



**Manchester
Metropolitan
University**

Marret, Fabienne, Bradley, Lee R, Tarasov, Pavel E, Ivanova, Elena V, Zenina, Maria A and Murdmaa, Ivar O (2019) The Holocene history of the NE Black Sea and surrounding areas: an integrated record of marine and terrestrial palaeoenvironmental change. *The Holocene*, 29 (4). pp. 648-661. ISSN 0959-6836

Downloaded from: <https://e-space.mmu.ac.uk/622413/>

Version: Accepted Version

Publisher: SAGE Publications

DOI: <https://doi.org/10.1177/0959683618824769>

Please cite the published version

<https://e-space.mmu.ac.uk>

1 **The Holocene history of the NE Black Sea and surrounding areas: an**
2 **integrated record of marine and terrestrial palaeoenvironmental change**

3

4 Fabienne Marret¹, Lee R. Bradley², Pavel E. Tarasov³, Elena V. Ivanova⁴, Maria A. Zenina⁴
5 and Ivar O. Murdmaa⁴

6

7 ¹ University of Liverpool, School of Environmental Sciences, Department of Geography and
8 Planning, Liverpool, L69 7ZT, UK

9

10 ² Manchester Metropolitan University, School of Science and the Environment, Manchester,
11 M1 5GD, UK

12

13 ³ Institute of Geological Sciences, Palaeontology, Freie Universitaet Berlin, Malteserstr. 74-
14 100, Haus D, 12249 Berlin, Germany

15

16 ⁴ Shirshov Institute of Oceanology, Russian Academy of Science, 36 Nakhimovsky Prospect,
17 Moscow, 117997, Russia

18

19 * Corresponding author: Email: f.marret@liverpool.ac.uk; Phone +44 151 794 2848

20

21 **Abstract**

22

23 Here we present an almost complete and integrated Holocene record of marine and
24 terrestrial palaeoenvironmental change from the NE shelf of the Black Sea. A dinoflagellate
25 cyst record used to reconstruct Holocene sea-surface conditions highlights that the NE shelf
26 was a brackish water environment, with a minimum of salinity of 7 psu in the early-Holocene
27 before changing at a gradual rate to a more saline environment with maximum salinities of
28 ~18 psu being reached around 3 cal ka. A warming phase was detected from 6 cal ka BP,
29 with warmest conditions between 3 and 2.5 cal ka BP. A pollen record is used to examine
30 the major climate and land-use changes in the eastern Black Sea region. Biome
31 reconstructions show that the temperate deciduous forest dominates throughout the record,
32 although with an overall decline. From early Holocene to the first hiatus around ~9 cal ka BP,
33 *Pinus* pollen dominates, while taxa representing a mixed oak-hornbeam-beech forest are
34 less abundant, indicating relatively cool and dry conditions. Between ~7.9 to ~6.1 cal ka BP,
35 a thermophilous deciduous forest established, suggesting an overall warming trend and
36 humid conditions. From 4 cal ka BP, *Pinus* dominates the pollen record, accompanied by an

37 increase of herbs, implying an opening of the landscape, which would coincide with the
38 beginning of the Meghalayan Age. The integrated record of the marine and terrestrial climate
39 indicators supports the notion that this change in landscape may have been triggered by a
40 combination of warmer and drier conditions and human activities in this region.

41

42 **Key Words:** Dinocysts; Black Sea; Holocene; Sea surface salinities; Pollen; Biomes

43

44 **1. Introduction**

45

46 Environmental change in the Black Sea during the Holocene has been increasingly
47 investigated using various proxies over the past two decades. Numerous published studies
48 agree that the reconnection of the Black Sea to the global ocean, via the Bosphorus Strait,
49 initiated between ~9.6 to 9 cal ka BP (e.g. Hiscott et al., 2002; Major et al., 2006; Ivanova et
50 al., 2015; Lister et al., 2015; Aksu et al., 2016; Hiscott et al., 2017; Yanchilina et al., 2017).
51 The initiation and development of the reconnection and the establishment of a two-way
52 exchange of water between the Black Sea and Marmara Sea was the primary control on
53 sea-level rise in the early and mid-Holocene (Balabanov, 2007; Brückner et al., 2010; Hiscott
54 et al., 2017). However, the baseline conditions prior to the establishment of the two-way flow
55 and the rate of change after ~9.6-9.0 cal ka BP are still contested. Two recently published
56 studies highlight this disagreement. According to Yanchilina et al. (2017), the Black Sea
57 palaeoshore was around 120 mbsl around ~9.3 cal ka BP, with a Black Sea disconnected to
58 the Marmara Sea. It was estimated that the filling of the Black Sea to reach the level of the
59 Bosphorus strait took less than 40 years. In contrast, the recent study of Aksu et al. (2016)
60 demonstrated that there was a strong Black Sea outflow in the Marmara Sea in the early
61 Holocene, suggesting that the sea level was either at the Bosphorus sill level or slightly
62 higher. Most recent studies agree that modern sea levels, albeit minor fluctuations, were
63 established ~4 cal ka BP (e.g., Balabanov, 2007; Brückner et al., 2010).

64

65 Secondary controls on the conditions of the Black Sea during the Holocene include regional
66 climate change and human activity. In comparison to studies examining the reconnection to
67 the global ocean, these secondary influences are less well investigated. However, a few
68 records show some interesting pattern of climate change during the Holocene, sometimes
69 conflicting. The Sofular Cave record (Göktürk et al., 2011) highlighted enhanced and more
70 intense precipitations in the southern Black Sea region between 9.6 and 5.4 cal ka BP, in
71 agreement with regional climatic trends reconstructed from pollen records from the east
72 Mediterranean (e.g., Kotthoff et al., 2008). However, further west, in the Marmara Sea, in
73 the Gulf of Gemlik, sedimentary records suggest dry conditions between 8.2 and 5.4 cal ka

74 BP followed by alternation of wet and dry climate conditions (Filikci et al., 2017). Pollen
75 record from Varna Lake suggests relatively humid conditions early Holocene until 5.6 cal ka
76 BP with continental conditions replacing oceanic ones (Filipova-Marinova et al., 2016). Few
77 climate reconstructions are available for the NE region of the Black Sea. A recent study
78 based on pollen records located in the Taman Peninsula from Bolikhovskaya et al. (2018)
79 shows alternations of warm/arid phases with humid intervals for the last 7400 years. Finally,
80 the pollen-based climatic reconstructions for Europe by Mauri et al. (2015) highlight the
81 contrast between the northern and southern region of the Black Sea. Holocene human
82 occupation around the Black Sea has been relatively well documented by archaeologists
83 (e.g., Anthony, 2007), notably in the west and north. Pollen record from the coastal NW
84 Bulgaria region of the Black Sea evidences human impact on the vegetation from around
85 7250 cal year BP (Tonkov et al., 2014). Other record of significant land use (deforestation)
86 was presented by Giosan et al. (2012) who showed the effects of catchment processes in
87 the late-Holocene in the area surrounding the Danube Delta, including on dinoflagellates.

88

89 Palynological records yield fundamental information about past vegetation, biogeography
90 and palaeoclimate reconstructions (e.g. Mauri et al., 2015). The Black Sea region has very
91 few Holocene terrestrial pollen records, despite being of high interest as a region of
92 vegetation refugia during the LGM (e.g. Leroy and Arpe, 2007). However, marine cores have
93 provided suitable palynological records, in particular in the NW and SW parts of the sea
94 (Cordova et al., 2009, Marinova et al., 2018). In the SE Black Sea basin (core 22-GC3/8)
95 has provided insights on the late Quaternary evolution of the vegetation, with evidence of
96 warmer than present-day conditions during the last interglacial period, ca. 125 ka, as well as
97 an increase of precipitation by 100-200 mm/year (Shumilovskikh et al., 2013). A detailed
98 pollen record from this core covering the entire Holocene interval (Shumilovskikh et al.,
99 2012) has been analyzed using a quantitative method of vegetation reconstruction, also
100 known as “biomization” (Prentice et al., 1996). This globally tested method (Prentice et al.,
101 2000; Wanner et al., 2008) uses plant functional types (PFTs), which are broad classes of
102 plants defined by growth and leaf form, phenology, and climatic adaptations. The PFT
103 concept allows objective assignment of palaeobotanical data (i.e. pollen and plant
104 macrofossils) to major regional vegetation types (i.e. biomes) and selection of a dominant
105 biome by calculating/comparing the numerical biome scores (Prentice et al., 1996). The
106 same PFT concept is also used in all climate-driven vegetation models, which can simulate
107 global and regional vegetation distributions (Prentice et al., 1992). The use of a common set
108 of PFTs in the biome reconstruction and simulation allows more robust climatic
109 interpretations of the analyzed palaeodata and facilitate data-model comparisons (Prentice
110 et al., 1996).

111 In contrast to the SW and NW, the NE region of the Black Sea has a paucity of Holocene
112 pollen records, either on the land or in basin (Mauri et al., 2015; Bolikhovskaya et al., 2018).
113 However, ostracod- and mollusc-based studies of benthic changes in this area show three
114 periods of differing environments (Ivanova et al., 2007, 2012, 2015; Zenina et al., 2017).
115 These studies have documented the dominance of Caspian-type assemblages from early
116 Holocene to 7.4 cal ka BP followed by a relatively short interval of co-habitation of Caspian
117 and Mediterranean types (between 7.4 and 6.8 cal ka BP). From 6.8 cal ka BP, ostracod and
118 mollusc fauna are progressively dominated by Mediterranean species. Very similar
119 assemblages were found in the SW shelf (Williams et al., 2018), except that the
120 disappearance of Caspian type occurred around 6.3 cal ka BP, about 500 years later than in
121 NE. Contrary to the ostracod records in the NE, proxy record of surface conditions is limited
122 to the incomplete record of dinoflagellate cyst (dinocyst) assemblages in core Ak-2575
123 published in Ivanova et al. (2015). Recent Holocene dinocyst records in the Black Sea (e.g.
124 Mudie et al., 2001; Marret et al., 2009; Verleye et al., 2009; Bradley et al., 2012;
125 Shumilovskikh et al., 2012; 2013) have demonstrated the richness in species and detailed
126 environmental changes in salinity conditions. Early Holocene assemblages show a
127 dominance of brackish species, *Spiniferites cruciformis* and *Pyxidinoopsis psilata*, although
128 presence of the euryhaline species *Lingulodinium machaerophorum* indicated marine
129 influence and salinity above 7 psu (e.g., Marret et al; 2009; Mertens et al., 2012). Full
130 modern conditions were reached around 4.1 cal ka BP.

131

132 This study aims to evaluate whether changes in water conditions (amplitude and timing)
133 across the Black Sea basin were contemporaneous during the Holocene as well as to
134 assess the impact of climatic changes in the NE region. To address these issues, we have
135 analysed core Ak-2575 retrieved on the northeastern shelf of the Black Sea (e.g., Ivanova et
136 al., 2012) for its integrated record of pollen and dinoflagellate cysts.

137

138 **2. Modern regional setting**

139

140 The Black Sea is a relatively deep-water basin, with a mean depth of 1315 m, and a
141 maximum of 2258 m at its centre (Figure 1); the sea shelves are in general narrow (only
142 occupying 25% of the basin) with the exception of the NW region where they extend for
143 more than 200 km. Its only connection to the world ocean is through the Bosphorus Strait
144 which is about 30 km long, with a depth varying between 20 and 100 meters. The Sea of
145 Azov in the NW region is a relatively shallow basin, with a maximum depth around 15 m and
146 it is connected to the Black Sea via the Kerch Strait. Three major rivers (Danube, Dnieper
147 and Dniester) in the NW region comprise most of the river input (80%); other important rivers

148 are the Caucasian rivers Kodori, Inguri, Rioni and Chorokhi which are classified as mid-size
149 rivers with a drainage area from 2000 to 50,000 km² (Mikhailov and Mikhailova, 2008)

150

151 INSERT FIGURE 1 HERE

152

153 The Black Sea is characterised by a permanent halocline and is strongly stratified, with a
154 well oxygenated surface water (up to 50 m water depth) and anoxic conditions and high
155 sulphide concentrations from 100 m to the bottom. Annual surface salinity ranges from ~15
156 psu (in the NW region, near river mouths, and south of the Kerch Strait) to 18-19 psu in the
157 middle of the basin (Figure 2b; Boyer et al., 2013). Bottom salinity is influenced by
158 Mediterranean waters flowing and averages 22 psu. Annual sea-surface temperatures (SST)
159 show a west-east gradient, with the lowest values in the Odessa Bay (~10°C) and the
160 highest off Sochi (~18°C), in the eastern region of the sea (Figure 2a). Movement of the
161 surface water mass is controlled by wind, river input and climate (temperature, evaporation
162 and precipitation). A cyclonic circulation, the Rim Current, is composed of two main cyclonic
163 gyres in the western and eastern regions respectively and a number of anti-cyclonic eddies
164 (Toderascu and Rusu, 2013).

165

166 INSERT FIGURE 2 HERE

167

168 Topography around the Black Sea is quite diverse, with plains in the west and north, and
169 mountainous in the east (Caucasus) and the south (Pontic) (Figure 1). The north-western
170 region is under the influence of a humid continental climate, whereas the southwest region
171 reveals Mediterranean-type climate. The northeastern side is characterised by humid
172 subtropical conditions, and the southern coast is dominated by an oceanic climate (Peel et
173 al., 2007). The studied region is the only coastal region in Russia to have subtropical
174 landscapes as well as humid to semi-arid landscapes (Petrooshina, 2003). Winter
175 temperatures average 3 to 5°C in winter up to 23-24°C in summer.

176

177 The vegetation in the studied region is characterized by the Colchic forest which is a relic of
178 Tertiary forest of Western Eurasia (Nakhutsrishvili et al., 2011). A succession can be
179 observed according to altitude, with in the lowland area, up to 500 m, a dominance of oak-
180 hornbeam (*Quercus pubescens* – *Carpinus orientalis*) forests, accompanied by *Fraxinus*
181 *excelsior* (Figure 3). From 300-800 m to 1000 m, a mixed sessile oak (*Quercus petraea*) –
182 hornbeam (*Carpinus betulus*, *C. orientalis*) forest is observed. Above this vegetation unit, the
183 Caucasian oriental beech forests dominate the landscape, up to 1800-2000 m. *Fagus*
184 *sylvatica* subs. *orientalis* is the dominant tree, accompanied by *Tilia*, *Acer*, *Ulmus*, *Castanea*

185 *sativa*. This forest also alternates with the west Caucasian fir-spruce forests (*Abies*, *Picea*).
186 High altitude areas are covered with grasslands with some patches of *Pinus* forests,
187 although pine can also be found in lower latitudes as they are eurythermic trees and their
188 presence may be associated with human activities, with sandy and/or stony locations (Bohn
189 et al., 2004).

190

191 INSERT FIGURE 3 HERE

192

193 **3. Material and methods**

194

195 The 186cm long sediment core Ak-2575 was collected in 2007 from the NE Caucasian outer
196 shelf (44°13.46'N, 38°38.03'E, water depth 99 m), during the cruise by RV *Akvanavt*. A semi-
197 liquid surface layer of unknown thickness, ~ 10 cm, was likely lost during the core Ak-2575
198 processing. Detailed lithology, an age model based on molluscs only as well as a preliminary
199 dinoflagellate cyst record can be found in Ivanova et al. (2015). The core was sliced into two
200 cm thick samples and a total of 45 samples were used for palynological analysis.

201

202 3.1 Age model of core Ak-2575

203

204 18 AMS radiocarbon ages were obtained on samples from core Ak-2575. These include
205 eleven dates on bivalve molluscs and seven from monospecific ostracod samples (Table 1).
206 For the extraction of the dated material, sediment samples were wet sieved and ostracods
207 were picked out and rinsed several times before being placed in glass vials and dried
208 overnight at 40°C. Samples were analysed at Scottish Universities Environmental Research
209 Centre (SUERC), Keck C Cycle AMS laboratory and Poznań Radiocarbon Laboratory
210 (UCIAMS). ¹⁴C dates were calibrated using IntCal13 (Reimer et al., 2013). A reservoir
211 correction of 404 ± 91 years for radiocarbon dates <7500 ¹⁴C years, 300 ± 125 for
212 radiocarbon dates between 7500 – 8400 ¹⁴C years, and 258 ± 55 years for ages >8400 ¹⁴C
213 years were applied (see Ivanova et al., 2015). The age-depth model for Ak-2575 (Figure 4)
214 was constructed using Bacon (Blaauw and Christen, 2011) in R (R Development core team
215 2018) using all samples listed in Table 1. Three hiatuses were inserted into the model using
216 sediment data and seismic profiles presented and discussed in Ivanova et al. (2015). Ages
217 used in this paper are given as mean ages and are reported as calibrated ages BP (0 cal BP
218 = AD 1950).

219

220 INSERT TABLE ONE HERE

221

222 3.2 Palynological preparation and analysis

223 Sample preparation follows that of Marret et al. (2009). Volume of sediments was first
224 estimated and followed by the addition of exotic markers (*Lycopodium clavatum*) enabling to
225 calculate palynomorph concentrations (specimens/ml). Sediments were then treated with
226 cold 10% hydrochloric acid, follow by cold 40% hydrofluoric acid to remove carbonate and
227 silicate content, respectively. Residues were then treated with 10% HCl to remove
228 fluorosilicates. Samples were neutralised between acid treatments with distilled water.
229 Residues were sieved with a 10 µm mesh and the larger fraction was mounted on a
230 microscope slide in glycerine jelly stained with safranine. Where possible, a minimum of 100
231 dinoflagellate cysts and a minimum of 300 pollen grains were counted. Dinocyst taxonomy is
232 based on Marret et al. (2004; 2009). *Spiniferites* spp. and *Brigantedinium* spp. comprise of
233 specimens that could not be identified at the species level due to poor orientation or hidden
234 diagnostic characteristics. Specimens of *L. machaerophorum* were often broken or folded,
235 and they were rare in many samples, so attempting to reconstruct past salinity using the
236 equation from Mertens et al. (2012) would not have been statistically reliable. Pollen
237 identification follows that of Beug (2004) and pollen reference collection at the Department of
238 Geography and Planning, University of Liverpool and Department of Palynology and Climate
239 Dynamics of the University of Göttingen. Dinocyst percentages were calculated on the whole
240 sum of dinocysts, and pollen percentages are based on arboreal and non-arboreal pollen
241 grains; but due to the over-representation of *Alnus*, the pollen percentages were calculated
242 with a sum excluding *Alnus*. Spores were excluded from the pollen sum but are presented in
243 the diagram. We also paid attention to occurrence of non-pollen palynomorphs as described
244 in Mudie et al. (2010) but surprisingly they were absent. The biomization approach applied in
245 this study follows a standard procedure described in Prentice et al. (1996). All terrestrial
246 pollen taxa found in the Ak-2575 record were assigned to the respective biomes following
247 Shumilovskikh et al. (2012). Biome affinity scores were calculated for each sample following
248 the equation published in Prentice et al. (1996).

249 Examining all biome affinity scores (and not only deriving the dominant biome name)
250 throughout a pollen record for more objective interpretation of reconstruction results has
251 been presented in various papers published elsewhere (i.e., Tarasov et al., 2005; Marchant
252 et al., 2006; Rudaya et al., 2009). For the purpose of the current study, we selected three
253 biomes for further discussion. Temperate deciduous (TEDE) forest biome reveals the
254 highest affinity score through the entire pollen record and is well represented in the natural
255 vegetation of the region (Shumilovskikh et al., 2012). Taiga (TAIG) biome includes the
256 following PFTs, including boreal evergreen conifers (e.g. *Picea*, *Abies*), eurythermic conifers
257 (*Juniperus*, *Pinus* s/g *Diploxylon*), boreal summergreen trees/shrubs (e.g. *Alnus*, *Betula*,
258 *Larix*), and shrubs of the heath family (Prentice et al., 1996). This biome is predicted by the

259 BIOME model at high elevations in the central European mountains, where winters are cold
260 and precipitation meets >75% of demand (Prentice et al., 1992). Steppe (STEP) biome
261 includes grass/shrub communities and is limited (under natural conditions) to the lower
262 elevations where climate is too dry and can not support forest vegetation. Thus,
263 reconstructed changes in the TAIG and STEP biome scores have potential to represent the
264 climatic/altitudinal extremes in the study region.

267 **4. Results**

269 4.1 Chronology

270
271 The ¹⁴C AMS ages (Table 1) show that site Ak-2575 recovered a section of Holocene
272 sediments with a basal age of ~9800 cal years BP. The age-depth model shows four phases
273 of sedimentation history (Figure 4) constrained by three hiatuses. The earliest phase of
274 sedimentation (9800- to 8950 cal year BP) suggests a relatively slow accumulation rate in
275 the earliest part of our record. The oldest hiatus (A) occurs between 8950-7950 cal yr BP
276 (164 cm). The second phase of the sediment record occurs between 7950-7770 cal yr BP.
277 At 156 cm there is an assumed very short-break in the record (<100 years, hiatus B) before
278 a third phase of the record between 7770 and 6020 cal yr BP. The sediment record shows
279 that hiatus B separates *Dreissena coquina* facies from a mixed mollusc fauna *coquina*
280 (Ivanova et al., 2015). The newly obtained date at 153 cm supports this hypothesis of a very
281 short-break in the record as well as the conclusion of Ivanova et al. (2015) that the dated
282 *Dreissena* sp. shell with raw age of 8215±30 ¹⁴C (9030-8430 cal year BP) is reworked.

283
284 INSERT FIGURE 4 HERE

285
286 The youngest break in the sediment record occurs between 6020-4130 cal year BP (42 cm)
287 and is highlighted in Figures 5, 6, and 7 as hiatus C. From ~ 4130 cal year BP to present,
288 the sedimentation rate slows and the modelled age errors increase. The dated ostracod level
289 at 32 cm (4820-4440 cal year BP) is older than the dated bivalve level at 37 cm (3830-3390
290 cal year BP). A similar situation repeats in the youngest section of the core where the dated
291 ostracod level at 9 cm (3390-3240 cal year BP) is older than the dated bivalve level at 19 cm
292 (2800-2360 cal year BP). The model assumes that core top is AD 2007. This suggests a
293 very slow sediment accumulation rate in the top 9 cm of this core and interpretation of
294 results from this section should be viewed with caution.

296 4.2 Dinoflagellate cyst assemblages

297

298 Dinocyst assemblages of core Ak-2575 are relatively diverse, with a total of 20 taxa,
299 dominated by *Lingulodinium machaerophorum* and *Spiniferites* species (Figure 5).
300 Concentrations (cysts/ml) are overall relatively low, with on average 4185 cysts/ml, ranging
301 from 140 cysts/ml to 27,599 cysts/ml. Three main assemblages can be observed between
302 the two main hiatuses (A and C). Prior to Hiatus A, from ~9.8 cal kyr, the assemblages are
303 dominated by two species of Caspian-brackish origin, *Pyxidinoopsis psilata* and *Spiniferites*
304 *cruciformis*. Accompanying taxa are *L. machaerophorum*, *Spiniferites belerius* and
305 *Spiniferites bentorii*. Cyst concentrations are at their lowest during this interval, with fewer
306 than 330 cysts/ml.

307

308 INSERT FIGURE 5 HERE

309

310 Between Hiatus A and Hiatus C, the species dominance has shifted to *L. machaerophorum*,
311 in particular its morphotype with short processes. *S. belerius* and *S. bentorii* are second.
312 Species of Mediterranean origin are occurring in low frequencies, such as *Operculodinium*
313 *centrocarpum*, *Spiniferites delicatus*, *Spiniferites mirabilis* and *Tectatodinium pellitum*. This
314 interval also sees the disappearance of *P. psilata* while *S. cruciformis* is still present, with
315 low percentages (up to 7.5%). Interestingly, this interval contains the only occurrences of
316 *Impagidinium caspiense* as well as sporadic presence of *Caspidinium rugosum*. Cysts of
317 *Pentapharsodinium dalei* appeared here for the first time in the record. Concentrations
318 reached their highest values during this interval, with a maximum (27,599 cysts/ml) around
319 6.9 cal ka.

320

321 The assemblages above Hiatus C show that *S. cruciformis* still occurs, albeit in low
322 percentages, similarly to the previous interval. *L. machaerophorum* still dominates this
323 interval but we note the very low occurrences of its morphotype with short processes.
324 Mediterranean taxa occur in higher percentages compared to the previous interval;
325 *Operculodinium israelianum* briefly appears between 2.9 and 2.3 cal ka. An unknown taxon
326 of *Spiniferites*, *Spiniferites* sp. 1 also temporarily occurs between 2.9 and 1.7 cal ka. This
327 cyst is of ovoidal shape, sometimes slightly cruciform, with a paratabulation expressed with
328 very developed sutural septa between all processes. The body size is around 40 microns by
329 32 microns and process length ~12 microns (Plate 1). The last 2000 years sees the
330 occurrence of euryhaline taxa, *Achomosphaera* sp. and *Ataxiodinium choane*.
331 Concentrations are lower than the previous interval, averaging 1834 cysts/ml.

332

333 4.3 Pollen assemblages and reconstructed biome scores

334

335 A total of 44 pollen taxa were identified and are overall dominated by tree species, in
336 particular by *Alnus* and *Pinus*, followed by *Quercus*, *Fagus* and *Corylus* (Figure 6).
337 Concentrations are higher compared to those of dinocysts, ranging from a minimum of 862
338 grains/ ml to a maximum of 56,413 grains/ ml, and averaging 15,770 grains/ml. Similarly to
339 the dinocyst record, three types of assemblages can be observed between the two main
340 hiatuses A and C. From the bottom of the record to Hiatus A, *Pinus* and *Quercus* dominate
341 pollen spectra, and are accompanied with low occurrences of *Carpinus*, *Fagus* and *Corylus*.
342 Concentrations are the lowest of the whole record, with a maximum of 9704 grains/ml. Herb
343 taxa are present, with a low diversity (13 species of a total of 21 herb taxa) and mainly
344 comprised of *Artemisia*, Poaceae and Amaranthaceae.

345

346 INSERT FIGURE 6 HERE

347

348 Between Hiatus A and Hiatus C, *Fagus* and *Corylus* dominate the tree taxa, whereas
349 *Quercus* occurs similarly as in the previous interval. *Carpinus* and *Alnus* have their highest
350 occurrence of the whole record. *Picea* is recorded only between ~7 cal ka and 6 cal ka.
351 *Ulmus* and *Abies* record their highest percentages from the whole spectra from 8 cal ka BP
352 to ~7 cal ka BP. *Ostrya* is observed only in this interval. *Fraxinus* is present throughout this
353 interval up to ~6.5 cal ka BP, always in low percentages. Herb taxa diversity is at its highest
354 and are still dominated by *Artemisia*, followed by Poaceae then Amaranthaceae.

355

356 From Hiatus C to the top of the core, tree pollen are dominated by *Pinus*, and secondarily by
357 *Alnus* and *Quercus*. There are rare occurrences of *Picea* around 3 and 2 cal ka. *Ulmus* and
358 *Carpinus* have their lowest relative abundance compared to the two previous intervals.
359 Significant percentages of *Taxus* are observed from 2 cal ka upward.

360

361 The biome score record (Figure 7) demonstrates that pollen taxa representing the low-
362 elevation temperate deciduous forest (TEDE) have a maximum contribution to the pollen
363 assemblages of the analyzed core. A progressive decrease in the TEDE biome scores is
364 recorded since 4 cal ka BP, accompanied by an increase in the STEP biome scores,
365 suggesting an opening of the landscape during this period forced by either climatic factors
366 or/and human activities. The TAIG scores reflecting pollen contribution from the boreal
367 evergreen and deciduous forest taxa show rather minor fluctuations, suggesting greater
368 stability of the higher-elevation forest belt.

369

370 INSERT FIGURE 7 HERE

371

372 **5. Discussion**

373

374 5.1 Contemporaneity of environmental change across the Black Sea Basin during the 375 Holocene?

376

377 Two of the main debates surrounding environmental change in the Black Sea during the
378 Holocene period are 1) baseline conditions around 10-9 cal ka BP and 2) subsequent rates
379 of change in sea level and salinity. This study suggests that on the NE Black Sea shelf, the
380 baseline conditions consisted of brackish water (>7 psu), sea level and salinity began to rise
381 after ~9.6-9.0 cal ka BP; rates of change were gradual (>1000 years) as shown by the slow
382 decline/disappearance of the Caspian/brackish species (Figure 7). Similar findings were
383 observed with the benthic bivalve community (Ivanova et al., 2007, 2012, 2015; Zenina et
384 al., 2017). The dinocyst species composition from core Ak-2575 is consistent with other
385 recent Holocene records from the Black Sea (Marret et al., 2009; Bradley et al., 2012,
386 Shumilovskikh et al., 2013, Verleye et al., 2009), albeit with a lower diversity compared to
387 the records from the SW. It is interesting to note that our record contains only two
388 heterotrophic taxa, with *Brigantedinium* spp. and *Peridinium ponticum*. This raises the
389 possibility of a preservation issue for the heterotrophic species as suggested by Zonneveld
390 et al. (2008); however, the anoxic character of the Black Sea suggests that other parameters
391 may explain this paucity of heterotrophic species. It could be that the prevalence of lower
392 productivity conditions in the eastern region compared to the west would have favoured the
393 dominance of autotrophic species, which is the case at present-day (Mudie et al., 2017). *S.*
394 *cruciformis* and *P. psilata* are the main components prior to ~9.8 cal kyr BP (Figure 5) and
395 highlight the dominance of Caspian/brackish taxa (Figure 7). There is a secondary influence
396 of climate on sea-surface conditions with thermophilic taxon being recorded ~2.5 cal ka BP.
397 Human-impact has limited effect on the sea-surface conditions with no toxic dinocysts such
398 as cysts of *Gymnodinium catenatum* recorded unlike in studies from other areas of the basin
399 such as the southwestern shelf (Marret et al., 2009; Bradley et al., 2012). These cysts were
400 thought to have been introduced from ship ballasts about 3000 years ago.

401

402 **Baseline (10 – 9 cal ka BP)**

403 Although there is a broad agreement as to when the reconnection took place, around 9.6-9.0
404 cal ka BP, a dispute remains with regards to the surface water level of the Black Sea prior to
405 the reconnection. According to Yanchilina et al. (2017), the Black Sea palaeoshore was
406 around 120 mbsl around 9.3 cal ka BP, with a rapid infilling of the basin, in less than 40

407 years, isolating this sea from the global ocean. On the opposite side, the recent study of
408 Aksu et al. (2016) demonstrated that there was a strong Black Sea outflow in the Marmara
409 Sea in the early Holocene, suggesting that the sea level was either at the Bosphorus sill
410 level (currently at 35 mbsl) or slightly higher. Both sets of evidence rely on geophysical,
411 geochemical and micropalaeontological data as well as radiocarbon dated material. The
412 sedimentation record (see Ivanova et al., 2015) from our site shows that the NE shelf was
413 water covered from at least 10 cal ka BP (Figure 4). There no evidence of reworked
414 palynomorphs and ostracods (Zenina et al., 2017) at this site which further supports that the
415 area was inundated prior to 10 cal ka BP.

416

417 Another disagreement is the salinity condition of the Black Sea prior to its reconnection, with
418 Ryan and co-workers (e.g. Ryan et al., 2002; Ryan, 2007) supporting the idea of a
419 freshwater environment, whereas other studies suggest brackish conditions (e.g. Mudie et
420 al., 2001; Marret et al., 2009; Mertens et al., 2012). Ivanova et al. (2015) and Zenina et al.
421 (2017) used mollusc and ostracod data to show that the benthic conditions were brackish in
422 this time period, estimating salinity to be around 7 psu. The dinocyst record, especially the
423 presence of *L. machaerophorum* and *S. mirabilis*, supports this conclusion and suggests that
424 the surface salinities were also a minimum of 7 psu prior to 9.6-9.0 cal ka BP. This is similar
425 to conclusions from studies examining surface conditions (e.g. Marret et al., 2009; Bradley et
426 al., 2012; Mertens et al., 2012; Bradley and Marret, 2013) and benthic conditions (Williams
427 et al., 2018) on the southwestern shelf.

428

429 **Transition to modern-day conditions**

430 Perhaps the most striking finding from the dinoflagellate cyst analysis is the occurrence,
431 albeit in low relative abundance, of Ponto-Caspian species in the mid to late Holocene. This
432 is in contrast to the findings of Marret et al. (2009) and Bradley et al. (2012) whose analysis
433 of Holocene sediment on the south-western shelf of the Black Sea showed the species such
434 as *S. cruciformis* and *P. psilata* only sporadically occurred after 6000 cal yr BP. Verleye et al.
435 (2009) found from core GeoB7625-2 taken from a deeper water site at -1242m that both
436 species were also present, again in a very low occurrence. The modern distribution of these
437 species shows that they are currently present in the Black Sea and Caspian Sea (Mudie et
438 al., 2017).

439

440 This leads to two possible explanations. The first and most likely is that current ecological
441 tolerance of *S. cruciformis* is broader than previously assumed. Mudie et al. (2017) using 45
442 sites show that the current distribution extends across the Marmara Sea, Black Sea,
443 Caspian Sea and Aral Sea. Previously this species was thought only to be present in low

444 salinity (4-15 psu) due to its modern occurrence in the Caspian Sea. The finding of the cyst
445 in the freshwater Lake Sapanca (Leroy and Albay, 2010) showed it to be tolerant to
446 freshwater/brackish conditions and thus meant it was unable to be used in the freshwater vs
447 brackish debate of early-Holocene Black Sea salinities (Hiscott et al., 2007; Soulet et al.,
448 2010;). *P. psilata* has been identified in recent sediments in low percentages (<4%) mostly in
449 the Black Sea, and some rare presence in the Marmara Sea and Caspian Sea. However, it
450 has been observed in abundance during the late Pleistocene to mid-Holocene period in the
451 Caspian Sea (Leroy et al., 2007; 2013, 2014), where conditions were more saline than
452 present-day conditions.

453

454 A second explanation may be linked to SSTs. Besides SSS, SST may play a role in the
455 occurrence of *S. cruciformis* during the mid- to late Holocene in the NE. Its current modern
456 distribution indicates that it can tolerate a relatively wide range of annual SST (12-20.5°C),
457 with peak abundance in the warmest waters. Warmer conditions are also suggested with
458 relatively high occurrences of the thermophilic species *S. mirabilis* from 6.1 cal ka BP
459 onward. A possible maximum of warm conditions may have occurred between 3.0-2.5 cal ka
460 BP, as highlighted by the occurrence of *O. israelianum*. This species has not been seen in
461 modern sediments from the Black Sea nor the Caspian Sea and mainly occurs in waters
462 where winter SST are above 14.3°C and summer SST more than 24.2°C and can tolerate a
463 salinity range between 30.3 to 39.4 (Zonneveld et al., 2013). Mudie et al. (2017) have
464 observed modern distribution of *O. israelianum* only in the Marmara Sea, where SST are
465 close to the range that this species lives in but with SSS 10 lower.

466

467 This warm episode is in agreement with the warm climatic conditions suggested by pollen
468 records in the Taman Peninsula between 2.9 and 1.5 cal ka BP (Bolikhovskaya et al., 2018)
469 but has not been recorded in the west by the dinocyst record.

470

471 Another evidence of contemporaneity across the Black Sea basin is a significant peak of the
472 thermophilic species *S. mirabilis* at ~2.0 cal ka BP, observed in our core as well as in cores
473 MAR05-13 (Bradley et al., 2012) and 22-GC3 (Shumilovskikh et al., 2013). Subtle peaks of
474 this species are also observed in cores MAR02-45 (Marret et al., 2009) and GeoB7625-2
475 (Verleye et al., 2009). Pollen records in the Tasman peninsula do suggest warm and humid
476 conditions around this date (Bolikhovskaya et al., 2018).

477

478 Establishment of present-day conditions may have happened within the last 1500 years but
479 the low-resolution sampling at the top of core prevents us to exactly pinpoint this change.

480 However, our dinocyst assemblage indicates cooler conditions with the decrease of *S.*
481 *mirabilis*.

482

483 5.2 Changes in vegetation

484

485 Core Ak-2575 provides the first Holocene pollen record for the NE of the Black Sea, albeit
486 with the hiatuses, and reveals some subtle but significant changes in the vegetation source.
487 There is no significant river discharge into the NE Black Sea near by the core location (cf.
488 figure 1) and therefore all the pollen is assumed to be from wind dispersal and reflects
489 regional signal (e.g. Cordova et al., 2009). At present the dominant wind blows from the NE
490 (Zecchetto and de Biasio, 2007) and therefore the pollen is assumed to be from the eastern
491 edge of the Black Sea and the Greater Caucasus mountains. This complex pollen source
492 area means that pollen is coming from both lowland coastal areas and mountainous areas of
493 the Caucasus.

494 Within the pollen source area at present, the NE region is currently dominated by the
495 Oriental hornbeam (*Carpinus orientalis*) and mixed oak forests, which is reflected in the
496 pollen record with the relative high occurrence of *Quercus* but a low representation of
497 *Carpinus* at the top of the core. The high percentages of *Alnus* is likely transported from
498 coastal areas. Biome reconstructions show that the TEDE biome dominates the record but
499 overall declines from the bottom of our record.

500 During the early Holocene, our pollen record indicates the dominance of *Pinus* taxa, with
501 some evidence of a mixed oak-hornbeam-beech forest, suggesting relatively cool and dry
502 conditions. At present, no other vegetation records from adjacent regions can be compared
503 with our data. Further south to our study site, pollen data from Georgia (e.g. Connor and
504 Kvavadze, 2008; Joanin et al., 2013) reflect lower humidity. Reconstructed climate
505 conditions based on pollen spectra in Europe (Mauri et al., 2015) suggest overall cooler and
506 drier conditions during the time interval prior to Hiatus A in our core.

507

508 The period between hiatuses A (~7900 cal yr BP) and C (~6000 cal yr BP) shows a steady
509 ratio for the tree/shrub/herb ratio (Figure 6) but the changes in the relative abundance of the
510 tree and herbs (green and yellow curves respectively in figure 6) suggest large scale
511 changes in vegetation of the eastern Black Sea shore and the Greater Caucasus mountains.
512 Significant increase of *Carpinus*, *Fagus* and *Corylus* accompanied by the decline of *Pinus*,
513 but also the presence of *Ostrya* and *Ulmus* suggest the development of a thermophilous
514 deciduous forest, indicating an overall warming trend and humid conditions. Such climate
515 conditions were also recorded in the Taman Peninsula (Bolikhovskaya et al., 2018) and
516 further south (Connor and Kvavadze, 2008). Interestingly, this onset of warm/humid

517 conditions coincides with the establishment of a mixed Caspian-Mediterranean benthic fauna
518 observed in our core (Ivanova et al., 2015).
519 Following Hiatus A, from around 4 cal ka BP, a remarkable dominance of *Pinus* pollen
520 among the tree taxa, accompanied by higher abundance of herb taxa and a steady increase
521 in the STEP biome scores suggest an opening in the landscape due to possibly a
522 combination of drier/warmer conditions and human impacts. This landscape opening more or
523 less coincides with the onset of the Meghalayan Age. However, our dinocyst record
524 suggests the onset of warmer water conditions around 6.1 cal Ka BP, prior to Hiatus A. It is
525 worth noting that the peak of thermophilic dinocyst taxa (figure 7) corresponds to a clear
526 decrease of TEDE biome scores, suggesting that most likely, changes in the vegetation may
527 have been triggered by climatic conditions rather than human activities around 3-2.5 cal ka
528 BP. The noticeable occurrence of the taxon *Taxus*, a taxon which belongs to the
529 intermediate temperate conifer PFT and is related to mild winters (i.e. mean temperatures of
530 coldest month between -2 and +5°C: Prentice et al., 1996), around 2 cal ka BP is
531 concomitant with the warm water conditions suggested by the peak of *S. mirabilis* across the
532 basin. The increase in the STEP biome scores during the last 2000 years may reflect a
533 combined effect of the warmer temperatures (i.e. increased evaporation) and intensified
534 human impact (i.e. opening of the landscape and spread of grassland/meadow vegetation).
535 Although humid and warm conditions were reconstructed further north (Bolikhovskaya et al.,
536 2018), their moisture reconstruction may represent local situation in the Kuban River delta
537 rather than the regional trend.

538

539

540

541 **6. Conclusion**

542

543 We provide here the first integrated record of climatic conditions and terrestrial
544 environmental changes from the NE region of the Black Sea for the Holocene period.
545 Despite the presence of two hiatuses, the dinocyst record has enabled us to confirm the
546 contemporaneity of the major changes that have occurred prior, during and after the
547 reconnection of the Black Sea with the world ocean. The dominance of the Caspian/brackish
548 species, *S. cruciformis* and *P. psilata*, accompanied with the euryhaline species *L.*
549 *machaerophorum* and other *Spiniferites* species supports the theory that the Black Sea was
550 brackish, with a minimum of surface salinity of 7 psu prior to the reconnection. The gradual
551 change in dinocyst species composition and their abundance further corroborates previous
552 findings from the NE and SW for a gradual infilling of the Black Sea rather than a
553 catastrophic flooding. The relative abundance of thermophilic species highlighted that the

554 eastern region was warmer than the west around 3.0-2.5 cal ka BP, which reflects the
555 current gradient of SST in the Black Sea. Contrary to the western region, our record does
556 not contain any toxic dinoflagellate species, which suggests a limited impact of human
557 activities in this region.

558 In parallel, our pollen record also provides the first regional biome reconstruction for the NE
559 Black Sea and shows that during the early Holocene, the vegetation was responding to the
560 regional climatic conditions, cooler and drier. The onset of warm and humid conditions
561 around 7.9 cal ka BP is recorded by the establishment of a temperate deciduous forest; this
562 biome is gradually changed towards an increase of open landscape and *Pinus* after 4 cal ka
563 BP likely due to a combination of climatic conditions and human activities.

564

565

566

567

568 **Acknowledgments**

569 We would like to thank Alan Henderson with the preparation of the samples for the
570 palynological analysis. This study was supported by Leverhulme Trust (FM and LRB; project
571 “The Black Sea environmental conditions during the Meso- and Neolithic period”, F/00
572 025/AN), project 0149-2019-0007 by Shirshov Institute of Oceanology RAS (EI, IM and MZ)
573 and by the NERC Radiocarbon Facility NRCF010001 (allocation number 1729.1013; FM).
574 We are grateful for the constructive comments from two anonymous reviewers which helped
575 to improve our manuscript.

576

577 **References**

578

579 Aksu AE, Hiscott RN and Yaltırak C. (2016) Early Holocene age and provenance of a mid-
580 shelf delta lobe south of the Strait of Bosphorus, Turkey, and its link to vigorous Black Sea
581 outflow. *Marine Geology* 380: 113-137.

582

583 Anthony D. (2007) Pontic-Caspian Mesolithic and Early Neolithic societies at the time of the
584 Black Sea flood: a small audience and small effects. In: Yanko-Hombach V, Gilbert AS,
585 Panin N, et al. (eds) *The Black Sea Flood Question*. Dordrecht: Springer, 345-370

586

587 Balabanov IP. (2007) Holocene sea-level changes of the Black Sea. In: Yanko-Hombach V,
588 Gilbert AS, Panin N, et al. (eds) *The Black Sea Flood Question*. Dordrecht: Springer, 711-
589 730.

590

591 Beug HJ. (2004) Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende
592 Gebiete. Pleif, E (Ed), 542p.
593

594 Blaauw M and Christen JA. (2011) Flexible Paleoclimate Age-Depth Models Using an
595 Autoregressive Gamma Process. *Bayesian Analysis* 6: 457-474.
596

597 Bohn U, Gollub G, Hettwer C, et al. (2004) Karte der natürlichen Vegetation Europas/Map of
598 the Natural Vegetation of Europe. Maßstab/Scale 1:2.500.000— Interaktive. Münster.
599 Landwirtschaftsverlag.
600

601 Bolikhovskaya NS, Porotov AV, Richards K, et al. (2018) Detailed reconstructions of
602 Holocene climate and environmental changes in the Taman Peninsula (Kuban River delta
603 region) and their correlation with rapid sea-level fluctuations of the Black Sea. *Quaternary*
604 *International* 465: 22-36
605

606 Boyer TP, Antonov J, Baranova OK, et al. (2013) *World Ocean Database 2013*.
607

608 Brückner H, Kelterbaum D, Marunchak O, et al. (2010) The Holocene sea level story since
609 7500 BP - Lessons from the Eastern Mediterranean, the Black and the Azov Seas.
610 *Quaternary International* 225(2): 160-179.
611

612 Cordova CE, Harrison SP, Mudie PJ, et al. (2009) Pollen, plant macrofossil and charcoal
613 records for palaeovegetation reconstruction in the Mediterranean-Black Sea Corridor since
614 the Last Glacial Maximum. *Quaternary International* 197: 12-26.
615

616 Filikci B, Eriş KK, Çağatay N, et al. (2017) Late glacial to Holocene water level and climate
617 changes in the Gulf of Gemlik, Sea of Marmara: evidence from multi-proxy data. *Geo-Marine*
618 *Letters* 37: 501-513.
619

620 Filipova-Marinova M, Pavlov D and Giosan L. (2016) Multi-proxy records of Holocene
621 palaeoenvironmental changes in the Varna Lake area, western Black Sea coast. *Quaternary*
622 *International* 401: 99-108.
623

624 Giosan L, Coolen MJL, Kaplan JO, et al. (2012) Early anthropogenic transformation of the
625 danube-black sea system. *Scientific Reports* 2.
626

627 Göktürk OM, Fleitmann D, Badertscher S, et al. (2011) Climate on the southern Black Sea
628 coast during the Holocene: Implications from the Sofular Cave record. *Quaternary Science*
629 *Reviews* 30: 2433-2445.

630

631 Hiscott RN, Aksu AE and Yaltrak C. (2017) Modelling the provenance of detritus flushed
632 through the Strait of Bosphorus, Turkey, during early Holocene outflow from the Black Sea to
633 the world ocean. *Marine Geology* 390: 147-169.

634

635 Hiscott RN, Aksu AE, Yaşar D, et al. (2002) Deltas south of the Bosphorus Strait record
636 persistent Black Sea outflow to the Marmara Sea since ~10 ka. *Marine Geology* 190: 95.

637

638 Hiscott, R.N., Aksu, A.E., Mudie, P.J., Marret, F., Abrajano, T., Kaminski, M., Evans, J.,
639 Çakıroğlu, A.İ., Yaşar, D. (2007). A gradual drowning of the southwestern Black Sea shelf:
640 evidence for a progressive rather than abrupt Holocene reconnection with the eastern
641 Mediterranean Sea through the Marmara Sea Gateway. *Quaternary International*. 167 (8),
642 19–34.

643

644 Ivanova, E.V., Murdmaa, I.O., Chepalyga, A.L., Cronin, T.M., Pasechnik, I.V.,
645 Levchenko, O.V., Howe, S.S., Manushkina, A.V., Platonova, E.A., 2007. Holocene
646 sea-level oscillations and environmental changes on the Eastern Black Sea shelf.
647 *Palaeogeography, Palaeoclimatology, Palaeoecology* 246, 228-259.

648

649 Ivanova EV, Murdmaa IO, Karpuk MS, et al. (2012) Paleoenvironmental changes on the
650 northeastern and southwestern Black Sea shelves during the Holocene. *Quaternary*
651 *International* 261: 91-104.

652

653 Ivanova EV, Marret F, Zenina MA, et al. (2015) The Holocene Black Sea reconnection to the
654 Mediterranean Sea: New insights from the northeastern Caucasian shelf. *Palaeogeography*
655 *Palaeoclimatology Palaeoecology* 427: 41-61.

656

657

658 Kotthoff, U., Pross, J., Muller, U.C., Peyron, O., Schmiedl, G., Schulz, H., Bordon, A.,
659 2008. Climate dynamics in the borderlands of the Aegean Sea during formation
660 of sapropel S1 deduced from a marine pollen record. *Quaternary Science Reviews* 27: 832-
661 845.

662

663 Leroy SAG and Albay M. (2010) Palynomorphs of brackish and marine species in cores from
664 the freshwater Lake Sapanca, NW Turkey. *Review of Palaeobotany and Palynology* 160:
665 181-188.
666

667 Leroy SAG and Arpe K. (2007) Glacial refugia for summer-green trees in Europe and south-
668 west Asia as proposed by ECHAM3 time-slice atmospheric model simulations. *Journal of*
669 *Biogeography* 34: 2115-2128.
670

671 Lister CJ, Hiscott RN, Aksu AE, et al. (2015) Compositional trends through the Holocene
672 mud succession of the southwestern Black Sea shelf: Implications for sedimentary
673 provenance and water-level history. *Sedimentary Geology* 316: 13-25.
674

675 Major CO, Goldstein SL, Ryan WBF, et al. (2006) The co-evolution of Black Sea level and
676 composition through the last deglaciation and its paleoclimatic significance. *Quaternary*
677 *Science Reviews* 25: 2031.
678

679 Marchant R, Berrio JC, Behling H, Boom A, Hooghiemstra H. (2006) Colombian dry moist
680 forest transitions in the Llanos Orientales – A comparison of model and pollen-based biome
681 reconstructions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 234: 28–44.
682

683 Marinova E, Harrison SP, Bragg F, et al. (2018) Pollen-derived biomes in the Eastern
684 Mediterranean–Black Sea–Caspian–Corridor. *Journal of Biogeography* 45: 484-499.
685

686 Marret F, Leroy S, Chalieu F, et al. (2004) New organic-walled dinoflagellate cysts from recent
687 sediments of Central Asian seas. *Review of Palaeobotany and Palynology* 129: 1-20
688

689 Marret F, Mudie P, Aksu A, et al. (2009) A Holocene dinocyst record of a two-step
690 transformation of the Neoeuxinian brackish water lake into the Black Sea. *Quaternary*
691 *International* 197: 72-86.
692

693 Mauri A, Davis BAS, Collins PM, et al. (2015) The climate of Europe during the Holocene: A
694 gridded pollen-based reconstruction and its multi-proxy evaluation. *Quaternary Science*
695 *Reviews* 112: 109-127.
696

697 Mertens KN, Bradley LR, Takano Y, et al. (2012) Quantitative estimation of Holocene
698 surface salinity variation in the Black Sea using dinoflagellate cyst process length.
699 *Quaternary Science Reviews* 39: 45-59.

700

701 Mikhailov VN and Mikhailova MV. (2008) River mouths. Handbook of Environmental
702 Chemistry, Volume 5: Water Pollution. 91-133.

703

704 Mudie PJ, Aksu AE and Yaşar D. (2001) Late Quaternary dinoflagellate cysts from the Black,
705 Marmara and Aegean seas: Variations in assemblages, morphology and paleosalinity.
706 Marine Micropaleontology 43: 155-178.

707

708 Mudie PJ, Marret F, Mertens KN, et al. (2017) Atlas of modern dinoflagellate cyst
709 distributions in the Black Sea Corridor: from Aegean to Aral Seas, including Marmara, Black,
710 Azov and Caspian Seas. Marine Micropaleontology 134: 1-152.

711

712 Nakhutsrishvili G, Zazanashvili N and K. Batsasashvili a. (2011) Regional Profile: Colchic
713 and Hyrcanic Temperate Rainforests of the Western Eurasian Caucasus. In DellaSala, D.
714 (Ed), Temperate and Boreal Rainforests of the World: Ecology and Conservation, 214-221.

715

716 Peel MC, Finlayson BL and McMahon TA. (2007) Updated world map of the Köppen-Geiger
717 climate classification. Hydrology and Earth System Sciences 11: 1633-1644.

718

719 Petrooshina M. (2003) Landscape mapping of the Russian Black Sea coast. Marine Pollution
720 Bulletin 47: 187-192.

721

722 Prentice IC, Cramer W, Harrison SP, Leemans R, Monserud RA, Solomon AM. (1992) A
723 global biome model based on plant physiology and dominance, soil properties and climate.
724 Journal of Biogeography 19 : 117–134.

725

726 Prentice, I.C., Guiot, J., Huntley, B., Jolly, D., Cheddadi, R., 1996. Reconstructing biomes
727 from palaeoecological data: a general method and its application to European pollen data at
728 0 and 6 ka. Climate Dynamics 12: 185–194.

729

730 Prentice, I.C., Jolly, D., Biome 6000 participants, 2000. Mid-Holocene and glacial maximum
731 vegetation geography of the northern continents and Africa. Journal of Biogeography 27:
732 507–519.

733

734 Reimer PJ, Bard E, Bayliss A, et al. (2013) Intcal13 and Marine13 Radiocarbon Age
735 Calibration Curves 0-50,000 Years Cal BP. Radiocarbon 55: 1869-1887.

736

737 Rudaya N, Tarasov PE, Dorofeyuk N, Solovieva N, Kalugin I, Andreev A, Daryin A,
738 Diekmann B, Riedel F, Tserendash N, Wagner M. (2009) Holocene environments and
739 climate in the Mongolian Altai reconstructed from the Hoton-Nur pollen and diatom records:
740 a step towards better understanding climate dynamics in Central Asia, *Quaternary Science*
741 *Reviews* 28: 540–554.
742
743
744 Ryan W. (2007) Status of the Black Sea flood hypothesis. In: Yanko-Hombach V, Gilbert AS,
745 Panin N, et al. (eds) *The Black Sea question; Changes in coastline, climate and human*
746 *settlement*. Dordrecht: Springer, 63-88.
747
748 Ryan WBF, Major CO, Lericolais G, et al. (2003) Catastrophic flooding of the Black Sea.
749 *Annual Review of Earth and Planetary Sciences* 31: 525-554.
750
751 Shumilovskikh LS, Marret F, Fleitmann D, et al. (2013) Eemian and Holocene sea-surface
752 conditions in the southern Black Sea: Organic-walled dinoflagellate cyst record from core 22-
753 GC3. *Marine Micropaleontology* 101: 146-160.
754
755 Shumilovskikh LS, Tarasov P, Arz HW, et al. (2012) Vegetation and environmental dynamics
756 in the southern Black Sea region since 18 kyr BP derived from the marine core 22-GC3.
757 *Palaeogeography, Palaeoclimatology, Palaeoecology* 337-338: 177-193.
758
759 Soulet, G., Delaygue, G., Vallet-Coulomb, C., Böttcher, M.E., Sonzogni, C., Lericolais, G.,
760 Bard, E. (2010) Glacial hydrologic conditions in the Black Sea reconstructed using
761 geochemical pore water profiles. *Earth and Planetary Science Letters*, 296 (1-2): 57-66.
762
763 Tarasov PE, Granoszewski W, Bezrukova E, Brewer S, Nita M, Abzaeva A, Oberhänsli H.
764 (2005) Quantitative reconstruction of the Last Interglacial vegetation and climate based on
765 the pollen record from Lake Baikal, Russia, *Climate Dynamics* 25: 625–637.
766
767
768 Toderascu R and Rusu E. (2013) Evaluation of the Circulation Patterns in the Black Sea
769 Using Remotely Sensed and in Situ Measurements. *International Journal of Geosciences* 4:
770 1009-1017.
771

772 Tonkov S, Marinova E, Filipova-Marinova M, et al. (2014) Holocene palaeoecology and
773 human–environmental interactions at the coastal Black Sea Lake Durankulak, northeastern
774 Bulgaria. *Quaternary International* 328-329: 277-286.
775

776 Verleye TJ, Mertens KN, Louwye S, et al. (2009) Holocene Salinity Changes in the
777 Southwestern Black Sea: A Reconstruction Based on Dinoflagellate Cysts. *Palynology* 33:
778 77-100.
779

780 Wanner, H., Beer, J., Bütikofer, J., Crowley, T.J., Cubasch, U., Flückiger, J., Goosse, H.,
781 Grosjean, M., Joos, F., Kaplan, J.O., Küttel, M., Müller, S.A., Prentice, I.C., Solomina, O.,
782 Stocker, T.F., Tarasov, P., Wagner, M., Widmann, M. (2008) Mid- to late Holocene climate
783 change - an overview. *Quaternary Science Reviews* 27 (19-20): 1791-1828.
784

785 Williams LR, Hiscott RN, Aksu AE, et al. (2018) Holocene paleoecology and
786 paleoceanography of the southwestern Black Sea shelf revealed by ostracod assemblages.
787 *Marine Micropaleontology* 142: 48-66.
788

789 Yanchilina AG, Ryan WBF, McManus JF, et al. (2017) Compilation of geophysical,
790 geochronological, and geochemical evidence indicates a rapid Mediterranean-derived
791 submergence of the Black Sea's shelf and subsequent substantial salinification in the early
792 Holocene. *Marine Geology* 383: 14-34.
793

794 Zecchetto S and De Biasio F. (2007) Sea surface winds over the Mediterranean basin from
795 satellite data (2000-04): Meso- and local-scale features on annual and seasonal time scales.
796 *Journal of Applied Meteorology and Climatology* 46: 814-827.
797

798 Zenina MA, Ivanova EV, Bradley LR, et al. (2017) Origin, migration pathways, and
799 paleoenvironmental significance of Holocene ostracod records from the northeastern Black
800 Sea shelf. *Quaternary Research* 87: 49-65.
801

802 Zonneveld, K.A.F., Versteegh, G., Kodrans-Nsiah, M. (2008) Preservation and organic
803 chemistry of Late Cenozoic organic-walled dinoflagellate cysts: A review. *Marine*
804 *Micropaleontology* 68 (1-2), 179-197
805

806 Zonneveld KAF, Marret F, Versteegh GJM, et al. (2013) Atlas of modern dinoflagellate cyst
807 distribution based on 2405 datapoints. *Review of Palaeobotany and Palynology* 191: 1-197.

808 **Figure captions**

809

810 Figure 1: The Black Sea: Bathymetry, rivers, core location and relief.

811

812 Figure 2: Maps showing annual sea-surface temperature (top) and salinity (bottom) based
813 on the World Ocean Atlas 2013 (Boyer et al., 2013) and created with Ocean Visual Display
814 software.

815

816 Figure 3: Vegetation map modified from Bohn et al. (2004) with location of core Ak-2575
817 (star) and vegetation profile from west to east across the Greater Caucasus.

818

819 Figure 4: Age-depth model for Ak-2575. Red = ostracods; Blue = Molluscs; Purple = Two
820 samples overlapping.

821

822 Figure 5: Percentage diagram of dinocyst taxa based on a sum comprising all dinocyst
823 species. Concentration (cysts/ml) curve is depicted on the right side of the diagram. Hiatuses
824 A and C are highlighted with grey bands, Hiatus B is not shown as it is very short-lived (less
825 than 200 years).

826

827 Figure 6: Percentage diagram of pollen taxa. Percentages were calculated on a pollen sum
828 that excluded *Alnus* due its over-representation in the spectra. *Alnus* percentages are
829 calculated on a total pollen sum. Pollen taxa are sorted according to vegetation types (Trees
830 in green and herbs in yellow). Hiatuses A and C are highlighted with grey bands, Hiatus B is
831 not shown as it is very short-lived (less than 200 years).

832

833 Figure 7: Summary pollen and dinocyst diagram. Lowland taxa (*Alnus* and *Corylus*), *Pinus*,
834 arboreal vegetation types (as grouped in figure 6), numerical scores of selected biomes
835 (steppe, taiga and temperate deciduous forest) and selected dinocyst species indicator of
836 water conditions are presented. Thermophilic group is represented by *O. israelianum*;
837 Mediterranean taxa include: *O. centrocarpum*, *S. delicatus*, *S. membranaceus*, *S. mirabilis*,
838 *S. ramosus*, *Achomosphaera* sp., *A. choane*; Euryhaline taxa include: *L. machaerophorum*
839 and its morphotypes, *S. belerius*, *S. bentorii*; Caspian/Brackish taxa consist of *S. cruciformis*,
840 *P. psilata*, *I. caspiense* and *C. rugosum*.

841

842 **Table caption**

843

844 Table 1. Details of radiocarbon dates, calibrated age range (2σ) and details of original
845 publication of radiocarbon dates.

846

847

848 **Plate caption**

849

850 Plate 1: Specimens of *Spiniferites* sp, 1 from core Ak-2575, depth 12cm (1-2; 4); depth 16cm
851 (3); depth 44cm (5-6). Scale bar represents 10 microns.

852

853