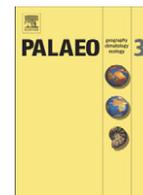




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## The early Quaternary palaeobiogeography of the eastern Ionian deep-sea Teleost fauna: A novel palaeocirculation approach

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## ABSTRACT

The early Quaternary stratigraphic and geographic distribution of teleostean fishes in the Ionian Sea (eastern Mediterranean) is examined based on the fossil otolith record. Through comparison between the western and the eastern Ionian early–middle Pleistocene deep-sea ichthyofauna, the stratigraphic distributions of nineteen taxa are revised. A new method of assemblage analysis is attempted, in order to discern the palaeoceanographic conditions prevailing at this time. The relative contributions of tropical, subtropical, temperate, and subpolar taxa to the surface, intermediate, and deepwater fish palaeofauna are calculated, using fossil material from Akrotiri (Kephallonia Island, Greece), Gerakas (Zakynthos Island, Greece) and Montalbano Jonico (Italy) sections, which span the Gelasian–Ionian time interval. Eleven distinct phases in the Ionian Sea palaeoceanographic evolution are distinguished, from prior 1.95 Ma to 0.61 Ma. Furthermore, a case study is conducted, to test the hypothesis that palaeoichthyofauna can be used to draw conclusions regarding the palaeocirculation patterns and their variability. In the Ionian Sea, the local production and/or Atlantic origin of the deep cold waters is registered already during the Gelasian. The presence of oceanic fish in the eastern Ionian can be explained by the existence of a strong anticyclonic gyre in the area during the early Quaternary, further indicating that the basin's geometry exhibited sufficient bathymetric variation to allow for the activation of the gyre.

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### 1. Introduction

Otoliths are the aragonitic incremental structures within the teleostean fish inner ear, which enable sound and balance perception. Fossil fish otoliths are a unique tool in the investigation of the palaeofauna, because of their taxon-specific morphology, high frequency in sediments of various environmental settings, ranging from lake to deep-sea deposits, and their generally good preservation (Nolf, 1985). They are quite valuable as palaeoecologic and palaeobathymetric indicators, and provide highly detailed and accurate palaeobiologic and palaeoclimatic information (Girone, 2000a, 2005).

The Pleistocene teleostean fish assemblages of the Mediterranean realm have been the subject of various studies over the past decades, both referring to the skeletal as well as the otolith material. Especially regarding the Ionian Sea, extensive studies have been carried out by Girone (2000a,b, 2003), Nolf and Girone (2000) and Girone et al. (2006), which examined the western part of the basin.

A brief examination of the fish fauna's evolution in the Mediterranean realm reveals a significant turning point at the Miocene/Pliocene boundary, which corresponds to the commencement of deepwater pelagic sedimentation over the Messinian shallow-water deposits, resulting in a sudden change in the fossil content. In the western Mediterranean, the direct interaction with the Atlantic Ocean leads to the re-establishment of a thermohaline circulation pattern, so that normal salinity and temperature conditions prevail soon after the opening of the Gibraltar Strait. In the eastern sub-basin however, the oceanic circulation was re-established later on. On the whole, the fish recolonization of the basin, following the opening of Gibraltar, was rapid. Notably, the proportions of currently living fish species increased from 17% in the late Miocene, to 75% during the Pliocene, and to 88% in the Pleistocene (Landini and Sorbini, 2005a). During the early and middle Pleistocene, the Teleost fauna shows a markedly more oceanic character than today; a trend which has been observed in the Mediterranean otolith associations since the early Oligocene (Girone et al., 2006). Gradually the Pliocene Indo-Pacific tropical and subtropical taxa are replaced by temperate taxa of Atlantic origin, which prevail to the present times. In particular, mesopelagic and deep benthopelagic fauna with more restricted North Atlantic affinities invades the Mediterranean from the Gelasian until the late Pleistocene.

The modern deepwater ichthyofauna of the Ionian Sea consists mainly of Atlantic and endemic Mediterranean species, as well as

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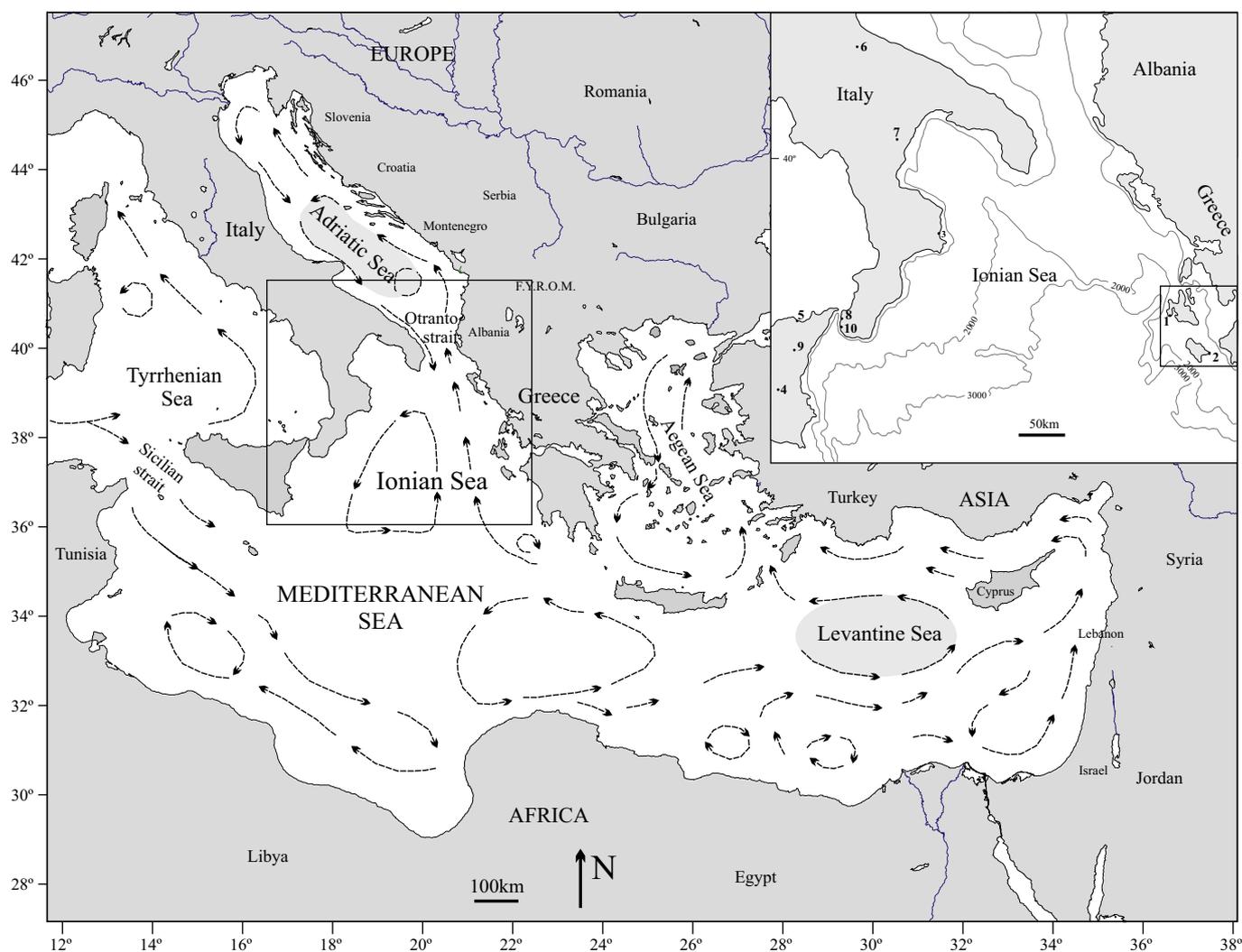
some cosmopolitan taxa of worldwide distribution. A recent study revealed an impoverished deepwater fish fauna in comparison to that of the Atlantic Ocean (D'Onghia et al., 2004). The recent origin of this deep-sea fauna in the Mediterranean, the “canal effect”, the high temperature, and the oligotrophy of the basin are considered the main reasons for this phenomenon (Fredj and Maurin, 1987; Bouchet and Taviani, 1992; Quignard and Tomasini, 2000). Madurell et al. (2004) supported that food availability is the main factor affecting the demersal fish assemblages in the Ionian Sea. Based on the assemblages' structure and distribution in the Ionian Sea deep waters, the fish fauna can be separated into three depth zones. The upper slope assemblages are bordered at 500 meters depth, whereas the middle to lower slope transition occurs at about 700 meters (Politou et al., 2008). The 700 meters barrier has also been noted for the adjacent areas (D'Onghia et al., 2004). Comparison between the eastern and the western part of the Ionian Sea does not reveal significant differences between the overall fauna (Mytilineou et al., 2005). However, the abundance of some species varies greatly between these two areas. According to D'Onghia et al. (2004), the differences in the assemblage composition and the abundance of certain species, between the eastern and the western Ionian upper slope, could be attributed to the different hydrographic conditions at the two sides of the basin, which result in water masses of

higher temperature and salinity affecting the eastern Ionian (Robinson and Golnaraghi, 1993; Theocharis et al., 1993).

In the present study the aims are three-fold: (a) to complement the Mediterranean teleostean fish distribution record for the Gelasian–Ionian time interval, (b) to present a new methodological approach to the palaeoenvironmental analysis of fish assemblages, and (c) to contribute to the Ionian Sea palaeoceanographic reconstruction, concentrating on the effects of oceanic circulation and climate variability on the distribution of Teleosts. To these ends, the otolith-based fish data obtained from two stratigraphic sections in the eastern Ionian realm is examined, compared and analyzed, in conjunction with the western Ionian record.

## 2. The study areas

In order to examine the evolution of the eastern Ionian Teleost fauna during the early Pleistocene and its palaeoecologic and palaeobiogeographic implications, the present study focused on the southern parts of Kephallonia and Zakynthos islands (Figs. 1 and 2), particularly sections Akrotiri (Kephallonia) and Gerakas (Zakynthos), where a very accurate stratigraphic framework has already been established by previous studies (Triantaphyllou, 1996; Triantaphyllou et al., 1997, 1999;



**Fig. 1.** Map of the eastern Mediterranean Sea indicating the study area. The arrows illustrate the main pattern of the present-day surface circulation, while the shaded areas mark the present-day intermediate and deepwater formation regions (The POEM group 1992, Theocharis et al., 1993). Map of the Ionian Sea (squared area), where the geographic distribution of the geological sections (1–10) used in this study is presented. 1. Akrotiri, 2. Gerakas, 3. Vrica, 4. Palione river, 5. Furnari, 6. Gravina, 7. Montalbano Jonico, 8. Archi, 9. Fiumefreddo, 10. Vallone Catrica. The indicated area inside the Ionian Sea map is presented in Fig. 2.

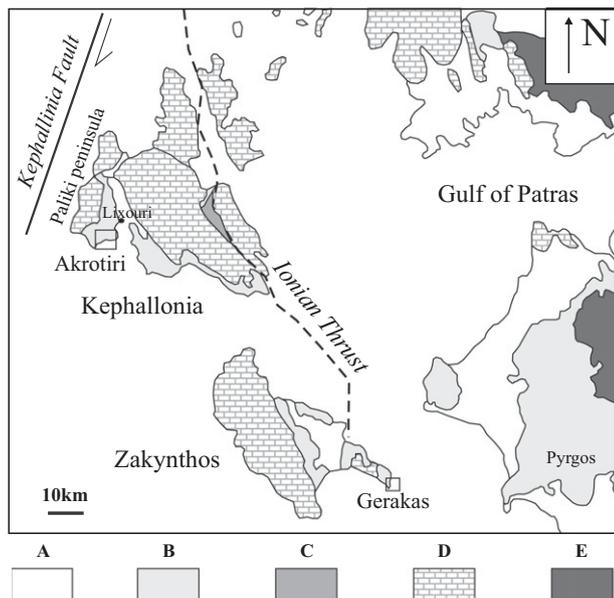


Fig. 2. Geologic map of Zakyntos and Kephallonia Islands (Underhill, 1989). A. Holocene alluvial sediments, B. Upper Miocene–Pleistocene, C. Middle–Upper Miocene, D. Mesozoic–Middle Miocene Preapulian and Ionian zone formations, E. Pindos zone formations.

Triantaphyllou, 2001; Papanikolaou et al., 2010, in press). The otolith associations identified in these areas are presented in Agiadi et al. (2010). The ages were provided through nannofossil biostratigraphy, based on the schemes of Lourens et al. (2004), Raffi et al. (2006), and Gibbard et al. (2009).

Kephallonia and Zakyntos Islands are located in the eastern part of the Ionian Sea, offshore western continental Greece (Figs. 1 and 2). They constitute part of the external Hellenides. Preapulian zone formations comprise the largest part of Kephallonia as well as the western part of Zakyntos, while in the eastern part of both islands outcrop the Ionian zone sediments. The Preapulian is separated from the Ionian zone by an important tectonic thrust (Underhill, 1989). Previous studies of the Neogene and Quaternary deposits in these areas have followed the prevailing chronostratigraphic scheme, which has recently changed, to place the Gelasian stage/age within the Pleistocene Series/Epoch and also to reaffirm the Quaternary as a full System/Period (Gibbard et al., 2009). In order to conform to this official position of the International Commission on Stratigraphy, the following chronostratigraphic data are presented accordingly.

On Kephallonia Island, the study area, Akrotiri, is located in the southern Paliki peninsula. Upper Miocene–Pleistocene sediments, in this area, consist mainly of marls, sands, silts, and calcarenites (Georgiadou-Dikaoulia, 1967), with early Pleistocene sedimentation taking place in well-formed basins within the Preapulian zone. The former Pliocene–Pleistocene boundary (prior to Gibbard et al., 2009) was located within these deposits through calcareous nannofossil biostratigraphy (Triantaphyllou et al., 1999).

Akrotiri section (Fig. 3) comprises 100 meters of marls with thin sand intercalations. A bioclastic calcareous bed forms the uppermost part, covered by a calcarenite layer. Based on the species abundance of calcareous nannofossil *Gephyrocapsa*, Triantaphyllou (2001) distinguished the first occurrence level of placoliths larger than 4–4.5  $\mu\text{m}$ , at 75 meters from the base of the section. This occurrence, which corresponds to the biozones MNN19a/MNN19b boundary level (Rio et al., 1990), is related to the Gelasian–Calabrian stage transition. In addition, the low abundance of *Discoasteridae* combined with the rare occurrence of planktonic foraminifer *Globorotalia inflata*, places the lower 20 meters of the section within the MNN18 biozone

(Triantaphyllou, 2001). These biostratigraphic studies placed the deposition of the Akrotiri section sediments between 1.66 and 1.98 Ma. Furthermore, the Cape Akrotiri deposits fall within biozone MNN19f (Ionian stage, middle Pleistocene), time constrained between 0.61 and 0.781 Ma.

The Zakyntos study area is located on the southeastern part of the island, along Gerakas coast (Fig. 2). The Neogene and Quaternary deposits of the central and southeastern Zakyntos form a monocline, which overlies the Cretaceous–Paleogene limestones, and can be separated into a lower, mainly calcareous sequence, and an upper, clastic sequence, which is placed in the Pleistocene. Gerakas Formation comprises these lower Pleistocene sediments, which outcrop well in the southeast and the eastern part of the island (Dermitzakis et al., 1979).

Along Gerakas coast, the lower part of the formation consists of 30 meters of marls with thin sand and silt horizons (Fig. 3). The sand horizons increase in density and thickness towards the upper part of the section. The upper part of the sequence is characterized by a thin sandy conglomerate at its base, followed by a 10-meter-thick brown sand bed. The remaining sequence, which outcrops at the eastern part of the coast, comprises 60 meters of clays and silts, deposited in relatively stable low-energy marine conditions (Triantaphyllou et al., 1997).

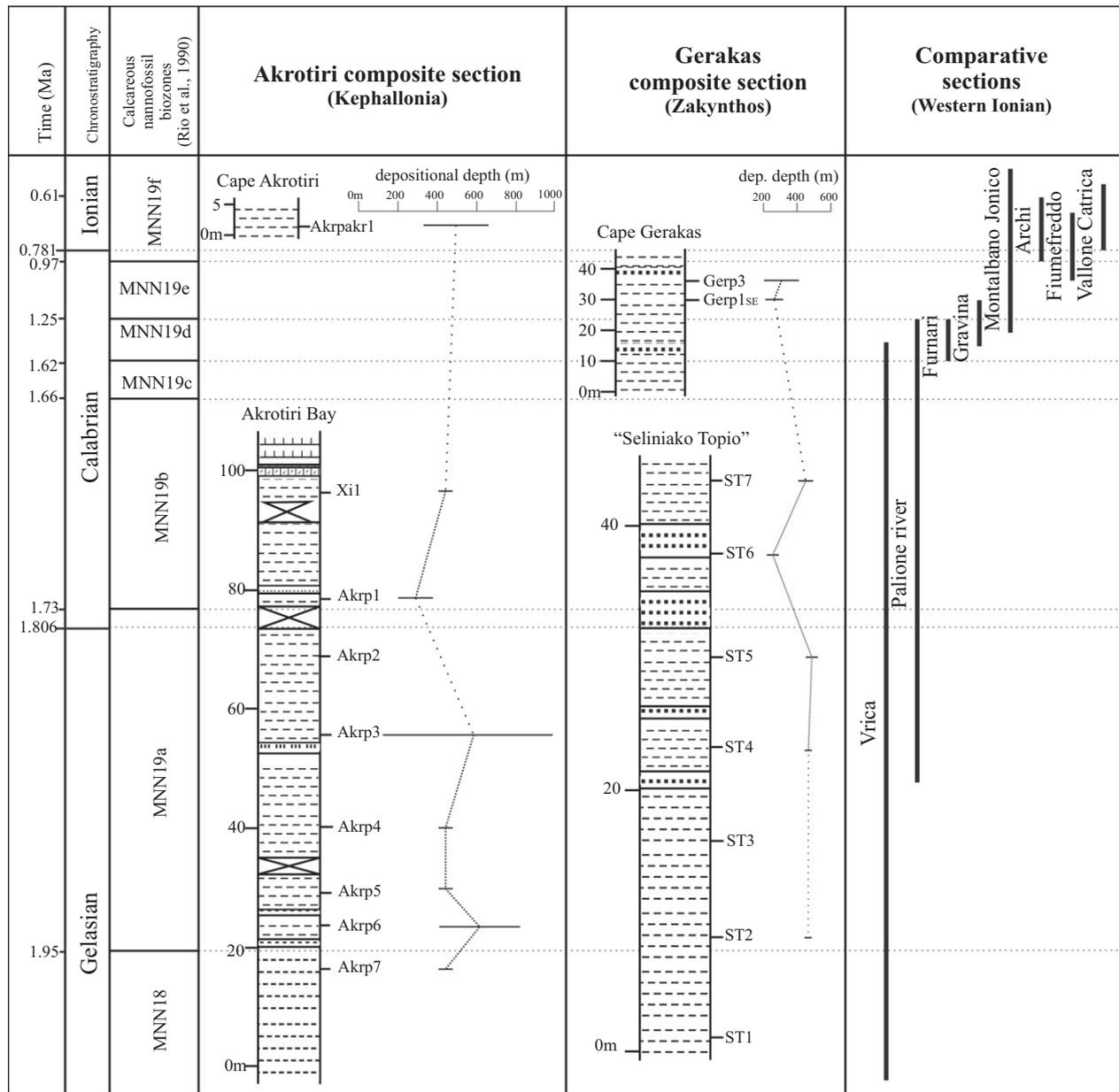
The biostratigraphic analysis of Gerakas sediments (Triantaphyllou, 1996; Triantaphyllou et al., 1997; Papanikolaou et al., 2010; Papanikolaou et al., in press) has placed the lower part of the section within the biozones MNN18 and MNN19a of Rio et al. (1990). The Gelasian–Calabrian stage boundary horizon has been determined by the first occurrence of normalized *gephyrocapsids*  $>4 \mu\text{m}$  at 36 meters from the section base. Within the upper part of the sequence, as observed on Gerakas coast, Triantaphyllou et al. (1997) have recognized biozones MNN19b,c, d, e, and MNN19f (Calabrian–Ionian). Based on these determinations, the studied Gerakas sediments span the 1.98–0.781 Ma time interval (Fig. 3).

### 3. Material and methods

#### 3.1. Samples and processing

On Kephallonia Island, seven samples (Fig. 3), weighing approximately 20 kg each, were taken from Akrotiri section (Akrp1–7), one sample from Cape Xi (Xi1), and one also from Cape Akrotiri (Akrkr1). The biostratigraphic analysis placed sample Xi1 within biozone MNN19b (Calabrian, early Pleistocene). Sample Akrkr1 is placed within biozone MNN19f (Ionian, middle Pleistocene), below the last occurrence of *Gephyrocapsa* sp.3, time constrained between 0.97 and 0.61 Ma. On Zakyntos Island, seven samples were taken from the lower part (ST1–7), and two from the middle part of Gerakas section (Gerp1SE and Gerp3); the latter are placed by Triantaphyllou (1996) within biozone MNN19e (Fig. 3). The samples were washed and sieved in plain water, using a 250  $\mu\text{m}$  diameter sieve. The otoliths were then handpicked from the sediment, under a stereoscope. The fish otolith identifications are presented in Agiadi et al. (2010) and some important species are also shown on Fig. 4.

The fossil otolith data from Akrotiri and Gerakas sections provide a continuous record of the fish assemblages for the time frame between 1.96 and 1.66 Ma, as well as isolated pictures of the fauna from 1.25 to 0.97 Ma, and from 0.78 to 0.61 Ma. In order to obtain a higher resolution of the palaeoceanographic reconstruction and a more robust justification of the conclusions, the otolith-based data presented in Girone and Varola (2001) and Girone (2000a,b, 2005) referring to the Montalbano Jonico section were also included in the palaeoenvironmental assemblage analysis. The Montalbano Jonico section has been studied extensively, and the fish data used here are well stratigraphically constrained between 1.25 and 0.97 Ma, and between 0.795 and 0.7 Ma (Ciaranfi et al., 2010; Maiorano et al., 2010). In addition three samples from Entalina section (Montalbano Jonico composite section), placed within biozone MNN19d were also included (Girone, 2005). Fish data were not available for the intervals between 1.66 and 1.45 Ma and 0.97–0.795 Ma.



**Fig. 3.** Stratigraphic columns of the studied geological sections and the referenced western Ionian localities. The biostratigraphy for Akrotiri and Gerakas section is based on the study of calcareous nannofossils and planktonic foraminifera (Triantaphyllou, 1996, 2001; Triantaphyllou et al., 1997; Papanikolaou et al., in press) and is in accordance with the nannofossil biozonation of Raffi et al., 2006 and the chronostratigraphic scheme for the Pleistocene by Gibbard et al., 2009. The palaeobathymetric estimates based on the fish otolith content are analyzed in Agiadi et al., 2010.

### 3.2. Assemblage analysis methodology

The palaeobiogeographic distributions of the identified teleost species, in the early and middle Pleistocene eastern Ionian Sea, were compared to the equivalent assemblages from the western Ionian realm, in order to fill the gaps in the fossil record, as well as to identify any ichthyofaunal differences and similarities, which may be attributed to palaeoenvironmental factors (Figs. 1 and 3, Tables 1 and 2).

The palaeoecologic analysis of the fish taxa identified in Akrotiri, Gerakas, and Montalbano Jonico sediments was based on modern ecological data (Table 3). Their relative abundances were calculated following the criteria proposed for bivalves by Di Geronimo and Robba (1976). Accordingly, the abundance of each taxon in the assemblage is the sum of the greatest number of the taxon's otoliths in the sample (either the number of left or the number of right otoliths) plus half of

the smallest number. The relative abundances of each taxon per sample for Akrotiri and Gerakas sections are given in appendices 1 and 2, and for Montalbano Jonico section are presented in Girone and Varola (2001) and Girone (2000a,b, 2005). The diagenetically modified otoliths, which may have been transported, were excluded from this analysis.

The assemblages were analyzed based on the modern depth, environmental preferences, and geographic distribution of the species that comprise them (Table 3). According to the depth they occupy in the water column, and their life mode, modern marine fish are separated into five main categories. Epipelagic fish live entirely in the euphotic zone (higher than 200 meters depth). Mesopelagic fish live entirely or in part between depths of 200 and 1000 meters in the water column. Bathypelagic fish occupy the lower part of the water column in the aphotic zone. Benthopelagic fish stay close to the sea

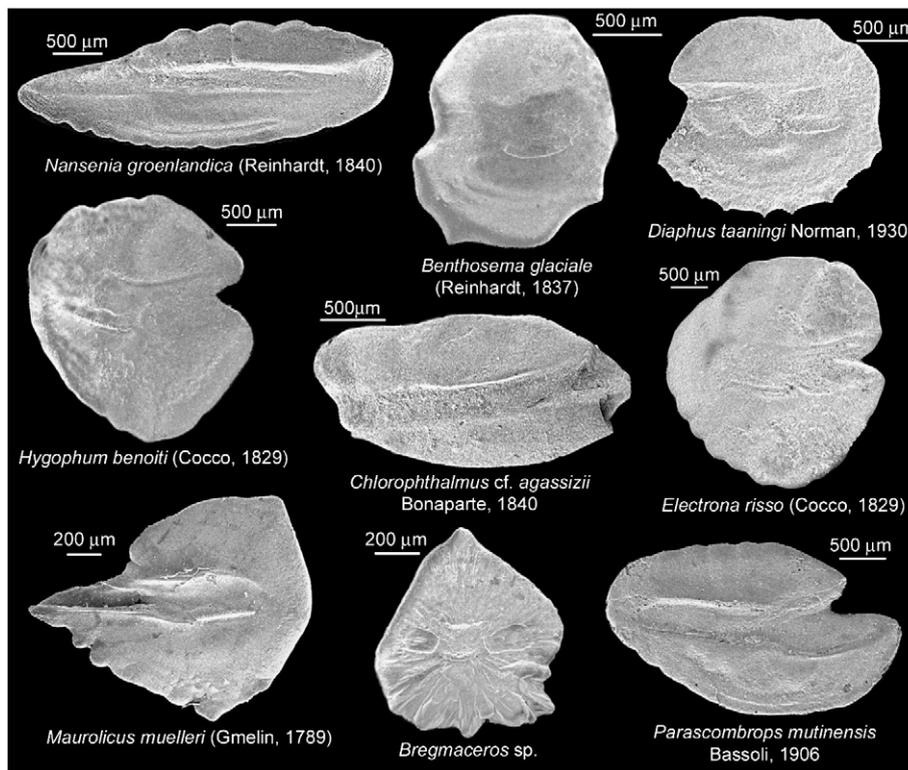


Fig. 4. Otolith specimens of the most significant fish taxa occupying the Pleistocene Eastern Ionian realm. All figured specimens come from the studied sections Akrotiri and Gerakas.

bottom. Finally, benthic fish live either on or directly above the bottom of the sea. The early–middle Quaternary Teleost assemblages of the Ionian Sea contain members of all five categories. The present-day geographic distributions of the identified extant taxa range from tropical to subpolar regions.

In order to study the fishes' response to different palaeoceanographic conditions along the depth of the water column, the identified taxa were placed in one or more of the following three categories based on their

depth distribution and life mode (Table 3). The surface group (S) comprises taxa occupying the upper 200 meters of the water column, the intermediate water group (I) incorporates taxa living between 200 and 500 meters, and the deepwater group (D) contains taxa occupying waters below 500 meters. The benthopelagic and benthic taxa contribute only to the deepest part of the water column depending on the palaeobathymetry of the examined sediment sample (Agiadi et al., 2010, presented here in Fig. 3; Gironé, 2000a,b; Maiorano et al., 2010) since they live near or on the sea bottom. When the palaeobathymetric estimate had indicated depths of less than 500 meters, the deepwater layer's (D) conditions could not be evaluated. In those instances, it was assumed that all otolith specimens of taxa living in the deeper zone had either been secondarily transported into the taphocoenosis, or these fish had a different palaeobathymetric distribution during the early–middle Quaternary than they do today.

Certain remarks on the present-day ecology of the examined taxa were considered especially important. Indeed, the small planktivore *Bregmaceros* has been reported in open waters between 0 and 1260 meters depth. However, it largely maintains an epipelagic way of life and is thus most abundant in the upper 200 meters (Castellanos-Galindo et al., 2006). Also, according to Whitehead et al. (1984), the distribution of *Hygophum benoiti* may be related to the oceanographic boundaries of the North Atlantic gyre system. As for the abundant species *Maurolicus muelleri*, it is known to display seasonal vertical migrations, in the Atlantic Ocean, occupying deeper parts of the water column during the summer. However, this does not hold true for the modern Mediterranean Sea, where adult specimens maintain a depth range between 200 and 400 meters during the daytime and feed in the surface waters at night (Whitehead et al., 1984). In addition, the present-day geographic distribution of the tropical–subtropical *Electrona risso* is discontinuous across the cyclonic gyre region, between the South Equatorial counter-current and the western branch of the Benguela Current (5°S–13°S), and is limited by the 10° and 15° C isotherms at 200 meters, and by productivity of 50 grams of carbon per square meter per year (Whitehead

Table 1

Environmental setting and relative references presenting the comparison data used in the current study for the Western Ionian Sea.

Locality (Stratigraphy)	Environmental setting	References
Vrica section (early Pleistocene)	Deep bathyal (above 500 meters)	Gironé et al. (2006) Landini and Menesini (1978)
Palliore river section (early Pleistocene)	Deep shelf–upper slope	Di Geronimo et al. (2003)
Furnari (early Pleistocene)	Deep bathyal	Gironé et al. (2006) Di Geronimo and La Perna (1997)
Gravina section (early Pleistocene)	Middle shelf to surface	Gironé et al. (2006)
Montalbano Jonico section (early–middle Pleistocene)	Deep bathyal progressively to deep upper slope, break shelf, and inner shelf	Gironé and Varola (2001) Gironé (2005)
Archi section (early–middle Pleistocene)	Deep bathyal (above 500 meters)	Di Geronimo et al. (1997) Gironé (2003)
Fiumefreddo section (early–middle Pleistocene)	Deep bathyal	Di Geronimo and Rosso, in Gironé et al. (2006)
Vallone Catrica (middle Pleistocene)	Bathyal	Di Geronimo and La Perna (1997)

et al., 1984). Finally, despite the fact that the otolith of *Alepocephalus* from the Akrotiri section cannot be identified to the specific level, all known modern *Alepocephalus* species exhibit distributions within the boundaries of the tropical to temperate zones, and dwell in the intermediate and deeper waters. Indeed, *A. rostratus*, the only *Alepocephalus* species occupying the Mediterranean today, has a bathymetric distribution between 300 and 2250 meters (Carrasson and Matallanas, 1998), which is also inclusive of the distributions of the other *Alepocephalus* species.

The relative abundances of tropical, subtropical, temperate, and subpolar fish taxa in the surface, intermediate, and deepwater environments (S, I, or D) were calculated for each sample (Fig. 5). Apart from being included in the previously described analysis, the relative contribution to the assemblages of *Nansenia groenlandica*, *M. muelleri*, *Benthoema glaciale*, *E. risso*, *Diaphus taaningi*, *Parascombrops mutinensis*, and *Bregmaceros* sp. were considered separately since these are regarded as the most significant palaeoecological indicators (Fig. 6).

### 3.3. Comparison with other available data

In order to distinguish between the palaeoceanographic changes occurring in the surface waters, and those affecting the deeper parts of the water column, the results of the present assemblage analysis were compared to those of the analysis of the calcareous nannofossil assemblages (Triantaphyllou, 1996; Triantaphyllou et al., 1997, 1999; Triantaphyllou, 2001; Ciaranfi et al., 2010; Maiorano et al., 2010). Since calcareous nannoplankton, as a phytoplankton group, occupies the euphotic zone, generally the uppermost 200 m, it is an important surface water proxy. The presence or absence, and the abundances of significant nannofossil indicators are especially considered in this respect. *Helicosphaera* spp. is a genus generally representing warm environments, while *Coccolithus pelagicus* is a typical cold water species (e.g. Triantaphyllou et al., 1999). *Braarudosphaera bigelowi* is indicative of increased fresh water input (e.g. Triantaphyllou et al., 2009a,b). Also, the presence of normal sized geophyrocapsids suggests higher surface temperatures (e.g. Triantaphyllou, 1996).

The Pleistocene epoch was a time of intense palaeoenvironmental changes, characterized by alternations between glacial and interglacial periods, generally following the orbital obliquity cycles, with glacial periods corresponding to maximum obliquity (Huybers, 2007). Based on this generally agreed upon model for the Pleistocene climate variability, the present fish data were correlated to the obliquity curve of Laskar et al. (2004), to infer the climatic impact on the fish assemblages.

## 4. Palaeobiogeography

The results regarding the geographic and stratigraphic distribution of the identified teleost taxa in the Ionian and the Mediterranean sediments are presented in Table 2. The occurrence of the deep-sea Atlantic species *Nansenia groenlandica* in the study areas is significant since it indicates its presence in the Mediterranean Basin during the Gelasian stage (nannoplankton biozones MNN18 and MNN19a). Previously, its distribution was limited to the Calabrian stage, and it was considered to be restricted to the western sub-basin, specifically the Messina Strait area (Girone, 2003; Girone et al., 2006). Similarly, the Atlantic species *Aphanopus carbo*, which was considered to have temporarily inhabited the Mediterranean Sea during the Calabrian age (Girone et al., 2006) is recognized here for the first time in the Gelasian stage of the eastern Ionian realm.

In addition, this is the first fossil record worldwide of the extant benthopelagic species *Chlorophthalmus agassizi*. Today, it is globally distributed in the tropical to temperate latitudes with high abundances in the central Mediterranean Sea (Whitehead et al., 1984). The modern Eastern Ionian distribution of this species is especially high around the island of Zakynthos in the bathymetric range of 300–700 meters, and it dominates the fish assemblages between 350 and

450 meters of depth (Anastasopoulou et al., 2006). In addition, Mytilineou et al. (2005) noted considerably higher abundance values of *C. agassizi* in the Eastern Ionian Sea as compared to the Western Ionian.

The present-day distribution of the tropical oceanic genus *Bregmaceros* is circum-global with only one published presence within the Mediterranean Sea (Whitehead et al., 1984). As a fossil, its stratigraphic distribution in the Mediterranean realm extended to the early Pleistocene (Nolf and Girone, 2000), and its departure from the basin was considered to be related to the climatic deterioration (Landini and Menesini, 1988). In Gerakas section, the high abundance of *Bregmaceros* found in Gelasian stage sediments is interpreted as a palaeotemperature maximum, as well as an indication of increased oceanic input in the area of southern Zakynthos.

## 5. Palaeoceanographic results and palaeocirculation inferences

The results of the new assemblage analysis methodology are presented in Fig. 5. The study areas are placed in the temperate climatic zone. Eleven phases in the Ionian Sea palaeoceanographic evolution are distinguished, from prior 1.95 Ma to 0.61 Ma (Fig. 5, pph1–11). During palaeoceanographic phase 1 (pph1), prior the MNN18/MNN19a biozone transition at 1.95 Ma, the fish species' relative abundances are widely distributed among the different ecological groups, in the surface and intermediate water levels. The high contribution of bathypelagic *E. risso* (19.67%), whose modern distribution is limited by the 10–15 °C isotherms and by productivity greater than 50gC/m<sup>2</sup>y (Whitehead et al., 1984), is combined with the increased presence of *M. muelleri* (23.78%) and *B. glaciale* (9.84%), which are mostly known from the upper temperate and subpolar zones (Whitehead et al., 1984; Mytilineou et al., 2005). Their presence indicates nutrient-rich relatively cold waters at this time. A medium-cold period for the surface waters with concurrent increased primary productivity, is derived from the palaeoecological study of calcareous nannofossils, interpreting the low abundance of *Helicosphaera* spp., contemporaneous with the extremely low abundance of the genus *Discoaster*, and the relative increase of *Coccolithus pelagicus*, followed by the intense presence of small *Gephyrocapsa* spp. (Triantaphyllou et al., 1997, 1999). Comparison to the obliquity curve indicates a possible correlation to the obliquity maximum at 1.98 Ma (Fig. 5).

The situation around 1.95 Ma (pph2, Fig. 5) appears homogenous throughout the water column (just above the biozone boundary MNN18/MNN19a). The introduction of *Hygophum hygomii* in the deeper water layers of Akrotiri (Appendix 1), as well as the decreased relative abundance of *B. glaciale*, in both areas, is perhaps due to an increase in deepwater temperature. However, the most dominant species in the assemblages (75% in the Gerakas assemblages, appendices 1 and 2), during this interval, is *Ceratoscopelus maderensis*, an exclusively temperate meso-bathypelagic species (D'Onghia et al., 2004). The high contribution of helicoliths suggests higher surface temperatures and an increase in fresh water input, which is also indicated by the presence of *Braarudosphaera* specimens. In addition, the presence of normal sized geophyrocapsids indicates higher surface temperatures (Triantaphyllou et al., 1997, 1999).

At about 1.9 Ma (pph3, Figs. 5 and 6), there is a maximum in the relative abundance of tropical taxa, namely *D. taaningi* and *Bregmaceros* sp., which today occupy the upper 500 meters of the water column. *D. taaningi* is presently considered a pseudo-oceanic species, occurring in environments which are close to land, or otherwise related to land-oriented food chains. In the eastern Atlantic, it has been reported from the Gulf of Guinea to the Mauritanian upwelling region and in the western Atlantic from the Caribbean Sea and the Gulf of Mexico in slope environments (Nafpaktitis et al., 1977). This positive shift of the tropical group abundance in the surface and intermediate waters, along with a decrease of both subtropical and temperate taxa, can be attributed to a climatic optimum at this time. This event, but to a lesser degree, is also

**Table 2**  
Palaeogeographic and stratigraphic distribution of the identified fish taxa in the Mediterranean realm.

Families	Taxa	Miocene	Pliocene		Pleistocene				
			Zanclean	Piacenzian	Gelasian		Calabrian		
					MNN18	MNN19a	MNN19b	MNN19c	
Microstomatidae	<b>Nansenia groenlandica</b>				<b>x</b>	<b>x</b>			
Alepocephalidae	<i>Alepocephalus</i> sp.				<b>x</b>				
Gonostomatidae	<i>Mauroliticus muelleri</i>	x	x	x	x	x	x	x	
Phosichthyidae	<i>Vinciguerria poweriae</i>	?x	?x	x	<b>x</b>	<b>x</b>	x	x	
Stomiidae	<i>Chauliodus</i> aff. <i>sloani</i>					<b>x</b>	<b>x</b>		
Chlorophthalmidae	<i>Chlorophthalmus</i> cf. <i>agassizi</i>								
Scopelarchidae	<b>Scopelarchus analis</b>	x	x		x	<b>x</b>			
Myctophidae	<i>Benthoema glaciale</i>	?x		x	x	x	x	x	
	<i>Electrona risso</i>		x	x	x	x	x	x	
	<i>Hygophum benoiti</i>			x	x	x	x	x	
	<i>Hygophum hygomi</i>	x	x	x	x	x	x	x	
	<i>Myctophum punctatum</i>			x	x	x	x	x	
	<i>Symbolophorus</i> aff. <i>veranyi</i>							x	
	<i>Ceratoscopelus maderensis</i>		x	x	x	x	x	x	
	<i>Ceratoscopelus</i> sp.1						<b>x</b>	<b>x</b>	
	<i>Diaphus holti</i>		x		<b>x</b>	<b>x</b>	x	x	
	<i>Diaphus rafinesquii</i>		x	x		<b>x</b>	x	x	
	<i>Diaphus taaningi</i>	x	x	x	x	x	x	x	
	<i>Diaphus</i> aff. <i>taaningi</i>	x	x	x	x	x	x	x	
	<i>Diaphus</i> sp.1					<b>x</b>	<b>x</b>		
	<i>Lampanyctus crocodilus</i>				x	x	x	x	
	<i>Lobianchia dofleini</i>	?x	x		x	x	x	x	
	<i>Notoscopelus elongatus</i>				x	x	x	x	
	<b>Scopelopsis pliocenicus</b>	x	x	x		<b>x</b>	<b>x</b>	<b>x</b>	
	Bregmacerotidae	<b>Bregmaceros</b> sp.	x		x		<b>x</b>	x	x
	Moridae	<i>Laemonema</i> sp.			x		<b>x</b>	x	x
	Phycidae	<i>Gaidropsarus</i> sp.					<b>x</b>		
Gadidae	<i>Gadiculus argenteus</i>	x	x	x	x	x	x	x	
	<i>Gadiculus labiatus</i>	x	x	x	x	x	x	x	
Bythitidae	<i>Bellottia</i> cf. <i>apoda</i>					<b>x</b>	x	x	
Acropomatidae	<b>Parascombrops mutinensis</b>					<b>x</b>			
Carangidae	<i>Trachurus</i> sp.			x		<b>x</b>	x	x	
Gobiidae	<i>Deltentosteus quadrimaculatus</i>			x		<b>x</b>	x	x	
	<i>Lesueurigobius</i> sp.		?x	x		<b>x</b>	x	x	
Trichiuridae	<i>Aphanopus</i> aff. <i>carbo</i>					<b>x</b>	<b>x</b>	<b>x</b>	

The taxa noted in bold have not been reported in the modern Mediterranean Sea. The presences in bold (x) note new data from the present study. The presences noted with “?” are questionable according to Girone et al. (2006). The bibliographic data for the Western Ionian Sea are analyzed in: <sup>1</sup> Agiadi et al., 2010, <sup>2</sup> Girone et al., 2006, <sup>3</sup> Di Geronimo et al., 2003, <sup>4</sup> Girone and Varola, 2001, and <sup>5</sup> Girone, 2003.

registered in the Akrotiri section. Indeed, the relative abundance of *D. taaningi* in the surface and upper intermediate waters (depth range 40–475 meters) is significantly increased at this level. However, the abundances of the cold-water species *N. groenlandica* and *B. glaciale*, which contribute mostly to the intermediate water layers, are also high. As a result, it appears that at this time the formation of deep water with lower temperatures than before took place, as also testified to by the occurrence of *Aphanopus carbo*. However, the locally high abundance of *D. taaningi* could indicate an increase in the river runoff into the Adriatic Sea, creating waters with major land nutrients input. The stratigraphic distribution of *D. taaningi* in the lower–middle Pleistocene sediments of the Montalbano Jonico section (western side of Ionian Sea) supports this hypothesis. In this section (Girone, unpubl. data), the relative abundance peaks of *D. taaningi* are correlated to maxima in the contribution of the planktonic foraminiferal assemblages of *Globigerinoides ruber* gr., which indicates warm, stratified, low salinity surface waters (Thunnel, 1978). At the same time, the higher occurrence of *Bregmaceros* sp. suggests greater mean surface temperatures than before, in the eastern Ionian Sea, which may be linked to a climate optimum forced by thermal stratification of the water masses as a consequence of this hypothesized increased river run-off. The simultaneous increase of normal sized *gephyrocapsids* >4  $\mu\text{m}$  (Triantaphyllou et al., 1997) in this level indicates higher surface water temperatures as well, but is also related to less

saline waters (Knappertsbusch, 1993; Winter et al., 1994; Triantaphyllou et al., 2009a,b, 2010).

The palaeoceanographic conditions appear generally stable until the upper part of MNN19a (pph4, Fig. 6), although the relative abundance of *D. taaningi* gradually deteriorates. Colder temperatures prevail especially in the Gerakas area, where an increase in the relative abundance of *M. muelleri* is combined with a decrease of *E. risso*. In the Akrotiri area, only the deeper parts of the intermediate water layers seem to follow the same pattern, mainly allowing for an increase in the abundance of *Nansenia groenlandica*. These observations coincide with the frequent occurrence of small–moderate (3–4  $\mu\text{m}$ ) *Gephyrocapsa* spp. forms (Triantaphyllou, 1996), which is considered indicative of higher surface productivity (Colmenero-Hidalgo et al., 2004) at the onset of winter convection (Triantaphyllou et al., 2010).

During the Gelasian–Calabrian transition at approximately 1.806 (pph5, Figs. 5 and 6), the relative abundance of *E. risso* increases again in both areas. In the uppermost Gelasian of Gerakas, the conditions return to temperate–subtropical, with a relative decrease in the contribution of the subpolar group in the entire water column. However, in the Akrotiri area during the lowermost Calabrian, the subtropical group shows a slight decline in the surface and intermediate waters, while the subpolar group increases significantly to 30% and 24% respectively (Fig. 5), due primarily to the high relative abundance of *M. muelleri* (36%).



**Table 3**  
Present-day ecological data for the identified fish taxa.

Taxon	Life style	Distribution	Depth (m)	Refs.
<i>Conger conger</i>	Benthic	Te, I + D	0–1171 m	12
<i>Argentina sphyraena</i>	Benthopelagic	Te-SP, I + D	50–700 m	12
<i>Nansenia groenlandica</i>	Bathypelagic	Te-SP, S + I + D	0–1400	1
<i>Alepocephalus rostratus</i>	Benthopelagic	Tr-ST-Te, I + D	300–2250	2
<i>Bonapartia pedaliota</i>	Meso-bathypelagic	Tr-ST, S + I + D	100–1200 m	1
<i>Gonostoma</i> spp.	Meso-bathypelagic	ST-Te	–	1
<i>Maurolucus muelleri</i>	Bathypelagic	Te-SP, S + I	day: 200–400, night: 0–100	1
<i>Polyipnus polli</i>	Benthopelagic	Tr, I + D	250–600 m	1
<i>Valencienellus tripunctulatus</i>	mesopelagic	Tr-ST, D + I	100–550	12
<i>Vinciguerra</i> spp.	Meso-bathypelagic	ST, S + I	50–1000	1
<i>Chauliodus sloani</i>	Bathypelagic	ST-Te, I	473–1192	3
<i>Chlorophthalmus</i> cf. <i>agassizi</i>	Benthopelagic	ST-Te, I + D	300–700	3, 15
<i>Scolecarchus analis</i>	Meso-bathypelagic	Tr-Te, S + I + D	0–820	4, 5
<i>Benthoosema glaciale</i>	Meso-bathypelagic	Te-SP, S + I + D	d: 375–1085, n: 12–200 and 600–800	1, 3
<i>Benthoosema suborbitale</i>	mesopelagic	Tr-ST, S + I + D	375–750	12
<i>Ceratoscopelus</i> spp.	Meso-bathypelagic	Te, S + I + D	d: 100–2500, n: 12–300 and 600–800	1, 6
<i>Diaphus holti</i>	Meso-bathypelagic	Te, S + I + D	d: 100–780, n: 80–235 and 400–600	1, 6
<i>Diaphus rafinesquii</i>	Meso-bathypelagic	Te, S + I + D	day: 400–675, nyctoepipelagic 0–600	1
<i>Diaphus taaningi</i>	Pelagic	Tr, S + I	40–475	12
<i>Electrona risso</i>	Bathypelagic	Tr-ST, S + I + D	d: 700–750, n: 150–200 and 400–700	1
<i>Hygophum benoiti</i>	Mesopelagic	Te, S + I + D	d: 100–1000, n: 12–400 and 700–1000	1
<i>Hygophum hygomii</i> (juveniles)	Bathypelagic	ST, D + I	400–750	1
<i>Hygophum hygomii</i> (adults)	Oceanic, Mesopelagic	ST-Tr, S + I + D	0–800	1
<i>Lampadena</i> spp.	Bathypelagic	Tr-Te, D + I	0–239	1, 12
<i>Lampanyctus crocodilus</i>	Benthopelagic	ST-Te, S + I + D	d: 200–1300, night at surface, adults non-migratory	1, 6
<i>Lobianchia dofleini</i>	Mesopelagic	ST, S + I + D	day: 375–600, night: 25–400	1
<i>Myctophum punctatum</i>	Mesopelagic	Te, S + I + D	d: 100–150 & 700–1000, n: 0–190 & 700–800	1
<i>Notoscopelus elongatus</i>	Mesopelagic	ST, S + I + D	day: 375–1000, night: 45–150	1
<i>Scopelopsis pliocenicus</i>	Meso-bathypelagic	ST-Te, S + I	74–400	7
<i>Symbolophorus</i> aff. <i>veranyi</i>	Pelagic	Te, S + I + D	0–800	1
<i>Bregmaceros</i> spp.	Pelagic	Tr, S	0–1260	8
<i>Laemonema</i> spp.	Benthic	Tr-ST, I	200–1200	9
<i>Gaidropsarus</i> spp.	Benthopelagic	Te, S + I	80–600	10
<i>Gadiculus argenteus</i>	Benthopelagic	ST, I + D	200–1000	1
<i>Gadiculus labiatus</i>	Benthopelagic	ST-Te	–	11
<i>Micromesistius poutassou</i>	Benthopelagic	Te, I + D	150–3000	9
<i>Phycis blennoides</i>	Benthopelagic	Te, S + I + D	10–1047	9
<i>Merluccius merluccius</i>	Benthic	Te, S + I	70–400	9
<i>Gaidropsarus biscayensis</i>	Benthopelagic	Te, I + D	80–600 m	10
<i>Phycis blennoides</i>	Benthopelagic	Te, I + D	10–1047 m	9
<i>Ophidion rochei</i>	Benthic	ST, S	?–150 m	13
<i>Ophidion barbatum</i>	Benthic	ST, S	?–150 m	13
<i>Echiodon dentatus</i>	Benthic	ST, I + D	120–3250 m	13
<i>Oligopus ater</i>	Benthopelagic	ST, S	Reef, coastal deep dweller, in rocky substratum	13
<i>Scorpaena</i> spp.	Benthic	ST, S	< 300 m	1
<i>Chelidonichthys lucerna</i>	Benthic	ST, S + I	20–318 m	12
<i>Bellotia apoda</i>	Benthopelagic	ST, S + I	30–700	3
<i>Trachurus</i> spp.	Benthopelagic	ST, S + I + D	0–1050	1
<i>Spicara smaris</i>	Benthopelagic	ST, S + I	15–328 m	12
Sparidae	Benthopelagic	ST-Te	–	1
<i>Dentex maroccanus</i>	Benthic	ST, S + I	20–500 m	12
<i>Coelorrhinus coelorhincus</i>	Benthopelagic	Te-ST, I	140–630 mostly 200–500	9
<i>Nezumia sclerorhynchus</i>	Benthopelagic	Tr-ST, I + D	130–3200 max abundance 450–800 m	9
<i>Cepola rubescens</i>	Benthic	ST, S + I	15–400 usually 15–200	12
<i>Blennius ocellaris</i>	Benthic	ST, S + I	10–400 m	14
<i>Deltentosteus quadrimaculatus</i>	Benthic	ST, S + I	0–333	6
<i>Lesueurigobius</i> spp.	Benthic	ST, S + I	0–337	3, 12
<i>Lesueurigobius suerii</i>	Benthic	ST, S + I	?–337 m	1
<i>Lesueurigobius friesii</i>	Benthic	ST, S	10–130	12
<i>Aphanopus carbo</i>	Benthic	Te-SP, S + I + D	200–1600	1

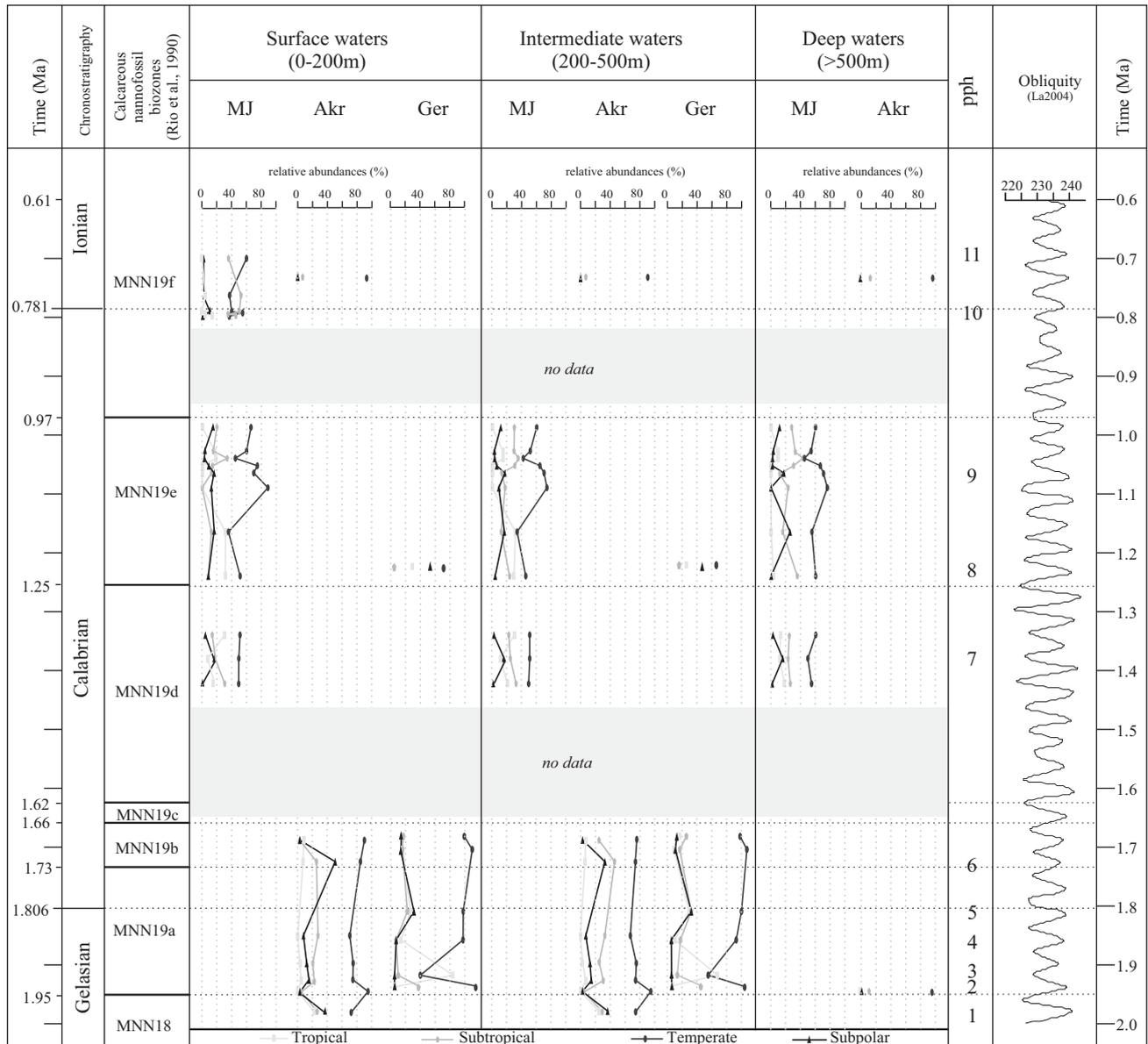
List of references: 1. Whitehead et al., 1984–1986, 2. Carrasson and Matallanas, 1998, 3. Mytilineou et al., 2005, 4. Riede, 2004, 5. Bogutskaya, 2007, 6. D'Onghia et al., 2004, 7. Girone, 2000a,b, 8. Castellanos-Galindo et al., 2006, 9. Cohen et al., 1990, 10. Svetovidov, 1986, 11. Girone et al., 2006, 12. Quero et al., 1990, 13. Nielsen et al., 1999, 14. Wheeler, 1992, 15. Anastasopoulou et al., 2006.

2001). Typical temperate fish, such as *Ceratoscopelus maderensis* and *Lampanyctus crocodilus*, are present along with *C. agassizi*, a dominant species today in the eastern Ionian Sea (Mytilineou et al., 2005), which has never been registered before as a fossil. This association possibly implies that the modern oceanographic conditions have prevailed in this area since the middle Pleistocene. Indeed the modern *C. agassizi* is a species well adapted to an oligotrophic environment, exploiting all available

niches of the eastern Ionian Sea deep-water habitats (Anastasopoulou and Kaporis, 2007).

## 6. Discussion and conclusions

The data presented here significantly improve the distribution record of several taxa in space and time. The stratigraphic distributions of six



**Fig. 5.** The surface, intermediate and deepwater taxa distribution among the different ecologic zones, i.e. tropical, subtropical, temperate and subpolar, for the Akrotiri, Gerakas, and Montalbano Jonico section sediments in a stratigraphic context and correlated to the obliquity curve (La2004). The eleven palaeoceanographic phases reflected in the fossil Teleost assemblages are referred to as pph 1–11.

teleostean species and two genera are extended back from the middle to the early Pleistocene, and the distribution gaps of ten additional taxa are filled. Most importantly, the presence of cold-water species *N. groenlandica* within the Gelasian stage sediments, in alternation with deposits rich in warm-water taxa such as *D. taaningi* and *Bregmaceros* sp., attest to the transitional nature and great variability of this time period, and reveal the high level of immediacy in the fish communities' response to such environmental changes. In addition, this is the first fossil record of *Chlorophthalmus* cf. *agassizi*, a species which exhibits great abundance in the present-day eastern Ionian Sea. Its presence in the Ionian stage sediments is considered especially significant, as it indicates that the palaeogeographic and/or at least some of the palaeoceanographic parameters prevailing in the eastern Ionian Sea had already taken their present-day form and value.

Modern observations have shown that oceanic circulation significantly modulates fish distribution worldwide. According to Landini and Sorbini (2005a,b), the climatic oscillations undoubtedly played an

important role in the major Mediterranean fish evolutionary events, during the early Pleistocene. However, these authors support that oceanic circulation variability as well as biotic interchange may have also been involved, since these events do not seem to act selectively. In the present study, we have used a new methodology to reconstruct the palaeoenvironment, based on the identified palaeoichthyofauna, which has enabled us to draw conclusions regarding the palaeocirculation patterns and their variability.

The present paper provides new input regarding the palaeoceanographic conditions prevailing in the Ionian Sea during the early Quaternary. It appears that the local production and/or the Atlantic origin of deep cold waters can be registered in the eastern Ionian Sea, already from the Gelasian age. This is denoted by the occurrence of several taxa, which today are restricted to the deep cold Atlantic waters. Meijer et al. (2004), modeling the Mediterranean thermohaline circulation, clearly observed a deep circulation cell in the eastern Mediterranean during the late Miocene, which according to them, was

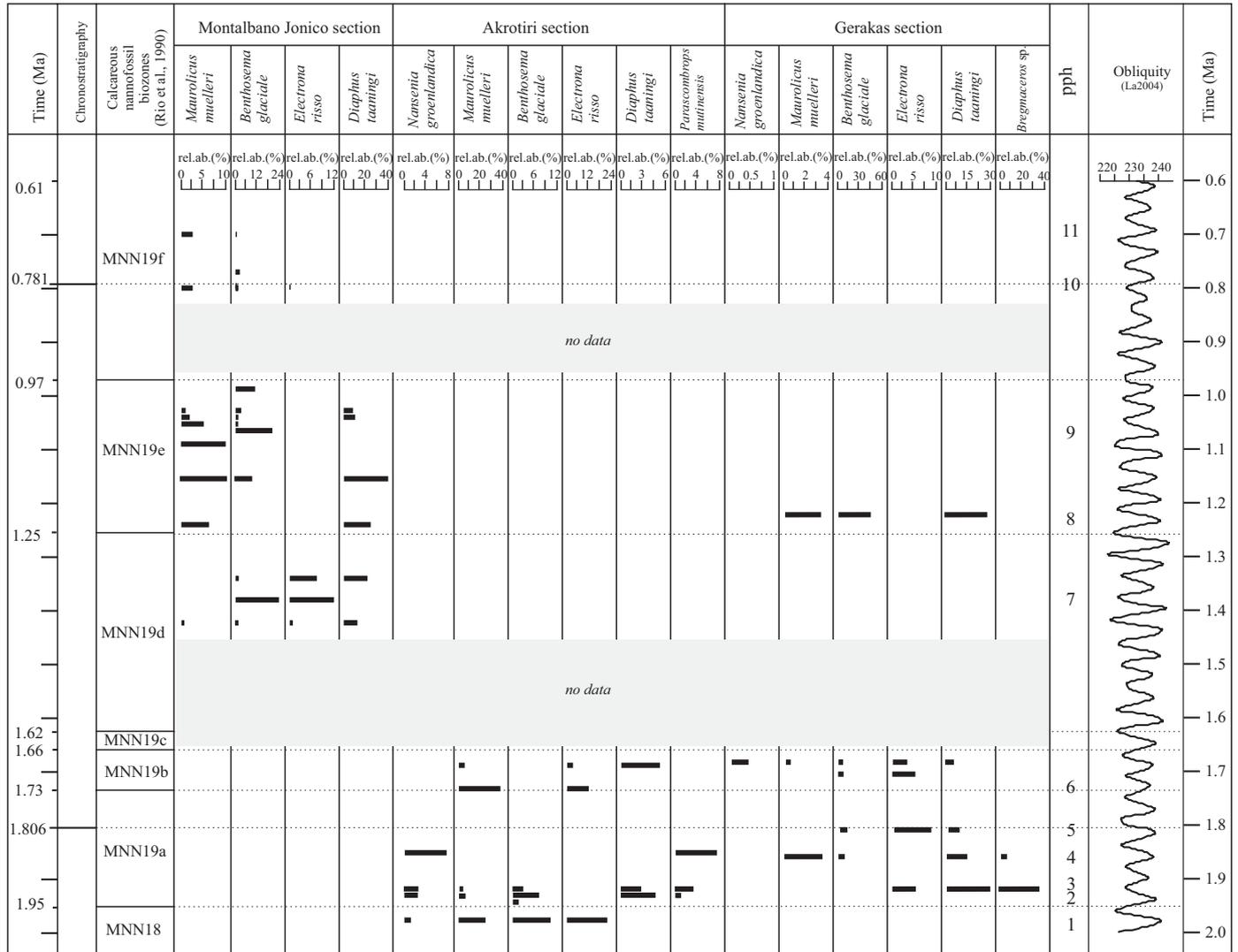


Fig. 6. The relative abundances of selected characteristic taxa in the samples from Akrotiri, Gerakas, Montalbano Jonico.

probably triggered by the outflow of dense water from the Adriatic Sea, an important location for deep water formation today (Robinson and Golnaraghi, 1993; Theocharis et al., 1993). This phenomenon is consistent with the data presented here for the early Pleistocene as well.

During the early Quaternary, local and global factors greatly influenced the compositions of the surface and intermediate water fish assemblages, which exhibit affinity to the modern Atlantic faunas. This is registered here for the eastern Ionian, as it has already been documented for the western part (Girone et al., 2006). Indeed, the geometric and bathymetric characteristics of the Ionian basin and the adjacent platforms strongly control the location of the intense anticyclonic gyre occupying the central part of the basin (Meijer et al., 2004). Thus, the surface water currents in the eastern Ionian Sea are influenced to a large degree by these characteristics. As a result, the presence of open sea and oceanic fish fauna in the eastern Ionian can be explained by the function of a strong gyre in the area during the early Quaternary, a development which, according to the above model, requires steep basin geometry and significant bathymetric variations within the Ionian basin.

The methodological requirements for the identification of fish paleofauna do not allow for the dense sampling obtained when

studying other fossil groups, e.g. nannofossils or foraminifera. However, the fish assemblages exhibit significant stability through time, so that the low resolution sampling does not hinder the isolation of important long term palaeoceanographic events. Fishes' ability to cope with environmental changes, by for example adjusting their depth distribution, trophic requirements and other life style attributes (Wootton, 1998), means that changes in a single environmental factor would probably not suffice, to alter the entire composition of the fish community. The pervasiveness by which, either tropical–subtropical or temperate–subpolar species keep recolonizing the Ionian Sea, within small time intervals, following severe environmental perturbations, is a clear indication in favor of this hypothesis. The extreme Pleistocene climatic variability, expressed in the glacial/interglacial stage alternations, cannot completely remove warm water taxa from the Mediterranean, such as *Bregmaceros*, nor admit *C. agassizi*. It simply shifts the distribution patterns on a local level, so that the fish can adjust to the new conditions. A result of this smoothing, is that the more pervasive palaeoenvironmental changes, such as the large scale palaeocirculation changes, can be clearly deciphered through the study of the fish record, as they are not solely controlled by climatic variability. Huybers (2007) describes the revolution from 40 to 100 Ka glacial cycles

observed during the middle Pleistocene, as an effect of continuous obliquity pacing, named the “Pleistocene progression”, indicating that the glacial/interglacial transitions, during the early and the middle Pleistocene are controlled by obliquity, with gradually more skipped cycles. This hypothesis could possibly justify the gradual changes observed in the fossil fish record. These major palaeoenvironmental perturbations are the ones we seek to identify when examining fossil fish and these indeed comprise relatively long time intervals of the scale of ten and hundreds of thousands of years.

Another factor to consider here is that, as has frequently been testified for modern teleosts (Chesson, 1985), although highly unpredictable environments have low species diversities, intermediate levels of disturbance might prompt diversity. In these moderate levels, species that would be unable to coexist, under stable conditions, because of competitive interactions, might all show positive population growth rates at low densities. This is especially the case with the oceanic palaeofauna studied here, where we observe the co-presence of warm and cold water pelagic species, such as *D. taaningi*, *Bregmaceros*, *Bonapartia pedaliota* and *Polyipnus polli* coexisting with *N. groenlandica* and *M. muelleri*. The alternating glacial–interglacial periods do not allow for the establishment of major competition, which would probably end in the exclusion of either the warm or the cold water fish group, but the ultimate establishment of the present day more stable palaeocirculation and palaeogeographic Ionian Sea regime does. This is also in agreement with previous analysis by Landini and Sorbini (2005a) who denote that the pattern of extinctions and originations in Mediterranean fish communities, during the Pleistocene, exhibits non-selectivity, in that it involves taxa with different habits and trophic, biogeographic and climatic behavior, and they suggest that other mechanisms besides climate, such as oceanic circulation, may influence the entire community structure.

According to Wootton (1998), Teleosts' spatial distribution reflects the individual response to several factors such as: current speed (circulation), temperature, salinity, physical structure of a locality (geography), and the presence of other fish (competitors, mates, etc.), while food availability only affects indirectly and only secondarily. This is because of the fishes' ability to change their

feeding ecology, and the fish community to easily adjust its trophic structure. Consequently, abiotic factors as well as interspecific and intraspecific competition and predation impact play a significantly more important role in fish distribution (Hopkins et al., 1996). Indeed these authors note that the predation pressure on the mid-water fish assemblage of the eastern Gulf of Mexico today indicates a tighter coupling of micronektonic fishes with higher levels of the trophic structure than with zooplankton. This theory could apply very well to the oceanic fauna examined here. As in the case of the modern Gulf of Mexico (Hopkins and Gartner, 1992), a relatively stable oceanic environment would offer opportunities for the coexistence of vast numbers of mid-water fish species, so that changes in the composition and diversity of the fauna would signify a major disequilibrium event. Evidently, it appears that the relationship between physical (abiotic) forcing and biological response may be indeed more linear than previously considered, in the case of fish assemblages.

The current study reveals the important role of fish otoliths in the reconstruction of deep-sea palaeoenvironmental conditions. Through the palaeoecologic analysis of the Teleost fauna, eleven distinct palaeoceanographic phases were determined, manifesting the great variability of climate and oceanography during early Quaternary times. Notwithstanding the general deterioration of climate, progressing into the Pleistocene, it appears that the Mediterranean palaeocirculation in conjunction with the basin geometry were modulated by the constantly changing global climatic conditions to produce a rather complex palaeoceanographic setting in the central part of the basin. In this respect, fish otoliths offer a unique opportunity to reconstruct the palaeoenvironmental evolution of the entire water column through time.

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**Appendix 1**

Fish otolith relative abundance in the Akrotiri section sediments									
Families	Taxa	Akrp7	Akrp6	Akrp5	Akrp4	Akrp3	Akrp1	Xi1	Akrakr1
<i>Pelagic</i>									
Nettastomatidae	<i>Nettastomatidae</i> sp. ind.			0.44					
Microstomatidae	<i>Nansenia groenlandica</i> (Reinhardt, 1840)	1.64		3.05	2.90	5.56			
Alepocephalidae	<i>Alepocephalus</i> sp.	1.64							
Gonostomatidae	<i>Gonostoma</i> sp.			1.31					
	<i>Gonostomatidae</i> sp. ind.			0.44					
Sternoptychidae	<i>Maurolicus muelleri</i> (Gmelin, 1789)	23.78		4.58	2.42		36.36	1.58	
Phosichthyidae	<i>Vinciguerria</i> cf. <i>lucetia</i> (Garman, 1899)			0.44					
	<i>Vinciguerria poweriae</i> (Cocco, 1838)	1.64		5.23	3.87	5.56			6.06
	<i>Vinciguerria</i> sp.			0.44					
Scopelarchidae	<i>Scopelarchus analis</i> (BRAUER, 1902)			0.87					
Myctophidae	<i>Benthoosema glaciale</i> (Reinhardt, 1837)	9.84	1.47	5.89	2.90				
	<i>Electrona risso</i> (Cocco, 1829)	19.67					6.06	1.58	
	<i>Hygophum benoiti</i> (Cocco, 1829)	18.85	2.21	5.01	19.32	16.67	6.06	7.87	
	<i>Hygophum hygomi</i> (Lutken, 1892)		2.94	0.44				11.02	
	<i>Hygophum</i> sp.				0.97	5.56			
	<i>Myctophum punctatum</i> Rafinesque, 1810	1.64	1.47	1.96		5.56		2.36	
	<i>Ceratoscopelus maderensis</i> (Lowe, 1839)	10.66	75.00	39.65	31.88	16.67	6.06	39.37	57.57
	<i>Ceratoscopelus</i> sp.1		3.68	1.31	1.45		6.06	4.72	
	<i>Diaphus holti</i> TANING, 1918			2.18	1.93			2.36	15.15
	<i>Diaphus rafinesquii</i> (Cocco, 1838)			0.65	1.45			3.15	
	<i>Diaphus taaningi</i> Norman, 1930			3.92	2.42			4.72	
	<i>Diaphus</i> sp.1		5.88	1.31	9.18	13.89		8.66	
	<i>Diaphus</i> sp.3	1.64							
	<i>Diaphus</i> sp.	4.92	1.47	1.96		8.33		3.94	9.09

(continued on next page)

Appendix 1 (continued)

Fish otolith relative abundance in the Akrotiri section sediments									
Families	Taxa	Akrp7	Akrp6	Akrp5	Akrp4	Akrp3	Akrp1	Xi1	Akrakr1
<i>Pelagic</i>									
Myctophidae	<i>Lampanyctus</i> sp.				0.97				
	<i>Lobianchia dofleini</i> (Zugmayer, 1911)			1.31	2.90				
	<i>Notoscopelus elongatus</i> (Costa, 1844)	2.46	2.94	9.80	10.63	11.11	6.06		
	<i>Scopelopsis pliocenicus*</i> (Anfossi & Mosna, 1976)			0.44			6.06		
<i>Benthopelagic</i>									
Chlorophthalmidae	<i>Chlorophthalmus</i> cf. <i>agassizi</i> (Bonaparte, 1840)								6.06
Myctophidae	<i>Lampanyctus crocodilus</i> (Risso, 1810)			1.96	1.93			3.94	6.06
Phycidae	<i>Gaidropsarus</i> sp.			1.31					
Gadidae	<i>Gadiculus argenteus</i> (Guichenaut, 1850)			0.44			6.06	1.58	
	<i>Gadiculus labiatus*</i> (Schubert, 1905)		2.94		0.97		15.15	1.58	
	<i>Gadidae</i> sp. ind.	1.64		1.31					
Carangidae	<i>Trachurus</i> sp.					5.56			
Sparidae	<i>Sparidae</i> sp. ind.							1.58	
<i>Benthic</i>									
Moridae	<i>Laemonema</i> sp.			0.65					
	<i>Moridae</i> sp. ind.			0.44					
Acropomatidae	<i>Parascombrops mutinensis</i> (Bassoli, 1906)			0.44	1.93	5.56			
Gobiidae	<i>Deltentosteus quadrimaculatus</i> (Valenciennes, 1837)						6.06		
	<i>Lesueurigobius</i> sp.			0.44					
Trichiuridae	<i>Aphanopus</i> aff. <i>carbo</i> (Lowe, 1839)			0.44					
Total identified otoliths		73	85	281	131	21	18	79	20

Appendix 2

Fish otolith relative abundances in the Gerakas section sediments									
Families	Taxa	ST2	ST3	ST4	ST5	ST6	ST7	Gerp1SE	
<i>Pelagic</i>									
Microstomatidae	<i>Nansenia groenlandica</i> (Reinhardt, 1840)						0.42		
Sternoptychidae	<i>Maurolicus muelleri</i> (Gmelin, 1789)			2.60			0.42		3.33
Phosichthyidae	<i>Vinciguerria poweriae</i> (Cocco, 1838)						1.25		
Stomiidae	<i>Chauliodus</i> aff. <i>sloani</i> (Schneider, 1801)						0.42		
Myctophidae	<i>Benthoosema glaciale</i> (Reinhardt, 1837)			2.60	15.55	3.08	2.98		45.00
	<i>Electrona risso</i> (Cocco, 1829)		4.44		8.89	4.62	2.70		
	<i>Hygophum benoiti</i> (Cocco, 1829)	7.41	11.11	29.87	20.00		22.61		
	<i>Hygophum hygomi</i> (Lutken, 1892)			5.20			1.04		
	<i>Hygophum</i> sp.			3.90			1.25		
	<i>Myctophum punctatum</i> (Rafinesque, 1810)					7.69	2.70		5.00
	<i>Myctophum</i> sp.						0.42		
	<i>Symbolophorus</i> aff. <i>veranyi</i> (Moreau, 1888)						0.42		
	<i>Ceratoscopelus maderensis</i> (LOWE, 1839)	22.22	11.11	24.68	24.44	49.23	24.07		8.33
	<i>Ceratoscopelus</i> sp.1				11.11	24.62	21.16		
	<i>Diaphus holti</i> (Taning, 1918)	14.82			4.44	7.69	0.62		
	<i>Diaphus rafinesquii</i> (Cocco, 1838)	11.11		2.60			0.83		
	<i>Diaphus taaningi</i> (Norman, 1930)		24.44	6.49	4.44		2.49		13.33
	<i>Diaphus</i> aff. <i>taaningi</i> (Norman, 1930)								
	<i>Diaphus</i> sp.1						0.42		
<i>Diaphus</i> sp.2								5.00	
<i>Diaphus</i> sp.		18.52	17.78	14.29	4.44		1.66		
<i>Lobianchia dofleini</i> (Zugmayer, 1911)							0.42		
<i>Notoscopelus elongatus elongatus</i> (Costa, 1844)				2.60			6.23	3.33	
<i>Scopelopsis pliocenicus*</i> (Anfossi & Mosna, 1976)		18.52							
Bregmacerotidae	<i>Bregmaceros</i> sp.		31.11	2.60					
<i>Benthopelagic</i>									
Myctophidae	<i>Lampanyctus crocodilus</i> (Risso, 1810)					6.67	2.08		3.33
Gadidae	<i>Gadiculus argenteus</i> (Guichenaut, 1850)			2.60					
	<i>Gadidae</i> sp. ind.						0.42		
Carangidae	<i>Trachurus</i> sp.						0.42		
<i>Benthic</i>									
Bythitidae	<i>Bellottia</i> cf. <i>apoda</i> (Giglioli, 1883)	7.41							
Gobiidae	<i>Deltentosteus</i> aff. <i>quadrimaculatus</i> (Valenciennes, 1837)								6.66
	<i>Lesueurigobius</i> sp.					3.08			3.33
Gobiidae	<i>Gobiidae</i> sp. ind.							3.33	
Trichiuridae	<i>Aphanopus</i> aff. <i>carbo</i> (Lowe, 1839)						0.62		
Total identified otoliths		15	28	47	26	40	404		33

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