Palaeogeography, Palaeoclimatology, Palaeoecology 446 (2016) 98–107

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Fish otolith assemblages from Recent NE Atlantic sea bottoms: A comparative study of palaeoecology

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ARTICLE INFO

Article history:
Received 16 September 2015
Received in revised form 7 January 2016
Accepted 10 January 2016
Available online xxxx

Keywords:
Otoliths
Recent sea bottom
Northeastern Atlantic
Bathymetry
Biogeography
Paleoenvironment

ABSTRACT

Reconstruction of the paleoenvironment, using fish otolith assemblages and depending on the modern analogue to provide precise reference information, has been applied on many marine Cenozoic sediments, although the composition of such assemblages on Recent sea bottoms in various environmental settings is still poorly known. This study aims at better understanding the characteristics of otolith thanatocoenoses from Recent sea bottoms. Otolith assemblages taken by box corers or Van Veen grabs on Recent sea bottoms of the Northeastern Atlantic and the North Sea, at various depths and at various latitudes, were analysed. The results reveal that the pelagic and benthic–benthopelagic taxa in the sea bottoms differ markedly in quantity and diversity. The composition of an otolith assemblage differs from location to location, reflecting its biogeographic characteristic, which is mainly determined by pelagic taxa in the oceanic assemblages. The bathymetry, on the contrary, can be better explained from the benthic–benthopelagic taxa, especially in the shallow water assemblages. In addition, otolith size-related distribution along the isobaths is discovered in *Lampanyctus crocodilus*, in which the proportion of larger specimens in deeper waters increases markedly, confirming the observations of its population stratification in the actual assemblages. The biogeography and bathymetry obtained from the otolith assemblages could therefore, in some cases, be used as an indicator of the present ecology.

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1. Introduction

The morphology of otoliths is very characteristic, which allows assignment of an otolith to a specific taxon in most cases with a relative degree of certainty. In paleontology, paleobathymetric interpretation using fossil otolith assemblages have been reported from many Cenozoic localities. Nolf and Brzobohaty (1992) proposed a method to determine the paleobathymetry based on the comparison of the identified taxa in a fossil assemblage with their Recent counterparts. In this analysis, the total number of potential presences of the taxa in each 100 m interval is counted and the interval with the highest total number determines the bathymetry (see 2.4 for detailed explanations of the method). Since then, this method has been applied in various studies estimating the paleobathymetry, e.g. from the Oligocene of northern Italy (Nolf, 1995) and Mississippi (USA) (Stringer and Miller, 2001), the Middle Miocene of the Central Paratethys (Brzobohaty, 1997, 2001), the Miocene to Pleistocene Caribbean coast (Aguilera and Rodrigues de Aguilera, 1999), the Plio-Pleistocene deposits from the western and eastern Mediterranean (Agiadi et al., 2010; Girone, 2000, 2003, 2005, 2007; Nolf et al. 1998). The paleobathymetric approach appears to be more applicable for the deep shelf and bathyal fossil otolith assemblages (Girone, 2005; Nolf and Brzobohaty, 1992). Girone (2003, 2005) proposed an integrated approach for Pleistocene associations, which contain a high percentage of extant species, in combination with a paleoecological analysis of the benthic–benthopelagic elements. This results in a more precise interpretation of the shallower environmental settings. In addition, several studies have focused on the paleobiogeographical and paleoclimatological significance of Cenozoic otolith assemblages: the Mediterranean area (e.g. Agiadi et al., 2011, 2013; Girone and Nolf, 2009; Girone et al., 2010; Hoedemakers and Batllori, 2005; Lin et al., 2015; Reichenbacher and Cappetta,1999), the Parathethys (e.g. Brzobohaty and Krhovsky, 1998; Nolf and Brzobohaty, 1994) the Aquitaine basin (e.g. Nolf and Brzobohaty, 2002; Nolf and Steurbaut, 2002) and the North Sea (e.g. Schwarzhans, 2010).

In spite of all the studies including a paleoecological and paleobiogeographical interpretation, it is, however, not certain whether fossil otolith assemblages directly reflect the ecology of a given time in the past. The mechanisms of otoliths entering the sediment and their transportation during taphonomic processes are not yet fully understood (Nolf, 1985, 1995). Otoliths discovered in Recent sea bottom sediments are derived from fishes, whose ecology is well-known. The study of such assemblages can provide elements for a better understanding of the paleoecology of fossil otolith assemblages, deposited in similar conditions. Wigley and Stinton (1973) reported on otoliths from the sea

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http://dx.doi.org/10.1016/j.palaeo.2016.01.022
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bottom sediments off Massachusetts, Martini (1974) from the top core sediments of two west Indian Ocean drilling sites, Gaemers (1978) described Recent otoliths from sea bottoms off Norway at depths varying from 77 to 407 m, Martini and Gaemers (1986) reported otoliths from southwest Pacific Quaternary sediments, and, more recently, Schwarzhans (2013) published a detailed case study on Recent sea bottom otoliths from the Gulf of Guinea and the Azores Islands, but these are about the only papers treating the subject.

In this study, we describe otolith assemblages from various depth ranges to understand better the characteristics of otolith thanatocoenoses from Recent sea bottoms. The analyses were performed in order to (i) identify the composition of otolith assemblages; (ii) determine how otolith assemblages can reflect both the depth and the biogeography; (iii) test the bathymetric method with known depth intervals to evaluate its precision.

2. Materials and methods

2.1. Sediment sampling and otolith preparation

The samples were collected and screenwashed through mesh sizes of 425 μm to 1 mm during the preparation, following the procedures of Prof. André Freiwald.

Sediments were collected from Recent North East Atlantic (NEA) sea bottoms. A locality map of the stations is shown in Fig. 1. Each station provided one single sample with otoliths. Several shallow water samples to the East of South Soester Island, off Norway, were collected during the ALKOR 232 (Alk232) cruise in 2003 (Pfannkuche et al., 2004b). Samples were collected from the Belgica Mound Area and the Kiel Mount of the high-latitude NEA during the METEOR Cruise M61/1 (Pfannkuche et al., 2004a) and the GeoB8045-1 cruises. The middle-latitude NEA samples include those from the Seine Seamount which were collected by the METEOR Cruise M60/1 (Christiansen, 2004), from the Ampère Seamount by the cruise R/V Victor Hensen VH-97, and from the Gulf of Cadiz (Cruise GeoB9002-1).

The Van Veen grab and box corer were employed during the sampling on board. Both devices were designed for sampling the uppermost bottom sediments, but it cannot be entirely excluded that some underlying sediments were grabbed in the process. There is, however, no positive evidence that this has occurred during the studied survey. The sediment samples with otoliths, ranging from depths of 64 to 1059 m, were used in the study. Table 1 gives a summary of the samples and the Appendix gives the coordinates and depth of each sample.

2.2. Quantitative analyses

Sampling procedures were not standardised, due to the use of different gears and to different cruise purposes. Therefore, the absolute otolith abundance (as in the Appendix) in a given quantity of sediment is not used, and the proportion of otoliths counted for a taxon in relation to others is presented to indicate abundance throughout the study, as in Schwarzhans (2013).

Otolith abundance of each taxon is expressed as a depth range to show any discussed taxon in relation to others in the sea bottom sediments. Samples from the high- and middle-latitude NEA were lumped together per 100 m interval, e.g. samples from depths of 130 m and 149 m were grouped together in the 100–200 m interval. Samples from the North Sea were lumped together per 25 m interval in order to enhance the analyses of the otolith assemblages. Additionally, taxa were divided into pelagic and benthic–benthopelagic groups, as

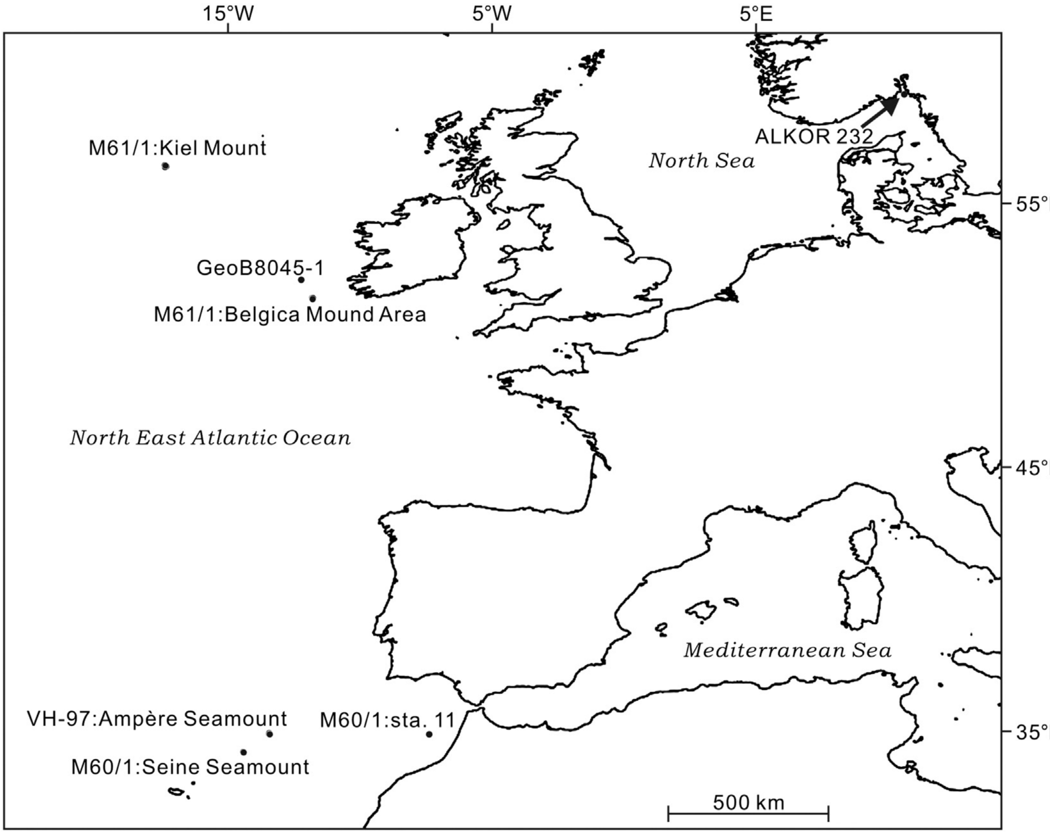


Fig. 1. Map showing the study areas: The North Sea, high (Belgica Mound Area, the Kiel Mount, and GeoB8045-1) and middle (Ampère Seamount, Seine Seamount, and Gulf of Cadiz) latitude North East Atlantic (NEA). See text for corresponding cruise names and Appendix for the coordinates and depth of each sample. Map derived from the EMODnet Bathymetry portal: http://www.emodnet-bathymetry.eu.

Table 1
Summary of Recent sea bottom samples in this study.

Investigated area	No. of stations	Depth range (m)	Main coordinates
The North Sea	12	64–110	59°N; 10°E
High-latitude NEA	17	646–1059	51°N; 11°W and 56°N; 17 W
Middle-latitude NEA	12	130–900	33°N; 14°W and 35°N; 12°W

suggested by Girone (2003, 2005, 2007), because of the significant difference in otolith abundance in the sediments and of the different ecological information they could furnish. Consequently, the dominance of any given pelagic taxon is presented as its percentage of the total pelagic otolith number counted in each 100 m interval. Similarly, the dominance of a benthic–benthopelagic taxon is presented as its proportion to the total benthic–benthopelagic otolith number counted, per 100 m interval.

2.3. Multivariate statistics

In order to make a clear relationship between the composition of otolith assemblages and the primary factor that influence the distribution of the taxa, multivariate statistical analyses, by means of cluster analysis (CA) and non-parametric multi-dimensional scaling (MDS) analysis, have been performed. The otolith count of each taxon was transformed as a proportion within a sampling station while performing multivariate analysis. Any taxon occurring only in a single sample and samples containing less than three taxa were excluded (Alk232 sta. 1135, Alk232 sta. 1140-2, Alk232 sta. 1145, Alk232 sta. 1151, Alk232 sta. 1157, Alk232 sta. 1160, M60/1 sta.11, M61/1 sta. 259, M61/1 sta. 311), under the assumption that they are less informative.

Hierarchical cluster analysis (CA) is a classification technique which joins groups of samples sequentially, based on their species content. CA was performed to classify all the samples in order to find out whether the content of the assemblages differs by sampling locality and how the samples from three geographically distinct areas are grouped. The UPGMA algorithm and the correlation distance coefficient were used (Ludwig and Reynolds, 1988).

The ordination method comparing samples of counted taxa was performed through the MDS using the Simpson similarity measure (Kruskal, 1964). The MDS was used to identify whether the content and abundance of taxa across assemblages can be interpreted by the water depth parameter. In this analysis, samples were arranged per 100 m interval, but the North Sea samples were excluded because of their simple composition and limited depth range. In addition, despite the large size of sampling sites during different cruises, samples without otoliths are not uncommon. Therefore, the oceanic high- and middle-latitude NEA areas were considered together to obtain a more continuous depth range in the MDS analysis. The analyses were carried out using PAST software (Hammer et al., 2001).

2.4. Paleobathymetric and paleoecological approach

A comparative study was carried out using Recent sea bottom samples of known depth to acquire a better understanding of the bathymetric methodology proposed by Nolf and Brzobohaty (1992) and Nolf and Cappetta (1988), which is an analysis to evaluate the bathymetry of fossil otolith assemblages.

The method is based on the analysis of an entire otolith assemblage, without differentiating between mesopelagic and benthic–benthopelagic taxa and, among various factors affecting the distributions of the fishes, only the taxonomic composition is taken into account. In such an analysis, the taxa are shown on one axis, while the bathymetry per 100 m interval is shown on the other. The bathymetric distribution of a given taxon is derived from that of its closest Recent relatives (species or genus), which is drawn along the latter axis. Once the depth range of each taxon has been established, the number of taxa occurring in each 100 m interval is counted and this number is expressed as a percentage of the total number of taxa (the first axis). The interval with the highest percentage suggests the potential bathymetry of the analysed assemblage.

3. Results

In total, 3209 otoliths were counted, of which 1119 could be identified to species, genus or family level. Their preservation was generally good. Most of the eroded specimens belong to the family Myctophidae or represent juveniles of others. As can be seen in Fig. 2, the pelagic taxa always outnumber the benthic–benthopelagic taxa. The proportion of the latter never exceeds 25% in any of the 100 m intervals of both the oceanic high- and middle-latitude NEA sampling sites.

The Appendix lists the taxonomic composition of each sample. The dominant taxa in each depth interval from the North Sea and high- and middle-latitude NEA are indicated as a percentage by the relative thickness of vertical lines in Fig. 3. In the North Sea, gadids (especially three species of the genus *Trisopterus*) dominate all the investigated depths, whereas characteristic neritic elements (such as *Echiodon* and gobiids) are found above the 75 m isobath. Pelagic taxa were not found in any of the neritic North Sea samples. The number of taxa drops gradually below that depth (Fig. 3a).

In the high-latitude NEA, sediment samples ranging from 600 to 1100 m contained otoliths of more than 31 pelagic taxa (27 taxa over 1% as in Fig. 3b) and of 13 benthic–benthopelagic taxa (see also the Appendix). Seventeen (16 taxa over 1% as in Fig. 3b) myctophid taxa

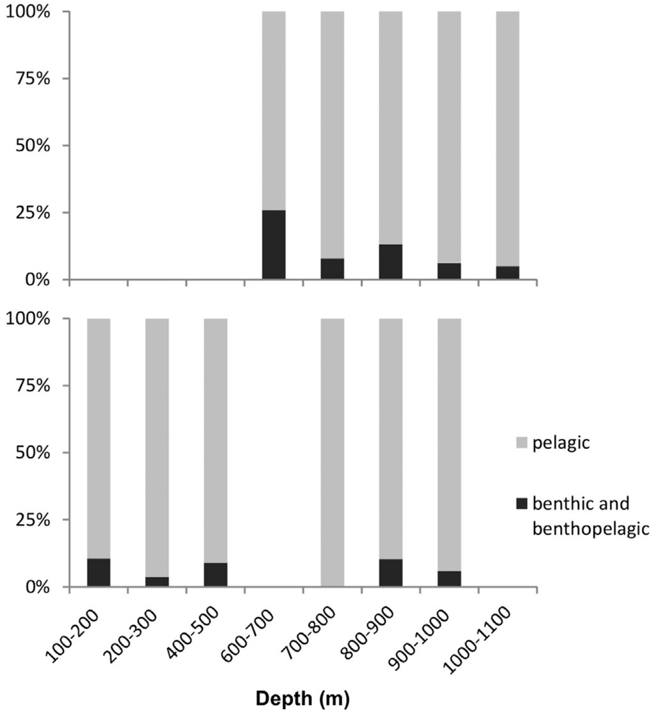


Fig. 2. Proportion of otolith number of pelagic taxa versus benthic–benthopelagic taxa recovered from Recent NEA sea bottoms. The pelagic taxa markedly outnumber the benthic–benthopelagic taxa. (a) Samples from high-latitude NEA; (b) samples from middle-latitude NEA. Note: samples are not continuous due to the absence of otolith-bearing samples, and pelagic taxa are not found in any of the North Sea samples.

occupy most of the water layers, of which *Benthosema glaciale*, *Lampanyctus crocodilus* and *Lampanyctus macdonaldi* are the most abundant at all the investigated depths. Other, non-myctophid pelagic taxa generally have a more scattered distribution with low abundance values (Fig. 3b), with the exception of *Scopelogadus beanii*, which is common to abundant in all investigated depth intervals. The benthic–benthopelagic group is mainly represented by gadids and macrourids. *Merluccius merluccius* and *Micromesistius poutassou*, taxa typically living along the continental slope (Whitehead et al., 1986–1989), are the most common and abundant. *Coryphaenoides* is also abundant but restricted to the samples below 800 m (Fig. 3b).

Otolith assemblages obtained from the middle-latitude NEA samples are also characterised by a high diversity and abundance of the family Myctophidae. Twenty-two (18 taxa over 1% as in Fig. 3c) of the 38 (28 taxa over 1% as in Fig. 3c) pelagic taxa belonged to this group, of which *Ceratoscopelus maderensis*, *Ceratoscopelus warmingii*, *Electrona risso*, *Hygophum benoiti*, *Hygophum hygomii* and, to a lesser extent, *Lobianchia dofleini* are the most common to abundant at various depths. Among the pelagic taxa, *Scopelarchus analis*, an oceanic fish with a worldwide distribution in the tropical and subtropical regions of all oceans, covers almost all the investigated depth ranges. *S. beanii* is occasionally found in samples deeper than 800 m. The composition of the benthic–benthopelagic group differs from shallow to deep water assemblages: *Glossanodon leioglossus*, sparids, *Spicara*, gobiids and *Capros aper* only occur in the shallowest depth, whereas congrids, *Hymenocephalus gracilis*, *Scorpaena notata* and *Epigonus constanciae* are recovered from slightly deeper slopes. *Coelorinchus*, *Coryphaenoides*, morids and *M. poutassou* are mainly from the deepest 700–1000 m intervals (Fig. 3c).

Cluster analysis shows three distinct clusters, corresponding to the three distinct geographic areas of the sampling stations: samples from the cruise ALKOR 232 formed a well-defined group, which also represents all the samples from the North Sea. Samples collected from the cruises M61/1 and GeoB8045-1 form another group, representing all the high-latitude NEA sampling sites. The rest of the samples form the third group, which is from the middle-latitude NEA (Fig. 4). The MDS analysis clearly discriminate the shallower samples from the deeper ones according to the negative and positive values of the first dimension, respectively (Fig. 5). The first dimension in the analysis is indicative of the depth.

4. Discussion

4.1. Taphonomy

Otoliths are exposed to taphonomic processes before entering the sediment. When passing through the guts of a predator, soft tissues and bones of fish are digested, but otoliths are mostly preserved in the excretions, albeit showing signs of acidic degradation (e.g. Clarke et al., 1995; Härkönen, 1986). Fitch and Brownell (1968), for example, reported 18,164 otoliths in 17 cetacean stomachs, with species mainly composed of mesopelagic preys. Isolated fish remains (teeth, vertebrae, etc.) in sediments are less abundant than the number of otoliths might suggest. In sediments that contain both otoliths and articulated fish remains, the latter mainly belong to larger piscivores (Nolf, 1985, 1995). The above observations imply that the mechanism of otoliths entering the sediment and their transportation during taphonomic processes is often controlled by predatory activities. However, many of our specimens (not specific to any taxa, but mostly the myctophids) still show translucent surfaces as if removed from a fresh fish, which is not like the appearance of having passed through an alimentary channel (see also Schwarzhans, 2013). In these cases, natural decay may be inferred.

Taxa older than the Quaternary have not frequently been found in the material in earlier studies (Beck et al., 2006; Christiansen et al., 2011; Pfannkuche et al., 2004a, 2004b). In addition, a rather high sedimentation rate in the shelf regions of the Portuguese coast region and the Bay of Biscay has been reported, ranging from 0.1 to 0.5 cm year^{-1} (Carvalho and Ramos, 1990; Dias et al., 2002), therefore the time-averaging effect is assumed to be limited.

4.2. Geographical distribution

As mentioned in 4.1, the predatory activity may affect the process of otolith taphonomy. Another factor to consider is the distance that foraging predators may cover. Remains of prey taken at one point may be excreted elsewhere, which can have an impact on the composition of otolith assemblages on sea bottoms. Such assemblages could potentially contain species transported from different environments (Nolf, 1985).

In this study, however, the geographical distribution of all the otolith-based species is in accordance with the actual biogeography. This is confirmed by the three distinct clusters of the cluster analysis (Fig. 4). The distinction of each main cluster is in the first place biogeographical rather than environmental because each contains samples from various water depths.

Several characteristic taxa which determine each cluster can be recognized: the North Sea samples are dominated by three benthopelagic species of the genus *Trisopterus*, namely *T. esmarkii*, *T. luscus* and *T. minutus*, which are all shallow water inhabitants on muddy bottoms and widely distributed in the temperate NEA (Cohen et al., 1990; Whitehead et al., 1986–1989). In the high-latitude NEA, most of the sediments contain subpolar to temperate mesopelagic species such as *Bathylagus euryops*, *Lampadena speculigera*, *L. macdonaldi* and *Protomyctophum arcticum* (Whitehead et al., 1986–1989). Temperate to subtropical mesopelagic species such as *S. analis*, *Bolinichthys indicus*, *H. hygomii*, *Cubiceps gracilis* (Whitehead et al., 1986–1989), on the other hand, can only be found in the middle-latitude NEA samples.

The composition of an otolith assemblage differs from location to location, reflecting its biogeographic characteristic. In the true oceanic high- and middle-latitude NEA assemblages, in particular, this biogeographic characteristic is mainly determined by pelagic taxa. Consequently, it seems that either mechanic or predatory transportation of otoliths over longer distances before deposition is limited (see also Schäfer, 1972: p.61), but cannot be totally excluded, because transportation (mechanic transportation in particular) results in poorly preserved specimens, often difficult to identify, whereas our material is generally well preserved.

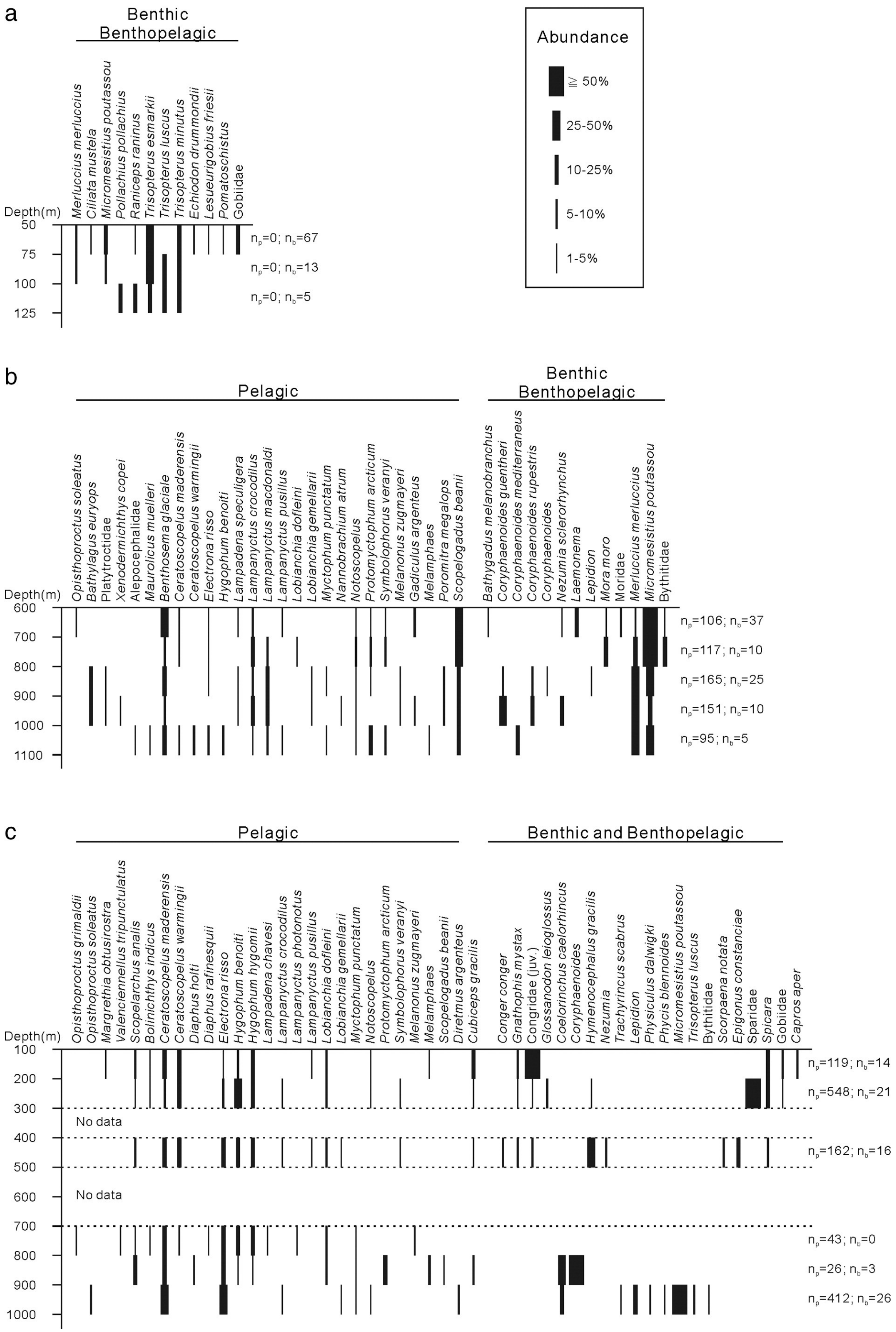
4.3. Otolith depth range

4.3.1. The North Sea otolith assemblages

Apparently, the composition of otolith assemblages varies with sampling locations and water depths. It reflects the typical composition of fish assemblages representing the environment in which the samples have been collected (Knijn et al., 1993), as summarized in Fig. 3a, although the otolith assemblages are not characterised by a very high diversity. Our results are very similar to the upper two otolith assemblages reported from the southern Norway Sea (Gaemers, 1978), although the first assemblage concerned gadids with abundant Pleuronectiformes.

4.3.2. The high- and middle-latitude NEA otolith assemblages

As shown in Fig. 3b and c, the distributions of most of the meso-bathypelagic components are very scattered and any robust separation concerning their depth range may be hazardous. Although the true bathypelagic taxa, such as *Bathylagus* and *Scopelogadus* (Whitehead et al., 1986–1989) reflect precisely the deep-water environment, a clearer separation of otolith depth range is shown by the benthic–benthopelagic group. The results of MDS analysis support the idea that the depth is the main factor affecting the distribution of the benthic–benthopelagic taxa (Fig. 5), and therefore this group could provide more precise bathymetric information with respect to the pelagic group.


a
Benthic
Benthopelagic
Merluccius merluccius
Ciliata mustela
Micromesistius poutassou
Pollachius pollachius
Raniceps raninus
Trisopterus esmarkii
Trisopterus luscus
Trisopterus minutus
Echiodon drummondii
Lesueurigobius friesii
Pomatoschistus
Gobiidae
Depth(m)
50
75
100
125
n_p=0; n_b=67
n_p=0; n_b=13
n_p=0; n_b=5
Abundance
≧ 50%
25-50%
10-25%
5-10%
1-5%
b
Pelagic
Benthic
Benthopelagic
Opisthoproctus soleatus
Bathylagus euryops
Platytroctidae
Xenodermichthys copei
Alepocephalidae
Maurolicus muelleri
Benthosema glaciale
Ceratoscopelus maderensis
Ceratoscopelus warmingii
Electrona risso
Hygophum benoiti
Lampadena speculigera
Lampanyctus crocodilus
Lampanyctus macdonaldi
Lampanyctus pusillus
Lobianchia dofleini
Lobianchia gemellarii
Myctophum punctatum
Nannobrachium atrum
Notoscopelus
Protomyctophum arcticum
Symbolophorus veranyi
Melanonus zugmayeri
Gadiculus argenteus
Melamphaes
Poromitra megalops
Scopelogadus beanii
Bathygadus melanobranchus
Coryphaenoides guentheri
Coryphaenoides mediterraneus
Coryphaenoides rupestris
Coryphaenoides
Nezumia sclerorhynchus
Laemonema
Lepidion
Mora moro
Moridae
Merluccius merluccius
Micromesistius poutassou
Bythitidae
Depth(m)
600
700
800
900
1000
1100
n_p=106; n_b=37
n_p=117; n_b=10
n_p=165; n_b=25
n_p=151; n_b=10
n_p=95; n_b=5
c
Pelagic
Benthic and Benthopelagic
Opisthoproctus grimaldii
Opisthoproctus soleatus
Margrethia obtusirostra
Valenciennellus tripunctulatus
Scopelarchus analis
Bolinichthys indicus
Ceratoscopelus maderensis
Ceratoscopelus warmingii
Diaphus holti
Diaphus rafinesquii
Electrona risso
Hygophum benoiti
Hygophum hygomii
Lampadena chavesi
Lampanyctus crocodilus
Lampanyctus photonotus
Lampanyctus pusillus
Lobianchia dofleini
Lobianchia gemellarii
Myctophum punctatum
Notoscopelus
Protomyctophum arcticum
Symbolophorus veranyi
Melanonus zugmayeri
Melamphaes
Scopelogadus beanii
Diretmus argenteus
Cubiceps gracilis
Conger conger
Gnathophis mystax
Congridae (juv.)
Glossanodon leioglossus
Coelorinchus caelorhincus
Coryphaenoides
Hymenocephalus gracilis
Nezumia
Trachyrincus scabrus
Lepidion
Physiculus dalwigki
Phycis blennoides
Micromesistius poutassou
Trisopterus luscus
Bythitidae
Scorpaena notata
Epigonus constanciae
Sparidae
Spicara
Gobiidae
Capros aper
Depth(m)
100
200
300
400
500
600
700
800
900
1000
No data
No data
n_p=119; n_b=14
n_p=548; n_b=21
n_p=162; n_b=16
n_p=43; n_b=0
n_p=26; n_b=3
n_p=412; n_b=26

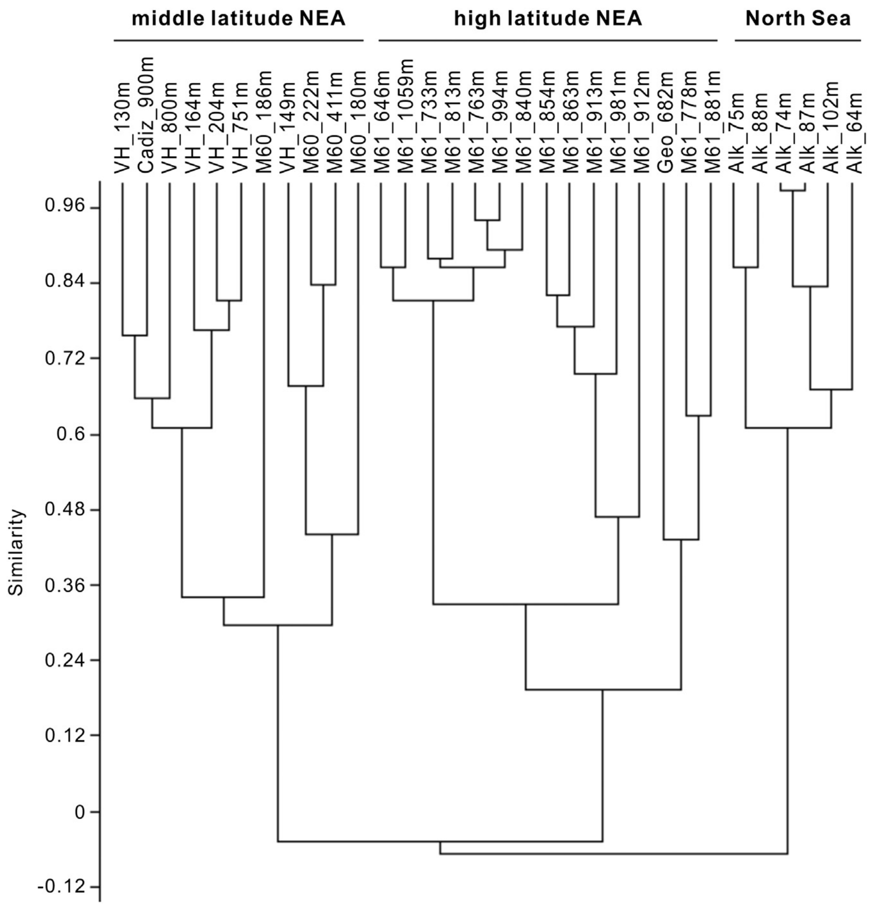


Fig. 4. Dendrogram of otolith samples from Recent NEA sea bottom. Cluster analysis using UPGMA algorithm and the correlation distance coefficient was performed. Three main groups corresponding to three main geographic sampling areas, the North Sea, high- and middle-latitude NEA, are well-resolved. Samples are coded by the cruise name and water depth.

Details of the composition of benthic–benthopelagic taxa in different depth assemblages reveal that they agree well with the modern communities. The macrourids (represented by the genera *Coryphaenoides*, *Nezumia* and *Trachyrincus*) characterise the deepest assemblages (below 600 m depth) which is in good agreement with their modern ecological features (Cohen et al., 1990; Massutí et al., 2004; Mauchline and Gordon, 1984). They have also been reported as characteristic taxa of the fossil otolith assemblages from the deep-sea deposits (Nolf and Brzobohaty, 1992; Brzobohaty, 1995; Girone, 2003). The shallowest samples, collected at the upper 200 m depths and negatively correlated to the first dimension of the MDS, are characterised by typical continental shelf taxa (e.g. sparids, *Spicara* and gobiids), which are also in agreement with the modern depth range of the living fishes (Whitehead et al., 1986–1989). In the Miocene to Pleistocene shallow water deposits of the Caribbean coast, for example, typical shallow water benthic–benthopelagic fishes are commonly found (Aguilera and Rodrigues de Aguilera, 1999). The assemblages from the 400–500 m depth range, correlating negatively with the first dimension of the MDS, are particularly interesting: their composition shows the concomitant occurrence of taxa typical of outer shelf and/or upper slope, such as *G. leioglossus*, *H. gracilis* and *E. constanciae* (Whitehead et al., 1986–1989) and of continental shelf taxa (e.g. congrids and gobiids). The latter are fishes that, in favourable conditions, can move from the deeper shelf to the very upper slope environment (Ungaro et al., 1995; Whitehead et al., 1986). Thus, these assemblages are essentially different from the deeper assemblages in composition, but similar to that from the shallower assemblages, they represent typical assemblages referable to a transitional environment.

The feature that many eroded specimens belonging to the family Myctophidae in these oceanic Recent sea bottoms compares well with the Neogene fossil assemblages that are often characterised by a very large number of eroded and juvenile myctophid otoliths. In addition, similar to many fossil oceanic assemblages, the quantity of mesopelagic species in the Recent sea sediments always outnumbers the benthic ones (Fig. 2). Diurnal mesopelagic fishes, such as myctophids, occur in large numbers along a large range of the water column, even in many shallow water sediments (see also Schwarzhans, 2013: Fig. 4). On the contrary, benthic–benthopelagic taxa usually are solitary, living close to the bottom, and their vertical movements are limited. Therefore, it is reasonable to consider benthic–benthopelagic taxa as the important indicator while inferring bathymetry.

4.3.3. Size-related distribution of *L. crocodilus*

Size-related stratification along the water column has been reported for some myctophids (Olivar et al., 2012). Species, such as *L. crocodilus*, have been shown to possess a habit shift during their growth: from mesopelagic in the juvenile stage to benthopelagic in the adult stage. Furthermore, the proportion of larger specimens of *L. crocodilus* increased considerably with depth and the occurrence of larger subadult and adult specimens is restricted to deeper assemblages, while the shallower ones are characterised only by the juvenile specimens (Stefanescu and Cartes, 1992). Consequently, despite the difficulty in

Fig. 3. Abundance of taxon along the sea depth. 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. (a) The North Sea assemblages; (b) high-latitude NEA assemblages; (c) middle-latitude NEA assemblages. Total number of identified otoliths is indicated for each depth interval and separated by pelagic (n_p) and benthic–benthopelagic (n_b) groups.

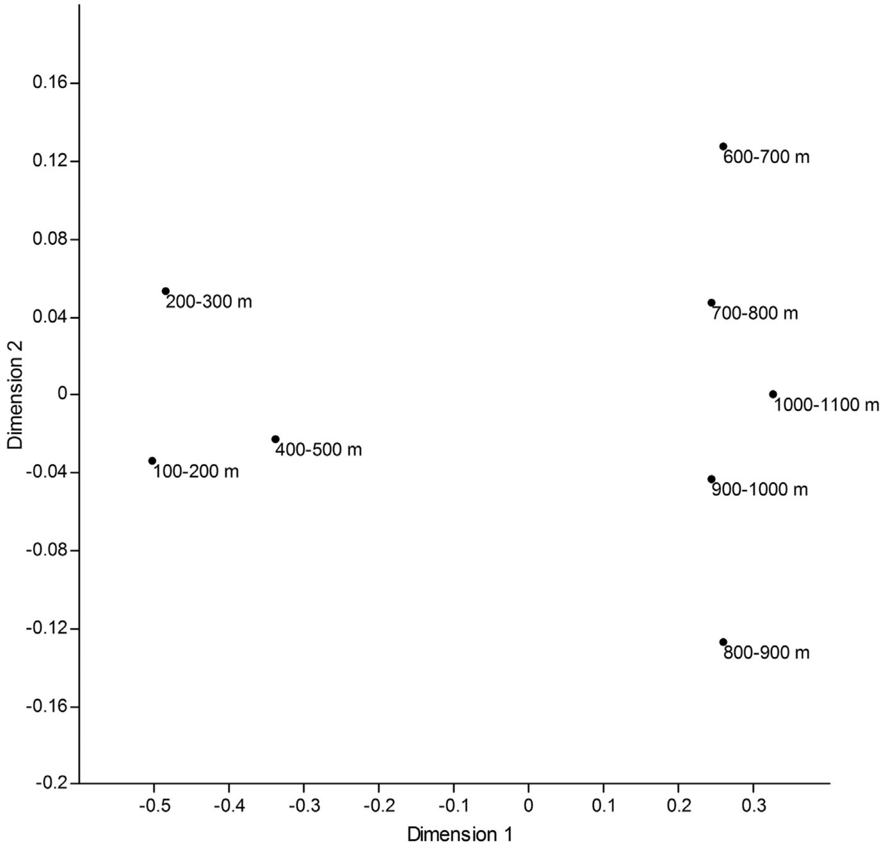


Fig. 5. First two dimensions of the non-parametric multi-dimensional scaling (MDS) ordination for the high- and middle-latitude NEA sampling stations. Only the benthic–benthopelagic taxa are considered and all the samples are arranged in 100 m intervals (see text). The first dimension indicates depth gradient, which distinguishes the shallow and deep assemblages.

bathymetric interpretation when using pelagic taxa as presented in Section 4.3.2, additional information may be obtained by analysing their population distribution at different water depths, given their considerable quantity in the sediments and age-related otolith size.

Girone (2003, 2005) first applied this size-related stratification feature to the Pleistocene fossil otolith assemblages to indicate sea level fluctuations in different layers of a section. Otoliths of *L. crocodilus* were grouped into three size classes (<1 mm, 1–2 mm and ≧2 mm) approximating their juvenile, subadult and adult otolith sizes. Analysis of all our Recent sea bottom samples containing this species resulted in a very similar pattern to what was observed in the actual ecology (Fig. 6), where the proportion of larger specimens increased considerably with depth and the juvenile specimens, though numerically rare, are confined to the shallower water. This supports the usefulness of the population structure analysis of *L. crocodilus*, which may allow a more detailed resolution on the bathymetry inference, and it also supports the paleobathymetric results of the fossil assemblages. However, such population stratification in the water was not clear in other pelagic taxa.

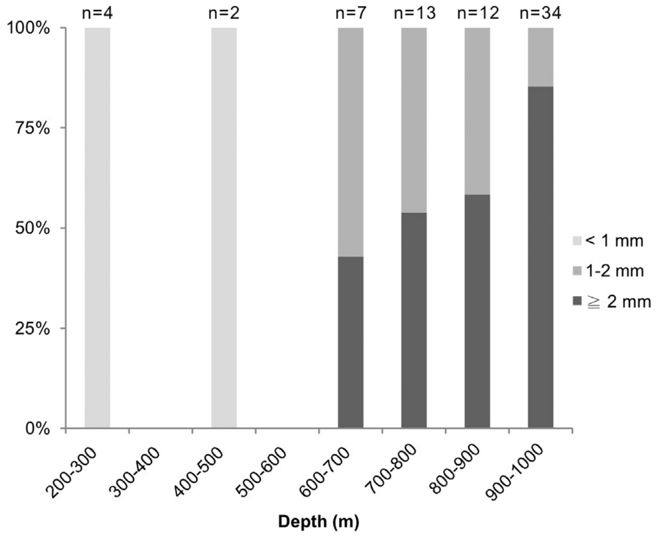


Fig. 6. Proportion of otolith size class versus water depth for *L. crocodilus*. Otolith size classes are indicated by colours. Smaller individuals are restricted to the shallow assemblages, whereas larger ones are found mainly in deep waters; additionally, the proportion of the largest size class increases with depth from 600 to 1000 m. $n =$ number of *L. crocodilus* otoliths in each depth interval.

4.4. Testing the bathymetric method: case studies

To evaluate the precision of Nolf and Brzobohaty's (1992) paleobathymetric method, all the samples were tested, three of which are shown here (Figs 7–9). The method resulted in a much deeper depth than the actual depth for six out of seven shallow (within 300 m) oceanic samples (e.g. Fig. 7a), which can be amended if only the benthic–benthopelagic taxa are considered (Fig. 7b), though apparently only two samples with more diverse benthic–benthopelagic taxa resulted in positive amendment. The expected values of the method become more accurate in the mid- to deep-water samples.

In general, the method is best interpretable for the mid-water assemblages. The calculation is obviously affected by the pelagic taxa in these assemblages because the expected bathymetry is determined by the total number of taxa identified (e.g. Fig. 8). In true oceanic samples, where the mesopelagic taxa are abundant, the values are always similar for the depths ranging from 400 to 800 m because of their high diversity and their similar occurrence over many samples within this range. This fact is also true even for some of the shallow water samples (e.g. Fig. 7).

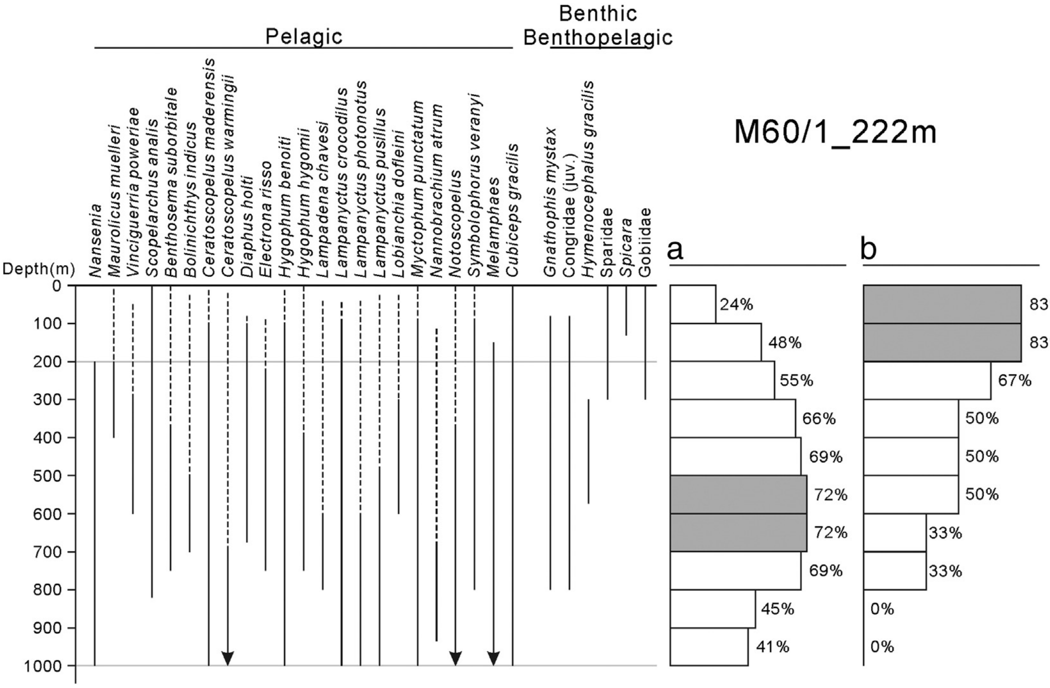


Fig. 7. Bathymetric method applied on Recent sea bottom sample (M60/1, station 765, depth 222 m). (a) results of all the taxa that have been identified; (b) results of the benthic–benthopelagic taxa (see text for further explanations). The estimation in this shallow water assemblage is more accurate if the pelagic taxa are excluded. Dotted lines indicate the distribution of mesopelagic taxa at night, which are not considered.

On the other hand, the benthic–benthopelagic taxa show different distributions from depth to depth. In fact, it is possible to estimate an accurate bathymetry by just considering the benthic–benthopelagic taxa in a single sample (Figs 7b, 8b and 9b). The reason may be that the effect of post-mortem transport is less important, given that these demersal taxa stay close to the sea bottom, and they can be regarded as autochthonous elements. These data support that the separation of the benthic–benthopelagic taxa and the mesopelagic taxa effectively improves the resolution while interpreting the bathymetry of fossil assemblages (Agiadi et al., 2010; Girone, 2003, 2005, 2007). Such fact seems especially true for the shallow water assemblages. However, the number of benthic–benthopelagic taxa that can be found in a single assemblage is

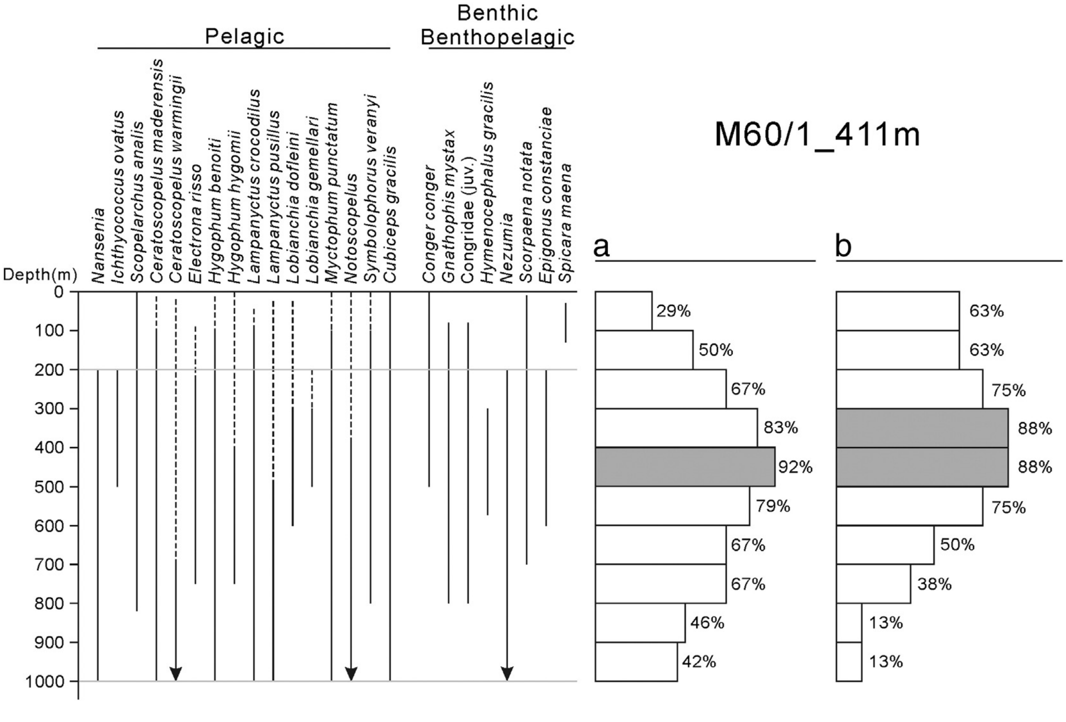


Fig. 8. Bathymetric method applied on Recent sea bottom sample (M60/1, station 309, depth 411 m). (a) Results of all the taxa that have been identified; (b) results of the benthic–benthopelagic taxa (see text for further explanations). The results of a and b are similar in this mid-water assemblage. Dotted lines indicate the distribution of mesopelagic taxa at night, which are not considered.

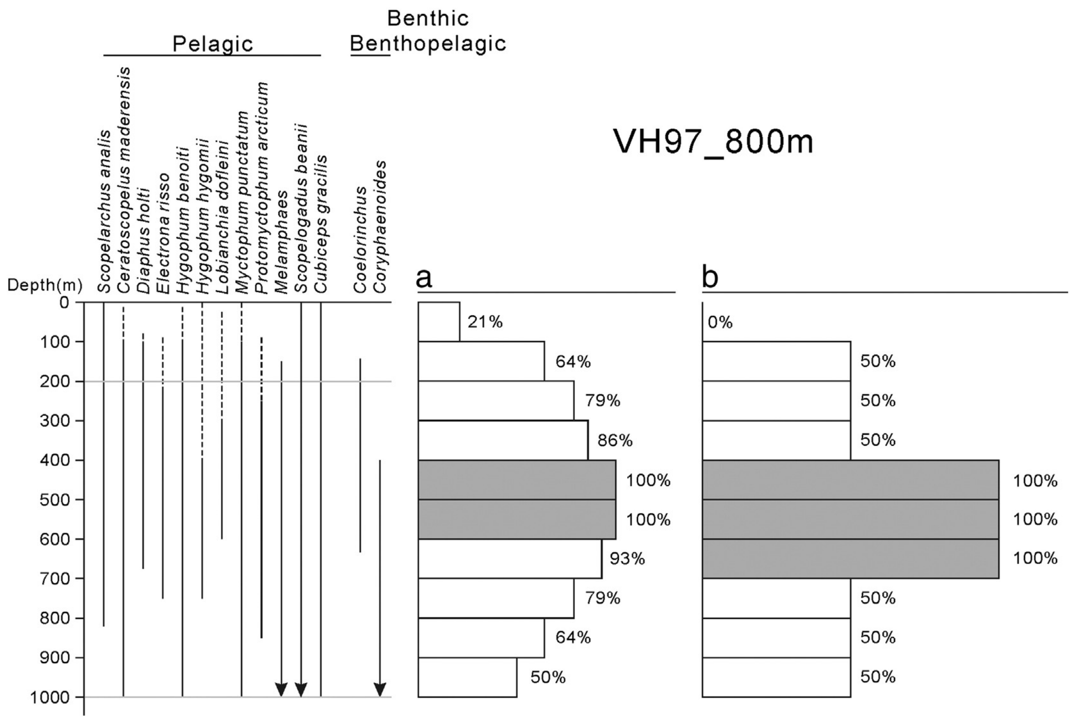


Fig. 9. Bathymetric method applied on Recent sea bottom sample (VH97, station 97, depth 800 m). (a) Results of all the taxa that have been identified; (b) results of the benthic–benthopelagic taxa (see text for further explanations). The results of a and b are similar in this deep-water assemblage. Dotted lines indicate the distribution of mesopelagic taxa at night, which are not considered.

critical. We found that the analysis from samples containing less than five benthic–benthopelagic taxa usually was not well-resolved (e.g. Fig. 9b).

5. Conclusions

In summary, otolith assemblages from the Recent sea bottoms of the NEA and the North Sea are indicative of the present biogeography and bathymetry of this region. This study reveals that:

1. The pelagic and benthic–benthopelagic taxa are two distinct groups which differ markedly in both the quantity and diversity in the Recent sea bottom sediments.
2. The composition of otolith assemblages from the sea bottom reflects the composition of the fish assemblages of the three defined geographic areas, transportation is not traceable. Consequently, an otolith assemblage represents its own biogeographic character. In the true oceanic high- and middle-latitude NEA assemblages, this is mainly determined by the pelagic taxa and can be a useful proxy for biogeographical analysis.
3. The benthic–benthopelagic taxa are more important for the bathymetric interpretation, especially in the shallow water assemblages; however, their low number is a major concern.
4. The bathymetric interpretation can be improved by analysing the population structure of such taxa as the mesopelagic *L. crocodilus*, which shows an otolith size-related distribution along the water depth: the proportion of larger specimens in deeper waters increases markedly.

Acknowledgements

We thank Prof. Dr. André Freiwald (Wilhelmshaven) and Prof. Dr. Bettina Reichenbacher (München) for providing precious sea bottom samples and otoliths. We also thank Mr. Kristiaan Hoedemakers for correcting and giving constructive comments on a first draft of our manuscript. Chien-Hsiang Lin was financially supported by the Ministry of Education, Taiwan, under the title "Government Scholarship for Overseas Study" during his Ph.D. program. The microscope laboratory at the Dipartimento di Scienze della Terra and Geoambientali, University of Bari Aldo Moro, was funded by Potenziamento Strutturale PONa3_00369 "Laboratorio per lo Sviluppo Integrato delle Scienze e delle Tecnologie dei Materiali Avanzati e per dispositivi innovativi (SISTEMA)".

Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at http://dx.doi.org/10.1016/j.palaeo.2016.01.022. These data include the Google map of the most important areas described in this article.

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