

Fish otoliths in superficial sediments of the Mediterranean Sea



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ABSTRACT

Otoliths represent a significant biogenic carbonate component in marine sediments that may provide valuable information for paleoenvironmental and biogeographic reconstructions. In spite of their importance, relatively little is still known about the taxonomic composition, abundance and early taphonomic characteristics of recent otolith death-assemblages, which would add to their value to interpret situations in the geological record. Here we present data on the distribution of fish otoliths from bottom sediments collected in the central Mediterranean Sea ranging in depth from 51 to 3300 m. The preservation of otoliths ranges from fresh semi-translucent (white) specimens to dull-coloured (dark) ones, although whitish specimens are predominant across all the samples. This diversity in lustre and colour and at times texture reflects the degree of early taphonomic processes undergone by these aragonitic bodies *post-mortem* under submarine conditions, never being exposed to diagenetic processes on-land. In general, a correlation with depth is observed, with best preservation observed in otoliths sampled at depths <500 m, while more degraded specimens occur deeper. In the upper depth range (<500 m), a substantial number of benthic and benthopelagic taxa is counted with respect to mesopelagic taxa, which prevail from 500 down to 3300 m. The taxonomic composition and relative abundance of each taxon of otolith death-assemblages at various depths conform well to the distribution of related Mediterranean modern fish communities. The occurrence of pre-modern subfossil taxa in the death-assemblages is evidenced at some bathyal sites by the overwhelming presence of many highly-degraded (worn, chalky, opaque and patinated) otoliths and locally extinct species. This is the case of *Protomyctophum arcticum*, a mesopelagic myctophid absent in the modern Mediterranean Basin that represents an Atlantic Pleistocene 'cold guest' fish in the Pleistocene of this basin.

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1. Introduction

Saccular fish otoliths represent a significant biogenic component of marine sediments although their major abundance is documented from the Cenozoic onwards (Nolf, 1985, 2013). They may at times even predominate in fossil assemblages, and this is especially true in hemipelagic and bathyal situations where other skeletal macrocomponents could be less represented in the sediments. Otoliths hold an important and independent role to achieve paleoenvironmental reconstructions since they are shed by mobile organisms from a variety of taxa living in different parts of the water column, from surface down to the benthic layer, in a wide bathymetric range and responding to a vast spectrum of salinity and oxygen content (e.g., Limburg et al., 2015). Besides their value as ecological indicators, these mineralized skeletal parts prove useful also as

archives to unravel delicate ecological as well as oceanographic problems (e.g., Brickle et al., 2016; Iacumin et al., 1992; Zazzo et al., 2006). Finally, their ecostratigraphic value is also significant (Kotlarczyk et al., 2006).

Since otoliths are calcified as metastable aragonite and more rarely as vaterite (Gauldie, 1993; Kalish, 1993), they are easily and quickly exposed to post-mortem taphonomic processes that could alter their texture until their ultimate dissolution (Cherns and Wright, 2009; Flügel, 2010). Otolith survival in the fossil record, therefore, largely results from certain ambient conditions, such as burial in fine-grained sediments. This explains also why fossil otoliths are more commonly found in muddy and mudstone lithologies deposited in outer-shelf to bathyal conditions (e.g., Brzobohatý et al., 2003; Girone et al., 2010; Lin et al., 2016b; Nolf and Steurbaut, 2004; Radwańska, 1992; Schwarzhans, 1985; Stringer, 1998), although they have been reported as abundant also from considerably shallower settings, such as the Eocene shallow neritic otolith assemblages from the Anglo-Belgian-Parisian Basin (Nolf, 1972; Nolf and Cappetta, 1976; Nolf and Lapierre,

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1979; Priem, 1906; Stinton, 1975) and the US Gulf Coast (Müller, 1999; Nolf and Stringer, 2003; Stringer, 2016).

All fossil assemblages are time-averaged (Kidwell, 2002; Kidwell and Flessa, 1995), and, in the case of otoliths, these are spatial-averaged vertically as well, since skeletal parts are added from different depths of the water column and from the sea-bottom. Furthermore, such otolith assemblages not necessarily reflect the ambient fish population only, since extra material may have been introduced into the burial place by a number of processes, both biological (feeding) and physical (turbidites, currents) (Nolf, 1985; Nolf and Brzobohaty, 1992; Schwarzhans, 2004). Therefore, there are a number of caveats to consider when approaching the study of recent death-assemblages with the scope of inferring valuable ecological information of paleobiological soundness. In general, the basic tenet of solving with confidence the paleoenvironment stays with the taxonomic resemblance between fossil and modern populations and upon the actualistic assumption of comparable ecological requirements between modern and fossil representatives. The reliability of such approach obviously diminishes with increasing geological age as well as with the intensity of taphonomic processes undergone by any fossil fauna (e.g., Behrensmeyer et al., 2000; and Elder and Smith, 1984, 1988 for fish remains).

A number of otolith-based paleoecological and biogeographic reconstructions could be tracked in the literature regarding the Cenozoic marine record of the Mediterranean region (e.g., Agiadi et al., 2011, 2013; Bassoli, 1906; Carnevale et al., 2006; Girone, 2000, 2003, 2005, 2007; Girone et al., 2006, 2010; Hoedemakers and Batllori, 2005; Lin et al., 2015, in press; Nolf et al., 1998; Nolf and Cappetta, 1988; Reichenbacher and Cappetta, 1999). Little is known, however, regarding the distribution of otoliths in superficial sediments of the Mediterranean Sea, which can further assist any paleoecological reconstruction in the basin since valuable information can be gained through the simple comparison of fossil assemblages with modern counterparts of known ecological niche. Here we present the first comprehensive study of otolith death-assemblages from bottom sediments in the Mediterranean Sea over a consistent bathymetric range from subtidal to bathyal depths. Our exercise sets a Mediterranean baseline to investigate the temporal relationships between otolith occurrence in sediments and fish distribution in the most recent past, in analogy with the scant literature on the subject (e.g., Elder et al., 1996; Gaemers and Vorren, 1985; Lin, 2016; Lin et al., 2016a; Schwarzhans, 2013, with references therein). Goals of this study are the evaluation of the ecological consistency between time-averaged death-assemblages and present fish distribution in the Mediterranean and to provide some qualitative information on taphonomy of otoliths under submarine conditions. This study offers the unique possibility to check the sea bottom otolith assemblages with respect to the formidable biogeographic changes that the Mediterranean fish population is experiencing at dramatic pace because of invasive species and meridionalization process (Azzurro, 2008; Galil, 2000; Kalogirou et al., 2012).

2. Materials and methods

2.1. Sediment sampling and otolith preparation

Sediments analyzed in this study for their otolith content are from a part of the marine sample collection stored in the repository of the Institute of Marine Sciences, National Research Council (ISMAR-CNR) in Bologna, Italy, formerly Laboratorio di Geologia Marina. Such samples were collected during several oceanographic cruises since the early '70s of the past century (Sartori, 1977) up to present. The large majority of samples was obtained by means of modified Van Veen grabs and chained geological dredges carried out onboard R/V *Bannock*. The rest were obtained by a few Van Veen large volume grab stations collected in 2014 by R/V *Urania* (cruise COCOMAP14). The area taken into consideration is a large sector of the central Mediterranean Sea and includes Tyrrhenian, Ionian and Adriatic Sea sites (Fig. 1, Table 1).

A total of 49 samples has been analyzed in the present study (Table 1, Appendix 1). Samples were weighed dry, and then two 50 g-subfractions per sample were taken and stored separately for archive purpose, except for samples from cruises T73 and COCOMAP14. Sediment samples were then wet-sieved over a 500 µm-mesh screen. All the otoliths were picked out from the 500 µm residue and grouped into two classes, i.e., identifiable and unidentifiable, irrespective to their preservation state. Whenever possible, otoliths have been identified at species level. The unidentifiable class is largely composed by juvenile and poorly-preserved specimens. The study material is deposited in the Institut royal des Sciences naturelles de Belgique, Brussels, Belgium (IRSNB) and a voucher collection is hosted in the ISMAR-CNR repository in Bologna.

2.2. Quantitative analyses

Otolith abundance was computed as otolith count/sediment weight (kg), and then plotted versus depth and locality. The otoliths and taxa were counted to indicate abundance and richness (Lin et al., 2016a).

Each taxon is recorded with its depth range to evidence distribution versus bathymetry. For convenience, samples <500 m depth were pooled together in each 100 m interval, while samples >500 m depth were pooled together in each 500 m interval. Taxa were further divided into pelagic and benthic-benthopelagic groups and treated separately to assess the dominance of any given taxon (see Lin et al., 2016a for details).

2.3. Multivariate statistics

The multivariate analysis was based upon the use of the PAST software; the UPGMA algorithm and the Correlation distance coefficient have been adopted for this study (Hammer et al., 2001). The otolith count of each taxon was transformed as a proportion to the total otolith count within each interval. Hierarchical cluster analysis was performed to classify all the intervals in order to find out how they are grouped; this analysis was based on both the taxonomic composition (quality) and relative abundance (quantity) within any given interval, in order to compare their similarity and difference with respect to the depth. Following Lin et al. (2016a), analyses based on all-taxa (pelagic plus benthic-benthopelagic taxa) and on benthic-benthopelagic taxa alone were conducted.

3. Results

3.1. Preservation status

An in-depth study of otolith taphonomy would unavoidably require a set of complex petrographical and chemical analyses complemented by detailed optical and SEM microscopy inspections to evaluate mineralogical and chemical compositional changes (Dufour et al., 2000), dissolution patterns and other circumstances affecting the overall modification of the original otolith sample. This approach is beyond the purposes of the present paper, and we limit our observations to a few qualitative features.

As noted by Schwarzhans (2013), the appearance and coloration of an otolith change during the fossilization process. The freshest otoliths display a semi-translucent lustre, turning progressively dull white with time. Otoliths could get yellowish, greyish, or brownish hues, in response to specific situations, such as the type of the embedding sediment or in response of their prolonged exposure on the sea bottom. All such situations are observed in the otolith specimens examined in this study, providing an indirect clue about relative aging of taphonomic processes, although only direct radiometric dating, when applicable, could in principle provide unquestionable ages. Otoliths also display considerable differences in their texture up to highly degraded chalky specimens and dark-patinated ones found especially at deeper stations.

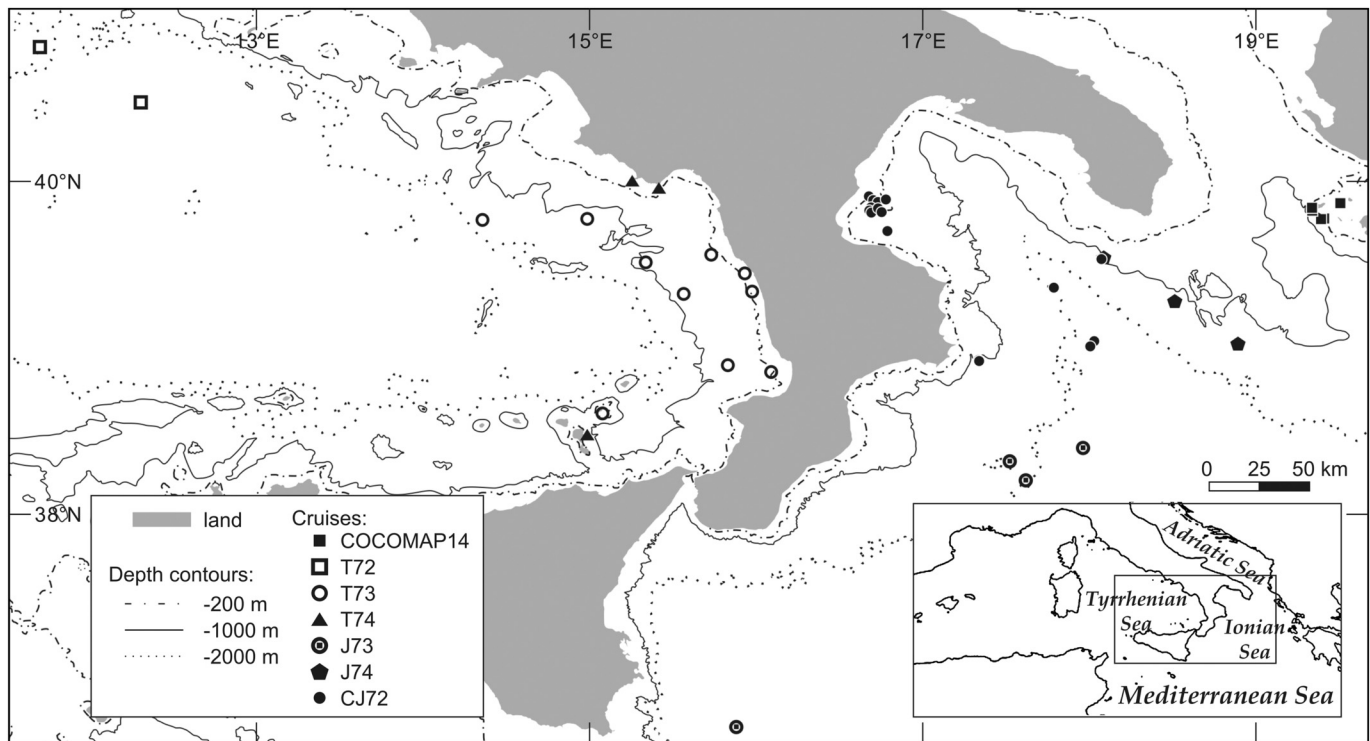


Fig. 1. Map showing the sampling sites in the central Mediterranean. See text for corresponding cruise names and Appendix 1 for the coordinates and depth of each sample. Map derived from the EMODnet Bathymetry portal: <http://www.emodnet-bathymetry.eu>.

As a general rule, most otoliths are white to light yellow in colour, with a substantial increase in the percentage of dark and brownish ones at depths > 1000 m, although mixed-coloured death-assemblages are not infrequent (e.g., J74-12 (1017–1060 m), Fig. 2i–k). An example of colour and texture modifications undertaken by otoliths is offered by the otoliths belonging to the pelagic species *Hygophum benoiti* (Fig. 2a–k), common in our samples. Otoliths preservation ranges from fresh semi-translucent (Fig. 2d, i) to dull white (Fig. 2a–c, e–h, j) up to yellowish-brownish ones (Fig. 2k), likely representing steps in their exposure to taphonomic processes on the sea bottom.

Overall, otoliths are well-preserved allowing identification at species or genus level possible (Appendix 2). The large majority of the unidentifiable otoliths occurs between 1000 and 2000 m, mostly belongs to the family Myctophidae, or to the juvenile individuals, plus very few eroded and very small specimens of neritic apogonids, mullids and gobiids; these otoliths are not considered further in this study. Best preservation is observed in the samples < 500 m depth, clearly reflecting the abundance of freshly-added modern to sub-recent otoliths to the death-assemblages; on the contrary, samples > 500 m often contain poorly preserved and highly-degraded specimens, suggesting the co-existence of various generations of otoliths at places interpreted as having been accumulated in a substantial albeit unassessed time span.

Table 1
Location and depth of stations providing otoliths considered in this study.

Cruise	No. of stations	Depth range (m)	Main coordinates
CJ72	20	51–2499	39°51'N; 16°41'E
COCOMAP14	7	79–527	39°77'N; 19°40'E
T72	2	1760–3300	40°27'N; 12°20'E
T73	10	61–1378	39°33'N; 15°44'E
T74	3	113–174	39°44'N; 13°48'E
J73	4	1115–2878	39°12'N; 17°38'E
J74	3	1017–1227	40°17'N; 17°16'E

3.2. Abundance

A list of taxa is recorded in Appendix 2. Six stations did not produce any otolith (all < 500 m: CJ72-4, 5, 10, 17; T73-7; T74-50). Lower abundance occurs in the shallowest sediments, although with some exceptions approaching 50–100 otoliths/kg. The abundance slightly increases in the 1000–2000 m depth range with numbers > 50 otoliths/kg; below 2000 m, the abundance decreases again but is still higher than at the shallower stations (Fig. 3). One station at 1017–1060 m (J74-12) proved the richest abundance with 874 otoliths/kg. However, our study does not identify any clear bathymetric trend for otolith abundance, which instead differs drastically from site to site, even at comparable depths (Fig. 3).

Both the otolith abundance and diversity (richness) of the pelagic group are much higher than those of the benthic-benthopelagic group are, although the diversity of benthic-benthopelagic component is higher than that of the pelagic one (34 versus 25 taxa) in the 0–500 m depth interval (Fig. 4). Besides comparing the abundance between the pelagic and benthic-benthopelagic groups, the highest abundance of the latter was obtained in the shallowest interval (295 otoliths) with respect to deeper intervals (0–77 otoliths).

3.3. Bathymetric trends

Generally, otoliths pertaining to pelagic fishes present a more uniform distribution throughout the water column, whereas those belonging to the benthic-benthopelagic taxa show more restricted repartitions along the depth, which is represented by patchy patterns (Fig. 5). Epipelagic taxa, *Engraulis encrasicolus* and *Sardina pilchardus*, are not common and mostly found in the shallow sediments. Otoliths of mesopelagic taxa such as *Maurolicus muelleri*, *Ceratospelus maderensis*, *Electrona risso*, *Hygophum benoiti*, *Hygophum hygomii*, *Lobianchia doleini*, *Myctophum punctatum*, and *Notoscopelus* spp. occupy a wide bathymetric range, although *M. muelleri* achieves more importance in samples < 500 m, and *C. maderensis* and *H. benoiti* are relatively more abundant

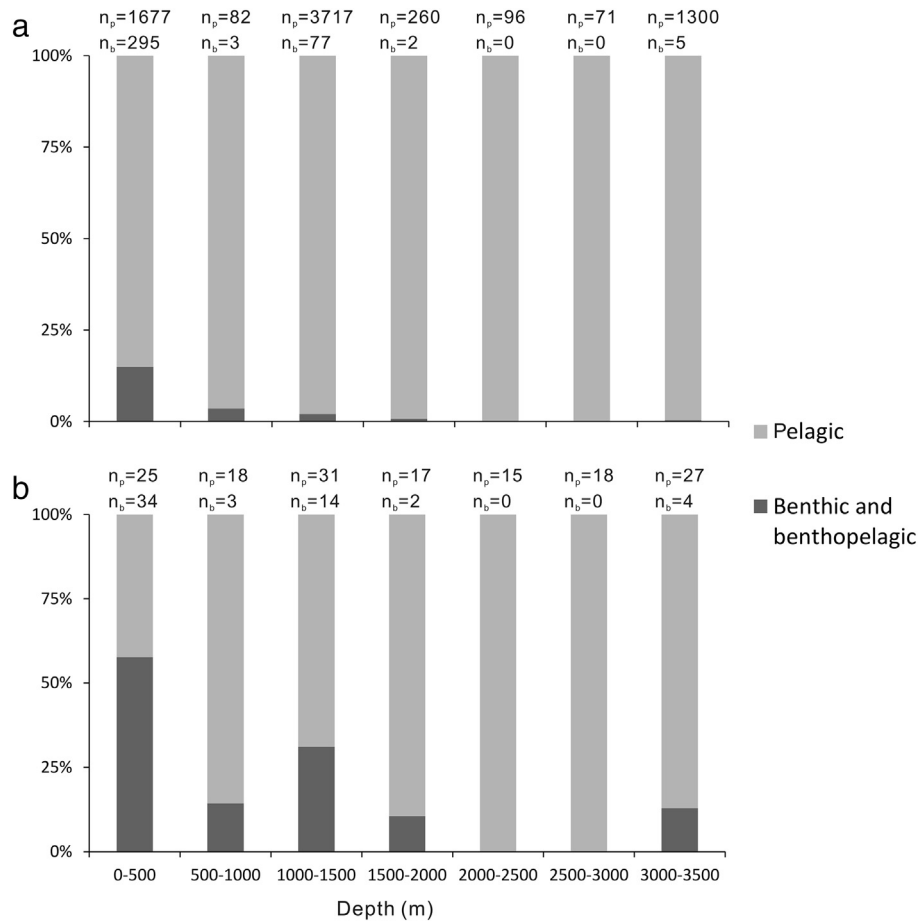


Fig. 4. Proportion of otolith number (a) and taxon number (b) of pelagic versus benthic-benthopelagic taxa. The pelagic taxa markedly outnumber the benthic-benthopelagic taxa in both abundance and richness, except that the richness in the 0–500 m interval, where more diverse benthic taxa were found. Total number of identified otoliths and taxa is indicated for each depth interval and separated by pelagic (n_p) and benthic-benthopelagic (n_b) groups.

than other mesopelagic taxa. *Ichthyococcus ovatus* and paralepidid otoliths characterize middle slope down to the deepest bottom sediments.

The otoliths of benthic-benthopelagic group show different taxonomic compositions with respect to bathymetry. Gobiid otoliths are numerically important in shallow water sediments, whereas in the upper to middle slope sediments (300–500 m), taxa such as congridids, *Chlorophthalmus agassizi*, *Coelorinchus caelorhincus*, *Micromesistius poutassou*, *Bellottia apoda* and several gobiids predominate. The abundance of *Epigonus constanciae* otoliths increases from the middle slope to lower slope region. Some reworking seems documented by the presence, in the deep 1000–1500 m interval, of several poorly preserved specimens of shallow water taxa such as *Apogon*, mullids and gobiids.

The results of the cluster analyses based on all-taxa (pelagic plus benthic-benthopelagic taxa) and on benthic-benthopelagic taxa alone successfully distinguish two main clusters grouping samples above and below 500 m depth, recognising shallow against deep-water otolith death-assemblages (Fig. 6a, b). However, we can observe a substantial difference in the similarity measure within the shallow and deep-water clusters between the all-taxa and benthic-benthopelagic taxa. The taxonomic composition and relative abundance in the benthic-benthopelagic taxa are very similar among the assemblages <500 m (similarity measure well above 0.84), but they are loosely related for those >500 m mainly due to their rare occurrences (Fig. 6b). On the contrary, in the all-taxa analysis the shallow water assemblages are quite distinct with each other, whereas the deep-water assemblages are nearly homogeneous (Fig. 6a).

4. Discussion

4.1. Otolith preservation and abundance

The differential degree in preservation is taken as an indication that the otoliths in the bottom sediment are not all coeval, although a rigorous evaluation of the degree of time averaging is not easy to establish solely on such qualitative observations. Otolith preservation (colour and appearance) from deep-water situations more commonly present a combination of semi-translucent (white) and dull-coloured (dark) specimens (Fig. 2). This fact can be primarily attributed to prolonged exposure on the sea bottom, easier to take place in the deep-sea because of the lower sedimentation rate compared to shallower environments. Otolith assemblages from such bathyal situations often include corroded and epifauna-encrusted specimens, usually benthic foraminifera (Fig. 2c, d, f, g, k).

The number of otoliths seems not strictly correlated with depth, nevertheless, otolith abundance is usually lower at depth < 500 m, while higher abundance is observed at bathymetries exceeding 500 m (Fig. 3). Wigley and Stinton (1973) on their study in the western Atlantic Ocean off Massachusetts between 27 and 567 m noticed a correlation between otolith abundance and depth. In general, our results are in fair agreement with data considering a greater depth range in the Atlantic Ocean (Elder et al., 1996; Lin et al., 2016a; Schwarzhans, 2013). The highest otolith richness recorded from an Ionian offshore station (J74-12), likely reflects a long temporal accumulation in a bathyal depth under sediment starved conditions.

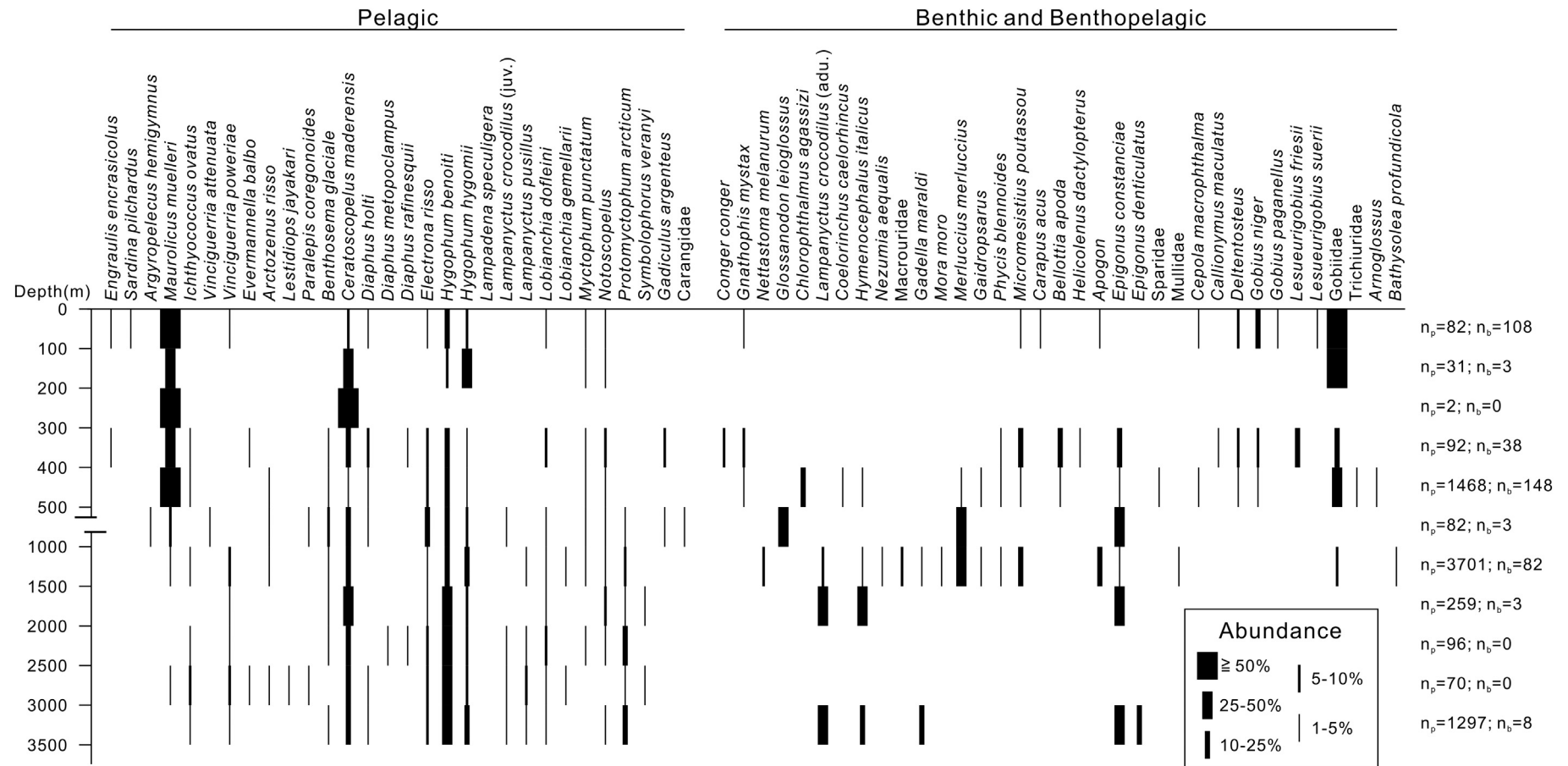


Fig. 5. Abundance of taxon with respect to bathymetry. The pelagic taxa and the benthic-benthopelagic taxa are regarded separately in the analysis. The thickness of the vertical lines indicates the relative abundance, and any taxon found lower than 1% is not shown. Total number of identified otoliths is indicated for each depth interval and separated by pelagic (n_p) and benthic-benthopelagic (n_b) groups. Note change of interval at 500 m.

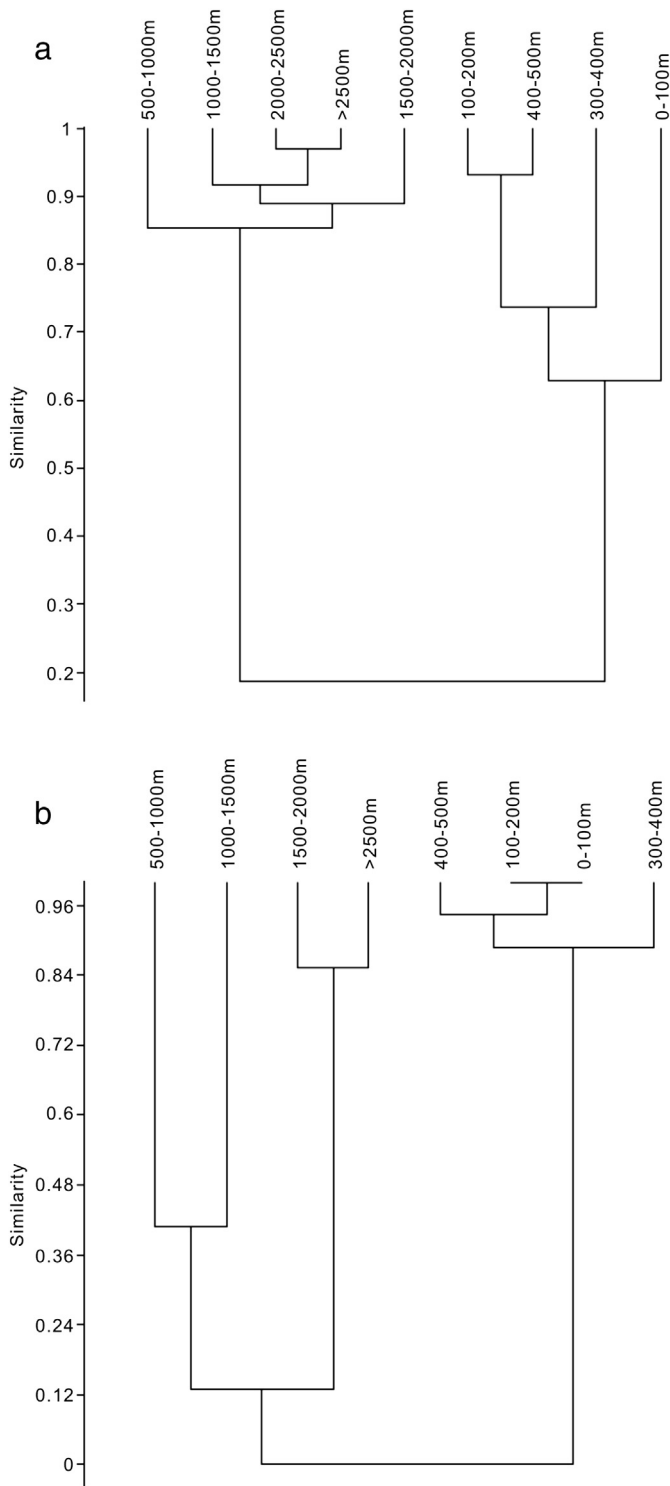


Fig. 6. Dendrogram of otolith depth intervals. Cluster analysis using UPGMA algorithm and the correlation distance coefficient was performed. (a) Cluster analysis based on all-taxa (pelagic and benthic-benthopelagic); (b) Cluster analysis based only on benthic-benthopelagic taxa. Two main clusters representing assemblages above and below 500 m intervals are well-resolved in both analyses.

It is also worth mentioning another aspect concerning the differences in richness and abundance between pelagic and benthic-benthopelagic components (Fig. 4), which has been demonstrated for both recent (Lin et al., 2016a) and fossil assemblages (e.g., Agiadi et al., 2010; Girone, 2003, 2005, 2007). In fact, the dead assemblage does not simply approach the numerical input of preservable individuals

over time, but it also relates to their degradation rate (Kidwell and Flessa, 1995; Kidwell, 2002). In the study of molluscan taphonomy, Cummins et al. (1986) reported that two distinct components of mollusc shells exist in the shallow water sediments: one, with substantial number, but less durable and decays very rapidly, and the other, rarer and long-term stable component. The mesopelagic (or pelagic) taxa contributing to otolith assemblages compare well with the short-lived, immensely abundant component reaching the sea bottom by pulses, while the benthic-benthopelagic taxa reflect a longer-term accumulation trend. In the recent, the mesopelagic taxa are a numerically significant component in the water column, being also largely responsible of the deep scattering layer (DSL, see e.g., Barham, 1966), situated at a lower trophic level (Cherel et al., 2010). The benthic and benthopelagic taxa (e.g., Gadiformes) are mainly long-lived species at a higher trophic rank (Drzen et al., 2008). With respect to their temporal preservation within death-assemblages, it should be noticed that mesopelagic taxa are typically represented by small and thin otoliths, prone to vanish earlier than the large and thick otoliths, pertaining to the benthic and benthopelagic species, comparable to the two components found in the molluscan study. Nevertheless, the significant otolith abundance of the former reflects their dominant biomass in the present ocean (Irigoién et al., 2014), even if wearing away rapidly. Indeed, both components in the death-assemblage represent two sets of ecological and trophic strategies related to turnover rate.

4.2. Ecostratigraphic aspects

A relevant outcome of the present study is the recognition within the otolith assemblages of faunal elements extinct in the present Mediterranean Sea. This is the case of the myctophid *Protomyctophum arcticum* (Lütken, 1892), an amphiatlantic subpolar to temperate Atlantic mesopelagic species, not recorded in the present Mediterranean fish fauna (Bailly, 2014; Whitehead et al., 1986–1989). Numerous otoliths of *P. arcticum* were identified from nine stations (CJ72-24, 25; T72-41, 43; T73-14; J73-5, 15; J74-12, 20) at depths between 494 and 3300 m (Appendix 2). Samples J74-12 and T72-41 proved to be the most productive, accounting for 337 and 215 specimens, respectively. In general, *P. arcticum* otoliths may contribute up to 10–25% of all pelagic taxa recovered in the central Mediterranean deep-water sediments under study (Fig. 5). Most *P. arcticum* otoliths display a surficial patina brown to almost black, and are fouled by the agglutinated foraminifer *Ammolagena clavata* (Jones & Parker, 1860) (Fig. 2l–p). No fresh or light-coloured otoliths of this species have been recovered in our samples, what is instead the case of co-occurring otoliths in some such assemblages, presumably younger in age. *Protomyctophum arcticum* otoliths were previously found at a single Tyrrhenian site at bathyal depth and considered of late Pleistocene age; however, older fossil records of this species have not been documented in the Mediterranean (Girone et al., 2006). We agree with this interpretation, although we cannot ascertain exactly to which part of the Pleistocene our material might belong, in absence of radiometric dating, and in consideration of slow sedimentation rates in these bathyal offshore situations. Thus, this nektonic taxon acquires the significance of a Boreo-Atlantic species of ecostratigraphic meaning, complementing the numerous and well-known benthic taxa identified thus far primarily among molluscs (e.g., Taviani, 2002; Sabelli and Taviani, 2014, with references therein), but also in other groups (Rosso and Di Geronimo, 1998). Other late Pleistocene Mediterranean fossil species, such as *Lampadena ionica* (Girone & Nolf, 2002) and *Scopelopsis pliogenicus* (Anfossi & Mosna, 1976), were not detected in our material.

4.3. Otolith depth range in the central Mediterranean

The cluster analysis indicates that depth is the main factor controlling the composition and relative abundance of otolith assemblages in sediments (Fig. 6). The results also strictly discriminate deep bathyal

assemblages (>500 m) from shelf-epibathyal assemblages (<500 m). In the shelf-epibathyal assemblages of all-taxa analysis, the increasing abundance of pelagic group with increasing depth (see Fig. 4) is detected, which separates each interval with low similarity measure (Fig. 6a), while in the benthic-benthopelagic analysis these intervals are strongly determined by several dominant taxa, such as the gobiids that occur over all assemblages (Fig. 6b). Nearly identical composition and relative abundance are demonstrated in the deep bathyal assemblages through the all-taxa analysis (Fig. 6a). However, a reliable statistical outcome was not obtained for benthic-benthopelagic taxa analysis because of the low otolith count (Fig. 6b). The 400–500 m interval is particularly interesting since it presents a close affinity with much shallower intervals, here interpreted as being a transitional zone related to the co-occurrences of several shallow water elements (see below).

The similarities of taxonomic composition between the otolith death-assemblages and related modern communities at various depths are most evident for the benthic-benthopelagic taxa, especially for those represented by higher abundance (Fig. 5, Appendix 2). The 0–200 m range is characterized by a very high frequency of gobiids (abundance >50%), a typical neritic group, and more sporadically by other neritic taxa like *Cepola macrophthalma* (Fig. 5). Such taxonomic composition not only compares well with the modern communities (Appendix 2), but also with the fossil otolith assemblages widely referred to shallow paleoenvironments in the Plio-Pleistocene deposits of the Mediterranean area (e.g., Nolf and Girone, 2000, 2006).

The shared benthic and benthopelagic taxa in the 300–500 m transitional middle slope, suggest another clear relation between otolith assemblages and the present deep-sea fish ecology (e.g., Angeletti et al., 2014, 2015; D'Onghia et al., 1998, 2011; Mytilineou et al., 2005; Taviani et al., 2016). In particular, *Micromesistius poutassou* is reported as a characteristic species of the upper slope in the Mediterranean (Cohen et al., 1990; D'Onghia et al., 1998; Mastrototaro et al., 2010). The occurrence of *Chlorophthalmus agassizi* in the 400 to 500 m otolith assemblages further confirms this relationship; *C. agassizi* is reported common to very abundant at this depth interval in the modern Mediterranean (D'Onghia et al., 2006; Mastrototaro et al., 2010; Mytilineou et al., 2005). The otolith occurrences of shelf elements such as gobiids are rarer than their occurrences in the upper 200 m, but they are still frequently found in several samples (Fig. 5). This is consistent with what is reported in the NE Atlantic Ocean between 400 and 500 m, and interpreted as the adaptive ability of these fish to live in deeper shelf and upper slope environment (Lin et al., 2016a). Several studies have documented the (fish) occurrence of *Lesueurigobius* and *Deltentosteus* in the Mediterranean at depths approaching or exceeding 300 m (Ahnelt and Dorda, 2004; Matarrese et al., 1996; Mytilineou et al., 2005), suggesting that their otolith occurrence at these deeper environments could still be considered as representatives of the original fish assemblages. Thus, the current opinion that gobiids are exclusively indicative of the shelf environment as proposed in many paleoecological reconstructions (e.g., Nolf and Girone, 2000) is only partly true, and thus paleobathymetric underestimates cannot be ruled out. Furthermore, the analysis of both taxonomic composition and relative abundance of all other benthic and benthopelagic taxa may be very useful to further constrain and refine any paleoenvironmental reconstruction. The combined results of this study and of NE Atlantic situation (Lin et al., 2016a) open a promising scenario in the paleoecological interpretation based on otolith assemblages, particularly in this complex slope environment.

Apart from the better-recognised otolith depth range of the benthic-benthopelagic taxa, nearly no other pelagic taxa could be considered as abundant at any specific depth interval (Fig. 5). Interestingly, moreover, we observe that the deepest otolith occurrence of some taxa exceeds the known range of their living representative (Appendix 2). It is possible that part of these small pelagic otoliths could be transported easily from shallow to nearby deeper environments, but it is a fact still requiring an explanation. The bathymetric range of two pelagic species provides interesting paleoecological insights. *Maurolicus muelleri* is very

abundant <500 m (Fig. 5); it is a cosmopolitan mesopelagic species which is most abundant at the continental shelf to slope at depths from 100 to 500 m (Armstrong and Prosch, 1991; Boehlert et al., 1994). This species is rather rare in the open ocean being mostly associated with land masses (Boehlert et al., 1994). This explains why it is nearly absent in the offshore NE Atlantic sea bottom (Lin et al., 2016a), being instead very abundant in the Mediterranean landlocked setting discussed here. *Gadiculus argenteus* is an epi-mesopelagic fish common between 200 and 400 m in the Mediterranean (Maurin, 1968; Bombace, 1972; Arena and Li Greci, 1973; Cohen et al., 1990; Mastrototaro et al., 2010) and displays higher otolith abundance in the 300–400 depth interval (Fig. 5). The environmental consistency between the present-day occurrence of *G. argenteus* and our results from otolith death-assemblages lends further support to analogue paleoenvironmental interpretation of Plio-Pleistocene Mediterranean deposits (Girone, 2005; Girone, 2007).

Lin et al. (2016a) concluded that analyses based solely on benthic-benthopelagic taxa are comparably more reliable for bathymetric interpretation, although biased by their objective scarcity in many assemblages. Otolith assemblages from the study area demonstrate a higher abundance and diversity of benthic-benthopelagic taxa at depths <500 m (Fig. 4), which are on the other hand extremely rare in the deeper water assemblages. For instance, 15 samples do not yield any benthic-benthopelagic taxon, and many deep-water assemblages contain a maximum of three benthic-benthopelagic taxa. Higher abundance and diversity of meso-bathypelagic taxa could be another discriminant element to take into due consideration for paleoecological interpretation, although their value is still to be fully assessed. Our results also unveil that the taxonomic composition and relative abundance (especially for meso-bathypelagic taxa) are nearly identical for samples >500 m (Fig. 6a), indicating a lesser ecological potential of the use of otolith assemblages in deep-water environments.

Overall, the composition of otolith assemblages agrees quite well with the general pattern of modern fish communities at various depths in the central Mediterranean with a decrease of species richness vs depth (e.g., Danovaro et al., 2010; D'Onghia et al., 2004; Follesa et al., 2011; Mytilineou et al., 2005). Most otoliths are represented by freshly-added individuals, a recurrent motif in such type of death-assemblages (e.g., Kidwell, 2002). In summary, the otolith assemblages largely reflect the actual ecological communities of area here considered.

Finally, invasive non-native fish species are by now overwhelming the autochthonous community in the southern Mediterranean (Goren et al., 2016), and many thermophilic species have expanded their range in the basin well northwards of our study area in the Tyrrhenian Sea (Azzurro et al., 2011). This epochal ecological turnover is not detectable in the otolith record of surface sediments of the central part of this basin because most sampling took place decades back in the past, before or at the dawn of the acceleration of this phenomenon. It would then highly desirable to re-occupy in the future our same stations to weight comparatively the current otolith bottom record with the pre-impacted situation here described.

5. Conclusions

Otoliths are a significant biogenic component of bottom sediments in the Mediterranean Sea, and they are especially abundant in bathyal settings. The preservation state of such otoliths is highly variable by degree of opaqueness (translucent to dull), colour and erosion. Although such observation is only qualitative, these characteristics document a first approximation of the earlier stages of diagenetic processes under submarine conditions, which is useful for a better interpretation of fossil counterparts. As a rule, most degraded otoliths occur in deeper water locations that are marked by slower sedimentation rates, suggesting a longer sedimentation time than at shallower depths, and consequently such otoliths are subjected to prolonged exposure at the water/

sediment interface. The absolute abundance of otoliths appears to be less correlated with water depth, although higher specimen counts are often related to deeper stations. Contrary to abundance, a higher diversity is clearly identified in the 0–500 interval, which is enriched by a number of demersal taxa. The different proportion between benthic-benthopelagic and pelagic taxa seems governed by two distinct ecological and trophic strategies, which is similar to their actual ecology: long-lived, but very rare for the former and very abundant with short turnover rate for the latter. Finally, a bathymetric trend is recognisable for the benthic-benthopelagic taxa. In fact, their representatives in the shelf-upper slope transitional zone and deeper death-assemblages mirror the present central Mediterranean Sea fish communities, except for the remarkable exception represented by the presence of a Pleistocene taxon (*P. arcticum*) found in deeper offshore situations.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2016.12.050>.

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