

Organic flux control on bathymetric zonation of Mediterranean benthic foraminifera

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Abstract

A data set of benthic foraminiferal faunas counted in 138 surface samples from the Mediterranean Sea has been used to investigate whether the bathymetrical distribution of the dominant taxa is controlled by the amount of labile organic matter transported to the sea floor. We find that most of the major taxa show a clear W to E shallowing of their upper or lower depth limit, coinciding with a W to E decrease in the surface water primary production, and in the estimated flux of the labile organic matter to the sea floor. This observation implies that the bathymetrical succession of these taxa is indeed determined by the organic flux. In the western Mediterranean, we find successions from more oligotrophic taxa at greater water depths to more eutrophic taxa in more shallow water. Towards the eastern Mediterranean, most eutrophic taxa tend to become increasingly rare, or even to disappear, whereas the more oligotrophic taxa show a clear shoaling of their depth range. Deep infaunal taxa are mainly limited to the western part of the Mediterranean. This is explained by their dependency on a relatively elevated organic flux, and by the fact that the bacterial stocks on which they feed may become unattainable when the redox front is positioned too deep in the sediment. The close similarity between the flux level controlling our main faunal boundary, and the flux levels coinciding with important faunal changes in other parts of the world ocean, suggests that a flux level of about 2–3 g labile C m⁻² y⁻¹ level corresponds to a benthic ecosystem threshold value of global importance. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

In a paper examining the relationship between organic carbon flux and deep-sea deposit feeding, Carney (1989) suggested that spatial and temporal

variations in the food supply to the benthic ecosystem would cause changes in the bathymetric distribution of food-limited taxa, and that benthic foraminifera could provide good examples of this interaction. With increasing waterdepth, and hence decreasing organic flux, a decreased overall faunal abundance should be expected, with a succession of species determined by differences in their trophic efficiency (Carney, 1989). If true, important spatial and temporal variability of the downward organic flux should lead to changing bathymetrical ranges of sensitive benthic

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foraminiferal taxa, explaining why most bathymetrical zonations are applicable only on a local scale (Murray, 1991).

Here, we examine the role of food supply on the composition of the benthic foraminiferal faunas and more specifically, on their bathymetrical distribution in the Mediterranean Sea (cf. Parker, 1958; Todd, 1958; Cita and Zocchi, 1978; Wright, 1978; Jorissen, 1987, 1988; De Stigter et al., 1998; De Rijk et al., 1999). The Mediterranean Sea is an extremely suitable basin to test Carney's hypothesis, because there is a very strong W–E gradient in surface water production, probably resulting in an even stronger W–E trend in the export production. Mediterranean primary production patterns were described recently by Antoine et al. (1995) based on satellite image analyses. Although the precise calibration between primary production and the satellite images is continuously under revision, relative trends likely represent true spatial variability.

The main food source for the benthic ecosystem is the downward flux of labile organic carbon (Gooday, 1988, 1993, and references therein). The vertical flux of organic carbon to the sea floor is determined by the exported fraction of surface water primary productivity, and losses due to degradation processes taking place in the water column (Suess, 1980; Berger et al., 1989; Berger and Wefer, 1990). In general, spatial differences in export production reaching the benthic ecosystem are amplified in comparison with those in surface water primary production (Berger et al., 1989). We compare quantitative estimates of organic flux reaching the sea floor with the spatial patterns in the bathymetrical distribution of the major benthic foraminiferal taxa. Our quantitative estimates of the amount of the organic carbon arriving at the sea floor are based on a combination of: (1) the primary productivity values of Antoine et al. (1995); (2) the water depth; and (3) the empirical flux equation proposed by Berger and Wefer (1990). This equation is valid in the open ocean, and its use in the Mediterranean may be questioned for two reasons. Firstly, Mediterranean deep waters are about 10°C warmer than the oceanic deep waters and degradation of organic matter in the water column will therefore be accelerated. Secondly, the equation ignores lateral fluxes of organic matter, which may be important in an enclosed marginal sea such as the Mediterranean.

Because of the first restriction, our estimated fluxes will probably be too high, but the fair homogeneously high temperatures in the deep water would make this a systematic offset, so that relative trends remain valid. The second problem concerns, in most cases, lateral advection of older organic material, which likely has an important refractory component, with probably a very limited direct nutritional value for the benthic foraminiferal faunas.

2. Material and methods

The present study uses a data set composed of a total of 138 surface sediment samples from a previous study of benthic foraminiferal thanatocoenoses (De Rijk et al., 1999). The water depth of the selected samples varies from 200 to 3000 m. Taxonomy follows Parker (1958) and Jorissen (1987); a description of the methodology and a short discussion on the most important species can be found in De Rijk et al. (1999).

No samples from 0 to 200 m waterdepth are included in this study. At shallow sites, primary productivity values may deviate from the general pattern because of increased production due to river-born nutrient input and benthic autotrophic production. In addition, primary productivity values for these shallow sites can not be derived reliably from satellite images (Antoine et al., 1995). For similar reasons we also exclude some deeper sites influenced by the seasonally nutrient rich Nile plume (Van Dijken and Arrigo, 1996).

We calculate the organic flux to the sea floor, a function of primary productivity and water depth (Suess, 1980; Martin and Bender, 1988; Herguera, 1992; Herguera and Berger, 1991), using the empirical relationship of Berger and Wefer (1990). This relationship distinguishes between a labile and a more refractory component in the organic flux, and takes the form:

$$J_z = kPP/z + rPP/\sqrt{z}$$

where $k = 2\sqrt{PP}$, $r = 5\sqrt{PP}$, PP = annual primary productivity ($\text{g C m}^{-2}\text{y}^{-1}$), and J_z is the annual organic flux at water depth z in meters. The first term represents labile organic matter (i.e. rapidly decaying matter), whereas the second term represents

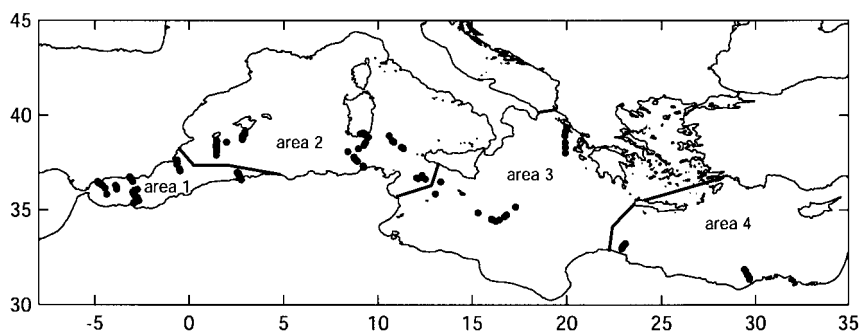


Fig. 1. Map of the Mediterranean Sea, indicating the sampling stations and the four areas recognised on the basis of the ranges of observed primary production values. See text for further explanation.

the slowly decaying, more resistant fraction. Since we do not consider the second term to be a major food source for most benthic foraminiferal species, we will compare the composition of our faunal assemblages with the first term only, representing the flux of labile organic matter. Annual primary productivity values are based on plate 4 of Antoine et al. (1995). This Mediterranean-wide map combines data from the western Mediterranean (Morel and André, 1991) with about 300 scenes over the eastern Mediterranean during 1979–1983 (Antoine et al., 1995). Although Antoine et al. (1995) do not claim to have

produced irrefutable numbers, the spatial gradients are believed to be represented reliably.

The benthic foraminiferal data set has been divided into four geographical areas, each with a specific primary productivity range (Fig. 1). For all samples, we calculated the labile organic carbon flux lines by feeding the annual primary production values of Antoine et al. (1995) into the J_z -equation (Berger and Wefer, 1990). In Fig. 2, these calculated labile organic flux data are shown for the four areas, as a function of water depth. Although there is some overlap between the various areas, the regression lines for the four geographical areas clearly show the

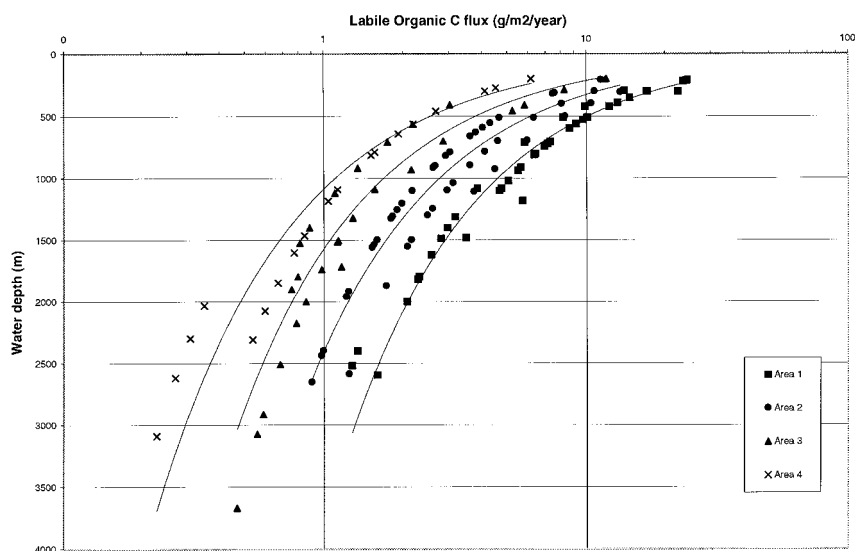


Fig. 2. Plot showing the relationships between water depth and the calculated downward flux of labile organic carbon for all 138 stations; different signatures are used for the four areas shown in Fig. 1.

Table 1
Overview of the water depths (in m) of various labile organic carbon flux-levels for the four areas. The calculated water depths are based on typical PP-values, which are different for the four areas; see text for further explanation

	Typical PP ($\text{g m}^{-2}\text{y}^{-1}$)	1 ($\text{g m}^{-2}\text{y}^{-1}$)	2 ($\text{g m}^{-2}\text{y}^{-1}$)	2.5 ($\text{g m}^{-2}\text{y}^{-1}$)	3 ($\text{g m}^{-2}\text{y}^{-1}$)	4 ($\text{g m}^{-2}\text{y}^{-1}$)	5 ($\text{g m}^{-2}\text{y}^{-1}$)	7.5 ($\text{g m}^{-2}\text{y}^{-1}$)	10 ($\text{g m}^{-2}\text{y}^{-1}$)
Area 1	175	4500	2300	1850	1550	1150	930	620	465
Area 2	125	2750	1400	1125	925	700	560	375	280
Area 3	90	1750	850	675	575	425	340	225	170
Area 4	65	1000	525	425	350	260	210	140	105

increasing oligotrophic conditions towards the eastern Mediterranean.

The first area (Figs. 1 and 2) includes the Alboran Sea and the transects north of Algeria and off southern Spain. Primary productivity values range from 125 to 250 $\text{g C m}^{-2}\text{y}^{-1}$. We consider 175 $\text{g C m}^{-2}\text{y}^{-1}$ as typical for this area; and use this value to calculate the average depths of the various regional isoflux lines (Table 1; Figs. 3–6). The second area comprises the remaining part of the western Mediterranean Sea, with primary productivity values between 100 and 175 $\text{g C m}^{-2}\text{y}^{-1}$; we use a typical value of 125 $\text{g C m}^{-2}\text{y}^{-1}$ to characterise this area (Table 1; Figs. 3–6). The third zone includes the western part of the Eastern Mediterranean, with primary productivity values from 65 to 125 $\text{g C m}^{-2}\text{y}^{-1}$, we use a value of 90 $\text{g C m}^{-2}\text{y}^{-1}$ to characterise this area. The fourth zone covers the Levantine basin, where average primary productivity values are between 50 and 100 $\text{g C m}^{-2}\text{y}^{-1}$; we use 65 $\text{g C m}^{-2}\text{y}^{-1}$ as a typical value.

3. Results

Percentages of the most important benthic foraminiferal taxa versus depth are plotted for each of the four Mediterranean subareas (Figs. 3–6). The benthic foraminiferal taxa are subdivided into four different groups based on their bathymetrical distribution and microhabitat:

- group 1 — taxa which in each area show a relative abundance increase towards deeper water (Fig. 3), and can thus be considered as relatively oligotrophic;
- group 2 — taxa, which, on the contrary, show a relative abundance increase towards shallower water (Fig. 4), and can thus be considered as more eutrophic;
- group 3 — taxa, which typically show an abundance maximum at mid-depth (Fig. 5);
- group 4 — the deep infaunal taxa *Bolivina alata* (Seguenza), *Chilostomella* spp. and *Globobulimina* spp (Fig. 6). (cf. Jorissen, 1999a,b).

3.1. Group 1

These taxa, which are typical for the deepest part of

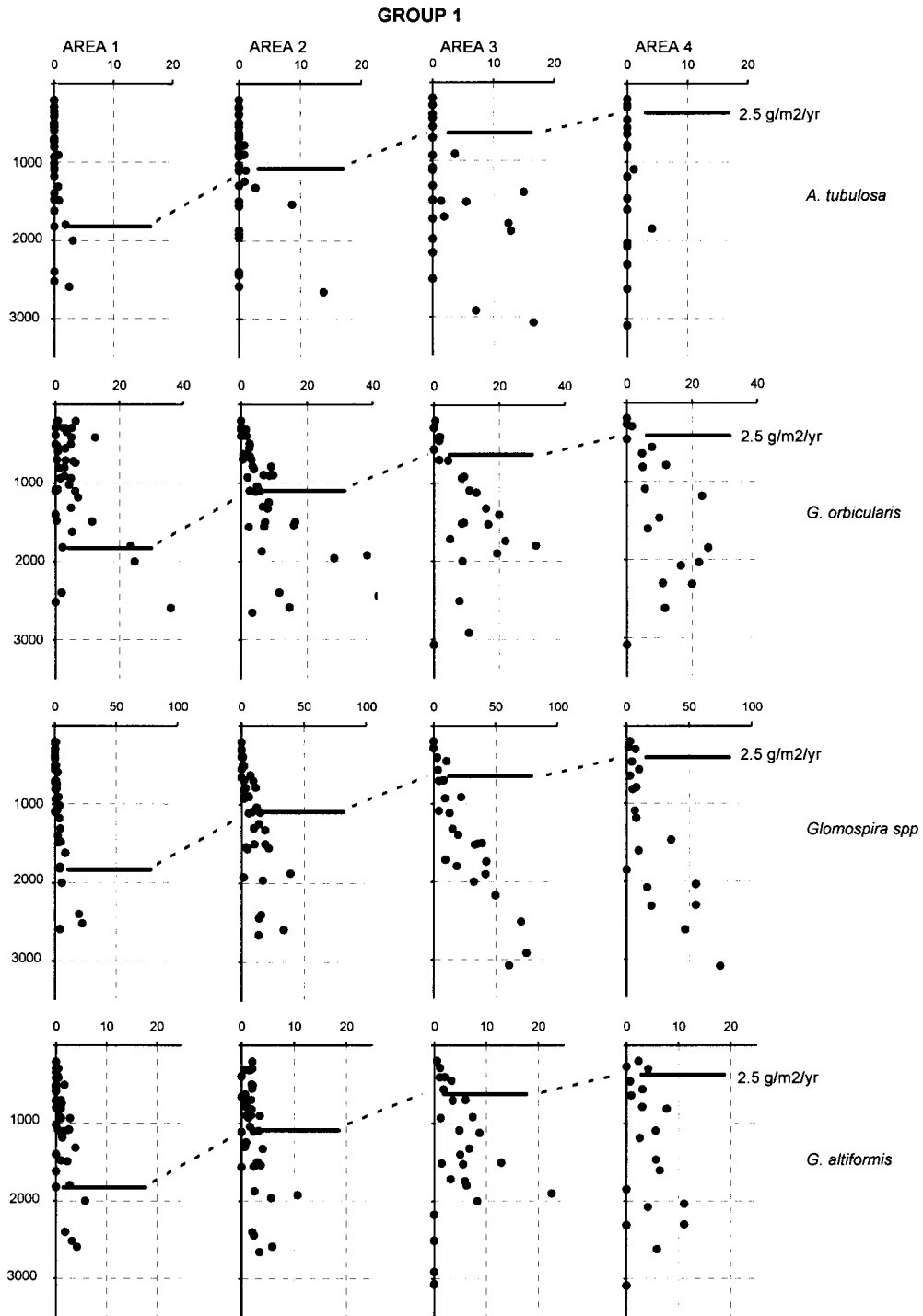


Fig. 3. Plots showing the percentage distribution of the dominant benthic foraminiferal taxa in function of water depth in the four areas. Values on the horizontal axes indicate the percentage of the taxon in the total benthic foraminiferal assemblage; values on the vertical axes indicate water depth in meters. In all figures the iso-flux line of 2.5 g labile C m⁻² y⁻¹ (based on typical PP-values for each area, see text) is shown.

the Mediterranean Sea, are generally considered as oligotrophic. *Articulina tubulosa* (Seguenza), *Glomospira charoides* (Jones and Parker), *Gyroidina altiformis* (Stewart and Stewart), and *Gyroidina orbicularis* (d'Orbigny) are typical examples.

Articulina tubulosa (Fig. 3) shows an eastward shallowing of its upper depth limit, from about 1800 m in area 1, 1200 m in area 2 and 800 m in area 3; it hardly occurs in area 4. This trend strongly resembles the eastward shallowing of the 2.5 g labile organic C m⁻² y⁻¹ iso-flux line (Fig. 3).

Gyroidina altiformis (Fig. 3) shows a distinct difference in its upper depth limit between eutrophic area 1 (500–750 m), and the other three areas (<300 m). The depth at which this species can reach about 5% is clearly shallow to the east, from about 2000 m in area 1, to 1000 m in area 2, 700 m in area 3, to 300 m in area 4. This trend roughly matches with that in the 3 g labile C m⁻² y⁻¹ line (Table 1).

High frequencies (>10%) of *Gyroidina orbicularis* (Fig. 3) are found commonly below 1500 m in area 1, below 800 m in areas 2 and 3 and below 600 m in the easternmost area 4.

Also *Glomospira charoides* shows a W–E shallowing trend (Fig. 3); its upper depth limit shifts from 1500 m in area 1, to 700 m in area 2, 400 m in area 3, and 250 m in area 4. This trend strongly resembles that of the iso-*Jz*-line of 4 g labile C m⁻² y⁻¹. *G. charoides* is only found in relative abundances above 40% in the deepest ranges (below 2000 m) of the two most oligotrophic (eastern) areas. Here, we calculate labile *Jz*-values below 0.7 g C m⁻² y⁻¹, conditions which are never met in the western basin.

3.2. Group 2

This group consists of *Bulimina marginata* d'Orbigny, *Cassidulina crassa* d'Orbigny, *Bulimina aculeata* d'Orbigny and *C. laevigata* d'Orbigny/*C. carinata* Cushman, taxa, which in all areas tend to show an increase in their relative abundances towards shallower water.

The lower depth limit of *Bulimina marginata* (Fig. 4) shallows from about 2000 m in area 1, to 1000 m in area 2, 700 m in area 3. It hardly occurs in the easternmost area. Hence, *B. marginata* is restricted to sites with a minimum *Jz*-value of 2.5 g labile C m⁻² y⁻¹.

Bulimina aculeata is mainly found in area 1 (Fig.

4), where occasional occurrences are seen in deeper samples, but where the bulk is found above 1500 m. In area 2, this species is mainly found above 700 m. In the other two areas *B. aculeata* occurs in low frequencies at sites shallower than 500 m. Here we observe a good correspondence with the trend in the 3 g labile C m⁻² y⁻¹ line (Table 1).

The lower depth limit of *Cassidulina crassa* gradually shoals from about 1500 m in area 1 to about 800 m in area 4 (Fig. 4). Although the eastward shallowing trend is clear, there seems to be no straightforward relationship with a specific *Jz*-level.

The lower depth limit of *Cassidulina laevigata/carinata* (Fig. 4) shows the same complication as *Bulimina aculeata* in area 1; one of the deeper samples (at 2520 m) shows an anomalously high percentage. Otherwise, the lower depth limit is positioned around 2000 m, around 1500 m in area 2, and 700 m in area 3. Similar to *B. marginata*, this species hardly occurs in the most oligotrophic area 4, with the exception of a single level at 2075 m depth, where the presence of *C. laevigata/carinata* can probably be explained by a downslope transport. The bathymetric trend shown by this taxon roughly corresponds with the *Jz* = 2.5 g labile C m⁻² y⁻¹ level.

3.3. Group 3

These taxa (*Uvigerina mediterranea* Hofker, *U. peregrina* Cushman, *Melonis* spp., and *Hoeglundina elegans* (d'Orbigny)) show peak occurrences in all areas around the middle of their depth range.

The lower depth limit of *Uvigerina mediterranea* (Fig. 5) shallows from west to east; in area 1 and 2 and it is about 1500 m, while in both areas from the eastern basin it is 1000–800 m. Relative abundances also show a distinct W–E diminution.

The lower depth limit of *Uvigerina peregrina* (Fig. 5) decreases from 2000 m in area 1, to 1600 m in area 2, 1200 m in area 3 (with the exception of one station of 1716 m depth), to 600 m in area 4, a trend which perfectly coincides with the *Jz* = 2.5 g labile C m⁻² y⁻¹ level. The overall abundance pattern with water depth also shows a W–E shallowing trend, with maximum relative abundances shifting from roughly 1400 m to roughly 500 m, respectively (coinciding with a flux level of about 3 g labile C m⁻² y⁻¹).

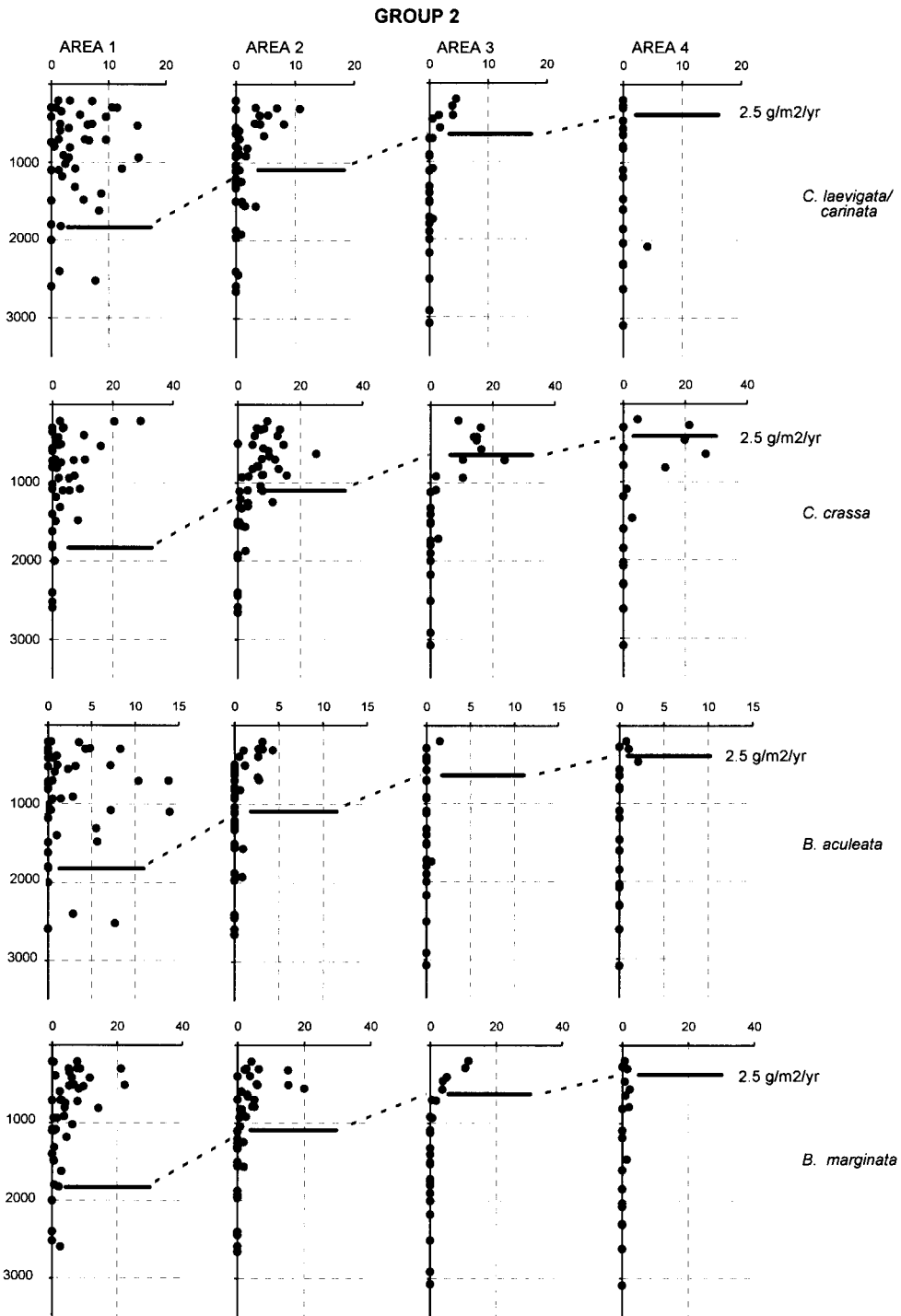


Fig. 4. Plots showing the percentage distribution of the dominant benthic foraminiferal taxa in function of water depth in the four areas. Values on the horizontal axes indicate the percentage of the taxon in the total benthic foraminiferal assemblage; values on the vertical axes indicate water depth in meters. In all figures the iso-flux line of 2.5 g labile C m⁻² y⁻¹ (based on typical PP-values for each area, see text) is shown.

In addition, there is a striking reduction in percentages from west to east in this species.

The lower depth limit of *Melonis* spp. does not display such a clear W–E trend; this may be a result of the grouping of two species (*M. barleeanus* (Williamson) and *M. parkeri* Uchio) with different trophic requirements and microhabitats.

Hoeglundina elegans only occurs in the western Mediterranean basin. The frequency distribution of this species shows a maximum around 1500 m in area 1, which shallows to about 1000 m in area 2. Also to upper depth limit shows a clear upward W–E shift.

3.4. Group 4

This group of deep infaunal taxa (Fig. 6) includes *Chilostomella* spp., *Globobulimina* spp. and *Bolivina alata*. The latter species is tentatively placed in this group because of its morphological resemblance (pore pattern, thin walled test) and its co-occurrence with the other two taxa in samples just before the Holocene sapropel S1 (Rohling et al., 1997). This group has its main occurrence in area 1, where it occurs at all water depths without showing a clear bathymetrical pattern. It occurs equally in some of the shallower stations of area 2, but is nearly absent in the other two areas.

4. Discussion

The percentage patterns shown in Figs. 3 – 5 indicate that the bathymetrical distribution of the dominant taxa of benthic foraminifera in the Mediterranean depends strongly on the flux of labile organic carbon to the sea floor. The overall trends are obvious, although certain species show occasional occurrences far below their usual distribution range. Closer inspection of these anomalous samples reveals a mixture of an autochthonous, deep fauna, with apparently displaced, much shallower elements. For instance, a site at 2520 m in area 1, with an anomalously high percentage of *Cassidulina laevigata/carinata* and *Bulimina aculeata* (Fig. 3), also contains shallow-living miliolids, suggesting that this assemblage shows a mixture of replaced and in situ sediments. Down-slope transport is a common feature in the Mediterranean, where the continental slope tends to be particularly steep (Stanley, 1985). The presence of

some anomalous points in the graphs presented in Figs. 3–6 is therefore not surprising.

The three groups that we distinguished on the basis of their bathymetrical distributions all show a clear W–E shift in their depth range. All deep-living species of group 1 show a W–E shallowing of their upper depth range. It is evident that these taxa are more successful in most oligotrophic parts of the basin, which are found at an increasingly shallow depth towards the east. The shallower living taxa of group 2, on the contrary, have a clear preference for the most eutrophic parts of the Mediterranean. For most of these species, the lower depth limit is close to the iso-flux line of $2.5 \text{ g labile C m}^{-2} \text{ y}^{-1}$. Consequently, they are found at a much greater depth in the western Mediterranean than in the eastern Mediterranean. Furthermore, their maximum percentage strongly decreases from west to east. In group 3, which contains species with maximum percentages at mid depth, the same phenomena can be observed in all taxa except *Melonis* spp. The lower depth limit shallows, and maximum percentage decrease significantly to the east. The latter phenomenon is particularly clear in both *Uvigerina* species.

The present data, therefore, unambiguously confirm Carney's (1989) hypothesis: the bathymetrical distribution of most of the dominant benthic foraminiferal taxa seems indeed to be controlled by the level of the organic flux to the sea floor. What has been described as a bathymetrical species succession before (Parker, 1958; Todd, 1958; Cita and Zocchi, 1978; Wright, 1978; Jorissen, 1988; De Stigter et al., 1998; De Rijk et al., 1999), is in essence a succession of taxa with different trophic requirements. Species indicative of eutrophic conditions are found in shallow water succeeded by more oligotrophic taxa towards deeper water. This whole species succession shifts to shallower depths towards the more oligotrophic eastern part of the Mediterranean.

The dependence on the organic flux is expressed in two different ways: (1) by the W–E changes of the lower or upper depth limit; and (2) by an eastward decrease of maximum abundances in the more eutrophic (shallower) taxa. The first parameter, the upper or lower depth limit of a taxon, probably depends on its competitive ability. The deeper, oligotrophic, taxa, which are only successful at J_z -values below $2.5 \text{ g labile organic C m}^{-2} \text{ y}^{-1}$, are

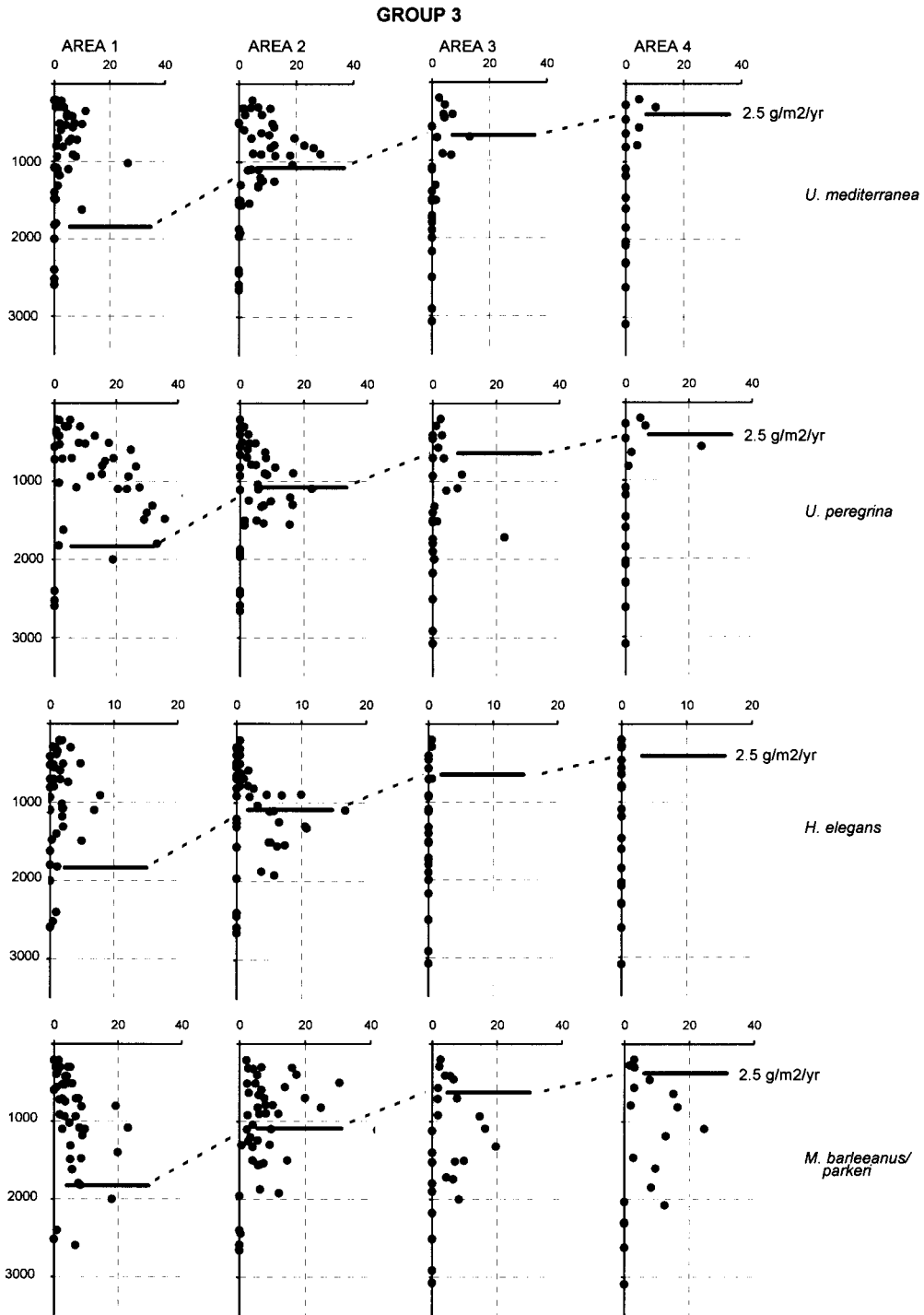


Fig. 5. Plots showing the percentage distribution of the dominant benthic foraminiferal taxa in function of water depth in the four areas. Values on the horizontal axes indicate the percentage of the taxon in the total benthic foraminiferal assemblage; values on the vertical axes indicate water depth in meters. In all figures the iso-flux line of 2.5 g labile C m⁻² y⁻¹ (based on typical PP-values for each area, see text) is shown.

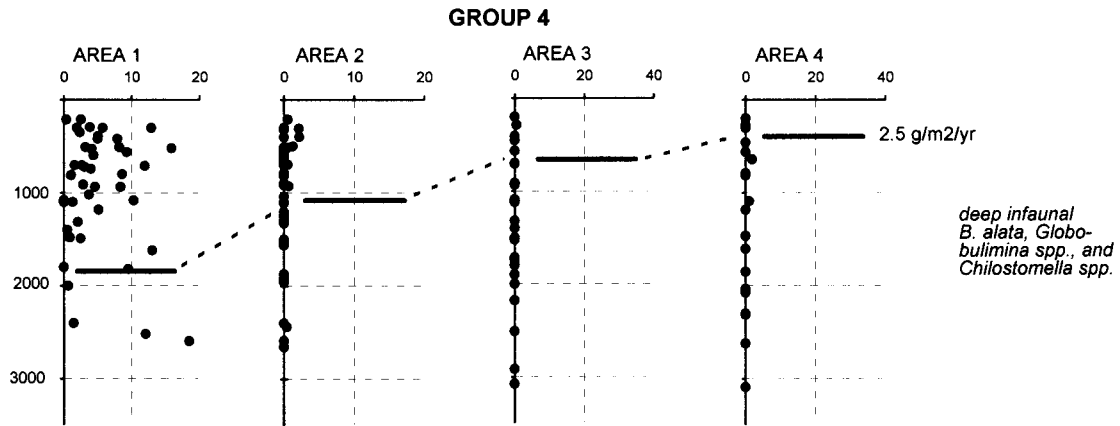


Fig. 6. Plots showing the percentage distribution of the dominant benthic foraminiferal taxa in function of water depth in the four areas. Values on the horizontal axes indicate the percentage of the taxon in the total benthic foraminiferal assemblage; values on the vertical axes indicate water depth in meters. In all figures the iso-flux line of $2.5 \text{ g labile C m}^{-2} \text{ y}^{-1}$ (based on typical PP-values for each area, see text) is shown.

outcompeted by more eutrophic shallower taxa when the organic flux rises above this level. This difference has probably to be explained by a (gradual) difference in ecological strategies between the two groups. The deep, oligotrophic, taxa, which apparently live in a strongly food-limited environment, can be considered as taxa with a life strategy aimed at very efficient utilisation of the scarce resources available. The shallower, more eutrophic taxa, on the contrary, may adopt a more opportunistic life style. As soon as the organic flux to the sea floor reaches a certain threshold value, a higher reproductive potential allows them to dominate the fauna. A similar gradual difference in opportunism may exist between groups 2 and 3.

The second reflection of the fauna's dependence on organic flux levels is a W–E trend of decreasing percentages found in many of the shallower taxa. Essentially this trend shows that species dominance decreases from west to east. We think that the species that show this trend most clearly (*Cassidulina laevigata/carinata*, *Bulimina aculeata*, *B. marginata*, *Uvigerina mediterranea* and *U. peregrina*), are the most opportunistic taxa found in the Mediterranean. In order to reach high standing stocks, these taxa should be dependent on an important supply of fresh organic matter, with a high nutritious value. Apparently, such conditions are much more common in the eutrophic western than in the more oligotrophic eastern part of the basin. We suggest that this

results from the fact that formation of organic aggregates (which are easily transported to a great water depth) is a common feature in the western Mediterranean, where important phytoplankton blooms occur in the frontal areas (Lohrenz et al., 1988; Prieur et al., 1993; Peinert and Miquel, 1994; Pujol and Vergnaud-Grazzini, 1995), but is almost non-existent in the eastern Mediterranean. Consequently, faunas living in the western Mediterranean are periodically fuelled by high quality organic matter, which allows the more opportunistic species to produce an important number of tests, whereas faunas living in the eastern part of the basin are subject to a more continuous flux of individual grains, with a much lower nutritious value. For this reason, the organic matter arriving on the sea floor in the eastern basin is more suitable for taxa adapted to high food utilisation efficiency, and less suitable for taxa with a more opportunistic lifestyle, explaining the W–E decrease in the percentages of the afore-mentioned taxa.

The deep infaunal species of group 4 are under normal conditions (with well-oxygenated sediment-water interface) living at several centimetres depth in the sediment, in dysoxic, or even completely anoxic conditions (e.g. Jorissen et al., 1998). Their specific habitat, relatively remote from the sediment-water interface where labile organic components are easily available, suggests that

they are not directly dependent on the flux of labile organic matter arriving at the sediment surface. It has been suggested (Caralp, 1989; Alve, 1990; Bernhard, 1992; Jorissen, 1999b) that they feed either on less labile organic components, or on stocks of nitrate and sulphate reducing bacteria, associated with the successive redox boundaries. This could explain why there is apparently no relation between labile organic flux levels and the bathymetrical distribution of intermediate (*Melonis* spp.) and deep infaunal taxa (Figs. 5 and 6).

Although the deep infaunal taxa do not show a preference for specific water depths (or a specific labile organic C flux-level), they do show a very conspicuous W–E decrease of their relative densities. In spite of their relative indifference regarding a precise labile organic flux level, they are much more frequent in the eutrophic than in the oligotrophic areas. This pattern coincides with the situation described in the Adriatic Sea, where Jorissen et al. (1995) show that deep infaunal taxa are fairly abundant down to 600 m depth, but are completely absent on the lower slope and in the deep southern basin. This situation strongly resembles that in area 2. The absence of deep infaunal taxa in the deeper, more oligotrophic (in our study: in areas 3 and 4) can be explained in two ways:

1. The downward organic flux could be too low to allow introduction of consumable organic matter (by bioturbation) into the sediment; almost all nutritious elements are exploited by the surface fauna, and the minor amounts of refractory organic matter introduced into the sediment are too small to sustain important bacterial stocks on which the deep infaunal elements could feed.
2. In the very oligotrophic areas of the deep Adriatic Sea, and in the eastern Mediterranean areas 3 and 4, the lower boundary of the oxic layer is probably situated at substantial depth. Jorissen et al. (1995) suggested that when the redox-boundary reaches below a critical threshold depth (around 10 cm depth), deep infaunal taxa that graze on stocks of nitrate and sulphate-reducing bacteria, are no longer capable of exploiting these resources.

In the Mediterranean Sea, a level of about 2.5 g labile organic carbon $\text{m}^{-2} \text{y}^{-1}$, seems to be an impor-

tant threshold value, coinciding with the lower depth limit of many eutrophic, relatively shallow taxa, and with the upper depth limit of many deeper, oligotrophic taxa. This value, which corresponds to a total flux (labile + refractory components) of about 4.0–4.5 g $\text{m}^{-2} \text{y}^{-1}$, is not very different from the value of 3 g organic C $\text{m}^{-2} \text{y}^{-1}$ (labile + refractory components) which forms an important faunal boundary off NW Africa (Altenbach, 1988). This flux level controls the boundary between a eutrophic biofacies dominated by *Uvigerina peregrina* and a more oligotrophic biofacies dominated by *Cibicidoides kullenbergi* (Parker). In a recent paper, Altenbach et al. (1999) confirm the validity of this important faunal boundary in a study concerning a major part of the Atlantic Ocean. Also in the South China Sea (Jian et al., 1999), a level of 3.5 g organic C $\text{m}^{-2} \text{y}^{-1}$ (labile + refractory components) separates a fauna dominated by detritus feeders (including *Bulimina aculeata* and *U. peregrina*) from a fauna consisting of suspension feeders (for instance *Cibicidoides wuellerstorfi* (Schwager) and supposedly ‘opportunistic’ species. The similarity between the calculated organic flux level at the main faunal boundary in the Mediterranean (present study), and in other sites of the world ocean (see above) strongly suggests a faunal boundary of global significance. The slightly higher projected values in our study could perhaps be explained by the higher sea water temperatures in the Mediterranean. These would cause more intense remineralisation of organic carbon in transit of the water column, so that the calculated values over-estimate the actual labile organic flux to the ocean floor.

5. Conclusions

1. In the Mediterranean Sea, the bathymetrical distribution of most dominant taxa of benthic foraminifera is controlled by the flux of labile organic matter to the sea floor. The upper and lower depth limits of numerous taxa show a close correspondence with the estimated iso-flux lines.
2. The bathymetrical succession of species found in the Mediterranean is almost entirely due to interspecific differences in food requirements; it should be considered as a succession from eutrophic (shallow living) to oligotrophic (deep-living) species.

Consequently, individual species are not indicative of a specific water depth, but of a certain level of organic flux to the sea floor.

3. Also the strong W–E decrease of deep infaunal taxa is suggested to be a the result of the increasing oligotrophy towards the east. Deep infaunal taxa become increasingly rare, either because the deeper sediment layers do no longer contain nutritious material, or because the anaerobic bacterial stocks on which these taxa may graze are situated too deep in the sediment to be exploited.
4. The similarity of the flux level of about $2.5 \text{ g C m}^{-2} \text{ y}^{-1}$, which corresponds to the main faunal boundary in the Mediterranean, and a total flux value of $3\text{--}3.5 \text{ g C m}^{-2} \text{ y}^{-1}$, which has been

mentioned several times in the literature, suggests the existence of a fundamental, constant faunal boundary of global importance.

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Appendix A. Taxonomical framework

<i>Articulina tubulosa</i> (Seguenza, 1862)	Parker, 1958, pl. 1, Figs. 12–13 and Figs. 18–19; Wright, 1978, pl. 1, Figs. 9–10
<i>Bolivina alata</i> (Seguenza, 1862)	Parker, 1958, pl. 1, Figs. 30–32
<i>Bulimina aculeata</i> d'Orbigny, 1826	Parker, 1958, pl. 1, Figs. 17–18; Jorissen, 1987, pl. 4, Fig. 5
<i>Bulimina marginata</i> d'Orbigny, 1826	Parker, 1958, pl. 1, Fig. 23; Jorissen, 1987, pl. 4, Fig. 6a and b
<i>Cassidulina carinata</i> Silvestri, 1896/ <i>Cassidulina laevigata</i> d'Orbigny, 1826	Parker, 1958, pl. 4, Fig. 15; Jorissen, 1987, pl. 1, Fig. 8
<i>Cassidulina crassa</i> d'Orbigny, 1839	Parker, 1958, pl. 4, Fig. 12; Jorissen, 1987, pl. 1, Fig. 3
<i>Chilostomella</i> spp.	Parker, 1958, pl. 4, Fig. 24
<i>Globobulimina</i> spp.	Parker, 1958, pl. 1, Figs. 24–28
<i>Glomospira charoides</i> (Jones and Parker, 1860)	Phleger et al., 1953, vol. 7, pl. 5, Fig. 1
<i>Gyroidina altiformis</i> Stewart and Stewart, 1930	Parker, 1958, pl. 3, Figs. 10–12; Jorissen, 1987, pl. 1, Figs. 7, 11 and 12
<i>Gyroidina orbicularis</i> d'Orbigny, 1826	Parker, 1958, pl. 3, figs. 7–9 and 13–18; Jorissen, 1987, pl. 1, Fig. 13a and b
<i>Hoeglundina elegans</i> (d'Orbigny, 1826)	Wright, 1978, pl. 5, Figs. 15 and 16
<i>Melonis</i> spp.	Parker, 1958, pl. 1, Figs. 36–39; Jorissen, 1987, pl. 4, Fig. 8
<i>Uvigerina mediterranea</i> Hofker, 1932	Parker, 1958, pl. 2, Figs. 39 and 40; Jorissen, 1987, pl. 1, Fig. 2
<i>Uvigerina peregrina</i> Cushman, 1923	Parker, 1958, pl. 2, Figs. 37 and 38; Jorissen, 1987, pl. 1, Fig. 4

Appendix B

Site locations and benthic foraminiferal census data for the taxa used in this paper. All counting data are given as a percentage of the total benthic foraminiferal fauna. A = *Articulina tubulosa*; B = *Bolivina alata*; C = *Bulimina aculeata*; D = *Bulimina marginata*; E = *Cassidulina carinata*/*C. laevigata*; F = *Cassidulina crassa*; G = *Chilostomella* spp.; H = *Globobulimina* spp.; I = *Glomospira charoides*; J = *Gyroidina altiformis*; K = *Gyroidina orbicularis*; L = *Hoeglundina elegans*; M = *Melonis* spp.; N = *Uvigerina mediterranea*; O = *Uvigerina peregrina*

Site	Depth (m)	Latitude (°N)	Longitude (°E)	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
T82/16	210	38.50	1.45	0.0	0.0	3.2	4.2	9.5	3.7	0.5	0.0	0.0	2.1	0.0	0.5	2.1	4.8	0.0
T82/17	320	38.49	1.45	0.0	0.0	1.0	15.2	7.3	2.6	0.0	0.0	0.0	1.6	1.6	0.5	4.2	11.0	0.5

(continued)

Site	Depth (m)	Latitude (°N)	Longitude (°E)	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
T82/18	555	38.43	1.42	0.0	0.0	0.0	20.0	8.2	2.6	0.0	0.0	0.0	2.1	2.6	0.0	13.8	12.3	0.0
T82/19	790	38.39	1.41	0.0	0.0	0.0	5.1	6.6	0.0	0.0	0.0	3.6	1.0	9.1	0.5	10.2	22.8	5.1
T82/20	900	38.37	1.41	0.0	0.0	0.0	1.0	7.8	0.0	0.0	0.0	2.1	1.0	9.8	4.7	11.9	28.5	7.8
T82/22	1500	38.25	1.45	0.0	0.0	0.0	0.0	0.5	0.5	0.0	0.0	18.9	3.0	16.4	5.0	4.0	0.5	1.5
T82/23	1960	38.09	1.45	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	17.0	5.7	28.3	0.0	0.0	0.0	0.0
T82/22	2400	37.89	1.42	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15.8	2.1	11.6	0.0	0.0	0.0	0.0
T82/6	315	38.95	2.86	0.0	0.0	4.3	2.2	13.5	10.8	0.0	0.0	0.0	0.5	0.0	0.0	2.7	1.6	0.0
T82/7	660	38.92	2.83	0.0	0.0	2.7	3.2	10.1	4.8	0.0	0.0	0.0	0.0	2.7	0.0	5.9	10.6	0.0
T82/8	820	38.89	2.81	0.0	0.0	0.7	1.3	13.1	2.0	0.0	0.0	2.0	2.0	3.9	2.6	24.8	26.1	0.0
T82/9	1562	38.89	2.82	0.0	0.0	1.0	1.9	2.4	3.4	0.0	0.0	4.8	0.0	2.4	0.0	5.8	1.0	1.4
T82/10	1920	38.76	2.82	0.0	0.0	0.9	0.0	0.0	0.9	0.0	0.0	1.8	10.7	38.4	5.8	12.1	0.4	0.0
T82/11	2440	38.73	2.81	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.4	13.9	2.4	41.8	0.0	0.4	0.0	0.0
T87/71	2654	38.93	10.59	13.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.8	3.4	3.4	0.0	0.0	0.0	0.0
T87/68	1538	38.68	10.74	8.6	0.0	0.0	0.0	0.0	1.2	0.0	0.0	3.7	3.7	16.0	7.4	7.4	3.7	7.4
T87/67	1326	38.66	10.75	2.7	0.0	0.0	0.0	1.4	0.0	0.0	0.0	18.9	4.1	8.1	10.8	4.1	6.8	6.8
T87/66	1102	38.65	10.76	1.1	0.0	0.0	0.0	8.0	0.0	0.0	0.0	14.9	2.3	5.7	5.7	2.3	6.9	5.7
T87/65	904	38.64	10.78	0.9	0.0	0.0	0.9	15.7	0.0	0.0	0.0	6.1	3.5	8.7	7.0	6.1	7.8	7.8
T87/64	630	38.59	10.83	0.0	0.0	0.0	2.9	25.2	0.0	0.0	0.0	7.2	0.7	0.7	0.7	2.9	7.9	7.9
T87/63	785	38.32	11.24	0.9	0.0	0.0	4.4	6.2	0.0	0.0	0.0	11.5	0.9	3.5	1.8	8.0	12.4	3.5
T87/51	592	36.71	12.03	0.0	0.0	0.0	1.2	9.8	0.6	0.0	0.0	1.2	1.8	1.8	1.8	6.7	1.8	2.5
T87/50	820	36.68	12.08	0.0	0.0	0.0	0.8	4.7	0.4	0.0	0.0	5.5	3.2	5.1	0.0	5.5	11.1	11.1
T87/49	1205	36.67	12.12	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	8.3	1.7	7.5	0.0	3.3	7.5	15.8
T87/55	1256	36.75	12.29	1.6	0.0	0.0	0.0	3.2	0.0	0.0	0.0	14.1	2.7	7.6	0.0	2.7	12.4	9.7
T87/56	917	36.78	12.31	0.0	0.0	0.0	2.6	3.4	1.7	0.0	0.0	16.2	6.8	6.8	0.0	2.6	17.9	8.5
T87/57	512	36.83	12.33	0.0	0.0	1.2	15.3	4.7	4.1	0.0	0.0	1.2	0.6	1.2	0.0	2.4	11.8	2.9
T87/48	1307	36.63	12.50	3.1	0.0	0.0	0.0	0.6	0.0	0.0	0.0	14.3	5.0	10.6	0.0	0.6	6.8	7.5
T87/4	200	39.32	20.01	0.0	0.0	1.5	11.6	9.1	4.5	0.0	0.0	0.0	0.5	0.5	0.5	2.5	2.5	2.5
T82/42	810	36.49	-3.00	0.0	0.0	0.0	14.3	1.5	6.6	2.0	1.0	0.5	1.0	5.6	0.5	8.7	3.1	26.5
T82/54	1080	36.15	-4.47	0.0	0.0	4.3	0.0	0.0	0.9	5.2	7.8	0.9	2.6	5.2	0.9	23.3	0.0	27.6
T82/53	1400	35.82	-4.38	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.0	2.5	0.0	12.5	0.0	20.0	0.0	30.0
T82/34	2520	37.06	-0.49	3.2	0.0	0.0	0.0	0.0	0.0	0.0	0.6	22.3	3.2	24.8	0.0	0.0	0.0	0.0
T87/90	1500	38.54	9.30	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	10.4	3.1	7.3	5.2	14.6	0.0	5.2
T87/83	1301	37.70	8.76	0.0	0.0	0.0	0.0	3.3	0.0	0.0	0.0	9.9	0.7	6.6	10.6	9.3	0.7	16.6
T87/84	1554	37.72	8.73	0.0	0.0	0.0	0.0	1.6	1.6	0.0	0.0	21.9	2.3	7.0	6.3	6.3	0.0	15.6
T87/85	1872	37.80	8.72	0.0	0.0	0.0	0.0	2.5	0.0	0.0	0.0	39.2	2.5	6.3	3.8	6.3	0.0	0.0
T87/87	2587	38.09	8.38	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	33.8	5.9	14.7	0.0	0.0	0.0	0.0
T87/62	1040	38.31	11.28	0.0	0.0	0.0	0.8	7.3	0.0	0.0	0.0	12.2	1.6	4.9	3.3	4.1	18.7	5.7
T87/61	1246	38.25	11.34	0.9	0.0	0.0	1.9	11.2	0.9	0.0	0.0	14.0	0.9	8.4	6.5	5.6	8.4	2.8
T87/128	296	35.49	-2.67	0.0	3.9	7.7	7.7	3.9	7.7	3.9	4.3	0.5	0.5	0.0	0.5	4.3	1.9	3.4
T87/96	397	39.03	9.25	0.0	0.5	0.5	3.8	5.4	5.4	1.6	0.0	0.0	0.0	1.6	0.5	17.4	2.2	0.0
T87/79	511	37.62	8.84	0.0	0.5	0.0	6.0	14.7	8.2	0.0	0.0	2.2	2.2	2.7	0.5	4.9	0.0	4.9
T82/40	300	36.70	-3.13	0.0	1.4	4.8	21.3	0.0	10.6	1.9	0.5	0.0	0.0	0.0	0.5	0.5	0.5	4.3
T82/41	510	36.60	-3.05	0.0	0.0	0.0	22.4	1.0	15.1	2.6	1.6	0.5	0.0	0.5	0.0	5.7	2.1	17.7
T82/45	1480	36.09	-3.85	0.0	0.0	1.1	0.5	8.6	1.6	0.5	2.7	4.8	1.1	4.8	4.8	8.6	0.0	35.8
T82/44	1720	36.19	-3.85	0.0	0.0	0.0	6.7	16.5	6.3	0.0	0.0	0.0	0.4	3.1	2.7	3.1	3.1	4.9
T82/49	210	36.03	-2.89	0.0	0.0	0.0	0.0	29.3	3.3	0.5	0.5	0.0	0.0	1.1	0.0	0.0	0.5	1.1
T87/137	218	35.91	-2.96	0.0	0.5	1.0	0.5	20.6	8.8	0.0	0.0	0.0	0.0	0.0	1.0	1.0	2.6	1.5
T82/48	390	36.04	-2.89	0.0	0.0	0.4	1.1	10.5	3.3	0.0	0.4	0.0	0.4	0.7	1.5	0.7	4.7	0.7
T87/129	419	35.63	-2.74	0.0	11.2	3.6	6.1	2.0	7.1	6.1	5.1	0.0	0.5	0.5	1.5	3.6	6.6	1.5
T87/130	509	35.64	-2.76	0.0	8.5	3.2	5.3	2.1	6.3	5.8	1.6	0.0	0.0	0.0	0.5	2.6	10.1	10.1
T87/136	528	35.90	-2.93	0.0	2.2	0.5	9.7	16.1	5.9	0.5	0.0	0.5	0.0	0.5	0.5	3.2	4.3	1.6
T87/131	704	35.73	-2.88	0.0	2.0	1.5	3.0	1.0	15.3	2.5	3.9	1.0	0.0	4.9	0.0	6.9	1.5	19.2
T87/134	705	35.89	-2.99	0.0	1.5	0.5	2.6	10.8	3.1	1.5	1.5	1.0	1.0	1.5	0.0	7.7	6.2	5.7

(continued)

Site	Depth (m)	Latitude (°N)	Longitude (°E)	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
T87/5	289	39.28	20.00	0.0	0.6	0.0	10.6	16.2	3.9	0.0	0.0	0.0	1.1	0.0	0.6	2.2	4.5	1.1
T87/6	409	39.27	19.99	0.0	0.0	0.0	5.0	14.9	1.7	0.0	0.0	2.8	1.1	1.7	0.0	5.5	7.2	0.0
T87/7	455	39.26	20.00	0.0	0.0	0.0	3.8	14.8	0.5	0.0	0.0	10.4	3.3	1.6	0.0	6.6	4.4	0.0
T87/8	701	39.25	19.97	0.0	0.0	0.0	0.5	10.4	0.5	0.0	0.0	8.2	6.0	1.6	0.5	7.7	13.2	0.0
T87/9	931	39.24	19.98	0.0	0.0	0.0	0.6	10.4	0.0	0.0	0.0	9.2	1.2	8.6	0.0	14.7	6.7	0.0
T87/10	1091	39.20	19.96	0.0	0.0	0.0	0.0	1.8	0.6	0.0	0.0	4.2	4.8	10.9	0.0	16.4	0.0	7.9
T87/11	1322	39.16	19.94	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15.3	6.7	16.0	0.0	19.6	1.2	0.6
T87/12	1505	39.11	19.92	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	39.3	12.9	9.2	0.0	9.8	0.0	0.0
T87/13	1740	38.93	19.90	0.0	0.0	0.6	0.0	0.0	0.6	0.0	0.0	42.6	5.9	21.9	0.0	6.5	0.0	0.0
T87/14	1999	38.57	19.92	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	32.6	8.3	8.8	0.0	8.3	0.0	0.5
T87/15	2510	38.31	19.92	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	70.8	0.0	7.9	0.0	0.0	0.0	0.0
T83/59	273	33.01	22.93	0.0	0.0	0.0	0.0	21.3	0.0	0.0	0.0	1.6	0.0	0.0	0.0	1.6	0.0	0.0
T83/60	462	33.04	22.93	0.0	0.0	2.1	0.7	19.9	0.0	0.0	0.0	4.3	0.7	0.0	0.0	7.8	0.0	0.0
T83/61	642	33.06	22.95	0.0	0.0	0.0	1.0	26.7	0.0	0.0	1.9	2.9	1.0	4.8	0.0	15.2	0.0	1.9
T83/62	815	33.08	22.95	0.0	0.0	0.0	0.0	13.6	0.0	0.0	0.0	4.9	7.8	4.9	0.0	16.5	0.0	1.0
T83/63	1093	33.12	22.98	1.1	0.0	0.0	0.0	1.1	0.0	0.0	1.1	6.7	5.6	5.6	0.0	24.7	0.0	0.0
T83/64	1185	33.13	23.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.7	2.6	23.1	0.0	12.8	0.0	0.0
T83/65	1603	33.18	23.04	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	9.7	6.5	6.5	0.0	9.7	0.0	0.0
T83/66	1849	33.21	23.06	4.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	25.0	0.0	8.3	0.0	0.0
T83/67	2075	33.24	23.09	0.0	0.0	0.0	0.0	0.0	4.2	0.0	0.0	16.7	4.2	16.7	0.0	12.5	0.0	0.0
T83/68	2310	33.29	23.12	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	20.0	0.0	20.0	0.0	0.0	0.0	0.0
T83/16	200	31.32	29.68	0.0	0.0	0.8	0.8	4.7	0.0	0.0	0.0	3.1	2.3	0.0	0.0	3.1	4.7	4.7
T83/17	300	31.36	29.67	0.0	0.0	1.0	1.6	0.0	0.0	0.0	0.0	7.3	4.2	1.6	0.0	3.1	10.5	6.3
T83/19	563	31.43	29.66	0.0	0.0	0.0	2.3	0.0	0.0	0.0	0.0	10.1	3.1	7.8	0.0	3.1	4.7	24.0
T83/20	790	31.55	29.61	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	8.1	3.0	12.1	0.0	2.0	4.0	46.5
T83/23	1465	31.88	29.41	0.0	0.0	0.0	1.4	2.9	0.0	0.0	0.0	35.7	5.7	10.0	0.0	2.9	0.0	0.0
T83/25	2034	32.17	29.29	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	55.6	11.1	22.2	0.0	0.0	0.0	0.0
T83/26	2300	32.37	29.20	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	55.6	11.1	11.1	0.0	0.0	0.0	0.0
T83/27	2620	32.75	29.12	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	47.1	5.9	11.8	0.0	0.0	0.0	0.0
T83/28	3090	32.75	29.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	75.0	0.0	0.0	0.0	0.0	0.0	0.0

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