models. To avoid undue weight in the analyses from related parameters, we cross-
345 correlated all parameters and where pairs correlated highly ($r > 0.7$) we removed the factor with
346 the lowest individual BIOENV (ρ) value from subsequent BIOENV analyses. Factors with no
347 significant relationship to the derived assemblage structure were also excluded from subsequent
348 analyses. We also excluded surface waterbody factors (included in table 3 for comparative
349 purposes) as less relevant to structuring benthic assemblages than bottom waterbody factors.

350 It is clear that factors relating to substrate and geographical position, as well as depth,
351 consistently have a stronger relationship to the observed assemblage structure than waterbody
352 nutrients and physical parameters. Rather than “cherry-pick” the strongest relationships for
353 inclusion in the combined models, we iteratively tested all possible combinations of up to five
354 factors (Table 3).

355 <<Table 3 about here>>

356 Combined models provided strong correlations with derived assemblage structure in both years.
357 The core of each model was geographic and substrate related factors, as well as depth; changes
358 in associated factors such as nutrients had only minor influence on the strength of the correlation.
359 To illustrate this we included simplified models, using only depth and the single substrate score;
360 it can be seen that these correlated only slightly less well with the assemblage structure than the
361 complex models with up to five factors (Table 3).

362 **3.5 *Phyllophora* distribution and abundance compared to historical data**

363 **3.5.1 Presence or absence of *Phyllophora* in 2006-08 compared to pre-eutrophication extent**

364 The presence or absence of *Phyllophora* spp. at detectable densities derived from video sampling
365 in 2006-08 was compared with pre-eutrophication extents derived from historical maps of
366 *Phyllophora* spp. distribution (Figure 5). Because the 2006 and 2008 surveys were not structured
367 with the sole objective of mapping the extent of current *Phyllophora* distribution, distribution
368 within the previous extents was not comprehensively sampled, and thus comparable estimates of
369 area are not available. Nonetheless it is clear that *Phyllophora* was present in 2006-08 in
370 detectable densities in the core of its former range, but not across all of it, which in 1962
371 extended southwest to include the Danube Delta front (Michaylov and Mashtakova, 1966), and
372 across deeper (>50 m) areas of the northwest shelf, to about 20 km west of the Crimean
373 peninsula at Cape Tarkhankut (Schapova, 1954).

374 <<Figure 5 about here>>

375 **3.5.2 Overall abundance and distribution patterns within the 1966 footprint**

376 Derived values for percent cover of the habitat-forming *Phyllophora* spp. at each station sampled
377 were plotted (Figure 6a and b) and overlaid on polygons digitised from the earliest available
378 percent cover estimates for the ZPF (Kalugina and Lachko, 1966).

379 <<Figure 6 about here>>

380 Maximum cover at any station was 9% in Summer 2006 (Station D5), and 13.3% in Spring 2008
381 (Station PHY1), whereas Kalugina and Lachko (1966), and other contemporary accounts, noted
382 extensive areas of 100% cover. *Phyllophora* spp. was not observed in continuous beds anywhere
383 in this study, but only as isolated patches. Wilcoxon’s matched-pairs signed rank test showed
384 that percent cover at the locations sampled in 2006 and 2008 was very significantly lower than in
385 1966 (2006: $p = 0.016$; 2008 and pooled years $p < 0.001$) (Figure 7). Although the percent cover
386 values compared in this analysis were derived using different methods, the differences observed
387 are so marked as to overcome any methodological bias.

388 <<Figure 7 about here>>

389 For each sample period, and for the pooled data from both years, correlation analyses were used
390 to determine whether the pattern of higher and lower percent cover of *Phyllophora* in 2006-08
391 corresponds to the 1966 pattern of percent cover. Spearman’s ranked correlations were not

392 significant between 1966 and 2006 ($n = 14$, Spearman's $\rho = 0.310$, $p = 0.278$), 2008 ($n = 19$, $\rho =$
393 0.283 , $p = 0.242$), or the pooled dataset ($n = 33$, $\rho = 0.218$, $p = 0.222$). In other words, the pattern
394 of *Phyllophora* percent cover within the historical footprint does not predict the sampled
395 distributions sampled in 2006-08. Since this analysis compares patterns of distribution (relatively
396 greater or lesser percent cover), rather than absolute values, methodological bias in the
397 estimation of percent cover is not considered a limitation here.

398 **3.6 Macroalgal abundance**

399 Fourteen stations were common to the Summer 2006 and Spring 2008 surveys, and these permit
400 comparisons of abundance of key components of the epibenthos between these two times.
401 Twelve stations were within the former extent of the former ZPF, and analyses therefore focus
402 on this important habitat-forming taxon, with opportunistic filamentous algae with which it is
403 associated. Figures 8a and 8b show the percent cover of both filamentous algae and *Phyllophora*
404 along a depth gradient for both sampling periods, corresponding to a cross-shelf transect through
405 the former ZPF. Two key differences are evident. Firstly, there is a very clear overall difference
406 between the percent cover of all macroalgae in 2006 compared to 2008 (Wilcoxon's signed ranks
407 test, $z = -2.746$, $p = 0.006$); secondly, this difference is much more marked in shallower water
408 (<35 m) than in deeper waters. There is a distinct bimodal distribution of *Phyllophora* spp. with
409 depth in the Summer 2006 survey (Figure 9), which is less evident in the Spring 2008 survey.
410 We suggest growth of filamentous algae and *Phyllophora* may be seasonal in warmer shallow
411 water during summer months, whereas in mesophotic depths (>35 m) *Phyllophora* is better able
412 to cope with low light availability, and not subject to shading and overgrowth by these faster
413 growing macroalgal forms. There is no overall difference in the percent cover of *Phyllophora*
414 spp. between the two sampling periods (Wilcoxon's signed ranks test, $z = -1.373$, $p = 0.171$).

415 <<Figure 8 about here>>

416 <<Figure 9 about here>>

417 **4 Discussion**

418 This study has illustrated that in 2006-08 there were distinct and relatively diverse macro-
419 epibenthic communities on the northwest shelf of the Black Sea, in contrast to the impoverished,
420 or absent, macrobenthic biota in the dead zones of the 1980s and 1990s.

421 The derived communities were statistically distinct in both years; and relatively consistent
422 between years, although there were some important differences. Inshore stations in both years,
423 particularly near the Dniester Inlet and the Danube Delta, were dominated by bioturbating
424 macrofauna, with only occasional clumps of live *Mytilus galloprovincialis*. In deeper waters, the
425 assemblage structure was dominated by varying combinations of bivalves (principally *Mytilus*),
426 ascidians, algae and sponges. Critically, in the Summer 2006 surveys, the keystone *Phyllophora*
427 spp, while present, did not play the primary structuring role in any derived assemblage, but
428 contributed 14 - 17% to within-group similarity of the two *Mytilus*-dominated groups, which
429 were otherwise distinguished by the very high (c.30%) contribution of ascidians in the *Mytilus* /
430 *Ascidians* group. In both years, *Phyllophora* was present in detectable quantities in the area of
431 the former Zernov's *Phyllophora* field, and as part of species complexes including high densities
432 of mussels *Mytilus*, ascidians *Ciona intestinalis* and other algae especially *Polysiphonia* spp.
433 However, only in the Spring 2008 surveys, and in a quite constrained distribution of nine stations
434 (*Algae* / *Mytilus* group) within a radius of c.44km, did *Phyllophora* appear as a structuring
435 element of the macrobenthos. This is heartening, but short of its pre-eutrophication role as the
436 major benthic biomass component and habitat engineer, as shown by the comparison between
437 1966 and 2006-08 percent cover. While it is not possible to properly test for seasonal effects

438 based on just two sampling periods, it is reasonable to infer that the observed differences in algal
439 species dominance and cover may relate to seasonal differences in water temperature and light
440 availability, which are more marked in shallower water. Certainly the dominance of
441 *Polysiphonia sp.* and the filamentous algal complex in 2006, and not in 2008, suggests this
442 relationship, perhaps facilitated by nutrient availability.

443 The key drivers for assemblage structure were substrate and depth, but consistently included
444 distance from input sources and a small nutrient contribution (principally forms of N). The
445 overgrowth of *Phyllophora* by faster growing filamentous algal forms in the Summer 2006
446 sampling event suggests that some nutrient enrichment, either from continuing inputs, or by
447 diffusion across the sediment-water interface, remained important at the time of the surveys.
448 Benthic nutrient flux was quantified at several stations (Friedrich et al., 2010), but not enough to
449 be included in the BIOENV models.

450 Comparing the release of nutrients from the sediments measured in 2006 and 2008 to that in the
451 1990s (Friedrich et al., 2010) reveals there is little difference in the rate of release of ammonia,
452 nitrate, phosphorus and silica between those times. This is an example of the sediment's memory
453 of eutrophication, whereby burial of organic matter from past eutrophication and its ongoing
454 decomposition leads to continued release of dissolved nutrients for decades after eutrophication
455 has ceased (Friedrich et al., 2010). In general, the highest nutrient release from the sediments
456 was found inshore where eutrophication was heaviest, and decreases towards the outer shelf; for
457 example, maximum flux of nitrogen (ammonia plus nitrate) from the sediments was found
458 adjacent to the mouth of the Dniester at $>4 \text{ mmol.m}^{-2}.\text{d}^{-1}$, but falling to $<0.8 \text{ mmol.m}^{-2}.\text{d}^{-1}$ at the
459 deeper *Phyllophora* field stations in 2006 and 2008 (*in situ* and *ex situ* sediment incubations,
460 Friedrich unpublished data).

461 The observed distribution of *Phyllophora* in 2006-08 provides clear evidence for recovery, in
462 that it was co-located within its historical range. However, within that historical footprint,
463 observed patterns of abundance (as percent cover) did not correlate with the available historical
464 patterns (Kalugina and Lachko, 1966). Unsurprisingly, on the path to recovery, fast-growing
465 opportunistic species may occupy newly formed niches; e.g., filamentous algae like
466 *Polysiphonia* have hindered the recovery of macroalgae like *Phyllophora* by overgrowth, and
467 ascidians such as *C.intestinalis* have replaced filter-feeding mussels (Friedrich & Janssen et al.,
468 2014). This 2006-08 data revealed a still fragile macrobenthic ecosystem that differed from the
469 pre-eutrophication state, and remained susceptible to anthropogenic and environmental impacts.
470 Clearly, recovery at that time was far from complete, in that percent cover of *Phyllophora*
471 remained very low compared to pre-eutrophication values, and it was not present in parts of its
472 former range. However, the relatively consistent cover of *Phyllophora* at depths greater than 35
473 m showed that it was re-establishing across its former depth range, and that in these deeper, more
474 offshore areas it was less affected by residual nutrients than in the shallower inshore waters. This
475 suggests that in 2006-08, there remained capacity for further recovery, if ongoing pressures are
476 removed or ameliorated; in particular, stringent measures to limit nutrient inputs should remain,
477 with ongoing monitoring to determine trends in riverine nutrient discharge and sediment/water
478 nutrient flux. This is particularly important in the context of modelling recovery trajectories.
479 Modelling by Capet et al. (2013) suggested that frequency of bottom hypoxia has declined much
480 less than other metrics for possible recovery (e.g., Langmead et al., 2009). This is further
481 confirmed by high-resolution time-series observations of bottom water oxygen in an hypoxia-
482 prone location on the shelf (Friedrich & Janssen et al., 2014; Friedrich et al., 2017; Friedrich et
483 al., 2019). This suggests that the recovery of Black Sea benthic biota subsequent to the reduction
484 of nutrient load may not have been as rapid, or extensive, as suggested for the pelagic ecosystem
485 (Kideys, 2002; Steckbauer et al., 2011). In contrast, Revkov et al. (2018), documented
486 macrozoobenthos distribution and biomass via grab sampling in 2010-13 (c. 5 years after this

487 study) and noted species richness comparable to, or greater than, pre-eutrophication data,
488 although this may in part be attributed to differing treatments of the samples. That study and the
489 present one are not comparable in terms of methods (grabs versus video), taxonomic resolution
490 or scope (macrozoobenthos versus epibenthos including algae); nonetheless they both point
491 towards a recovery trend, while suggesting differing points along that continuum.

492 Recovery of large-scale (<1000 km²) dead zones elsewhere has been rarely, if ever, been
493 documented. Of the two largest dead zones (Diaz et al., 2010), hypoxic conditions in the Baltic
494 Sea over an area of >40,000 km² have persisted since the 1960s (Carstensen et al., 2014),
495 prompting calls for controversial “engineered” solutions (Conley, 2012). The extent of the dead
496 zone in the northern Gulf of Mexico varies between about 5,000 and 20,000 km² with catchment
497 rainfall, and therefore river flow volumes (Diaz and Rosenberg, 2008), indicating a clear link
498 with catchment-sourced nutrients (Boesch et al., 2009). In both cases there is no apparent
499 recovery trend, despite seasonal variation and efforts to mitigate nutrient inputs (Rabotyagov et
500 al., 2014). Elsewhere, dead zones continue to occur seasonally in hundreds of locations. Diaz et
501 al. (2010) note measurable recovery in 55 previously hypoxic locations, including the Black Sea,
502 but with that exception, these are all very small (mostly <100 km²), and in most, periodic
503 hypoxia still occurs. The meta-analysis by McCrackin et al. (2016) showed a huge variation in
504 time to recovery of dead zones from less than a year to over a century, and emphasises the need
505 for long-term studies to better understand recovery timescales, and assess the effectiveness of
506 policy measures.

507 **Conclusions**

508 Set in this context, the signs of recovery in the northwest shelf of Black Sea, documented in this
509 and other studies (Revkov et al., 2018; Samyshev and Zolotarev, 2018) although far from
510 complete, are all the more remarkable. The recovery of this ecosystem after its earlier ecological
511 collapse appeared, in 2006-08, to be at a stage characterised by: slow recovery of *Phyllophora*
512 abundance; a shift in benthic communities towards opportunistic species with short life cycles;
513 and a shift in the baseline conditions relative to the situation prior to eutrophication (Friedrich &
514 Janssen et al., 2014). It is ironic that the observed turnaround in nutrient inputs to the Black Sea
515 is in large part due to the collapse of the Soviet Union and the ensuing social and political
516 restructuring of the region (Rabotyagov et al., 2014), rather than the co-ordinated actions of
517 interested parties, as well as European Union regulations governing nutrient inputs via the
518 Danube (Artioli et al., 2008). At present, the region faces significant geopolitical instability
519 (Christakis, 2015; Hansen, 2015) and stark choices about the future use of the resources of the
520 Black Sea and its catchments (Langmead et al., 2009; O'Higgins et al., 2014; Dungaci, 2015). It
521 is therefore critically important that the regional players, including the EU, recognise the
522 progress that has been made, and continue to press for regional-scale agreements in areas such as
523 nutrient inputs and fisheries management (O'Higgins et al., 2014), as well as a commitment to
524 long-term studies (McCrackin et al., 2016). Encouraging progress has been made in the
525 declaration of a marine reserve over a large proportion of Zernov's *Phyllophora* field (Kostylev et
526 al., 2010; Revkov et al., 2018), and the adoption of contemporary adaptive management
527 approaches (Douvere and Ehler, 2011) by several of the Black Sea member states. However,
528 predicted scenarios for the Black Sea ecosystem suggest significant declines (Akoglu et al.,
529 2014b) if current policy settings are retained. The risk remains, especially if regional tensions
530 around resource use are not resolved, of sliding into another of Hardin's (1968) “tragedy of the
531 commons”.

532

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542

543 **Dedication**

544 In memory of our colleague, mentor, co-author and dear friend Laurence Mee, who passed away
545 during the preparation of this manuscript. Laurence made an enormous contribution to the
546 understanding and management of our oceans; he is sorely missed.

547

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773 northwestern Black Sea. *Annals of the Zoological Museum of the Academy of*
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777 **Tables**

778

779 **Table 1:** Description of video sampling effort

Item	Summer 2006	Spring 2008
Number of stations	29	36
Total distance (m)	7552	8124
Total area (m ²)	3020	3250
Total number of frames	1392	1794
Mean frames/transect	48	49.8
Taxa or Indicators	14	18

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In review

783 **Table 2:** SIMPER analysis of contribution to within-group similarity a) Summer 2006, b) Spring 2008. Only
 784 contributions up to 90% included. Taxon refers to phylum or growth form, except for key species.

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786 a)

Group	Taxon		Contribution
Bioturbators	Burrows		47.4%
	Tracks		46.7%
Mytilus / Ascidians	Mytilus		44.8%
	Ascidians		29.7%
	Phyllophora	10.3%	16.5%
	Polysiphonia	6.2%	
Mytilus / Algae	Mytilus		73.7%
	Phyllophora		14.7%
	Ascidians		4.1%

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788 b)

Group	Taxon		Contribution
Bioturbators	Tracks		35.5%
	Burrows		28.8%
	Mytilus		20.6%
	Hydroids		6.2%
Sponges / Ascidians	Sponges		46.9%
	Ascidians		33.6%
	Bryozoans		9.0%
	Phyllophora		3.7%
Algae / Mytilus	Other filamentous algae	27.1%	50.1%
	Phyllophora	15.8%	
	Polysiphonia	7.2%	
	Mytilus		19.4%
	Cnidarians		19.4%
	Ascidians		4.4%

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791 **Table 3:** Best-fit models of combinations of abiotic drivers for macro-epibenthic assemblage structure in Summer
 792 2006 and Spring 2008. Spearman's ranked correlation ρ values from BIOENV. All correlations are highly
 793 significant, $p < 0.001$ (determined by randomisation) in every case. Highly correlated factors ($r > 0.7$), surface
 794 nutrients, combined substrate score and non-significant individual factors were not included in the BIOENV.
 795 Models are ranked by correlation value, and factors within each model are listed in the order of individual
 796 correlation. Correlation values for simplified models including the combined substrate score are given below the 5th
 797 model in each case.

Summer 2006 Models	Spearman's ρ
Sand/mud + depth	0.715
Sand/mud + <i>Mytilus</i> shell + depth + bottom temperature + bottom NH ₄	0.702
Sand/mud + distance to Danube + <i>Mytilus</i> shell + depth + bottom NH ₄	0.698
Sand/mud + distance to Danube + distance offshore + <i>Mytilus</i> shell + depth	0.695
Sand/mud + distance to Danube + <i>Mytilus</i> shell + depth + bottom PO ₄	0.692
Combined substrate score + depth	0.680
Spring 2008 Models	Spearman's ρ
Sand/mud + distance offshore + depth + <i>Mytilus</i> shell	0.599
Sand/mud + distance offshore + depth + <i>Modiolus</i> shell + bottom NO ₂	0.596
Sand/mud + distance offshore + depth	0.594
Sand/mud + distance offshore + depth + <i>Mytilus</i> shell + bottom NO ₂	0.583
Sand/mud + distance offshore + depth + bottom SiO ₂ + <i>Mytilus</i> shell	0.588
Combined substrate score + depth	0.579

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801 Figure Captions

802 **Figure 1:** Location map, including the extent of Zernov's *Phyllophora* Field from Kalugina and Lachko (1966), and
803 the State Botanical Preserve declared in 2008. The box on the main map shows the approximate extent of
804 subsequent maps.

805 **Figure 2:** Sampling distribution for Summer 2006 and Spring 2008. Fourteen stations were sampled in both periods
806 (transect centroids within 500m).

807 **Figure 3:** Benthic assemblage structure, Summer 2006. A) (top) nMDS of 4th root transformed abundance data
808 showing three clearly defined groups. The vectors illustrate the contribution of main growth forms. B) (bottom) map
809 of derived groups. Group names are derived from the most influential taxa in the BIOENV analyses.

810 **Figure 4:** Benthic assemblage structure, Spring 2008. A) (top) nMDS of 4th root transformed abundance data
811 showing three clearly defined groups. The vectors illustrate the contribution of main growth forms. B) (bottom) map
812 of derived groups. Group names are derived from the most influential taxa in the BIOENV analyses.

813 **Figure 5:** Presence / absence of *Phyllophora* spp. at detectable densities from towed video sampling in 2006-08,
814 compared to mapped extents of ZPF pre-eutrophication. Maps digitised and georeferenced from Minicheva (2005)
815 and Zaitzev and Mamev (1997).

816 **Figure 6:** Sampled percent cover of *Phyllophora* spp. overlaid on percent cover class polygons from Kalugina and
817 Lachko (1966). A) (top) sampled percent cover in Summer 2006. B) (bottom) sampled percent cover in Spring
818 2008.

819 **Figure 7:** Mean percent cover of *Phyllophora* spp. compared to percent cover from Kalugina and Lachko (1966) at
820 the points sampled in Summer 2006, Spring 2008 and for both periods combined. Values for 1966 derived from the
821 lower value of the cover class at the sampled point. Number of points sampled in each case is given in the legend.

822 **Figure 8:** Percent cover of macroalgal forms at 12 stations representing a cross-shelf transect through Zernov's
823 *Phyllophora* field. Note that the scale of the Y-axes are different. A) (top) sampled percent cover of macroalgae in
824 Summer 2006. B) (bottom) sampled percent cover of macroalgae in Spring 2008.

825 **Figure 9:** Percent cover of *Phyllophora* spp. at 12 stations representing a cross-shelf transect through Zernov's
826 *Phyllophora* field in Summer 2006 and Spring 2008.

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Figure 1.JPEG

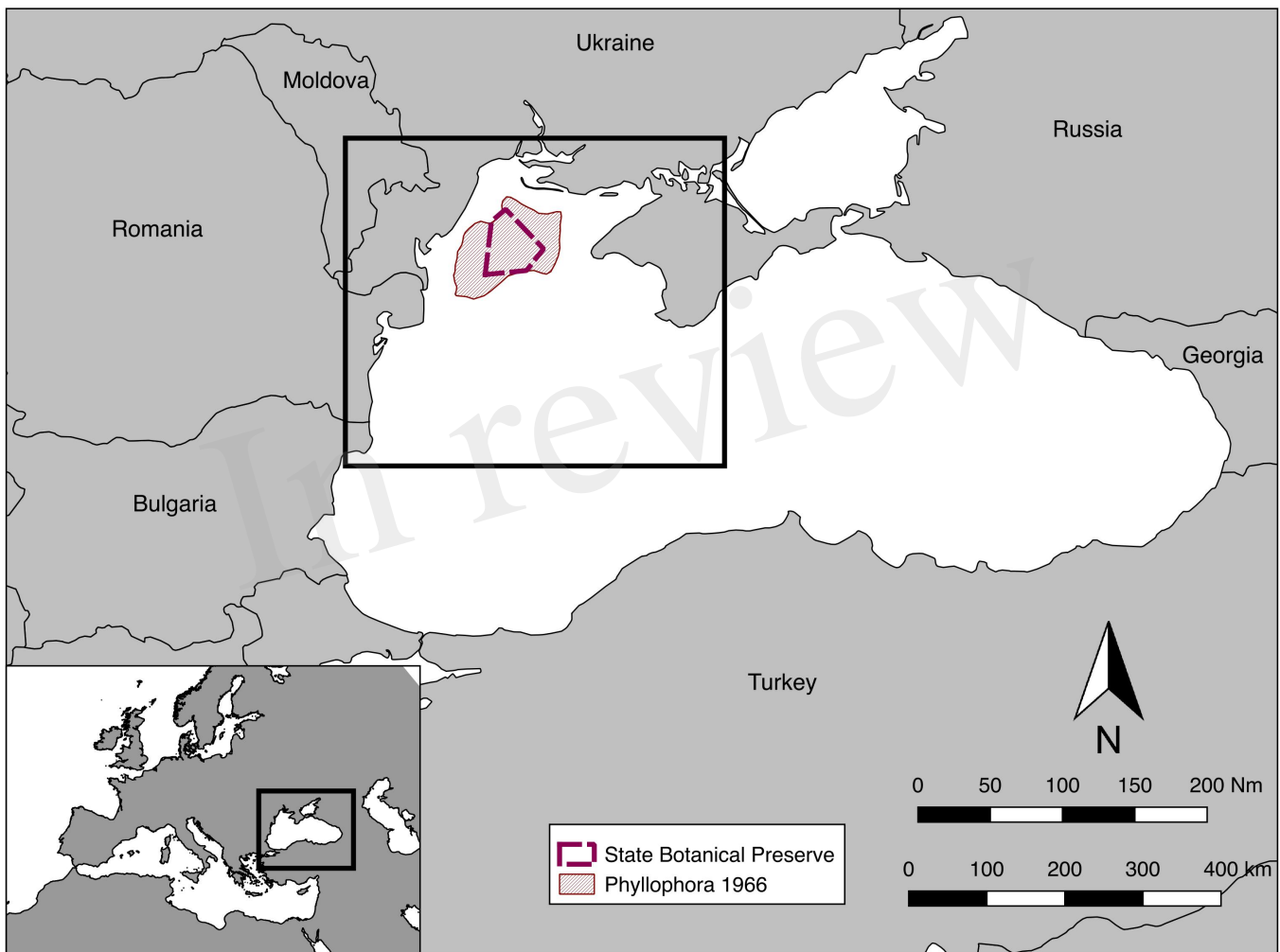


Figure 2.JPEG

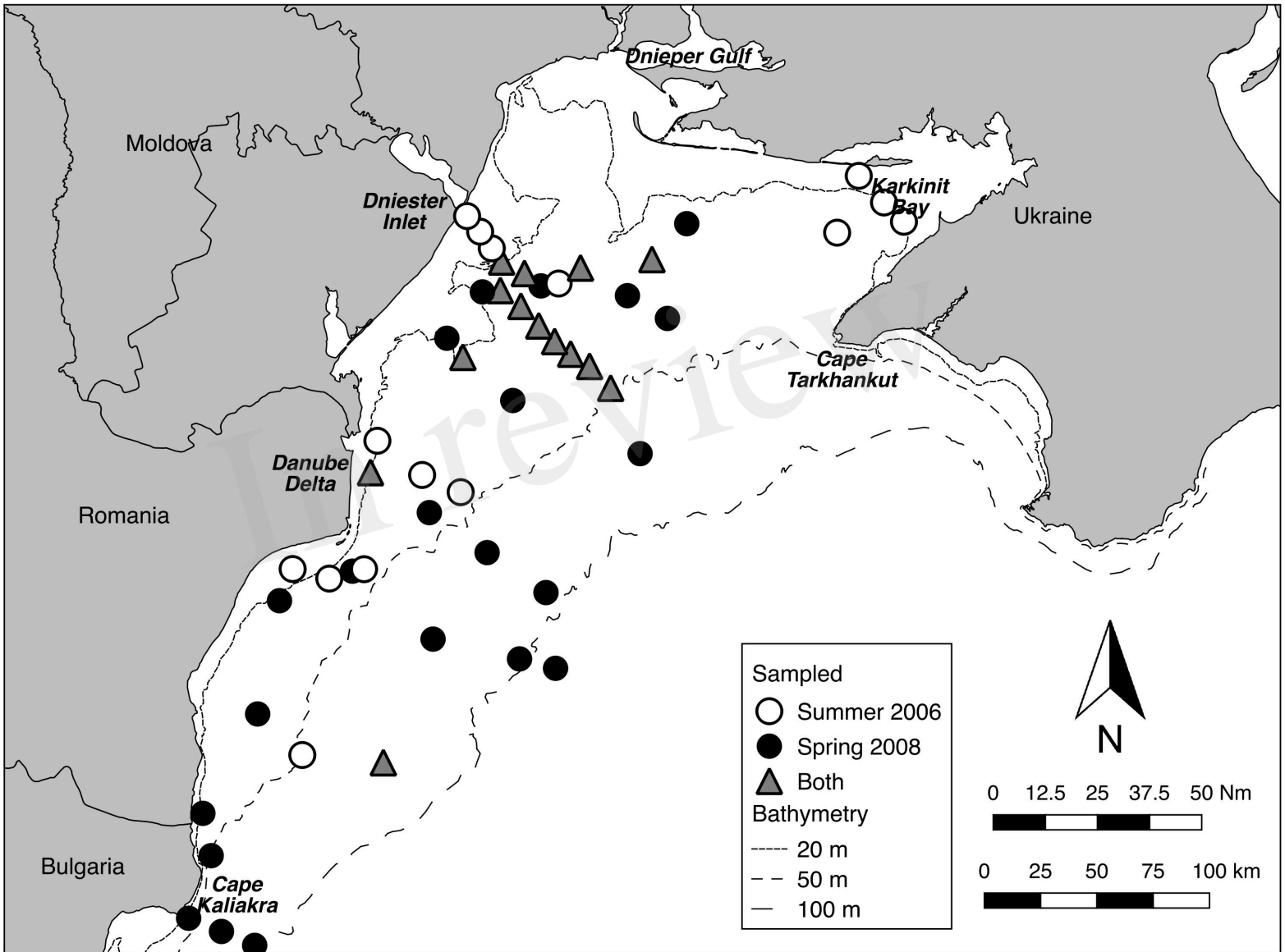


Figure 3.JPEG

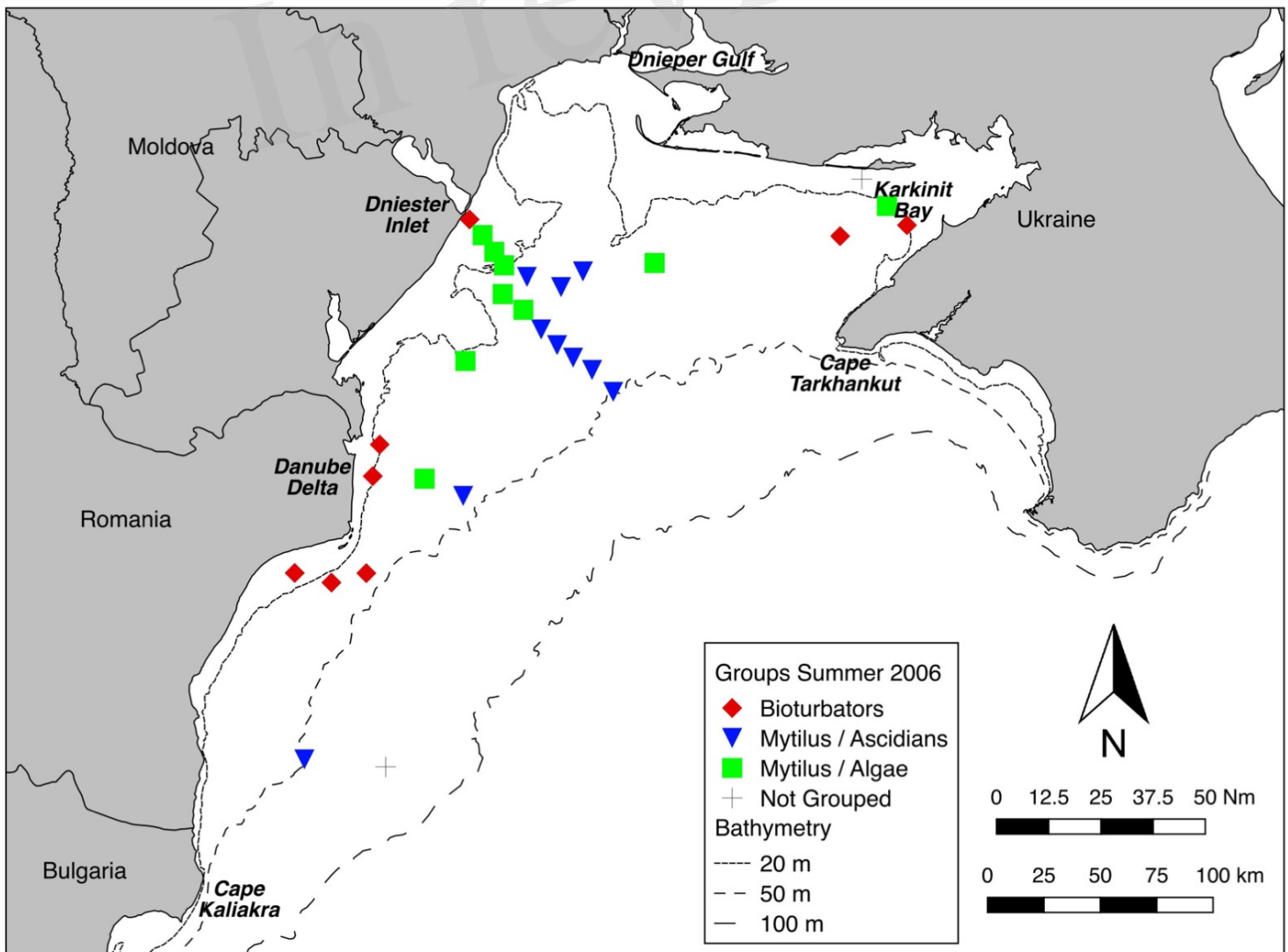
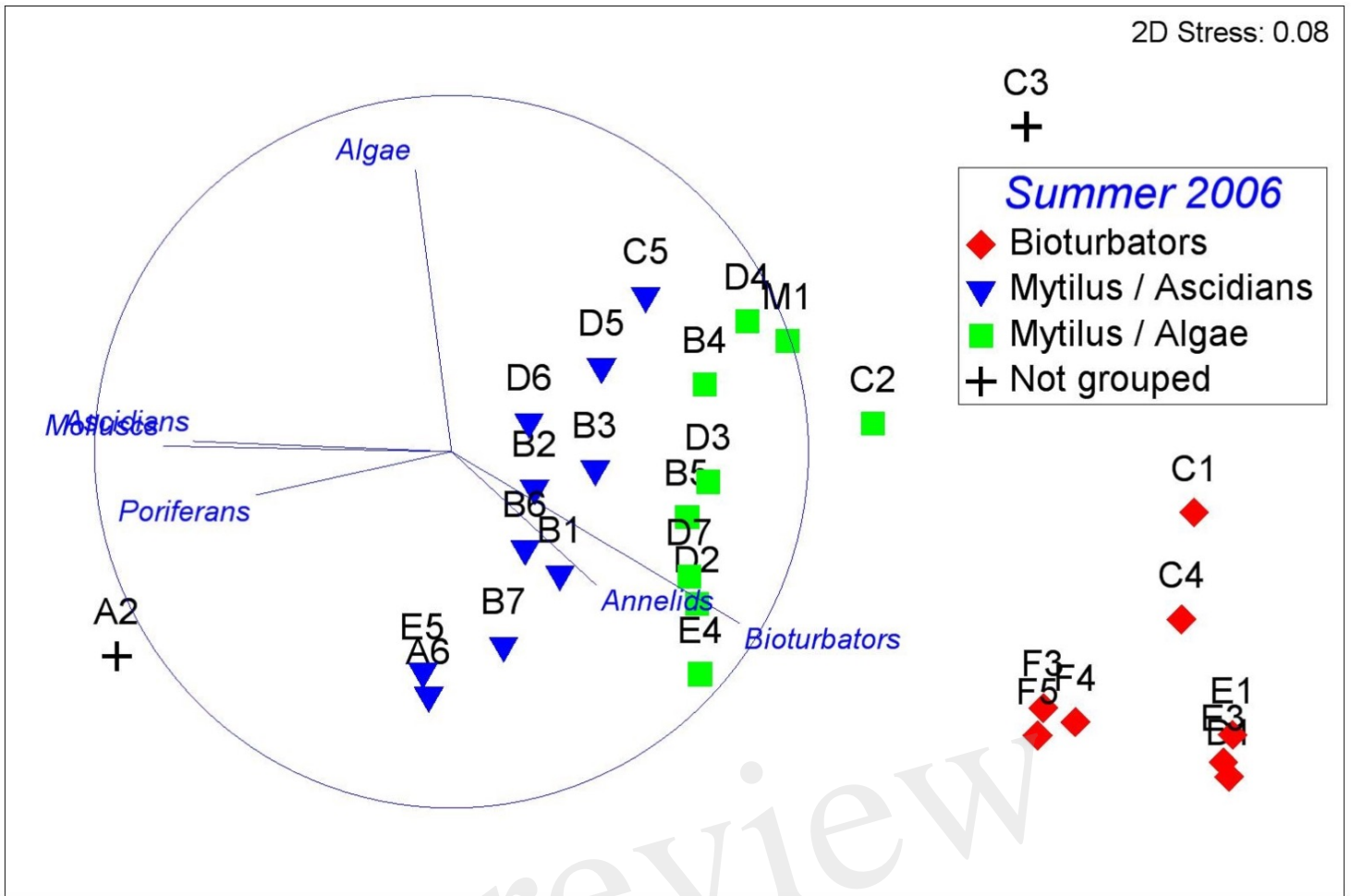


Figure 4.JPEG

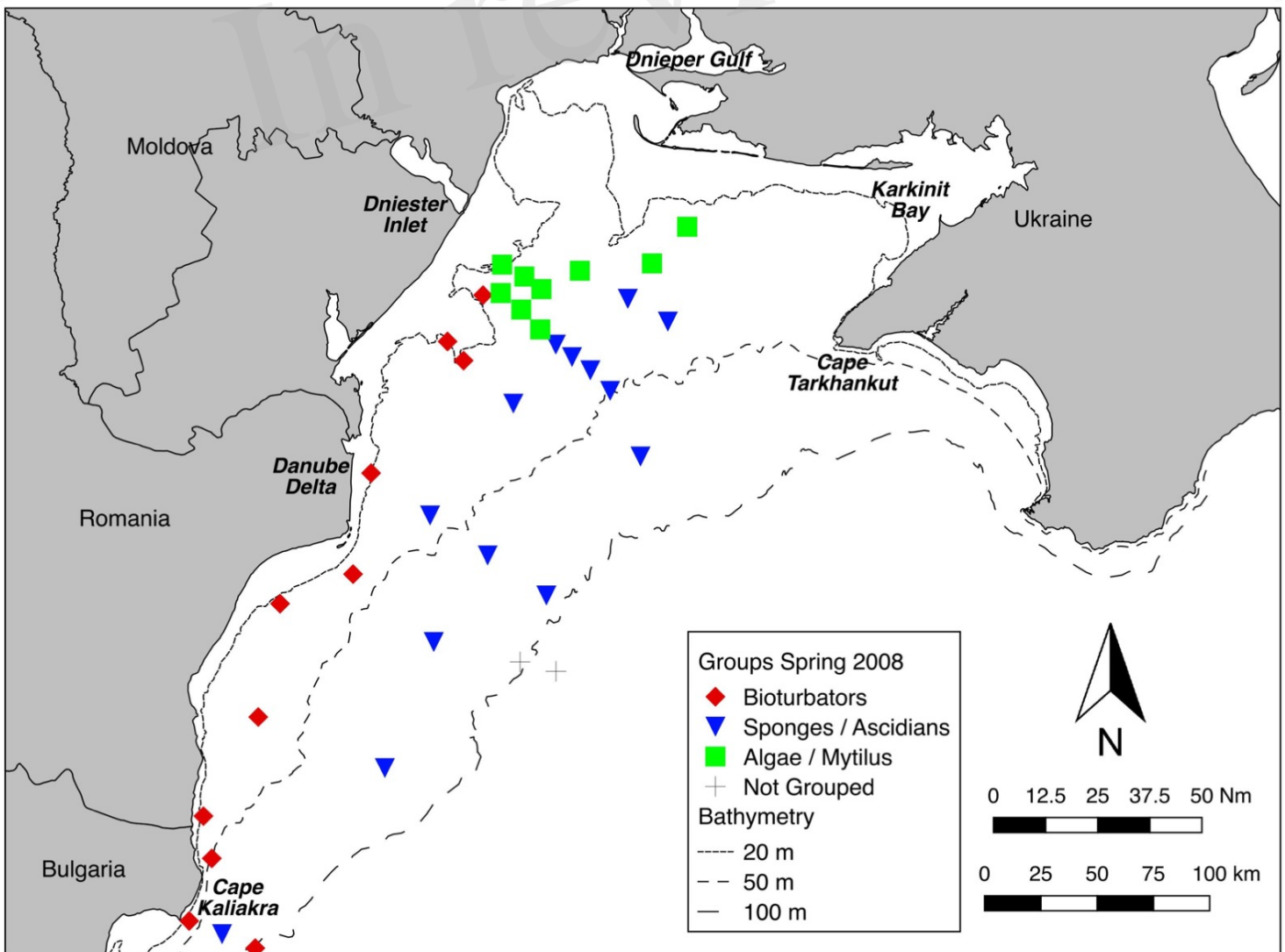
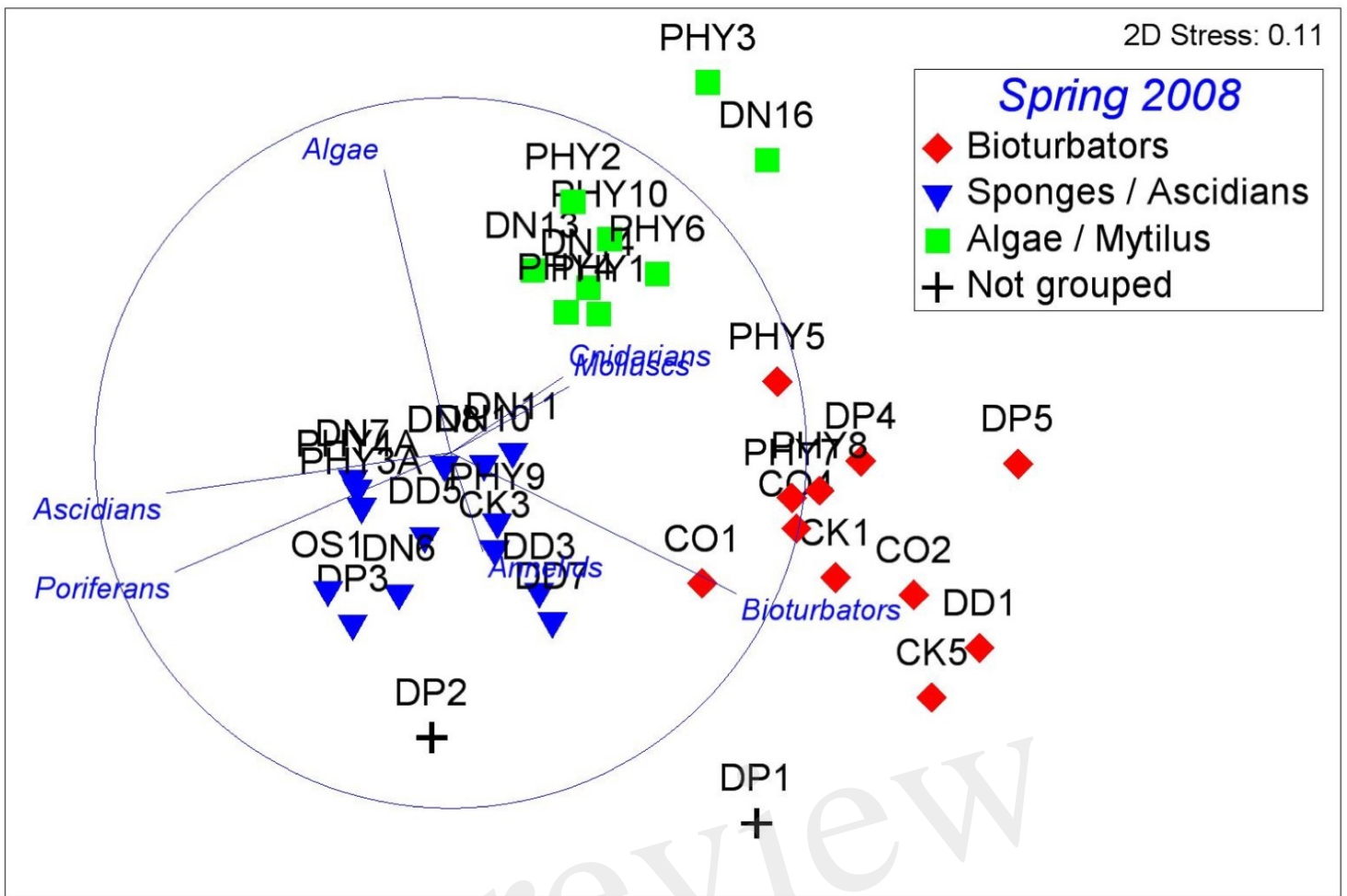


Figure 5.JPEG

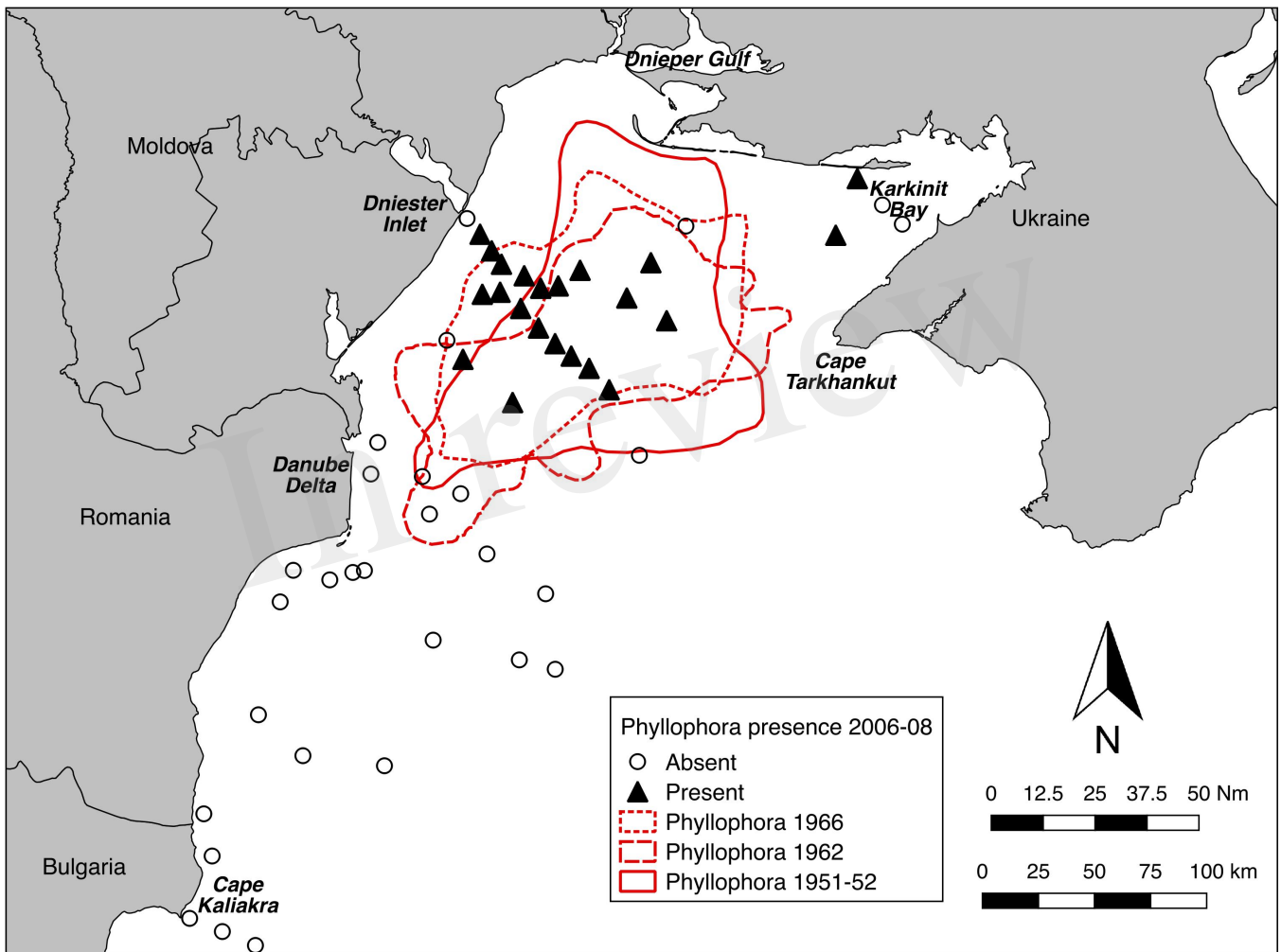


Figure 6.JPEG

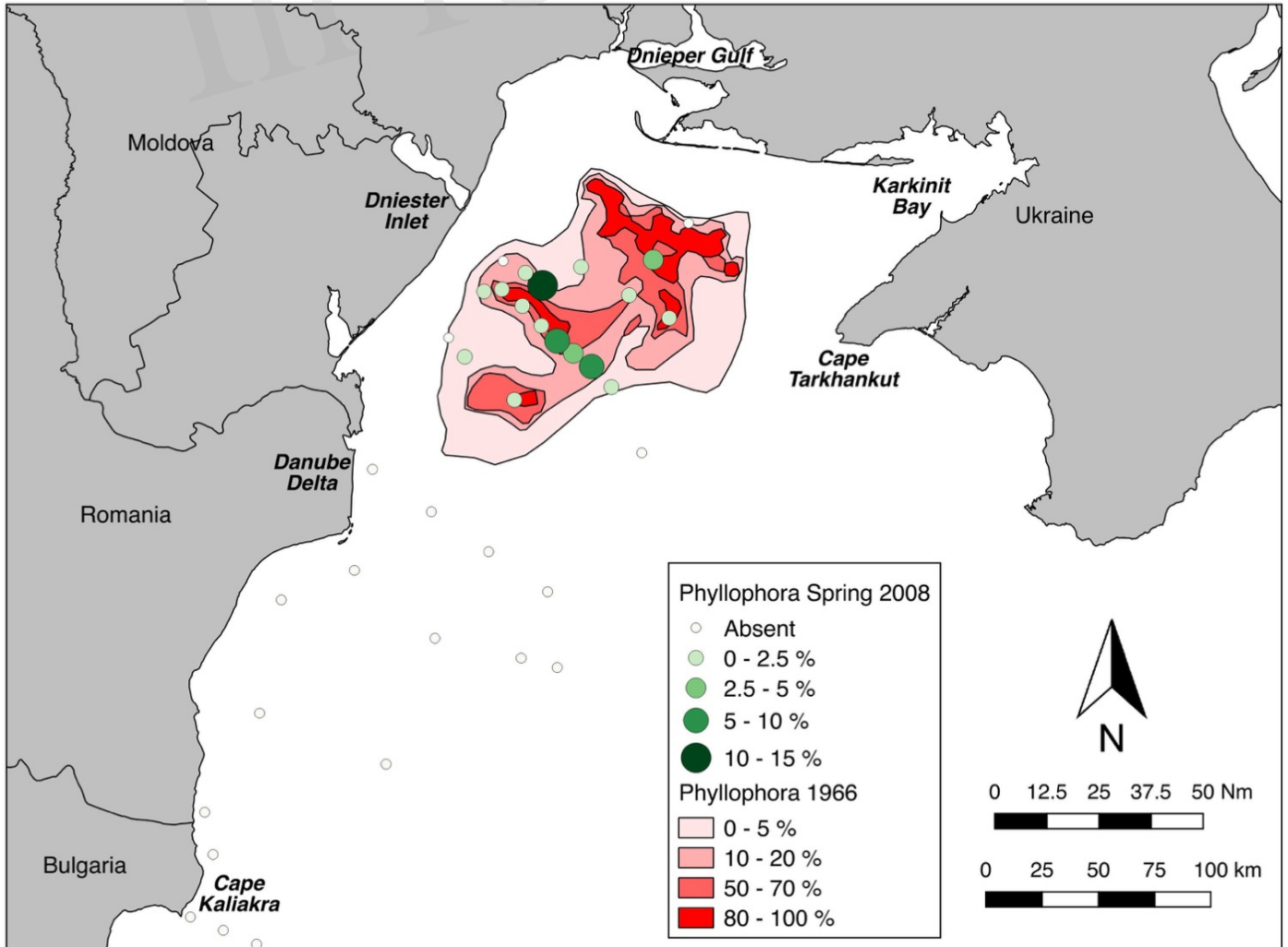
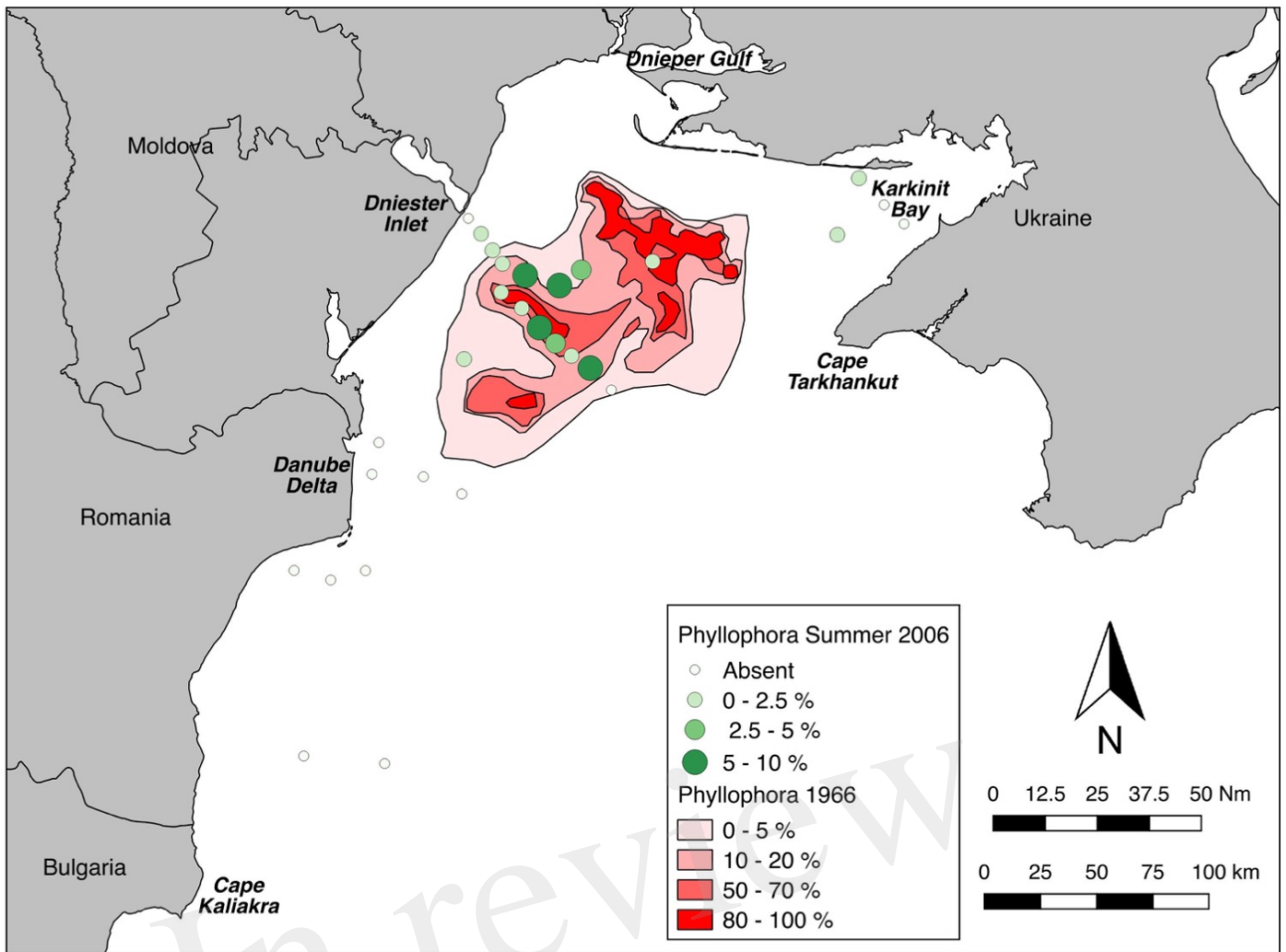
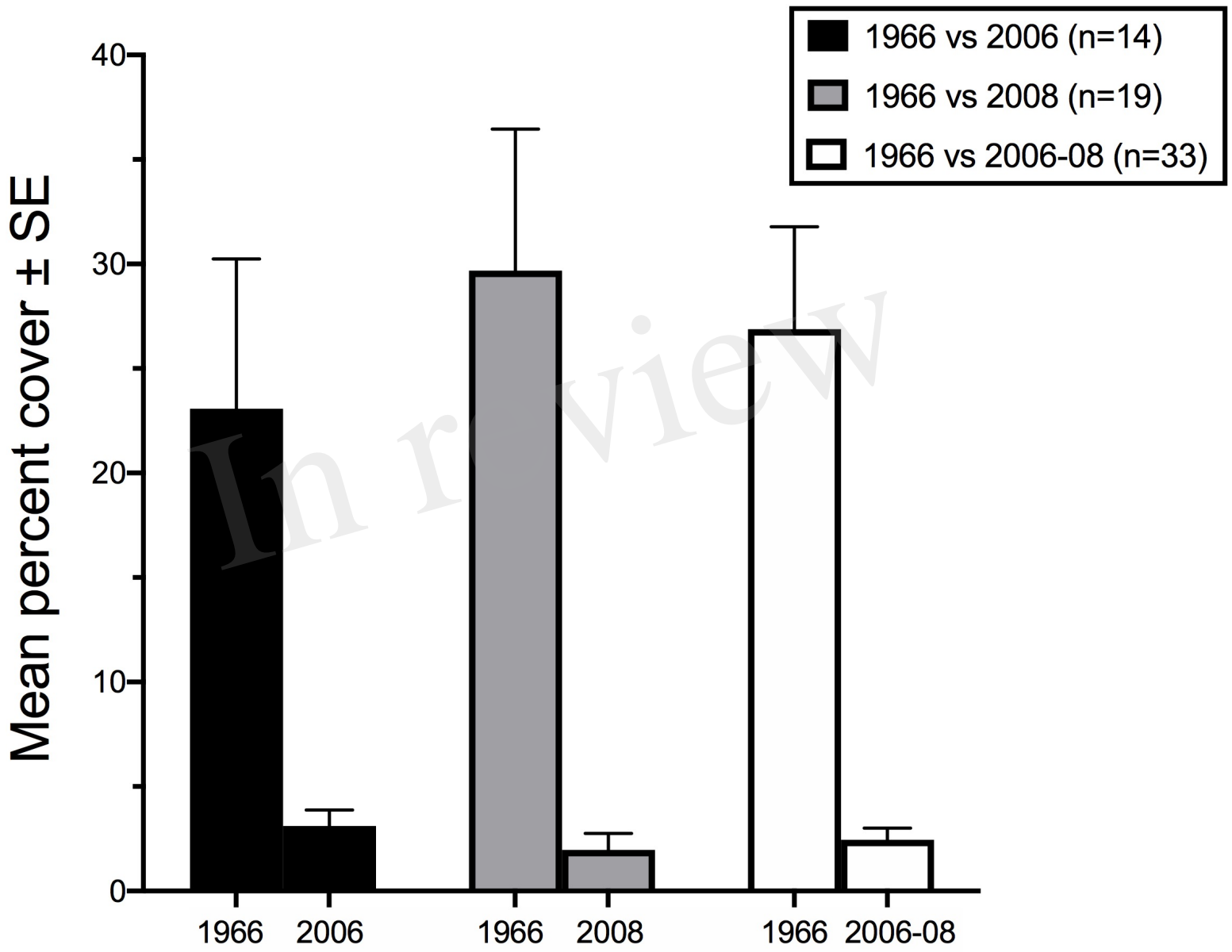


Figure 7.JPEG



Summer 2006

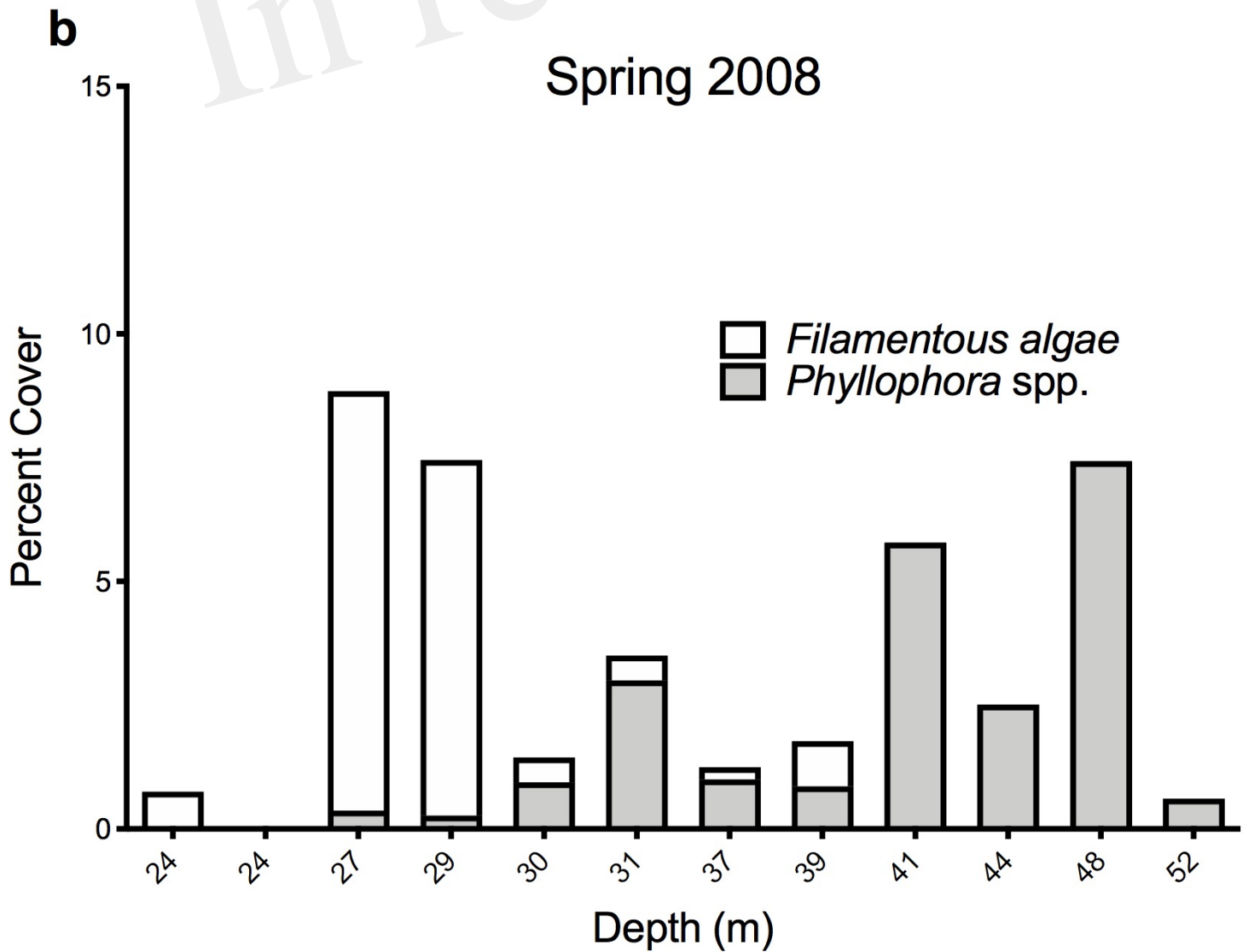
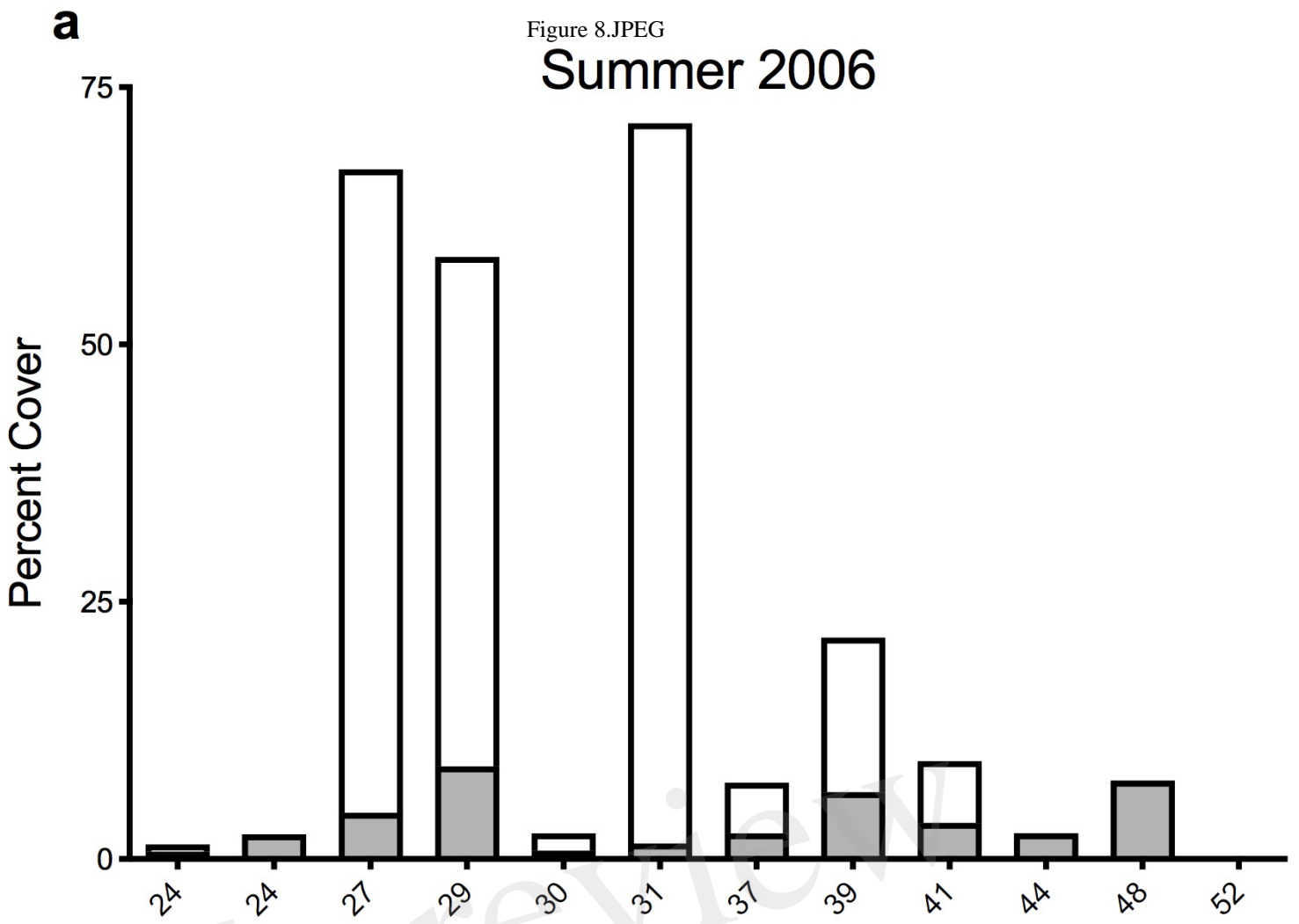


Figure 9.JPEG

