MIS 5–1 dinoflagellate cyst analyses and morphometric evaluation of Galeacysta etrusca and Spiniferites cruciformis in southwestern Black Sea

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1. Introduction

The salinity of the Black Sea is controlled by the inflow of marine water through Marmara Sea and its shallow straits (Fig. 1) during marine highstands, and by precipitation and the volume of runoff from vast rivers draining Europe and Western Russia during and immediately after glacial marine regressions (Major et al., 2006). The unusual configuration and unique oceanographic features of the semi-isolated Black Sea makes it a fascinating biome to study unusual dinoflagellate cysts (Mudie et al., 2007; Ivanova et al., 2012; Yanko-Hombach et al., 2013, 2014) that have been able to adapt to large-scale salinity fluctuations and can tell us about these past environmental changes. Some of these cysts are relics of the Pliocene Paratethyan Seas, while others are more recent Mediterranean immigrants (Marret et al., 2015). Here we provide new data on late Pleistocene to early Holocene dinoflagellate cyst assemblages recovered from DSDP Site 380 in deep water at the base of the western continental slope apron, 2107 m water depth. Morphological changes seen in two of the most abundant relic Paratethyan endemic dinoflagellate cyst species present, Galeacysta etrusca and Spiniferites cruciformis, are combined with dinoflagellate assemblage data to evaluate a possible morphological response of the cysts to changes in sea-surface salinity and to examine the impact of sea-level changes and the history of the connections.

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http://dx.doi.org/10.1016/j.quaint.2016.07.035
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Furthermore, discriminant analysis is performed to verify the morphometric variations between these two different dinoflagellate species. DSDP Site 380 (Fig. 1) was selected for its proximity to the narrow Bosphorus Strait as drops in eustatic sea level during the glacial disconnected the Black Sea from Marmara and the Aegean Sea, creating a change from higher salinities to more brackish water conditions that should be evidenced at the studied site. These salinity changes were further overprinted by fluctuations in evaporation (E) relative to total freshwater input (P) derived from runoff, melt water and rainfall and will be discussed as well (Major et al., 2006; Wegwerth et al., 2016).

Debate exists on the exact timing of connections between the low salinity Black Sea and more saline Mediterranean between the last interglacial maximum (high salinity phase, MIS 5e) and the Holocene interglacial (MIS 1). Two main scenarios exist for the Late Pleistocene—Holocene marine reconnection: 1) a rapid (Catastrophic Flood model (Ryan et al., 1997, 2003; Major et al., 2006; Lericolais et al., 2007; Soulet et al., 2011) around 8.4 ka BP, and 2) the Progressive or Gradual Flood model starting around 11 ka BP (Hiscott et al., 2007; Aksu et al., 2002a). In addition to debates over the timing of the Holocene marine transgression in the Black Sea, there are significant disagreements regarding the timing and manner of marine reconnections between the Aegean, Marmara and Black Seas during MIS 3 and regarding the salinity of the Black Sea after MIS 5e (Karangatian highstand 130–115 ka BP). Benthic foraminifera (Yanko-Hombach, 2007) and some mollusk data (e.g. Aksu et al., 2002b; Panin and Popescu, 2007) indicate a marine incursion in the southwestern Black Sea during MIS 3 (Tarkankutian beds, dated 40–27 ka BP; Surozhian interstade 40–25 ka BP) and show that during the Karangatian, salinity was higher, being comparable to that of the present Mediterranean, ranging from ca. 30–37 psu (practical salinity unit). Dinoflagellate cyst assemblages in the southeastern Black Sea (Shumilovskikh et al., 2013) also indicate a higher salinity and temperature for MIS 5e. Oxygen isotope records from Sofular Cave (Badertscher et al., 2011) indicate marine connections only during MIS 5e and the Holocene, as also evident in the absence of an Aegean Sea sapropel between the end of MIS 5 (71 ka BP) and early MIS 1 (Işler et al., 2016). In contrast, there are three MIS 5 sapropel layers in the northern Aegean Sea (S3, S4 and S5), with well constrained median termination ages at 70.8, 96.2 and 121.0 ka BP (Işler et al., 2016).

2. Regional setting

The Black Sea is a large, deep semi-enclosed basin located between southeastern Europe and Asia (Fig. 1). The Black Sea is thought to have evolved from a freshwater lake to a brackish—marine basin around the Oligocene – Miocene (Muratov et al., 1978). From the Miocene onwards, the basin has been characterized by successive fluctuations between brackish to fresh water conditions (Muratov et al., 1978). The present marine connection to the Mediterranean Sea is complex as the shallow Bosphorus Strait first connects the Black Sea to the Marmara Sea, which then connects to the Aegean and Mediterranean seas through the deeper Dardanelles strait (Fig. 1). The Bosphorus strait is relatively shallow (average 40 m), with a minimum depth of about 30 m near Istanbul, Turkey. The depth of this connection limits the salinity, stratification and oxygen exchange within the Black Sea (Kerey et al., 2004). In addition to this marine connection, the Black Sea is connected to the almost freshwater (<11 psi) Sea of Azov through the narrow Strait of Kerch. At a maximum depth of 15 m, the Sea of Azov is the presently shallowest sea in the world. At present, it provides a constant freshwater outflow to the Black Sea via the Don River (Kosarev et al., 2008) and it was probably a large river valley during intervals of lower sea level. However, during the late Pleistocene, it was connected to the Caspian Sea via the Manych River valley (Major et al., 2006) from which reddish-brown “chocolate” clays flooded into the northern and western Black Sea around 16–18 cal ka BP (Major et al., 2006). Although the Black Sea hydrographic configuration is largely controlled by fluvial inputs from
the discharge of other large rivers such as the Danube, Bug, Dniepr, Dniestr, and the Rioni, the shallow connection to the Marmara Sea plays a pivotal role in the hydrographic balance of the Black Sea. This precarious situation has led to periodic interruption and resumption of marine flow between the two bodies of water.

3. Material and methods

DSDP Site 380 of Leg 42B is located at 42°05.94′N and 29°36.82′E in a water depth of 2107 m in the southwestern Black Sea north of the Bosphorus Strait (Supko et al., 1978). Site 380 refers to DSDP Hole 380 that was drilled in 1975 during DSDP Leg 42B, using conventional drill-hole coring techniques which penetrated to 370.5 m sub-bottom and recovered 159.5 m of sediment by continuous coring of 40 core barrels, each of length 9.5 m. Only the top 70 m of Site 380 (Cores 1–8) were analyzed for this project. The units sampled (Units 1b to 1d of Ross et al., 1978) are from Unit 1 (Cores 1–5) composed of terrigenous sediments including muds and sandy silts, and from Unit II, a diatomaceous mud, including intervals of marine diatom species in Cores 6 and 8, and calcareous oozes in Cores 7, 8, and at the 6/5 boundary. The lower half of Core 7 was tentatively assigned to the Emiliania huxleyi zone. The age of the base of Unit 1d was estimated as ~100,000 yr BP (late MIS 5) and the Unit 1d/c boundary at 42 m (Core 5, base section 4) was assigned an age of 70,000 yr BP (Muratov et al., 1978) which is near the start of glacial stage MIS 4.

Although Muratov et al. (1978) do not specify the basis for the age assignments, it appears from the shipboard descriptions (Ross et al., 1978) that it is based on the appearance of E. huxleyi (with, at that time, a youngest first occurrence datum of 110 ka BP). The assignment of a 70 ka BP age for the Unit 1d/c boundary is presumably based on correlation with the termination of the fluctuating warmer–cooler intervals of interglacial MIS 5 and the start of glacial conditions of MIS 4 (now dated at 71 ka BP by the Lisiecki and Raymo (2005) marine isotope record). We support these tentative age assignments based on the occurrence of the highest pre-Holocene sapropelic mud (TOC > 0.6%) near the top of Core 5 and tentatively correlated with sapropel S3 (median termination age 70.8 ka BP in North Aegean). A second sapropelic mud interval (presumably S4 equivalent) occurs in Core 6 and a third sapropel occurs at the bottom of Core 7 down to 76 m that would logically correspond with Aegean sapropel S5 (1210 ka BP). Subunit 1c (24–42 m) are muds and sandy silts, the top of which is correlated with Unit III of Ross et al. (1974) and which includes some sapropel mud (<0.9%) in Core 4, suggestive of the warmer MIS 3 interstadial phase. Subunit 1b (0–2 m) consists of olive-gray sapropelic mud with pinstripe laminae from 0150 cm and is correlated with Unit II of Ross et al. (1974). Below 150 cm in Subunit 1b, there is bioturbated mud, then massive dark gray muds interlayered with light brown interbeds that continue to the base of Core 1 and possibly correspond with the late MIS2 chocolate clays of Black Sea piston cores. These reddish clastic units are not present in the Subunit 1c sediments of Core 2 (9.5–19 m) but they re-appear as thicker beds in Core 4 (27.5–38 m) below the sapropelic mud. Core 3 at DSDP 380 was void (Ross et al., 1978). Twenty grams of sediment were sampled at 50 cm intervals wherever available between depths of 67.47 and 0.52 m. Poor recovery from 59 to 54 m, 47.5–43 m, and no recovery from 29.5 to 19 m hindered sampling, however 40 samples from the least disturbed sediments were selected as suitable for analysis. Samples were processed using the CENEX-SHELL method. All samples were treated with HCl and HF to digest unwanted carbonates and silicates. ZnCl₂ (density of 2.00 g/ml) was used as a density separator to float and concentrate the palynomorphs. The residues were sieved at 10 μm, and the remaining fraction was mounted in glycerol (density of 1.23 g/m³).

An Olympus BX41 microscope and oil immersion 60× or 100× magnification objectives were used for dinoflagellate cyst analysis. Microphotographs were taken using a QCapture camera with a 0.5× coupler, and managed with QCapture software. A minimum of 300 identifiable dinoflagellate cysts were counted on each slide. Reference slides and bibliographic material from the Center of Excellence in Palynology (CENEX) library were used to identify the cysts at the species level. Identification of the dinoflagellate cysts was based on comparison with curated dinoflagellate cysts from the CENEX-SHELL collection and on published Black Sea studies including those of Marret et al. (2009), Verleye et al. (2009), and Caspian studies of Marret et al. (2004). However, for morphotypes of Lingulodinium machaerophorum we used the classification similar to Marret et al. (2004) for Caspian morphotypes C and D with processes greater or less than ca.7 μm. Precisely, we divided the L. machaerophorum into two sub-groups: “long” processes (>5 μm but <15 μm), and “short” processes (<5 μm). No “true long” processes as defined by (Mertens et al., 2009), with an average process length of 15 μm or greater were observed. Therefore, the L. machaerophorum processes present in this section are on average smaller than L. machaerophorum processes present in the Black Sea in other studies.

Dinoflagellate cysts were recovered grouped according to their ecological requirements as follows (a) marine stenohaline taxa typically restricted to marine sea-surface conditions (Ataxiodinium choane, Impagidinium spp., Impagidinium caspiense, Impagidinium inaequalis, Spiniferites bentorii sensu stricto, and Spiniferites mirabilis; (b) marine euryhaline species tolerating wider ranges of sea-surface conditions such as Nematosphaeropsis labrinthus, other Spiniferites spp. (excluding Spiniferites cruciformis), Achomosphaera cf. andalusiensis, and Lingulodinium machaerophorum (form with long processes); c) brackish species endemic to the Paratethyan basins, including Galeaestra eustraca, Spiniferites cruciformis and Pyxinodopsis psilata.

Morphological changes for Galeaestra eustraca and Spiniferites cruciformis were measured by tracking four dimensions: the lengths and widths of the endocyst (Lₑₑₑₑ and Wₑₑₑₑ) and ectocyst (Lₑₑₑₑ and Wₑₑₑₑ) (Fig. 2), following the methodology defined by Popescu et al. (2009) for the Mediterranean and Paratethys Sea regions. First, multivariate descriptive analyses (Principal Component Analysis and Linear Discriminant Analysis) of the morphometric variability of the two taxa were conducted based on these four initial variables. Second, according to these first results a time series analysis of G. eustraca based on three synthetic morphometric descriptors was conducted. These descriptors are (after Popescu et al., 2009):

\[ X = \log(\sqrt[3]{\text{LEN} \times \text{WEN} \times \text{LEX} \times \text{WEX}}) \]

where X is the log-transformed geometric mean of the four initial variables; it is an estimate of the overall size of the dinoflagellate cyst;

\[ Y = \log(\text{LEN} \times \text{WEN}/\text{LEX} \times \text{WEX}) \]

where Y is the log-transformed ratio of the endocyst size to ectocyst size;

\[ Z = \log(\text{LEN} \times \text{LEX}/\text{WEN} \times \text{WEX}) \]

where Z is the log-transformed ratio of the lengths to widths.

All statistical analyses were conducted using the PAST v. 2.10 freeware (Hammer et al., 2001).

4. Results

4.1. Dinoflagellate cyst distribution at DSDP Site 380

More than 16,000 dinoflagellate cysts were counted during this study, yielding a total of 23 taxa (11 in situ species and 12 reworked species). The preservation of specimens was moderate to good, and
particular effort were made to identify the “brackish endemic species” as defined by Popescu et al. (2009) because they show a large morphologic spectra that appear to be related to sea-surface physical parameters including temperature, salinity and nutrient content variability (Popescu et al., 2007, 2009). Dinoflagellate cysts recovered include eight marine taxa (Fig. 3), with varying amounts of stenohaline and euryhaline marine species and alternating with larger amounts of brackish Paratethyan basin species, and sometimes with large amounts of reworked taxa. The marine species (Fig. 3) mostly show a low relative abundance (between 1% and 12%), except in two deeper samples, where these species respectively reach 16% (at 62.95 m) and 42.3% (at 67 m). The overall assemblage at DSDP Site 380 is clearly dominated by high abundance of the brackish taxa (Fig. 3; Plate 1), with Pyxidinopsis psilata and Galeacysta etrusca making up to 90% of relative abundance, and Spiniferites cruciformis achieving its maximum relative abundance (less than 20%) between 0 and 10 m depths.

Additional species recovered of reworked taxa include Areoligeracean taxa (Cretaceous — Paleogene) (Williams et al., 1998), Oligosphaeridium spp. (Upper Cretaceous — Paleogene) (Williams et al., 1998), Paleogene — Eocene Enneadocysta sp. (Fensome et al., 2007), Eocene Glaphyrocysta spp. (Williams et al., 1998), Homotryblum sp. (Paleogene — Miocene) (Williams et al., 1998), Late Eocene — Early Oligocene Deflandrea phosphoritica (Williams et al., 1998), Wetzeleilla symmetrica (Oligocene) (Williams et al., 1998), Hystrichokolpoma sp. and Virgodinium sp. both with a last appearance in the Miocene (Sütő-Szentai, 1986; Warny and Wrenn, 2002), and Miocene — Early Pliocene Spiniferites bentorii pannonicus (Sütő-Szentai, 1986).

Four dinoflagellate cyst zones were identified based on dinoflagellate cyst distributions and relative abundances of paleoecological groups (Fig. 3).

**Dinoflagellate cyst zone 1** (68–67 m) is defined by the highest relative abundance of marine dinoflagellate cysts (42.3% relative abundance).
abundance at 67.47 m) including Spiniferites mirabilis, Spiniferites sp., and Lingulodinium machaerophorum. The brackish species group, with a relative abundance of 57.7%, is dominated by the most widespread (Spain to Caspian Sea) Paratethyan relic taxon Galeacysta etrusca with 57% (at 67.47 m). Brackish species Spiniferites cruciformis and P. psilata were present but in very low amounts with only two cysts of S. cruciformis and one cyst of P. psilata observed within this zone. Reworked dinocysts have a relative abundance of 10% at 67 m depth.

**Dinoflagellate cyst zone 2** (67–38 m) is characterized by a reduction in marine taxa which never dominate the studied section again above dinoflagellate cyst zone 1 and by a change in the dominant brackish species, with G. etrusca being replaced by P. psilata by the top of this zone. G. etrusca makes up 99% of the assemblage (at 62.5 m) in the lower part of the zone, and P. psilata begins increasing in the middle of the zone and ends up dominating the assemblage with 84% (at 41 m) towards the end of this zone. Brackish S. cruciformis remains rare only reaching up to 4% within this zone. In zone 2, marine taxa reach their highest abundance of 10% total dinoflagellate cysts at 40 m. Euryhaline taxa L. machaerophorum, Spiniferites spp., and Achomosphaera cf. andalousiensis are present and as well as the stenohaline taxon Spiniferites mirabilis. Lastly, zone 2 is also marked by the highest and most continuous relative abundance of reworked taxa within the studied section reaching its highest presence of 20% at 52 m.

**Dinoflagellate cyst zone 3** (38–11 m) is characterized by the first appearance of stenohaline taxon Ataxiodinium choane, and the continuance of assemblage dominance by brackish P. psilata. Pyxidinopsis psilata has a relative abundance of 95% or more in all but one sample (82% at 16 m where G. etrusca briefly increases to 6%). S. cruciformis is rare in this zone with a maximum relative abundance of 1% at 16 m depth. Marine abundances remain low throughout zone 3 with euryhaline Spiniferites spp. and L. machaerophorum cysts appearing most consistently. Organic matter is low.

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**Plate 1.** Light photomicrographs of DSDP Site 380 dinoflagellate cysts with sample depth (slide number) and England Finder coordinates for each specimen. Scale bar = 20 μm. 1–8 Galeacysta etrusca 1 60.02 m (2) K12/0; 2 42.45 m (3) K37/0; 3 60.02 m (2) S10/0; 4 34.46 m (2) R22/4; 5 60.02 m (3) M24/2; 6 60.02 m (3) T16/2; 7 60.02 m (2) M20/1; 8 62.50 m (1) V15/0. 9–16 Spiniferites cruciformis 9 34.46 m (1) W46/1; 10 34.46 m (2) P38/2; 11 8.495 m (1) Q12/2; 12 0.97 m (2) O28/1; 13 2.50 m (2) V28/4; 14 33.5 m (1) J34/0; 15 41.50 m (1) J10/3; 16 0.97 m (1) T14/4.

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throughout and sediments are predominantly red and gray banded muds with traces of “chocolate brown” laminae possibly related to flood events from Caspian Sea overflow through Manych Strait (see Major et al., 2006). Reworked cysts range from 0 to 2% within this zone. Note there is a 9.5 m interval of no sediment recovery in the middle of this zone (19–28.5 m).

**Dinoflagellate cyst zone 4 (11–0.52 m)** is characterized by the highest relative abundance in *S. cruciformis* recovered in the studied section (up to 20% at 3.5 m), with an average of 6% throughout the zone. This zone is also associated with minor increases in marine taxa including the first appearances of stenohaline taxa *Impagidinium* sp., *A. choane*, and *Spiniferites bentorii sensu stricto*. Euryhaline taxa *Spiniferites* spp., *A. cf. andalusiensis*, and *L. machaerophorum* once again occur consistently throughout this zone and slightly increase in low abundances here. The relative abundance of total marine taxa reaches its peak of 6% in the uppermost sample (0.52 m). Brackish taxon *G. etrusca* increases slightly but remains relatively rare and the dinoflagellate cyst assemblage is dominated by *S. cruciformis* and *P. psilata*. The relative abundance of *P. psilata* ranges between 95% at 8 m and 62% at 3.5 m. Reworked dinoflagellate cyst occurrence is low with a maximum abundance of 2% (at 6.49 m, and 0.52 m) in zone 4.

### 4.2. Statistical morphometric analysis of *Galea cysta etrusca* and *Spiniferites cruciformis*

Intraspecific changes in dinoflagellate cyst morphology are known to be linked to changes in controlling environmental conditions, particularly salinity as first indicated by Wall et al. (1973) for late Pleistocene – early Holocene Black Sea assemblages of *S. cruciformis* and *P. psilata* (as *Tectatodinium psilatum*). The variable length of *Lingulodinium machaerophorum* processes is a well-established case (Mertens et al., 2009, 2012), but as discussed above, other species such as *G. etrusca* and *S. cruciformis* are also known to have a morphology influenced by sea surface salinity, SSS (e.g., Mudie et al., 2001, 2016; Sorrel et al., 2007; Popescu et al., 2009). Because these brackish water indicator species are abundant at our site, a detailed morphometric analysis was conducted on the variability of their size, using only well-preserved specimens (i.e. torn cysts and partially covered cysts were not measured). Four dimensions (the lengths and widths of the endocyst, *L*\(_{EN}\) and *W*\(_{EN}\), and the ectocyst, *L*\(_{EX}\) and *W*\(_{EX}\)) were measured for both *Spiniferites cruciformis* \((n = 65)\) and *Galea cysti etrusca* \((n = 1074)\) (Fig. 2).

Morphometric variability for both species was analyzed: (i) through a Principal Component Analysis (PCA) and Linear Discriminant Analysis (LDA) of Log-transformed measurements, and (ii) by graphing the X, Y, and Z synthetic descriptors (see Methods).

The PCA shows that the overall morphometric variability of *G. etrusca* and *S. cruciformis* can be decomposed into three principal components (PCs), which are independent linear combinations of the four measured dimensions and were used in a previous study of morphometric variability (Popescu et al., 2009). Together, these three PCs explain 93.6% of the total variability (Table 1, Fig. 4). PC\(_1\) (57.0% of the total variability) is an overall-size descriptor (a large PC\(_1\) value indicates a large overall size for the specimen). PC\(_2\) (21.1% of the total variability) sets the two EN-descriptors against the two EX-descriptors, thus being an EN:EX descriptor (a large PC\(_2\) value indicates a large EN:EX ratio, i.e., a large endocyst size relative to the ectocyst size). PC\(_3\) explains 15.5% of the overall variability and sets the two L-descriptors against the two W-descriptors, thus being an L:W descriptor (a large PC\(_3\) is related to a small L:W ratio, i.e., a more rounded shape). The fourth PC which explains less than 7% of the overall variability is likely a “noise-parameter” accounting for the inter-individual variability.

Histograms of *G. etrusca* and *S. cruciformis* specimen coordinates on PC\(_1\), PC\(_2\) and PC\(_3\) are used to evaluate how similar/dissimilar the two species are morphometrically (Fig. 5). The large amount of overlapping between the two species clearly gives evidence to their overall morphometric similarities based on the linear combinations of the four measured variables as defined by PCA. Both species project on the same range of PC\(_1\) and PC\(_2\) values (Fig. 5A and C), but not on the same PC\(_2\) values (Fig. 5B). This indicates that the main source of morphometrical dissimilarity between the two species is from the EN:EX-size ratio marking endocyst size relative to that of the ectocyst. *S. cruciformis* individuals show more negative PC\(_2\)-values, and thus possess a smaller ratio of endocyst size to ectocyst size than *G. etrusca*, while they both share similar “overall size” (PC\(_1\)), and L:W ratios (PC\(_3\)).

Based on this first exploratory result, we further evaluated the ability of the four measured descriptors to accurately separate the two species through a linear Discriminant Analysis (DA) coupled with a Hotelling’s test (Hotelling’s T\(^2\) = 353.4, \(p\)\(>\)0.99; same multivariate means) = \(3 \times 10^{-16}\)) for equality between two multivariate means, showing a highly significant difference between *G. etrusca* and *S. cruciformis*. The DA results show that the two species are morphometrically distinct, with an overall “leave-one-out” (jackknife) probability of correct classification of 88.67% (Fig. 6).

Finally, mixture analyses were performed for the three synthetic descriptors X, Y, and Z on the five most sampled (abundant) levels for *G. etrusca* to identify possible mixtures of morphometrically distinct sub-groups within this species and use it to evaluate paleo-SSS. As illustrated by the most abundant sampled depth (\(n = 298\)) (Fig. 7), these distributions are unimodal, indicating that *G. etrusca* is morphometrically homogeneous throughout our studied section. This is in contrast to Popescu et al.’s (2009) results for Zanclean-aged sediment at the same study site (828.02-841.91 m in Hole 380, which indicated the presence of four morphometrically distinct *G. etrusca* groups. The presence of only one morphometric group for our study is further confirmed by comparing the [X, Y] distribution of the sampled specimens to those of Popescu et al. (2009) (Fig. 8). The comparison shows that, even if including rather small-sized specimens, the *G. etrusca* group present in MIS 5–1 estimated age sediment from DSDP Site 380 is similar to *G. etrusca* group ‘b’ defined by Popescu et al. (2009) as a marine group, indicating that this site is characterized by relatively stable marine salinities at least throughout MIS 5e to 4 where *G. etrusca* is found in statistically significant abundances. The presence of *G. etrusca* starts to decline at MIS 5a, depth of 39.9 m, and continues to have a limited presence for the rest of the studied section into MIS 1.

### 5. Discussion

#### 5.1. Environmental reconstruction based on dinoflagellate assemblages

Based on the environmental affinities described above, the high abundances of brackish taxa recovered in all samples from DSDP Site 380 indicate that this area of the Black Sea experienced low sea-surface salinity ranging between about 12 and 22 psu throughout most of the interval studied. This observation is in accord with the persistent presence of *Lingulodinium machaerophorum* which does not grow in salinities of less than 7 psu, and is most common in a salinity range of ca. 13–18 psu in the modern Ponto-Caspian region (Mertens et al., 2012). Despite the low resolution sampling interval of our study, some paleoenvironmental changes are nevertheless inferred based on observed assemblage differences.

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5.1.1. Dinoflagellate cyst zone 1 (68–67 m): interglacial marine environment

A relative abundance of 42.3% marine taxa at depth 67.47 m, combined with the presence of sapropel sediment and coccoliths (reported by DSDP Leg 42B Ross et al., 1978) indicate a connection between the Aegean Sea and the Black Sea within this latest MIS 5e interglacial interval. This connection caused SSS to increase in the Black Sea from a previous glacial stage (MIS 6) salinity of 5 psu up to 22 psu for the southeastern Black Sea (S.-M. Popescu, personal communication). In comparison, today’s seawater enters the Bosporus Strait at an average bottom water salinity of 34.9 psu (Murray et al., 2005) and mixes with lower salinity surface water as it pours into the Black Sea to form a bottom water layer of ca. 24 psu (Mertens et al., 2012). However, the high freshwater river input relative to evapotranspiration keeps the Black Sea SSS between about 16 psu on the shelves and 18 psu in the basins. The maximum diversity of marine dinoflagellate cysts and the peak occurrence of stenohaline taxa also indicates a full marine connection. However, L. machaerophorum specimens present throughout zone 1 exhibit a mixture of “long” (>5–<15 μm), and “short” (<5 μm) processes (Fig. 9), but no fully developed processes >15 as found in Marmara and Aegean Seas. Absence of normal long processes indicates that salinity conditions were relatively low in this part of the Black Sea following the inflow of marine waters to the formerly isolated lacustrine environment at the beginning of MIS 5e. High relative abundance of the marine morphometric group of G. etrusca along with the low abundance of P. psilata characterize dinoflagellate zone 1. The presence of some reworked species in sediments at 67 m may indicate higher erosion of Cenozoic western Black Sea sediments associated with the Bosporus inflow and subsequent strengthening of the Rim Current.

Table 1
Summary of the numerical results of the correlation matrix-based PCA of G. etrusca + S. cruciformis. The three first PCs, together explain 93.6% of the total morphometric variance, and convey morphometric information analogous to the X, Y and Z synthetic descriptors, respectively.

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<td>59.55</td>
<td>17.34</td>
<td>16.29</td>
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Correlation between original variables and PCs:

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<td>0.588</td>
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<td>0.104</td>
</tr>
<tr>
<td>WEX</td>
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<td>0.074</td>
<td>0.615</td>
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<td>0.268</td>
</tr>
<tr>
<td>WEN</td>
<td>0.581</td>
<td>-0.531</td>
<td>0.034</td>
<td>0.268</td>
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</tr>
<tr>
<td>LEN</td>
<td>0.804</td>
<td>-0.07</td>
<td>-0.512</td>
<td>-0.295</td>
<td>0.295</td>
</tr>
</tbody>
</table>

Meaning of the resulting PCs.

PC1: Overall size (large PC1-value = large overall specimen size).
PC2: EN vs. EX size (large PC2-value = small EN/EX-size ratio).
PC3: Lengths vs. widths (large PC3-value = small L/W ratio).
PC4: Noise.

5.1.1. Dinoflagellate cyst zone 1 (68–67 m): interglacial marine environment

A relative abundance of 42.3% marine taxa at depth 67.47 m, combined with the presence of sapropel sediment and coccoliths (reported by DSDP Leg 42B Ross et al., 1978) indicate a connection between the Aegean Sea and the Black Sea within this latest MIS 5e interglacial interval. This connection caused SSS to increase in the Black Sea from a previous glacial stage (MIS 6) salinity of 5 psu up to 22 psu for the southeastern Black Sea (S.-M. Popescu, personal communication). In comparison, today’s seawater enters the Bosporus Strait at an average bottom water salinity of 34.9 psu (Murray et al., 2005) and mixes with lower salinity surface water as it pours into the Black Sea to form a bottom water layer of ca. 24 psu (Mertens et al., 2012). However, the high freshwater river input relative to evapotranspiration keeps the Black Sea SSS between about 16 psu on the shelves and 18 psu in the basins. The maximum diversity of marine dinoflagellate cysts and the peak occurrence of stenohaline taxa also indicates a full marine connection. However, L. machaerophorum specimens present throughout zone 1 exhibit a mixture of “long” (>5–<15 μm), and “short” (<5 μm) processes (Fig. 9), but no fully developed processes >15 as found in Marmara and Aegean Seas. Absence of normal long processes indicates that salinity conditions were relatively low in this part of the Black Sea following the inflow of marine waters to the formerly isolated lacustrine environment at the beginning of MIS 5e. High relative abundance of the marine morphometric group of G. etrusca along with the low abundance of P. psilata characterize dinoflagellate zone 1. The presence of some reworked species in sediments at 67 m may indicate higher erosion of Cenozoic western Black Sea sediments associated with the Bosporus inflow and subsequent strengthening of the Rim Current.
5.1.2. Dinoflagellate cyst zone 2 (67–38 m): late interglacial brackish environment with brief marine fluctuations

It is unclear what drives the fluctuations observed between *G. etrusca* and *P. psilata* throughout zone 2 which includes the time from MIS 5d–MIS 5a. The rarity of stenohaline marine taxa indicates that there was a weaker Mediterranean connection, but the sapropelic sediments indicate presence of stratified water and not uniformly brackish or well-mixed conditions. The presence of common Atlantic/Mediterranean stenohaline *Spiniferites* spp. are never found in the Caspian Basin suggesting that the salinity here was higher than that of the Caspian SSS (ca. 13–15 psu). Reworked dinoflagellate cysts reach abundances of 20% (at 52 m), which is the

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**Fig. 6.** Discriminant analysis of *G. etrusca* (grey) vs *S. cruciformis* (black) specimens based on the four measured dimensions (lengths and widths of the endocyst and ectocyst; Fig. 3). For each specimen, the Discriminant Score (DS) is calculated from the linear discriminant function $DS = (22.225 \times \log(LEN)) + (25.513 \times \log(WEN)) - (40.197 \times \log(LEX)) + (-25.954 \times \log(WEX)) + 43.3652$, clearly evidencing the main source of morphometrical difference (the endocyst/ectocyst size ratio) as also identified by the PCA (Figs. 4 and 5). The jackknifed confusion matrix gives the number of correctly classified and misclassified specimens for each species based on a “leave-one-out” procedure.

**Fig. 7.** Gaussian (plain) and kernel (dotted) density distributions of X, Y and Z synthetic descriptors for the 298 measured specimens of *G. etrusca* from the most abundant level (depth: 62.5 m) of the analyzed time series. At this depth as for all other tested depths, the three empirical distributions do not show any marked evidence of multimodality, illustrating the morphometrical homogeneity of *G. etrusca* in the DSDP Site 380 studied interval.

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Please cite this article in press as: Ferguson, S., et al., MIS 5–1 dinoflagellate cyst analyses and morphometric evaluation of *Galeacysta etrusca* and *Spiniferites cruciformis* in southwestern Black Sea, Quaternary International (2016), http://dx.doi.org/10.1016/j.quaint.2016.07.035
Fig. 8. Biplot of X and Y synthetic descriptors contrasting the Galeacysta etrusca (black dots; dark-grey ellipse: 70% binomial Confidence Interval) and Spiniferites cruciformis (grey dots and light-grey ellipse) specimens from DSDP Site 380 with the distributions of Popescu et al. (2009) morphometric groups ‘a’–‘d’ (colored ellipses, 70% binomial CI; group ‘a’ is related to brackish conditions, group ‘b’ to marine conditions, group ‘c’ to freshwater, and group ‘d’ to high nutrient levels).

Fig. 9. Lingulodinium machaerophorum individuals present throughout studied section at DSDP Site 380. Our “long” processes are defined as being >5 μm but <15 μm in length, and our “short” processes are defined as being <5 μm in length. No “true long” processes being ≥15 μm (as defined by Mertens et al. (2009)) were present. Dinoflagellate cyst assemblage zones are shaded.
maximum borehole depth indicating high river discharge causing erosion and re-deposition of Cenozoic shelf sediments northwest of the DSDP 380 drillhole site. More than halfway up of zone 2 (at 48 m), *L. machaerophorum* reaches an acme again, with a mixture of long and short processes (Fig. 9), likely marking a brief salinity increase and is coeval to the decrease of *P. psilata* and occurrence of sapropelic mud possibly correlative with MIS 5e. These changes suggest minor increase in SSS and SST associated with periodic minor influxes of warmer marine waters, and a marine connection to the Black Sea just before the Unit 1c/b boundary during MIS 1. Alternatively, changes in evaporation relative to freshwater supply by rainfall and rivers may have changed the salinity, as reported for MIS 4–2 in the southeastern Black Sea (Wegwerth et al., 2016), but that model would not account for presence of the sapropelic mud intervals in this zone.

5.1.3. Dinoflagellate cyst zone 3 (38–11 m): cold brackish conditions with brief salinity rises

Here, two salinity increases are indicated by two episodes of increased abundance in *L. machaerophorum* with relatively long processes (>5–15 µm) at 33.5 and 16 m depths in DSDP Hole 380. These saline intervals are coeval with the presence of marine *Spiniferites spp.*, *A. cf. andalusiensis*, as well as a peak of reworked dinoflagellate cysts immediately after both episodes and following glacial stage MIS 4. This may indicate short-lived warmer interstadials that characterize MIS 3, within a zone that appears to be predominantly cold with brackish conditions as also recorded by the low percentage of marine taxa and dominance of *P. psilata* as reported for MIS 4 and 2 in the SE Black Sea basin (Shumilovskikh et al., 2014). Alternatively, these changes may again correspond to fluctuations in evaporation relative to precipitation during MIS 3 as reported by Wegwerth et al. (2016). No sapropelic sediment is present, and TOC values are very low throughout the massive banded clastic sediments. At the deepwater DSDP Site 380, there is also a notable absence of freshwater algae throughout this zone, in contrast to the (Shumilovskikh et al., 2014) record for the SE basin.

5.1.4. Dinoflagellate cyst zone 4 (11–0.52 m): late glacial brackish waters with minor interglacial salinity influence

Although brackish *P. psilata* remains the predominant species and reworked dinoflagellate cysts are rare (2% maximum), there are peaks of *Spiniferites cruciformis* that has a wider salinity range in surface sediments of the present-day Ponto-Caspian basins (Zonneveld et al., 2013; Marret et al., 2015). Several minor marine influxes in zone 4 are also indicated by the presence of marine stenohaline taxa *Impagidinium* sp., *Ataxodinium choane*, and *S. bentorii*, along with an increase in *L. machaerophorum* with “long” processes (Fig. 9) in many samples (Fig. 3). The *S. cruciformis* acme in this zone (ca. 20%) is notable and corresponds to the well known late Pleistocene intervals described for Marmara Sea and other Black Sea cores (e.g. Mudie et al., 2004; Marret et al., 2009; Shumilovskikh et al., 2013). The low diversity of total dinoflagellate species in this zone and absence of peridinioiid taxa which characterize both interglacial stages MIS 5e and MIS 1 (Shumilovskikh et al., 2013), show that the DSDP Site 380 samples do not include the mid-late Holocene sediments where diversity increases to around 34 taxa (Marret et al., 2009; Bradley et al., 2012).

5.2. Environmental significance of the assemblage recovered from DSDP Site 380

*Galea cysta etrusca*, one of the most common species recovered at our site, is known to occur as four biometrically determined morphotypes in relation to qualitative assessments of salinity or nutrient variability (Groups ‘a’–‘d’ of Popescu et al., 2009). In their paper, Popescu et al. (2009) indicate that the species most likely originated from Pannonian basins (Hungary) and/or from the Eastern Paratethys basins (Southern Romania, Black and Caspian Seas) and later migrated to the Mediterranean Sea during late Miocene and early Pliocene highstands. These periodic widespread migrations into the Mediterranean possibly imply a greater sea surface temperature (SST) tolerance and opportunistic species characteristics for this taxon compared to the other brackish Paratethyan species.

The second endemic taxon recovered in large quantity within this study is *Spiniferites cruciformis*. This species was first described for samples of Black Sea sediments by Wall et al. (1973) and was attributed an early Holocene age. However, since then this species has been reported for late Miocene to early Pliocene sediments in the Black Sea at Site 380 (Popescu, 2006), southern Romania (Popescu, 2001), latest Miocene of Italy (Bertini, 1988), in late Pleistocene — early Holocene sediments from Greece (Kouli et al., 2001), and in Pleistocene—Holocene sediments in the Black, Aral, Marmara and Caspian Seas (Mudie et al., 2001, 2002; Marret et al., 2004; Sorrel et al., 2006; Leroy et al., 2007; Londeix et al., 2009). In late Pleistocene sediments of Marmara Sea, this species and *P. psilata* increase during the Bolling–Allerød warm periods (ca. 14.7–12.7 ka BP), indicating a preference for warmer surface waters during glacial–interglacial transitions (Popescu, 2000; Shumilovskikh et al., 2013, 2014). The sea-surface salinity preference of *S. cruciformis* is a matter of debate. Wall and Dale (1973) described it as a “plastic” species that can present important morphological differences. It is classically accepted as a brackish water species (where brackish is defined as a salinity of ca. 3–11 psu) by in (Mudie et al., 2011, 2016) except by Kouli et al. (2001) that argue for a freshwater preference of *S. cruciformis* based on its occurrence in a freshwater lake in Greece. Leroy and Albay (2010) also show that small amounts of *S. cruciformis* form 3 can live in the Turkish freshwater Lake Sapanca. However, Mudie et al. (2001) show that the salinity range of *S. cruciformis* form 1 in early Holocene sediments of Marmara Sea is ca. 12–22 psu, as measured by calibration with oxygen isotope values of co-occurring planktonic foraminifera. Present-day distribution of *S. cruciformis* includes sites in the fully marine Mediterranean Sea (Zonneveld et al., 2013).

The last so-called Paratethyan endemic species to dominate the assemblage is *Pyxidinioopsis psilata*, which is known to appear since the late Miocene in the Black Sea (Popescu, 2008), as well as in Black Sea MIS 6 sediments (Shumilovskikh et al., 2013), in late Pleistocene sediments from the Marmara Sea (Mudie et al., 2001, 2002, 2004; Londeix et al., 2009), and in Black Sea sediments before the last connections between the Marmara and Mediterranean seas which occurred around 10 cal ka BP (Mudie et al., 2001; Popescu, 2008; Verleye et al., 2009; Bradley et al., 2012). Generally, this species increases during glacial periods possibly indicating a preference for cooler surface waters (Popescu, 2008) but it is found in modern sediments of the Caspian Sea where annual SST is 16–18°C and in subtropical water off Florida (Zonneveld et al., 2013). The presence of this species in the Black Sea where the sea surface salinity ranges between 7 and 20 psu, and its sparsity in the Caspian Sea were its associated SSS ranges between 5 and 12 psu (Mudie, unpublished data) indicates a probable SSS range between 7 and 12 psu as suggested by its concurrence with *L. machaerophorum* for the early Holocene of the southwest Black Sea (Marret et al., 2009; Mertens et al., 2012).

*Lingulodinium machaerophorum* is one of the few cosmopolitan marine dinoflagellate cyst species recovered in this study. As discussed previously, this species is known to show a wide range of process lengths, which is correlated with salinity (Mertens et al., 2005, 2012). Its presence has been recorded in coastal sediments from subtropical to tropical regions of the Southern Hemisphere, and from tropical to temperate regions in the Northern Hemisphere. It is distributed in marine environments characterized by a
sea surface temperature (SST) between about 1.5 °C (winter SST; rarely found from 0 to −1.5 °C) and from 10 to 29.1 °C (summer SST), with sea surface salinity (SSS) between 8.5 and 39.5 psu (summer − autumn), and with nutrient ranges of 0.06−1.1 mM for phosphate and 0.04−12.0 mM for nitrate (Marret and Zonneveld, 2003, updated in Zonneveld et al., 2013). This species is common in low salinity environments such as the Black Sea and Marmara Sea (Wall and Dale, 1973; Wall et al., 1973; Mudie et al., 2001, 2004, 2011; Marret et al., 2009), Caspian Sea (Marret et al., 2004), Baltic Sea (Elleegaard, 2000), or in periodically hypersaline conditions of the endorheic Aral Sea (Sorrel et al., 2006). L. machaerophorum appears to respond to salinity stress by a reduction in process lengths from long spines to short bulbous processes, and therefore presence of shortened processes is commonly used as a proxy for past sea-surface salinity (Mudie et al., 2001; Sorrel et al., 2006; Marret et al., 2009), conclusions about endocyst shape and salinity changes remain tenuous. Our PCA analysis of morphotypes found within Holocene sediments of the Black Sea (Mudie et al., 2004; 2011; Mudie et al., 2001; Sorrel et al., 2006; Marret et al., 2009; Mertens et al., 2009) and Dale, 1973; Wall et al., 1973; Mudie et al., 2001, 2004, 2011; Marret et al., 2009), Caspian Sea (Marret et al., 2004), Baltic Sea (Elleegaard, 2000), or in periodically hypersaline conditions of the endorheic Aral Sea (Sorrel et al., 2006). L. machaerophorum appears to respond to salinity stress by a reduction in process lengths from long spines to short bulbous processes, and therefore presence of shortened processes is commonly used as a proxy for past sea-surface salinity (Mudie et al., 2001; Sorrel et al., 2006; Marret et al., 2009; Mertens et al., 2009; Verleye et al., 2009). Long processes are present during times of relatively normal marine salinity and little to no stress, while short/bulbous processes indicate times of low salinity and severe stress to the taxa (Mertens et al., 2009; Verleye et al., 2009). Most of these studies (Mudie et al., 2001; Marret et al., 2009; Mertens et al., 2012) classified L. machaerophorum with processes longer than >15 µm as long processes, and short processes ranging from <5 to 10 µm in length. However, in our study, it is notable that true long processes were not present, and that (as noted in the method section) the “long” processes reported herein are >5 but <15 µm, with short processes are defined as being <5 µm. The absence of normal long processes (>15 µm) at DSDP Site 380 may relate to its position downstream from the Danube Shelf where modern populations of L. machaerophorum have short processes within the river discharge plume, and indicates low salinity for the entire record (Mudie, unpublished data). Also notable is the sparse occurrence of L. machaerophorum cyst with bulbous processes in the DSDP Hole 380 samples; this morphotype is rare in the Caspian Sea but it is common in more saline waters of the Black Sea (Marret et al., 2015).

Regarding S. cruciformis and other cruciform dinocyst species, Eaton (1996) suggested that this rare endocyst shape may be a stress response to low salinity waters of less than 12 psu. Comparisons of G. etrusca and S. cruciformis distributions at DSDP Site 380 do show that cruciform taxa are correspondingly more abundant at different depths, but without measurement of morphometric heterogeneities within G. etrusca in the style of Popescu et al. (2009), conclusions about endocyst shape and salinity changes remain tenuous. Our PCA analysis of S. cruciformis morphometrical variation based on endocyst: ectocyst size ratios (Fig. 4) would also indicate a more complex relationship with SSS, at least for MIS 5–1, as these species appear in salinity possibly higher than 12 psu, and S. cruciformis with typical morphology can be present in surface sediment of Marmara and the Mediterranean Sea at salinities up to at least 29 psu (Zonneveld et al., 2013). Mudie et al. (2001) encountered the same problem for the S. cruciformis morphotypes found within Holocene sediments of the Black Sea and Marmara Sea region where five morphotypes were identified based on process lengths and development of sutural septa. Neither multivariate regression of abundance against foraminiferal oxygen isotope estimates of salinity nor comparisons to the sea-level curve allowed them to propose concrete salinity reconstructions for the different morphotypes other than an overall estimation of brackish to low salinity marine conditions.

5.3. Marine reconnections and chronology on and timing of the last reconnection

The main problems in trying to reconstruct a marine reconnection model from our DSDP Site 380 dataset are largely due to the limited sample distribution, as well as the poor recovery, lack of high resolution magnetostratigraphy, and limited microfossil age markers for this DSDP Site. The drilling did not recover the mid-late Holocene sediment which contains a higher diversity of dinoflagellate species (ca. 25−30), including many heterotrophic taxa (Marret et al., 2009; Bradley et al., 2012; Shumilovskikh et al., 2013) such as the Holocene endemic species Peridinium ponticum that has a first appearance around 5.5 ka BP in the Black Sea. Furthermore no samples were available between 28 and 17 m (most of MIS 3 according to our age estimates), preventing precise age reconstruction and calculation of marine reconnection rates. Another issue is the lack of an oxygen isotope curve from the Black Sea because of the absence of planktonic foraminifera in the low salinity (<18 psu) Black Sea although they live in the semi-marine Marmara Sea where SSS is ca. 22−26 psu. Despite these limitations, some observations can be made by comparison with more complete late Pleistocene sections elsewhere in the Black Sea. Verleye et al. (2009) proposed that the Black Sea was close to fully connected to the Aegean at 7.97 ka BP as evidenced by the presence of 95% of marine dinoflagellate cysts (Operculodinium centrocarpum sensu stricto and Spiniferites spp.) at a slope site southeast of Bosphorus Strait, in the path of the marine bottom water overflow. Such abundance of marine species were not seen at the deeper water of DSDP Site 380 north of Bosphorus Strait which is at the terminus of the counterclockwise circulation of both surface and bottom water in the Black Sea, but a small increase in marine palynomorphs was observed near the top of dinoflagellate cyst zone 4. This event is marked by increases in in situ euryhaline marine species (Spiniferites spp. a. c. andalusiensis [now extinct throughout the region but present in latest Pleistocene] and L. machaerophorum) along with the appearance of stenohaline marine species Axatodinium choano, and the highest abundance of L. machaerophorum with “long” processes.

Comparison can also be made with the palynological studies of MIS 5e and MIS 4–2 in deep basins of the southeastern Black Sea (Shumilovskikh et al., 2013, 2014; Wegwerth et al., 2016). These studies show that in this part of the Black Sea, both the Eemian and Holocene interglacials are marked by a succession from lacustrine brackish taxa (P. psilata, S. cruciformis, and Caspidinium rugosum) to more marine assemblages (L. machaerophorum, Spiniferites ramosus complex and up to 20 other autotrophic and heterotrophic dinoflagellate cyst taxa) which is attributed to inflow of saline Mediterranean water. During MIS 5e, this marine connection persisted from ca, 128−119 ka BP, with SSS reaching ca, 28−30 psu, and between 127.5 and 121 ka BP a relatively high SST is evident due to the high abundance of Tuberculodinium vancampoae and Bitectodinium tepikiense (Shumilovskikh et al., 2013). In contrast, the absence of these warm water indicators, lower diversity and absence of heterotrophic taxa at DSDP Site 380 suggests that our studied samples did not cover the full suite of interglacial conditions.

For the interval from 64 to 25 ka BP in the southeastern Black Sea, there is a comparable dominance of Pyxidinopsis psilata and Spiniferites cruciformis in the dinocyst record, indicating brackish water, with a decrease in marine indicators around 54 ka BP and a further freshening of Black Sea from ca, 32−25 ka BP (Shumilovskikh et al., 2014). Notably, species diversity in the SE Black Sea records shows higher diversity of autotrophic species, but G. etrusca is rare or absent throughout this densely sampled interval (152 levels) and Caspidinium rugosum, a Caspian endemic dinoflagellate cyst is commonly present in contrast to its absence at Site 380. In the SE basin, there is also an almost ubiquitous presence of freshwater algae which is not found at the deeper water location of DSDP Hole 380. High resolution pollen studies on the southeastern core 25GC1 from 418 m water depth (Shumilovskikh et al., 2014)
show there were alternating arid/humid phases in the region which were expressed as minor salinity and water level changes, with interstadials having higher dinoflagellate cyst concentrations probably related to increased temperature, runoff, and nutrients. Drier conditions with increased salinity mark stages MIS 4 and MIS 2 and stadials within MIS 3. Overall, there is no indication of a full marine reconnection in the eastern Black Sea basins between the end of MIS 4 and MIS 2.

Minor oscillations in dinoflagellate species are observed in the low resolution study of MIS 4–2 at DSDP Site 380, despite the missing Core 3 interval that represents the middle part of MIS 3 (probably −54–44 ka BP). The observed increase in marine taxa and appearance of the typical deep water Mediterranean taxa Impagidinum sp. and Nematosphaeropsis clearly indicate some brief influx of marine water to the western region which is not recorded in the SE basin cores of Shumiliyskikh et al. (2013, 2014) where N. labirinthus disappears after MIS 5e. This brief salinity increase appears to correspond to the Tarkan-Kutan and Surozhian interstadi al intervals dated ca. 40–27 ka BP and is marked by a peak occurrence of Pterocysta cruciformis on the SW Black Sea shelf (Rochon et al., 2002). P. cruciformis is very rare at the deep water DSDP Sites, as also found in a deep basin core from Marmara Sea where it is reported for the late Pleistocene (Londeix et al., 2009).

6. Conclusions

The dinoflagellate cyst analysis of late Pleistocene—Holocene samples from DSDP Site 380 located at the base of the western Black Sea’s continental slope is constrained by low resolution sampling and limited age control, but it provides further evidence for past connections between the Black and Mediterranean Seas and the paleoenvironmental changes from late MIS 5 to early MIS 1. Brackish species Pyxidinopsis psilata, Galeacytus etrusca, and Spiniferites cruciformis were the dominant taxa found in all samples from Site 380. P. psilata is more abundant during glacial periods, while G. etrusca and S. cruciformis are associated with warmer sea surface temperatures at the end of MIS 5 and end of MIS 2, respectively. Species with a primarily marine affinity mainly include Lingulodinium machaerophorum, Spiniferites bentorii, Achomosphaera cf. andalousiensis, and Nematosphaeropsis labyrinthus; these common Mediterranean taxa are present during the later interstadial phases of the interglacial MIS 5, and together with presence of sapropelic muds, indicate at least intermittent connections between the Black and Mediterranean Seas at times of high sea levels before the glacial regression of MIS 4 and 2. The reconnection intervals appear as small differences in sea surface salinity for the southwestern Black Sea during the Last Glacial Climatic Cycle, towards the middle of MIS 3 when the salinity most likely fluctuated between the restricted ranges of 12 and 22 psu as indicated by the morphometric analyses of Galeacytus etrusca. No freshwater, low salinity brackish or high nutrient morphometric subgroups were seen in G. etrusca at any sampled depths, indicating that the salinity in the western Black Sea remained brackish to low-salinity marine throughout the sampled interval at DSDP Site 380. Finally, discriminant analysis between Galeacytus etrusca and Spiniferites cruciformis show that the two Paratethyan relic species are morphometrically distinct, with an overall probability of correct classification of 88.67% based on the four morphologic measurements alone. In the deep water western Black Sea basin, G. etrusca has its last peak abundance in MIS 5a whereas S. cruciformis is most abundant in late MIS 2 and early MIS 1. Lower species diversity, absence of heterotrophic taxa (including endemic Peridinium ponticum) and absence of thermophiles such as Tuberculodinium vanCampae apparently distinguish assemblages at the bathyal western DSDP Sites from those of mid-depth cores from the southeastern basin.

Acknowledgments

This paper is primarily a summary of S. Ferguson’s M.S. thesis. Thanks are extended to speranta Popescu for her substantial guidance and contribution during Ferguson’s Master Thesis (Ferguson, 2012). She thanks her committee members for constructive remarks, and the LSU Department of Geology and Geophysics for financial assistance. Thanks are also extended to Martin Head (Brock University) for assistance with the identification of some dinoflagellate cyst species and ranges of reworked taxa, and to Crawford White for valuable figure and editing support. We also thank two anonymous reviewers for their constructive and helpful comments.

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