**Late Quaternary Ponto-Caspian Dinoflagellate cyst assemblages from the Gulf of Corinth, Central Greece (eastern Mediterranean Sea)**

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### Abstract

We present here the first long Quaternary record of organic-walled dinoflagellate cyst assemblages analysed from sediment cores retrieved during the International Ocean Discovery Program (IODP) Expedition 381 in the Gulf of Corinth. Site M0078A is located in the central part of the Gulf of Corinth (GoC), a semi-isolated marine basin that was repeatedly isolated and reconnected to the Mediterranean Sea during the Quaternary glacial/interglacial cycles. Our results show that dinoflagellate cysts are sorted in two major ecogroups, each group alternating between marine and isolated/brackish conditions. The marine intervals are characterised by high dinocyst diversity whereas the isolated intervals are dominated by taxa thriving in low-salinity conditions such as *Spiniferites cruciformis* and *Pyxidinopsis psilata*. In several of these assemblages, *S. cruciformis* is so prevalent that it forms almost monospecific assemblages. The low salinity dinocyst assemblages are reported for the first time outside the Ponto-Caspian region and they show a close affinity to modern assemblages from the Black Sea, Caspian Sea and Marmara Sea. The alternations between marine and brackish conditions recorded in the Gulf of Corinth reflect changes in surface water salinity (SSS) and temperature (SST), in response to the Quaternary glacial-interglacial cycles. These seem to be in good agreement with regional and global marine isotope and sea-level records. Our findings suggest that the study region sensitively responds to climate forcing at orbital time scales and that local factors most likely drive shifts in dinoflagellate species composition and diversity.

Keywords: glacial/interglacial cycles; sea-level change; dinoflagellate cyst assemblages; sea-surface salinity; northeastern Mediterranean Sea

1. Introduction

Organic-walled dinoflagellate cysts are the resting phase in the life cycle of a single-celled eukaryotic plankton of the phylum Dinoflagellata (e.g., Fensome et al., 1993; Head, 1996). They are mostly free-living micro-organisms occupying a wide range of environments from fresh water to the open ocean, and from the tropics to high latitudes (e.g., Marret et al., 2020; Van Nieuwenhove et al., 2020). Dinoflagellate cyst assemblages are mostly encountered in marine environments, but they can also be found in low salinity and freshwater conditions (Evitt et al., 1985; Kouli et al., 2001; McCarthy et al., 2011; Panagiotopoulos et al., 2014; Mudie et al., 2017). Previous studies have highlighted their strong potential as biostratigraphic and palaeoenvironmental indicators (e.g., Mudie, 1987; Louwye et al., 1999; Mudie et al., 2002b; Louwye et al., 2004; Mudie et al., 2004; Marret et al., 2004; De Schepper et al., 2009; Dybkjær et al., 2007; Mertens et al., 2009a, Mertens et al., 2012b; Zonneveld et al., 2013; De Schepper et al., 2015; Mudie et al., 2017; Londeix, 2018; Matthiessen et al., 2018; El-Soughier et al., 2019; Zorzi et al., 2019; Marret et al., 2020; Van Nieuwenhove et al., 2020), in particular in environments where other proxies are rare or absent.

Connectivity between lakes, seas and oceans plays a critical role in shaping the physical and geochemical conditions within each basin by facilitating the exchange of water and biota. The connection to the open sea can significantly impact the basin's circulation pattern, water chemistry and depositional environment as well as its biodiversity. Nowadays, the Gulf of Corinth is connected to the Gulf of Patras (Ionian Sea) through the Rion Strait (Figure 1), creating a bathymetrically restricted ‘fjord-like’ marine embayment with fully marine conditions (Poulos et al., 1996). This connection to the Mediterranean Sea is governed by the interplay between eustatic sea level and changes in sill geometry at the Rion Strait in the west (Perissoratis et al., 2000; Stanev et al., 2001; Rohling et al., 2014; Mc Neill et al., 2019a) and tectonic uplift to the east (Collier and Thompson, 1991; McMurray and Gawthorpe, 2000; Papanikolaou et al., 2015; Pallikarakis et al., 2019).

The link to climate-driven sea-level fluctuations observed in other low salinity, semi-enclosed or endorheic basins located eastwards (i.e., Marmara, Black and Caspian Seas) have resulted in the isolation and reconnection of the these basins with the Mediterranean Sea (Kvasov 1975; Svitoch et al. 2000; Mudie et al., 2017). These three seas were connected during the late Miocene (Popov et al., 2006) but since then, the Caspian Sea became isolated and occasionally reconnected with the other basins after ca. 2.6 Ma, during the Akchagylian period (Forte and Cowgill, 2013) and remained periodically connected during the Pliocene, the Pleistocene and the early Holocene (Boomer et al., 2000; Naderi Beni et al., 2013; Haghani et al., 2016). The Black Sea was also isolated from the north Aegean Sea until ca. 12,000 years BP when the Mediterranean Sea penetrated the Dardanelles Strait (Aksu et al., 1999b; Aksu et al., 2002b; Karatsolis et al., 2017; Dimiza et al., 2020; Aksu and Hiscott, 2022). Studies of recent dinoflagellate cyst assemblages across the Aegean-Black-Caspian Sea corridor have demonstrated the sensitivity of dinoflagellate cysts to different salinities and have been successfully applied to reconstruct past salinity gradients (e.g., Mudie et al., 2004; Marret et al., 2004; Mertens et al., 2009; Mertens et al., 2012b; Bradley et al., 2012; Mudie et al., 2017).

The Black Sea is the largest anoxic marine basin in the world, it is shallow in the northeast and is intensely influenced by river inputs (Aksu et al., 2000; Sorokin, 2002; Chepalyaga, 2007). Based on the analysis of paired Sr isotope and palaeosalinity data, the Black Sea appears to be strongly influenced by variations in glacial extent within the Dnieper River catchment and the resultant erosion of Sr from granitic basement rocks, where the Sr ratios are high (Bista et al., 2021). During the last interglacial period, the Black Sea received a meltwater influx from the Fennoscandian ice sheet, freshening the Marmara and the Aegean Seas and eventually the eastern Mediterranean Sea (Vadsaria et al., 2022). The Marmara Sea is a small tectonic trench with narrow straits and shallow sills that link the Black Sea to the Aegean Sea (NE Mediterranean Sea; Aksu et al., 2000; Aksu et al., 2002; Mudie et al., 2017), while the Caspian Sea is the largest intracontinental lake (Marret et al., 2004; Chepalyga, 2007). The Gulf of Corinth, despite its smaller size (105 km long, 30 km wide) and the significantly lower riverine input, is quite comparable with these basins. It is quite similar to the Marmara Sea with regard to size, bathymetry, watershed, climate and sedimentation rates; they both underwent the same palaeoenvironmental changes during the Quaternary (McHugh et al., 2008; Mudie et al., 2002a) with a disconnection from the open sea during the Late Glacial Maximum (MIS 2; Campos et al., 2013).

The evaluation of the timing and type of transition from lacustrine (isolated) to brackish (semi-isolated) or marine conditions can be accurately traced through aquatic palynomorph analysis (i.e., freshwater algae, dinoflagellate cysts and foraminiferal organic linings). One of the main advantages of studying dinoflagellate cyst assemblages throughout successive glacial-interglacial intervals is the continuous presence and preservation of these palynomorphs in alternating environmental conditions. Calcareous microfossils, such as foraminifera and coccolithophores are restricted to intervals when the GoC was connected to the global ocean. Organic-walled dinoflagellate cysts (dinocysts) are generally abundant and well-preserved in the sediments of the Black Sea Corridor (BSC). In the low-oxygen stratified waters of these brackish water basins, dinocysts are the main proxy for studying changes in sea-surface conditions and phytoplankton biodiversity (e.g., Mudie et al., 2002a; Marret et al., 2004; Sorrel et al., 2006; Bradley and Marret, 2013). The high potential of dinocysts as environmental indicators in the BSC is because 1) calcareous phytoplankton are frequently poorly preserved (Giunta et al., 2007) and 2) in the BSC, planktonic foraminifera occur only in the Marmara Sea (Mudie et al., 2002a). The analysis of the dinoflagellate cyst assemblages contributes to further comprehending and reconstructing the salinity gradients that developed during the transition of the basin from marine to isolated conditions. The surface salinity signal inferred from the dinoflagellate cysts in those aforementioned neighbouring basins reveals the changes in the depositional palaeoenvironment and determines the relationship among the climate-driven marine ecosystem response and the other mechanisms controlling basin subsidence, sill elevation and eustatic sea level.

The main scope of this study is to examine the alternations between marine and isolated/semi-isolated depositional environments in relation to the eustatic sea level changes and active tectonics in the Gulf of Corinth using a record of the resting phase of dinoflagellates. Preliminary studies in the IODP retrieved deposits from the Gulf of Corinth confirmed the preservation of dinocysts in all depositional environments in contrast to other marine/aquatic biotic proxies that present discontinuous occurrences (McNeill et al., 2019b). Therefore, the salinity-sensitive dinoflagellate cyst assemblages are an excellent tool for the reconstruction of the palaeoenvironmental shifts during glacial and interglacial periods in the Gulf of Corinth basin.

1. Area setting

The Gulf of Corinth extensional basin is an ESE-trending arm of the Ionian Sea, with a length of ca. 120 km and a surface area of ca. 2300 km2 (Figure 1). It reaches the open sea in the west, through the 2 km wide Rion Strait. The Rion strait has a maximum depth of 62 m and a prominent terrace is formed at a 60–62 m water depth (Perissoratis et al., 2000). To the east, the Gulf is separated from the Saronic Gulf by the 6 km-wide and up to 90 m high Corinth Isthmus, where a ship canal has been dug during the late 1800s. The eastern part has two arms: the Lecheon Gulf in the south, which adjoins the isthmus and is up to ca. 200 m-deep, and the Alkyonides Gulf in the north, separated from the Gulf by the Perachora Peninsula (Perissoratis et al., 2000).

The submarine bathymetry of the Gulf of Corinth consists of four main physiographic provinces: a) the continental shelf; b) the continental slope; c) the continental rise and d) the abyssal plain. This system is completed by the Delphic Plateau and the Alkyonides Basin (Heezen et al., 1966). Water depth in the abyssal plain, in the central basin of the Gulf of Corinth, reaches more than 800 m. This flat area is characterised by gentle gradients <0.5º (Poulos et al., 1996). The water masses within the basin are separated into two main categories: a) euphotic zone (0–200 m) wherein temperature and salinity seasonally vary with depth; and waters below 200 m, where temperature and salinity remain almost constant. Sea-surface temperature and salinity range between 25°C and 38.55 psu (summer) and 14.3°C and 38.35 psu (winter), respectively. Below 200 m, they remain almost constant at 13.3°C and 38.57 psu (summer) and 12.8°C and 38.41 psu (winter), respectively (Anderson and Carmack, 1973). Seasonal fluctuations in the concentration of dissolved oxygen are observed, with higher saturation values between February and August (Friligos et al., 1985) and maximum saturation (>80%) just below the sea surface. However, the water column from the sea floor to just below -200 mis oxygenated, indicating renewal processes. Water circulation is dominated by a semi-diurnal baroclinic tide generated in the deep centre of the GoC (Drakopoulos and Lascaratos, 1998) that is characterised as a microtidal environment (Tsimplis, 1994). In the central part of the GoC, the velocity of the currents is very low (<8 cm/s, Poulos et al., 1996), whereas high-velocity bottom currents and upwellings are generated in the western part at Nafpaktos bay where the Mornos River is discharging (Rubi et al., 2022). The surface water circulation is dominated by the funnelling of both wind and water through the narrow Rion Strait, where near-surface current velocities can exceed 100 cm/s (Piper et al., 1990).

In the Corinth Rift area, more than 2.5 km of sediments accumulated during the last approximately 5 Ma, recording its complete geological history within the onshore and offshore deposits (Nixon et al., 2016). Quaternary sediment accumulation in the GoC has been controlled by the position of the sea level relative to the Rion Strait sill and alluvial sediment input from rivers resulting in alternating marine and lacustrine sediments (e.g., Ori, 1989; Gawthorpe et al., 1994; Rohais et al., 2007; Backert et al., 2010; Palyvos et al., 2010; Leeder et al., 2012; Ford et al., 2013). When the sea level fell below the level of the Rion Strait sill, the GoC became isolated. However, when the sea level was only a few meters above the Rion Strait sill, it remained connected with the Ionian Sea, characterised by marine conditions together with high input of freshwater conditions. When the sea level was significantly higher, open marine conditions were restored. Under marine conditions, low gradient (suspended load) deltas, such as those entering the Gulf of Corinth, deposited most of their sediment on the shelf, but supplied lacustrine turbidites by underflow when the Gulf was isolated (e.g., Hemelsdaël et al., 2021; Cullen et al., 2022). Steep gradient (bed load) deltas like the Selinous and Vouraikos Rivers of Peloponnese supply turbidites to the basin floor under both marine and lacustrine conditions, but the importance of mass movement appears greater under lacustrine conditions (Perissoratis et al., 2000). Before 400 kilo-annum (ka), the connection of the GoC with the open ocean was mainly from the east, through the Saronic Gulf and the present-day Corinth Isthmus (Collier and Thompson, 1991; Pallikarakis et al., 2019; Gawthorpe et al., 2022).

The IODP Exp. 381 ‘Corinth Active Rift Development’ drilled three sites (M0078, M0079 and M0080 in the Alkyonides Gulf) and sampled the most recent syn-rift deposits (~1-2 Ma) reaching a maximum depth of 705 m below sea floor (mbsf). The preliminary sedimentological, micropalaeontological and geochemical analyses of the recovered deposits allowed the identification of two major lithostratigraphic units. The upper LU1 (further subdivided into subunits from LU1.1 up to 1.16) represents an interval of periodical isolation and reconnection of the GoC with the Mediterranean Sea in response to the global sea-level fluctuations; the lower LU2 characterises a more isolated environment (Shillington et al., 2019). Several subunits of the M0078 core were characterised by the relatively high abundances of benthic and/or planktonic foraminifera, suggesting marine conditions (e.g. LU1.1, 1.3, 1.7), whereas, in other intervals, foraminifera were completely absent (McNeil et al., 2019b). The occurrence of marine diatoms and calcareous nannoplankton also suggests marine conditions, whereas they were absent in the isolated subunits (e.g. LU 1.2, 1.4, 1.6) (McNeil et al., 2019b). In contrast to the discontinuous occurrence of these calcareous and siliceous proxies , dinocysts are present all through the sequence and their assemblages represent well the alternations between the isolated intervals and the marine transitions.

The age constraints of the deposits are mainly based on the study of site M0079 which reported significant climate-driven changes in palaeoenvironment, sediment accumulation and geochemistry during the last ~850 ka, correlating well with the Marine Isotopic Stages (McNeill et al., 2019a; McNeill et al., 2019b; Gawthorpe et al., 2022). The identified Brunhes/Matuyama boundary (0.773 Ma) and several dating points were correlated with the reference PISO-1500 RPI curve, providing a high-resolution age-depth model (Maffione and Herrero-Bervera, 2022) for the deposits. The Brunhes/Matuyama reversal has been also recognized at site M0078 at the depth of 385.99 mbsf (McNeill et al., 2019b). The deposits of sites M0079 and M0078, both originating from the central GoC, have been correlated in detail by Gawthorpe et al. (2022), providing the age frame for the present study.

1. Material and Methods

Site M0078, drilled during IODP Exp. 381, is a long record of the syn-rift sedimentation (McNeill et al., 2019b). It is located in the central part of the Gulf of Corinth (38°8′41.802″N 22°45′30.251″E) at a water depth of 859.5 m (Figure 1). The sedimentary sequence drilled 610.43 mbsf that were divided into two main Lithostratigraphic Units (LU). Deposition during the upper one, LU1 (0–385.14 mbsf), is primarily controlled by eustatic sea level and dominated by detrital clay- and silt-grade carbonate (Figure 2). This interval has been divided into 16 subunits (LU1.1-1.16) with respect to the alternation of marine and isolated/semi-isolated intervals, with several facies associations (FA) have been described (McNeill et al., 2019b; Figure 2). Below 385.14 mbsf, LU2 is composed almost entirely of weakly laminated to homogeneous highly bioturbated mud (FA12). The boundary between LU1 and LU2 is sharp and marked by an abrupt change from laminated greenish-grey muds to homogeneous light-grey muds downhole (McNeill et al., 2019a).

### 3.1 Sampling and laboratory procedure

The sampling of core M0078A for palynological analysis was carried out at ~1.8 m intervals in 2018 at the Bremen Core Repository at the University of Bremen, Germany. For the present study, a total of 294 samples distributed within LU1 were studied. Approximately three grams of dry sediment were prepared for palynological analysis using the same chemical preparation protocol developed during the IODP Exp. 381 onshore phase in Bremen Core Repository (McNeill et al., 2019b). Samples were treated at the Laboratory of Historical Geology and Palaeontology of the National and Kapodistrian University of Athens using hot hydrochloric acid (HCl 37 %), placed in a hot water bath for ~20 min and cold hydrofluoric acid (HF 38 %), for approximately three days. The residues were repeatedly washed with distilled water until they were neutralised, and then sieved through a 10 μm sieve. One *Lycopodium* tablet (Batch No.: 483216/18583 spores) was added at the start of treatment for estimating the concentration of palynomorphs in each sample. The residue was finally transferred to 1.5ml Eppendorf tubes for storage and mounted in glycerine.

### Microscopic Analysis

Palynological analysis has been conducted under the transmitted light microscope Zeiss Axilla 5 at magnifications of ×400 and ×1000. Microscopic photographs of specimens were taken with a Zeiss AxioCam 208 colour camera. All samples processed were analysed for their dinoflagellate cysts content to determine the palaeoenvironmental conditions. The encountered dinocysts were exceptionally well preserved in the vast majority of the samples analysed. Where possible, 200 dinoflagellate cysts were counted; samples containing fewer than 50 cysts were excluded. In the few cases where relatively poor preservation and/or low counts of dinoflagellate cysts were observed, e.g., in the interval 207–237 mbsf, these samples were excluded from the analysis.

The identification of dinocysts was based on the work by Wall and Dale (1974), Head et al. (1993), Rochon et al. (1999), Mudie et al. (2001), Rochon et al. (2002(, Mudie et al. (2002b), Marret and Zonneveld (2003), Marret et al. (2004), de Vernal and Marret (2007), Mertens et al. (2009a, b ; 2012a; 2017a, b; 2018a, b; 2020), Zonneveld et al. (2013), Zonneveld and Pospelova (2015), Mudie et al. (2017), Soliman and Riding (2017), de Vernal et al. (2018), Londeix et al. (2018), Gurdebeke et al. (2018) and Van Nieuwenhove et al. (2020). Microscopic analysis revealed two distinct morphotypes of *Lingulodinium machaerophorum*. This species exhibits great variability in the length of the processes in response mainly to salinity variations (Wall et al., 1973, Mertens et al., 2009a, Mertens et al., 2012b). Therefore, *L. machaerophorum* with short processes (<10μm) as *L. machaerophorum* s.p. and *L. machaerophorum* with long processes (>10μm) as *L. machaerophorum* s.l. were distinguished. *Operculodinium centrocarpum* has been recorded to exhibit variations in processes and based on that *O. centrocarpum* sensu Wall and Dale, 1966 is the morphotype with “normal” (> 7 μm) and *O. centrocarpum* with the morphotype with “reduced” (< 5–7 μm) processes (Mudie et al., 2017). Only *O. centrocarpum* sensu Wall et Dale, 1966 with normal processes was recognized during the microscopic analysis.

### Statistical Analysis

A visual representation of the square-root transformed data matrix was achieved through a shade plot (Clarke and Gorley, 2015).

The results of the microscopic analysis were processed statistically. Percentages of each taxon were calculated based on the total sum of counted specimens. Taxa not identified at the species level (e.g., *Spiniferites* spp., *Impagidinium* spp.) were excluded from the statistical analysis as these groups may contain species with different ecological requirements. The dataset was subjected to non-metric multidimensional scaling (nMDS) and Principal Component (PCA) analyses. The PCA was selected to test the qualitative palaeoenvironmental results. The nMDS analyses the transposed dataset in order to demonstrate differences between the species. Prior to the nMDS analysis, percentages were square-root transformed to stabilize the variances (Clarke and Gorley, 2015). A Bray-Curtis similarity index was used to identify possible species – environment relationships (Clarke and Gorley, 2015). All statistical analyses were performed using Primer version 7 (Clarke and Gorley, 2015).

### Results

The dinocyst assemblages are characterised by high concentrations, especially in intervals representing isolated conditions in the GoC, with a mean concentration of 26,630 cysts/g. The cyst diversity is extremely low, with, in several cases, an almost monospecific assemblage. Opposingly, in the marine intervals, assemblages are characterised by high diversity, while the cyst concentration is generally lower, with a mean concentration of 24,633 cysts/g.

Microscopic analysis showed several alternations of diverse dinocyst assemblages that may be grouped into two main palaeoenvironmental conditions (Figure 3). The palynological analysis has shown that the low salinity intervals and the marine intervals correlate well with the Lithostratigraphic Units (McNeill et al., 2019b). Plotted results (Figure 3) highlight the dominance of *S. cruciformis* and *P. psilata* in the isolated intervals; monospecific assemblages consist of cysts of *S. cruciformis*. The results of the microscopic analysis are presented in detail below.

#### **Isolated/semi-isolated intervals:**

The dinocyst assemblages encountered within the intervals described below consist of the low salinity indicators *S. cruciformis*, *P. psilata*, *Caspidinium rugosum,* *Impagidinium caspienense* and *Lingulodinium machaerophorum* s. p. These assemblages support the notion of the occurrence of distinct isolated/semi-isolated intervals of the Gulf of Corinth when brackish water conditions should have been occurring. *Spiniferites cruciformis* and *P. psilata* are the most dominant species during those intervals, however, a distinct variability in those assemblages is recorded. Representative dinoflagellate cyst species are illustrated in Plate 1.

LU1.2 (21.43 –91.62 mbsf, 56 samples): The dominant taxa are *P. psilata* and *S. cruciformis, C. rugosum*, with high abundances reaching mean values of 75%; only a few representatives of *I. caspienense*, and *L. machaerophorum* s.p. are present (Figure 3). The following species *Tuberculodinium vancampoae, Polysphaeridium zoharyi*, *Operculodinium centrocarpum* sensu Wall et Dale 1966*, L. machaerophorum* s.l*., Nematosphaeropsis labyrinthus, Tectatodinium pellitum,* representatives of the *Impagidinium* group, *Spiniferites* group and several brown cysts are present in very low concentrations.

LU1.4 (123.765– 177.59 mbsf, 45 samples): This zone is characterised by the dominance of *S. cruciformis, reaching* 88%*. P. psilata* has a strong presence, whereas *C. rugosum* and *L. machaerophorum* s.p. are almost absent.

LU1.6 (188.45–198.52 mbsf, 7 samples): This zone is characterised by the co-dominance of *S. cruciformis* and *P. psilata*, whereas the presence of *C. rugosum* is observed only by a few representatives.

LU1.8 (206.22–235.65 mbsf, 28 samples): *S. cruciformis* is the dominant taxon reaching 90% in this interval. *P. psilata* is present in lower abundances and *C. rugosum* is almost absent.

LU1.10 (260.37–286.67 mbsf, 29 samples): In contrast to the other LUs, this Unit is characterised by the dominance of *P. psilata* which exceeds 80% of the assemblages in some samples (e.g., 268.07, 283.81, 285.6 mbsf). Although *S. cruciformis* shows a strong signal, it becomes completely absent when *P. psilata* is dominant.

LU1.12 (303.32–323.01 mbsf, 20 samples): *S. cruciformis* is the major component of the dinocyst assemblage (mean -representation is 90%)*,* whereas *P. psilata* is characterised by lower relative abundances.

LU1.14 (334.16–365.48 mbsf, 6 samples): The assemblage is characterised by the strong signal of *P. psilata,* while *S. cruciformis* occurs in lower relative abundances.

LU1.16 (370.3–384.3 mbsf, 1 sample): The most dominant taxon in this sample was *S. cruciformis* with percentages of 96%. A few *P. psilata* cysts complement the assemblage.

#### **Marine intervals**

The dinocyst assemblages recovered within the marine intervals of M0078A record are characterised by a high diversity (30 different species) and with mean concentrations of 24,632 cysts/g, as well as with many representatives of the *Spiniferites* group, *N. labyrinthus*, *O. centrocarpum* sensu Wall et Dale 1966, *L. machaerophorum* s.l., *P. zoharyi, T. pellitum, Bitectatodinium tepikiense*, representatives of *Impagidinium* group and some brown cysts. The assemblages of each Lithostratigraphic Unit are described in detail below and featured in Figure 3.

LU1.1 (0.00–20.19mbsf, 20 samples): This interval is characterised by the highest dinocyst diversity throughout the sequence. The *Spiniferites* group representatives are *S. belerius*, *S. bentorii*, *S. bulloideus*, *S. membranaceus*, *S. mirabilis*, *S. ramosus*, *S. lazus* and a few cysts of *S. cruciformis*, which could be characterised as tolerant to marine conditions. From the *Impagidinium* group, *I. aculeatum*, *I. paradoxum*, *I. patulum*, *I. sphaericum* and *I. strialatum* are present. Other species such as *Achomosphaera* spp., *Ataxodinium choane*, *O. centrocarpum* sensu Wall et Dale 1966*, L. machaerophorum* s.l*.*, *N. labyrinthus, P. zoharyi,* cysts of *Pentapharsodinium dalei, T. pellitum* and *B. tepikiense* are encountered, while the brown cysts *Brigantedinium* spp. (*B.* *cariacoense* and *B. simplex*), *Echinidinium* spp*.*, *Lejeunecysta oliva, Quinquecuspis concreta, Selenopemphix quanta* and *Selenopemphix nephroides* complement the assemblages.

LU1.3 (95.05–121.88mbsf, 22 samples): The dinocyst assemblages appear similar to the LU1.1 ones, however less diverse. However, in this interval, *T. vancampoae* is observed. Interestingly, in the interval 100.35-105.7mbsf (represented by four samples), *S. cruciformis* was the most dominant taxon, whereas a lack of several marine species (e.g., representatives of the *Spiniferites* group) and a total absence of all brown cysts are recorded.

LU1.5 (180.69–187.82, 8 samples): The most characteristic species of this assemblage were *N. labyrinthus*, *S. mirabilis*, *S. ramosus* and *O. centrocarpum* sensu Wall et Dale 1966.

LU1.7 (199.9–205.62, 7 samples): The species encountered were *Achomosphaera* spp., *A. choane*, *C. rugosum*, *I. aculeatum*, *I. paradoxum*, *I. patulum*, *I. sphaericum*, *I. strialatum*, *O. centrocarpum* sensu Wall et Dale 1966, *L. machaerophorum* s.I*.*, *N. labyrinthus*, *P. zoharyi*, cysts of *P. dalei*, *P. psilata, S. belerius*, *S. bentorii*, *S. bulloideus*, *S. membranaceus*, *S. mirabilis*, *S. ramosus*, *S. lazus*, *T. pellitum*, *B. tepikiense*, *Brigantedinium* spp., *Echinidinium* spp., *L. oliva*, *Q. concreta*, *S. quanta*, and a few specimens of *P. psilata* and *S. cruciformis*. *S. cruciformis* was present in high percentages in the last two samples (205.27 and 205.62mbsf).

LU1.9 (236.43–259.72mbsf, 23 samples): Poor dinocyst preservation was recorded in several samples within this interval, whereas some others were barren of any palynological content. In the samples with good dinocyst preservation, the occurring species were *A. choane*, *O. centrocarpum* sensu Wall et Dale 1966, *S. mirabilis*, *S. ramosus*, *S. lazus*, *B. tepikiense, Brigantedinium* spp., *L. oliva*, *Q. concreta, S. quanta* as well as a few specimens of *P. psilata* and *S. cruciformis*.

LU1.11 (288.06–298.4mbsf, 12 samples): The species characterising this interval are *A. choane*, *I. aculeatum*, *I. paradoxum*, *I. patulum*, *I. sphaericum*, *I. strialatum*, *O. centrocarpum* sensu Wall et Dale 1966, *L. machaerophorum* s.l., *N. Labyrinthus*, *P. zoharyi*, cysts of *P. dalei*, *S. mirabilis*, *S. ramosus*, *S. lazus*, *B. tepikiense*, *Brigantedinium* spp., *L. oliva*, *Q. concreta, S. quanta* as well as a few specimens of *P. psilata* and *S. cruciformis*. However, four samples (289.47–291.84mbsf) were barren similarly as in LU1.9.

LU1.13 (324.04–333.15mbsf, 8 samples): In this interval the samples 324.04–326.8 mbsf are characterised by high diversity. The *Spiniferites* group representatives are *S. belerius*, *S. bentorii*, *S. bulloideus*, *S. mirabilis*, *S. ramosus*, *S. lazus*,whereas a few cysts of *S. cruciformis* were also encountered. From the *Impagidinium* group, *I. aculeatum*, *I. paradoxum*, *I. patulum*, *I. sphaericum* and *I. plicatum* were observed. Other species such as *O. centrocarpum* sensu Wall et Dale 1966, *L. machaerophorum* s.l., *N. labyrinthus*, *P. zoharyi*, cysts of *P. dalei*, *T. pellitum*, *T. vancampoae* and *B. tepikiense* are encountered, whereas the brown cysts *Brigantedinium* spp. (*B.* *cariacoense* and *B. simplex*), *L. oliva*, *Q. concreta* and *S. quanta* complement the assemblages. The most dominant species in both samples were *L. machaerophorum* s.l.*, S. ramosus* and *Brigantedinium* sp. The sample at 328.51 mbsf was barren. Below the depth of 329.74 mbsf, *S. cruciformis* dominated and was accompanied by a few representatives of *P. psilata* and *C. rugosum*.

#### **Statistical results**

The PCA analysis (Figure 4) yielded two main different groups of dinocyst assemblages. The first principal component explains 62.2% of the total variance and shows positive loadings for all species except for *S. cruciformis*. The positive loadings can be related to marine assemblages and the remaining low-salinity indicators, such as *P. psilata, I. caspienense, C. rugosum* and *L. machaerophorum* s.p. Negative loadings are related to the most dominant taxon, *S. cruciformis*.

The second principal component axis explains 21.7% of the total variance and shows positive loadings for *S. cruciformis, P. psilata, C. rugosum*, *I. caspienense* and*Achomosphaera* sp. (which is very close to zero) and negative loadings for all marine assemblages and species (except *Achomosphaera* sp.). The positive loadings appear to be related to brackish assemblages, which are accompanied by increases in percentages of *S. cruciformis*.

In the nMDS analysis (Figure 5a), *S. cruciformis, P. psilata, C. rugosum*, *I. caspienense* and *L. machaerophorum* s.p. have negative scores and are shown in the top part of the diagram, indicating that they have similar environmental preferences. All other species have positive scores and are grouped in the bottom of the diagram and most of them on the right, while only two species are on the bottom left side (*S. nephroides* and *I. plicatum*).

### Palaeoenvironmental Interpretation - Discussion

The dinoflagellate cyst record of M0078A shows distinct alternations between marine and brackish assemblages in good agreement with the lithostratigraphic unit scheme from McNeill et al. (2019b). Those alternations can be associated with Quaternary isostatic sea-level fluctuations and are clearly observed in Figure 2 (PC1 curve). The PCA analysis sorts the samples into two main groups with distinct dinocyst assemblage compositions and confirms the occurrence of distinct palaeoenvironmental conditions during the study intervals (Figure 4). Interestingly, in some cases, samples that are assigned to marine (or isolated/semi-isolated) intervals based on the LUs, appear displaced from marine to brackish (or from brackish to marine) assemblages. Those samples mostly correspond to transitional intervals. The nMDS analysis (Figure 5b) shows a clear separation between the marine and the low-salinity assemblages. All brackish species are on the top part of the diagram, while marine species accumulate at the bottom (Figure 5a). The alignment of *P. zoharyi* and *T. vancampoae* is most likely related to their similar temperature preferences as both species are reported as thermophilic (e.g., Mudie et al., 2017).

### 5.1. Marine Dinocyst Assemblages

Marine dinocyst assemblages are characterised by high diversity. Several representatives of the *Spiniferites* group, as well as *N.* *labyrinthus*, *O.* *centrocarpum* sensu Wall et Dale 1966, *L. machaerophorum* s.l., *P. zoharyi*, *T. pellitum*, *B. tepikiense*, representatives of *Impagidinium* group and some brown cysts, are the main taxa encountered.

Several dinocysts found in high relative abundances in the GoC have oceanic and fully-marine distribution or can be found in great numbers in high-productivity areas, such as upwelling regions and areas influenced by river discharge. *N. labyrinthus*, *O. centrocarpum* sensu Wall et Dale 1966, *S. mirabilis*, *S. ramosus* and *B. tepikiense* have an oceanic distribution (Wall et al., 1977; Harland, 1983; Dale and Dale, 1992; Matthiessen, 1995; Rochon et al., 1999, Zonneveld et al., 2013; Marret et al., 2020); *S. mirabilis* and *S. ramosus* occur in high-productivity areas although they can be found in open ocean waters as well (Zonneveld et al., 2013; Mudie et al., 2017). *Spiniferites mirabilis* can also be considered as a warm species (Global SST: -0.8-29.8 °C; SST Marmara and Black Seas: 5.5 °C - 24 °C; Marret and Zonneveld 2003; Zonneveld et al., 2013; Mudie et al., 2017), however, in the GoC deposits, it was always found with the oceanic species *S. ramosus* and *B. tepikiense*. *Tectatodinium pellitum,* another species recorded in the GoC, has a widespread distribution in deep, fully marine waters, as well as in regions of high productivity and a wide range of bottom water oxygen (Zonneveld et al., 2013). *Impagidinium* species encountered in the Gulf of Corinth such as*I. aculeatum*,*I. paradoxum*, *I. patulum*, *I. sphaericum* and *I. strialatum* (Figure 3), are fully marine and have an oceanic distribution. Specifically, *I. strialatum* has an open oceanic distribution, from temperate to equatorial regions with well-ventilated bottom waters. *Impagidinium aculeatum* has a widespread distribution, although it exhibits its highest abundance in central oceanic oligotrophic environments. *Impagidinium paradoxum* is present in temperate to equatorial areas, from restricted to fully marine environments. *Impagidinium sphaericum* can be found from coastal areas to open ocean and regions with low seasonal salinity due to melting ice, whereas *I. patulum* occurs in temperate to equatorial areas and sporadically in subpolar and polar regions (Zonneveld et al., 2013; Marret et al., 2020). In the Gulf of Corinth, the *Impagidinium* species were mostly encountered in marine intervals (i.e., LUs 1.1, 1.2, 1.7 and 1.13), in low abundances, with *I. aculeatum* appearing to be the most common representative (Figure 3). *I. sphaericum, I. patulum* and *I. strialatum* occur in lower abundances and seem to be grouped on the right side of the nMDS (Figure 5a).

Opposingly, *S. membranaceus*, *S. hyperacanthus*, *S. bulloideus*, *S. bentorii*, *S. delicatus* and *L. machaerophorum* s.l. are exhibiting a neritic or coastal distribution (Marret and Zonneveld, 2003; Zonneveld et al., 2013; Zonneveld and Pospelova, 2015). *S.* *nephroides* and *I. plicatum* are encountered in low abundances in our record and are grouped together in the bottom left side of the nMDS analysis (Figure 5a). Both species areknown mostly from restricted to coastal waters of temperate to equatorial regions (Zonneveld et al., 2013; Zonneveld and Pospelova, 2015). *Selenopemphix nephroides* is usually found in seasonally mesotrophic to eutrophic upwelling or oligotrophic areas whereas *I. plicatum* is observed in oligotrophic to mesotrophic areas. They prefer well-ventilated bottom water, but *S. nephroides* is tolerant to anoxic conditions (Zonneveld et al., 2013; Zonneveld and Pospelova, 2015; Mudie et al., 2017).

The presence of the thermophilic species *T. vancampoae* and *P. zoharyi* that were observed in marine dinocyst assemblages from sites in the Levant, the Red Sea, the Gulf of Oman, and the northern Arabian Sea (Rossignol, 1962; Wall and Dale, 1967; Bujak et al., 1980; Marret and Zonneveld, 2003; Elshanawany and Zonneveld, 2016; Mudie et al., 2017) suggests the occurrence of warm surface water conditions in the Gulf of Corinth during interglacial periods.

The dinocyst assemblages of LU1.1, 1.3, 1.7, 1.9 and LU1.11 (Figure 3) indicate the occurrence of fully marine conditions, confirming the connection of the Gulf of Corinth with open sea during interglacials as a result of sea-level rise (McNeill et al., 2019b). However, some interesting variations in the assemblage composition of each interval are observed. The highest diversity of dinoflagellate cysts is observed in LU1.1 (corresponding to the Holocene), while in LU1.5 (corresponding to MIS 7a/c; Gawthorpe et al., 2022) the assemblages are characterised by the dominance of *N. labyrinthus, O. centrocarpum* sensu Wall et Dale 1966, *S. mirabilis* and *S. ramosus*. Within LU1.3 (correlating to MIS 5c/e; Gawthorpe et al., 2022), the presence of thermophilic species such as *T. vancampoae* indicates warmer climatic conditions (Zonneveld et al., 2013; Zonneveld and Pospelova, 2015; Mudie et al., 2017). The temporal increase of *S. cruciformis* abundance at 100.35– 105.7mbsf (Figure 3) indicates salinity fluctuations during MIS 5. The Last Interglacial Complex (LIC, MIS 5) is known for its climatic variability as it is characterised by the succession of cool and dry stadial (MIS 5b and 5d) and warm and wet interstadial (MIS 5a, 5c and 5e) phases (e.g., Shackleton, 1969; Shackleton et al., 2003; Tzedakis et al., 2004a; Sánchez-Goñi, 2007; Brewer et al., 2008; Capron et al., 2010; Tzedakis et al., 2012; Sánchez-Goñi et al., 2013; Milner et al., 2016; Sinopoli et al., 2018, Sinopoli et al., 2019). The temporal isolation of the Gulf of Corinth could tentatively be correlated with the increase of ice volume and drop of sea level occurring during such a stadial phase, most probably the MIS 5d (Figure 2). MIS 5d is the first cooling event in the MIS 5, and it is characterised by reduced temperatures and precipitation (Tzedakis et al., 2007; Brewer et al., 2008) in many European sites (e.g., Les Echets and La Grande Pile: Guiot et al., 1989; Guiot et al., 1990; Tenaghi Philippon: Milner et al., 2013; Milner et al., 2016), while in other sites, this reduction is less pronounced (e.g., Lake Ohrid: Sinopoli et al., 2018; Sinopoli et al., 2019). The LU1.5-1.6-1.7 are associated with MIS 7 (see Figure 2). According to our data, this stage seems to be divided by two low salinity peaks, a very distinct one (LU1.6) and a very small peak (within LU1.5). MIS 7 is the shortest interglacial period of the mid-late Quaternary (Figure 2), which is divided into 5 sub-stages, 3 interstadial periods (MIS 7e, 7c and 7a) and 2 stadials (deep stadial 7d and brief stadial 7a) (Tzedakis et al., 2004b; Desprat et al., 2006; Roucoux et al., 2008; Fletcher et al., 2013; Donders et al., 2021). The LU1.9, LU1.11 and LU1.13 are correlated with the MIS 9, 11 and 13, respectively. The poor preservation of dinocysts in several samples of LU1.8 and 1.9 could be connected to the bed type classification of graded beds (G1a, c, d) recognized also in the correlated site M0079 (Gawthorpe et al., 2022).

The occurrence of brackish assemblages within the identified as marine LUs (McNeill et al., 2019b) has been recorded in LU1.7 (205.27 and 205.62 mbsf), LU1.11 (296.29 and 297.62 mbsf) and at the lower part of LU1.13 (329.74–333.15 mbsf; Figure 3), indicating short periods of isolation of the GoC from the Mediterranean Sea. The low-salinity character of these assemblages is further confirmed by the PCA (Figure 4). However, they most probably feature the occurrence of transitional conditions as they are mainly recorded either at the beginning or at the end of each LU. Finally, LU1.13 seems to be more complex, as the two first samples record fully marine conditions, whereas the others have brackish dinocyst assemblages.

### 5.2. Brackish/ isolated assemblages

The glacial and interglacial cycles reflect the expansion and the decrease of the continental ice, related to the variability of the incoming solar radiation caused by the Earth’s orbit. During glacial periods, the global sea level drops due to the extension of ice sheets, causing gulfs and semi-isolated regions to disconnect from the open ocean, such as the confined region of the Gulf of Corinth. When the sea level fell below the level of the Rion Strait sill (which is today at -62 m), the GoC was transformed into an isolated system or, if the sea level was a few meters above the Rion Strait sill, into a marine area with a high freshwater content (see section 2, Area setting). The low salinity assemblages of the M0078A sedimentary archive are a striking feature of the dinocyst record and document periods when the GoC was isolated from the Mediterranean Sea. Those isolated/semi-isolated intervals, also recorded in the neighbouring site M0079, correlate with the eustatic low sea level during the glacial intervals (McNeill et al., 2019a). These eustatic sea-level cycles are similar to those recorded in the Black Sea during the last 430 ka BP (Hoyle et al., 2021). In the Black Sea, six minor sea-level cycles were identified, three sea-level cycles existed starting at about 480 ka BP, followed by another three minor cycles mostly at lowstands (Winguth et al, 1997).

The low salinity assemblages of the Gulf of Corinth mainly consist of *S. cruciformis*, *P. psilata*, *C. rugosum*, *I. caspienense* and *L. machaerophorum* s.p. (Plate 1). *S. cruciformis* is the dominant species in the GoC (Figure 3) and thrives in low-salinity conditions or even sometimes freshwaters (Wall and Dale, 1973; Kouli et al., 2001; Mudie et al., 2001; Mudie et al., 2002b). In the Gulf of Corinth, *S. cruciformis* forms 1–4 described in Mudie et al. (2001) were encountered (Plate 1); in contrast to other sites, this species lacks the membranous flange or consists mostly of morphotype B or C (Lake Pannon: Mudie et al., 2017; Lake Kastoria: Kouli et al., 2001; Caspian Sea: Marret et al., 2004). The occurrence of the four forms in the brackish assemblages of the GoC most probably indicates fluctuations in sea-surface salinity (Mudie et al., 2001; Mudie et al., 2002b; Mudie et al., 2004). This species occurs today in brackish environments with seasonal SSS between 12.1 to 18.3 psu in the Black and Caspian Seas (Mudie et al., 2001; Marret et al. 2004; Mudie et al., 2004; Mudie; et al., 2017) and rarely, in the Mediterranean Sea (Zonneveld et al., 2013). Recent findings show its presence in brackish environments (Marret et al. 2004; Mertens et al., 2012a). Limited fossil occurrences of the species in the freshwater lakes of Kastoria in Greece (Kouli et al. 2001) and Sapanca in Turkey, alongside other low salinity indicators (Leroy and Albay, 2010) imply its possible tolerance to freshwater conditions. However, *Spiniferites cruciformis* has never been found until now in recent freshwater settings (Mertens et al., 2012a).

*Pyxidinopsis psilata* is encountered in high abundance (even becoming dominant in several samples; Figure 3) in the Gulf of Corinth and it is characterised as a low salinity indicator. In the study area, it was found mostly with smooth wall and a rhomboidal, spherical, or cruciform central body (Plate 1), in contrast to the Black and Marmara Seas where the smooth wall morphotype was found only in low abundances and in the Caspian Sea the verrucate morphotype was rare (Mudie et al., 2017). This species can be considered as a euryhaline, temperate, sub-tropical to tropical species (Zonneveld et al., 2013; Zonneveld and Pospelova, 2015). Even though *P. psilata* was found mostly in coastal sites, it is not restricted to coastal areas (Zonneveld et al., 2013). This species is common in late Pleistocene to early Holocene intervals in shelf and deep basin cores of the Marmara and Black Seas, as well as intervals of deep-water cores of the Caspian Sea, where it was recorded with other brackish indicators such as *S. cruciformis* and *I. caspienense* (Mudie et al., 2017; Mudie et al., 2018).

*Caspidinium rugosum* is encountered in the GoC in high abundance in LUs 1.2, 1.4 and 1.6, while in the other LUs, it is just present (Figure 3). In the GoC, this species was found with a reduced size (starting from 20 μm, see Plate 1) compared to previous studies reporting the same species from Central Asia Seas (Marret et al., 2004). It is known to be present in reduced salinity conditions and moderate temperatures (Mudie et al., 2017). *Caspidinium rugosum* is largely restricted to the Caspian and Aral Seas, with the only other occurrence being one specimen at each of five scattered sites in the northern Black Sea (Mudie et al., 2001; Marret et al., 2004; Mudie et al., 2004; Mudie et al., 2017).

In the low salinity assemblages of M0078A, cysts of *L. machaerophorum* s.p. (Plate 1) appear to have shorter processes arranged close to each other, per previous observations that have shown the strong relationship between the length of the processes and their number and density (Mertens et al., 2012b). In the Gulf of Corinth, it is present in low abundances in marine and isolated intervals (LU1.1, 1.2, 1.3, 1.4, 1.5, 1.11), most likely indicating tolerance to higher SSS and changes in SST. The process-length variation was initially related to salinity variations in the Black Sea (Wall et al., 1973), while in the Caspian Sea the process length (<10μm) was related to higher annual SST and lower SSS (Mertens et al., 2012b). High abundances were also observed in sediments near upwelling areas or in highly stratified waters such as the Black and Marmara Seas (Mertens et al., 2012b). In Figure 5a, this species is clearly grouped with the brackish indicators but is also plotted near *Achomosphaera* sp., indicating a distribution both in neritic and shelf regions (Zonneveld et al., 2013; Zonneveld and Pospelova, 2015; Mudie et al., 2017). This species is continuously present in Black Sea sediments since its reconnection with the Mediterranean Sea during the Holocene (Mudie et al., 2001; Mudie et al., 2004; Marret et al., 2009; Mertens et al., 2012).

Finally, the low salinity indicator *I. caspienense* is observed only in the uppermost isolated interval of the Gulf of Corinth (LU1.2), which might explain the great distance between *I. caspienense* and the other low salinity indicators in the nMDS diagram (Figure 5a). This taxon has been commonly associated with oligotrophic, low-productivity conditions (Marret et al., 2004; Mudie et al., 2017). It is considered as an endemic species, found in high abundance (also as dominant species) in the Caspian and Aral Seas (Marret et al., 2004; Mudie et al., 2017). This taxon was present in low abundance in Holocene sediments from Marmara Sea (Roberts, 2012) and the SW Black Sea (Marret et al., 2009), but it has not been encountered in cores from deeper water (Mudie et al., 2017). However, it must be highlighted here that the phylogenetic study of this species by Mertens et al. (2017) concluded that it was not endemic to the Caspian Sea but also occurring in the Baltic Sea, the cyst being produced by the thecate *Gonyaulax baltica*. This thecate has been observed to produce spiniferate and impagidinioid specimens, possibly in relation to environmental conditions, notably salinity.

The two uppermost isolated/semi-isolated LUs of the M0078A core (LU1.2, and 1.4) record two very distinct brackish assemblages. During LU1.2, *S. cruciformis*, *P. psilata* and *C. rugosum* have very high relative abundances, with *S. cruciformis* and *P. psilata* being codominant, suggesting the occurrence of low salinity conditions in the GoC. The presence, in very low abundances even meagre, of *T. vancampoae* and *P. zoharyi* and other marine representatives in several samples within the LU1.2 most likely indicate fluctuations in temperature as well as occasional connection with the open sea. The LU1.2 correlates with MIS 2-5a (Gawthrope et al., 2022), a period marked by significant millennial climate variability which could explain the fluctuations observed in the Corinth record. MIS 5a is characterised by temperate conditions in the region and it is included in the warm and wet interstadial periods of MIS 5 (Helmens et al., 2014; Panagiotopoulos et al., 2014; Sadori et al., 2016; Ferguson et al., 2018; Sinopoli et al., 2019). In MIS 4-2, the two glacial maxima have been recognized in the regional palaeoclimatic record (e.g., Tzedakis et al., 2002; Panagiotopoulos et al., 2014; Wulf et al., 2018). MIS 2 is the most recent glaciation and includes the coldest climatic conditions of the last glacial cycle, the Last Glacial Maximum (LGM; Yokoyama et al., 2000; Fletcher et al., 2010; Hughes et al., 2015; Ferguson et al., 2018; Ishiwa et al., 2019, Leontaritis et al., 2020). MIS 4 also reaches full glacial conditions in Europe and the North Atlantic Ocean (Guiot et al., 1989; Mangerud et al., 2011; Anjar, 2012; Ferguson et al., 2018; Shackleton et al., 2021). MIS 3 is characterised by climatic warming phases, the Dansgaard-Oeschger (DO) events, which are rapid transitions from cold stadial to warm interstadial phases, followed by a slow return to cold stadial conditions (e.g., Cacho et al., 1999; Capron et al. 2010; Panagiotopoulos et al., 2014). The DO warm events can be compared to MIS 5c and 5a (Oppo et al., 2006; Engels et al., 2008; Ferguson et al., 2018). During the MIS 3, within some stadials, the Heinrich (HEs) events also took place (Heinrich, 1988). These events are characterised by abrupt climatic changes. According to our results, the LU1.2 is characterised mainly by brackish conditions. However, marine species, such as *T. vancampoae, P. zoharyi*, *O. centrocarpum* sensu Wall et Dale 1966*, L. machaerophorum* s.l*.* and *N. labyrinthus*, have also been encountered in very low concentrations, indicating that the GoC was temporally connected and disconnected from the Mediterranean Sea (Figures 2 and 3). These marine conditions and the presence of warm species in several samples could be correlated with the 5a interstadial period.

In LU1.4, *S. cruciformis* is the most dominant species suggesting that the GoC was significantly more isolated, compared to the last glacial period. The LU1.4 is correlated with MIS 6, which is characterised by very cold and dry conditions, especially during the second part of this glacial period (Roucoux et al., 2006; Rohling et al., 2014; Sinopoli et al., 2019; Leontaritis et al., 2022).

In LU1.6 and LU1.8, *S. cruciformis* continues to be the most dominant species downcore, which points to an isolated environment, whereas in LU1.10, the most dominant species is *P. psilata*, possibly indicating an increase in SST. The LU1.6 corresponds to the stadial MIS 7d (see section 5.1). The LU1.8 and LU1.10 are correlated with MIS 8 (Fletcher et al., 2013) and 10, respectively.

The LU1.12, 1.14 and 1.16 are characterised by the dominance of *S. cruciformis* in very high concentrations and reflect a very restricted environment, with very low salinity or even freshwater conditions. The LU1.12 is correlated with the MIS 12 (Koutsodendris et al., 2019; Gawthorpe et al., 2022; Maffione and Herrero-Bervera, 2022).

The lower part of LU1 ends at 385.99 mbsf (end of LU1.16) and it is correlated with the Brunhes – Matuyama Boundary (~773 ka; McNeill et al., 2019b; Gawthorpe et al., 2022; Maffione and Herrero-Bervera, 2022).

Some samples in this interval such as 21.43 mbsf (LU1.2), 248.01 mbsf (LU1.8) and 260.31 mbsf (LU1.10) were displaced, in the PCA plot (Figure 4) and were grouped with marine assemblages. Most likely transitional conditions occurred during these intervals as these samples are mainly recorded either at the beginning or the end of each LU.

The dinocyst assemblages described from the GoC record show strong affinities to the Black Sea, the Sea of Marmara, and the Caspian Sea assemblages (Stanev et al., 2001; Rochon et al., 2002; Gómez et al., 2004; Marret et al., 2004; Leroy et al., 2007; Marret et al., 2009; Mertens et al., 2012b; Zonneveld et al., 2013; Jansson et al., 2014; Zonneveld and Pospelova, 2015; Mertens et al., 2017b; Mudie et al., 2017; Lewis et al., 2018; Marinova et al., 2018; Richards et al., 2018; Hoyle et al., 2019; Hoyle et al., 2021). Most of the taxa recorded in the GoC deposits, especially in brackish intervals, have been previously reported from the Black and the Marmara Seas, while similarities with the Caspian Sea dinocyst assemblages are also evidenced. The brackish dinocyst assemblages encountered in the GoC were identified for the first time outside the Ponto-Caspian region. Among these low-salinity species, only *S. cruciformis* has been found in coastal areas of the eastern Mediterranean and Aegean Seas (Zonneveld et al., 2013). Opposingly, *P. psilata*, *C. rugosum* and *I. caspienense* are reported only from the Marmara, Black, and Caspian Seas (Table 1). These low salinity indicators of the Gulf of Corinth are only a few brackish representatives of the identified brackish assemblages of the Marmara, Black and Caspian Seas.

### Conclusion

The sedimentary record of the Gulf of Corinth is characterised by distinct shifts in the dinoflagellate cyst assemblages, revealing fluctuations in surface water salinity and temperature, in response to the global sea-level changes and trace orbital-driven climate shifts as shown in the global Marine Isotope Record. Dinoflagellate cysts are sorted into two major ecogroups reflecting alternations between marine and isolated/brackish conditions.

During the interglacial periods, the Gulf of Corinth is characterised by a high diversity of the dinoflagellate cysts assemblages as a result of the prevalence of fully marine conditions as the Gulf was connected with the Mediterranean Sea. The presence of thermophilic species indicates higher temperatures in comparison to other eastern Mediterranean sites. Opposingly, during glacial periods, the dinocyst assemblages are less diverse and dominated by low salinity dinocysts, indicating the isolation of the Gulf of Corinth. The dominance of *S. cruciformis* cysts in selected isolated intervals, corresponding to MIS 6, 8 and 12 implies the occurrence of very restricted, low salinity conditions during those glacial periods.

The GoC dinoflagellate cyst assemblages, especially the brackish, show distinct similarities to those described in other regional basins such as Black Sea, Caspian Sea, Marmara Sea. The low-salinity dinoflagellate cysts encountered hold an amazing and unique feature as, apart from *S. cruciformis,* they are recorded for the first time outside the boundaries of Ponto-Caspian region.

The occurrence of species of the *Impagidinium* group during the marine intervals in the Gulf of Corinth confirms a wide communication with open sea and the occurrence of well-oxygenated, deeper waters and higher salinity than in the other basins.

The sedimentary sequence of the Gulf of Corinth has the potential to become a long and high-resolution regional archive of palaeoenvironmental changes for the eastern Mediterranean Sea. Downcore dinoflagellate cyst analysis is part of ongoing research (Fatourou et al. in prep). The correlation of dinocyst findings with other biotic and abiotic proxy analyses such as other marine microfossils, pollen, sediment properties or geochemistry, combined with a robust age-depth model based on magnetostratigraphy, tephrochronology and other absolute dating methods will allow the establishment of this new regional reference record.

**Acknowledgements**

The study material was retrieved during the IODP Exp. 381. The research work was supported by the Hellenic Foundation of Research and Innovation (H.F.R.I) under the “First Call for H.F.R.I. Research Projects to support Faculty members and Researchers and the procurement of high-cost research equipment grant” (Project Number: 1026, Quaternary Environmental Changes in the Corinth Rift Area: the IODP 381 palynological record: QECCoRA). The authors are very grateful for the constructive comments from the two reviewers and the editor.

**Figure captions**

Figure 1: Map showing the topography of the Gulf of Corinth, the study site M0078A (modified from McNeill et al., 2019a and Gawthorpe et al., 2022) and regional setting. In the inset map the shorelines during lowstand (-100m) intervals are featured in grey.

Figure 2: Site M0078A: Lithostratigraphic Units (LU), facies associations (FA), samples analysed (in red triangles), Brackish/Marine dinoflagellate cyst curve and PC1 of the samples curves. FA1: Homogenous mud, FA2: Greenish, grey mud with dark grey to black silty-to-sandy beds (cm-scale) FA3: Light grey to white sub-mm laminations (cc or aragonite) alternating with mud-silt beds, FA4: Laminated greenish grey to grey mud with muddy beds, FA5: Greenish, grey mud with homogeneous cm-thick grey mud beds, FA6: Green bedded partly bioturbated mud, silt and sand,FA10: Interbedded mud/silt and dm-thick sand beds, FA11: Interbedded mud/silt and cm-thick sand beds, FA12: Light grey to buff, homogenous. to weakly stratified mud. Facies associations and LUs are from McNeill et al., 2019b. Sediment lithology coloured according to facies association

Figure 3: Shade plot: visual representation of the species encountered in the different LUs (LU1.1 to LU1.16). Samples were arranged based on core depth. White colour indicates absence, black the highest abundance in the dataset, while all the different colours suggest low (blue colour), medium (green colour) and high presence (orange and red).

Figure 4: Plot of the first two axis of the Principal Component Analysis.

Figure 5: nMDS – species (a), nMDS – samples (b): non-metric Multidimensional Scaling Analysis for the samples and species.

Plate 1: Light microphotographs of the main species encountered in brackish/isolated intervals of the Gulf of Corinth. Scale bar= 20μm. 1–9: *Spiniferites cruciformis*, 10–14: *Pyxidinopsis psilata*, 15– 16: *Caspidinium rugosum* and 17–18*: Lingulodinium machaerophorum* s.p. (<10μm).

Plate 2: Light microphotographs of the main species encountered in marine intervals of the Gulf of Corinth. Scale bar= 20μm. 1-2: *Ataxodinium choane*, 3-4: *Lingulodinium machaerophorum* s.l., 5-6: *Nematosphaeropsis labyrinthus*, 7-9: *Operculodinium centrocarpum* sensu Wall et Dale 1966, 10-11: *Polysphaeridium zoharyi*, 12-14: *Spiniferites mirabilis*, 15-16: *Quinquecuspis concreta*, 17: *Brigantedinium* sp., 18: *Brigantedinium simplex*.

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