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Recent benthic foraminiferal assemblages in deep high-energy environments from the Gulf of Cadiz (Spain)

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Abstract

The benthic environment in the Gulf of Cadiz, north-eastern Atlantic, is strongly affected by the Mediterranean outflow water undercurrent (MOW) which flows northwards along the western Iberian Margin at 500-1500 m water depth. Foraminiferal census counts of living and dead assemblages from 27 surface samples ranging from 103 to 1917 m water depth, and the examination of hard substrates reveal a close correlation of the fauna with the local hydrography and sediment facies. Four different faunal groups are separated by factor analysis of the living fauna. Assemblage 1 contains typical lower slope species and dominates samples from the lower MOW core layer and in the North Atlantic deep water below. Shelf edge foraminifera are common in assemblage 2a which shows the highest proportions in samples from 103 to 272 m. Assemblage 2b is dominated by upper slope species and suspension-feeders that are frequent in the upper MOW core layer and in distal settings between 396 and 901 m. Species from assemblage 3 prefer epibenthic habitats and are recorded with high proportions exclusively in the immediate flow paths of the upper MOW between 496 and 881 m. Colonisation structures and species composition of epibenthic assemblages from the proximal facies largely differ from those in distal settings. In general, epibenthic foraminifers only use elevated substrates under the influence of near-bottom flow. Under high current velocities, epibenthic foraminifers prefer large and heavy objects. They colonise high attachment levels where a maximum yield of advected food particles can be achieved. In distal settings at lower flow velocities, the elevation height does not exceed 20 mm above the surrounding sediment surface. This level is related to a hydrologic transition layer with high concentrations of suspended particles. The comparison of microhabitat preferences and faunal structure under high and low current velocities reveal that substrate stability may be a confining environmental variable for endobenthic and shallow epibenthic foraminifers. The observations also indicate that the preferential settling height of epibenthic foraminifera is related to the highest lateral flux rates of food particles within reach from the sea floor. A dynamic selection of elevated microhabitats is only used by 7.8% of all species recognised in the Gulf of Cadiz area. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: benthic foraminifera; epibiotism; continental slope; East Atlantic Ocean

1. Introduction

Benthic foraminifera are widely used for pa-

laeoenvironmental reconstruction. Before application to the fossil record, index species, assemblages or faunal indices have to be calibrated with scaling ecological parameters. A growing number of studies on the recent distribution of living (Rose Bengal-stained) benthic foraminifera prove

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a substantial relationship with the flux of particulate organic matter to the sea floor (Lutze and Coulbourn, 1984; Altenbach and Sarnthein, 1989; Herguera and Berger, 1991; Gooday, 1994; Altenbach et al., 1999; Loubere and Fariduddin, 1999), the oxygen content of ambient bottom waters (Koutsoukos et al., 1990; Hermelin, 1992; Alve, 1995; Bernhard and Sen Gupta, 1999), and high levels of environmental stress (Sharifi et al., 1991; Yanko et al., 1994; Alve, 1995; Hess and Kuhnt, 1996; Stott et al., 1996).

Water turbulence leaves also a certain impact on benthic foraminiferal assemblages. This has been demonstrated indirectly in most cases by a coincidence of changes in assemblage composition at the depth of the wave base and the shelf break where water turbulence markedly decreases (Pujos, 1971; Pujos-Lamy, 1973; Seiler, 1975; Lutze, 1980; Schiebel, 1992; Levy et al., 1993; Debenay and Redois, 1997). In shallow-water, high-energy environments, lateral displacement of foraminiferal tests is common and obstructs environmental interpretations if the living, autochtonous fauna is not considered (Murray, 1970; Murray et al., 1982; Williamson et al., 1984).

Little is known about foraminiferal assemblages in deep high-energy environments. As in shallow waters (Dobson and Haynes, 1973; Haward and Haynes, 1967; Semeniuk, 2000), epibenthic habitats are used with greater abundances under the impact of near-bottom flow regimes (Mullineaux, 1988; Schönfeld, 1997, 1998), and suspensionfeeders are frequent in adjacent places where water turbulence decreases and suspension load settles (Lutze and Altenbach, 1988; Mackensen et al., 1985; Thomsen, 1998). The patchy and sparse distribution of appropriate elevated habitats (Oschmann, 1990) may lead, if not sampled or analysed, to a misinterpretation of the dead assemblage in the near-surface sediment (Mackensen, 1987). Nonetheless, the observations made to date rely only on a few tens of samples from selected areas. The deep, high energy facies deserves attention, however, because it is well established in sea straits which provide pathways for interbasinal faunal exchange and deep-water circulation.

In the present paper, I demonstrate how the

benthic foraminiferal assemblage composition is structured by the influence of the Mediterranean outflow water (MOW) contour current in the Gulf of Cadiz, Spain. Observations of microhabitat colonisation structures reveal the influence of substrate properties, current strength, and the strategies of foraminifera to prevail in this deep high-energy environment.

2. Study area and hydrography

The Gulf of Cadiz forms a southwest-facing, arched embayment of the north-eastern Atlantic ocean between the Gibraltar Strait and Cape San Vincente. The shelf is covered with sand and rock outcrops in places with strong exposure, in particular south of the Algarve and to the east of Cadiz up to Gibraltar (López-Galindo et al., 1999). Extended mud drapes occur on the shelf close to the river mouths of Huelva and Guadalquivir, and in the inner part of the Gulf of Cadiz (Nelson et al., 1999). Glauconitic sands prevail at the shelf edge and pass into muds with intercalated sandy contourite beds on the upper slope (Heezen and Johnson, 1969; Faugères et al., 1984; Sierro et al., 1999). The shelf environment is under influence of North Atlantic Central Water (NACW) from the thermocline (approximately 30-100 m) down to 430 and 600 m depth at maximum (Wüst, 1936). The flow regime in the near-surface water is from northwest to southeast (Lobo et al., 2000).

The MOW is present between 450 and 1500 m. It is the most outstanding hydrographic component in this area and shows higher temperatures and salinities than the NACW (Heezen and Johnson, 1969; Zenk, 1975a). The MOW enters the Gulf of Cadiz through the Gibraltar Strait at depths of 150-280 m (Lacombe et al., 1964). On entering the Atlantic, it cascades down to 700 m depth and rapidly mixes with ambient NACW (Zenk, 1971, 1975b; Ambar and Howe, 1979a). Then it turns clockwise closely following the slope in a narrow vein that divides and reunites again downstream (Madelain, further 1970). The MOW's buoyancy is in disequilibrium with the ambient NACW and it is held upwards only by

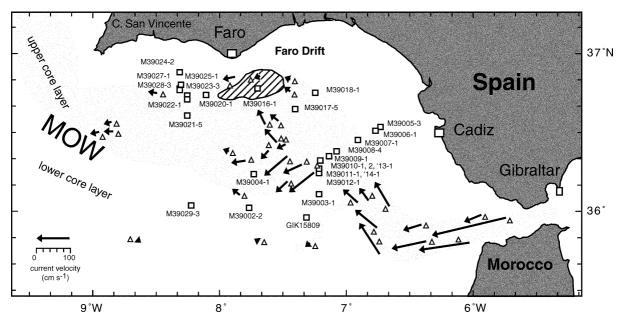


Fig. 1. Location of sampling sites (open squares) in the Gulf of Cadiz, north-eastern Atlantic. The spreading of the MOW is depicted in light and medium grey. The MOW flow strength and direction as obtained from current meter moorings (open triangles) are marked with arrows (after Heezen and Johnson, 1969; Madelain, 1970; Zenk, 1975b; Zenk and Armi, 1990; Nelson et al., 1993). The Faro Drift (hatched area) is given for comparison (Faugères et al., 1984).

Coriolis force (Baringer and Price, 1997). When the current is slowed down at slope-perpendicular ridges or at canyons, the outflow water further descends and spreads at its equilibrium density level between 1000 and 1400 m water depth forming the lower MOW core layer (Zenk, 1975b; Thorpe, 1976; Gründlingh, 1981; Baringer and Price, 1999). Close to the Gibraltar Strait, the current speed is rather high, up to 200 cm s⁻¹ (Bøyum, 1963; Lacombe et al., 1964; Kinder and Bryden, 1987). In the northern branch, the current in the upper core layer slows down to 100 cm s⁻¹, and the velocity further decreases to about 13 cm s^{-1} in distal settings off Cape San Vincente (Meincke et al., 1975; Ambar and Howe, 1979b; Nelson et al., 1993). The currents are slow in the lower core layer, where only $5-10 \text{ cm s}^{-1}$ are recorded (Heezen and Johnson, 1969).

The bottom sediments in the MOW depth interval also reflect the decrease in current strength from east to west. Hard rock outcrops and gravel lags occur in proximal areas in the east (Heezen and Johnson, 1969; Nelson et al., 1993). Sand and sandy silt covers the sea floor along the main flow paths, and silt and clayey silt prevails in quiet zones outside and in between the MOW veins (Nelson et al., 1999). The MOW flow has also resulted in the build up of the Faro Drift and other sediment drift bodies in the west that consist of sandy to silty sediment accumulated and sorted under the current regime (Fig. 1) (Gonthier et al., 1984; Faugères et al., 1984, 1999; Stow et al., 1986).

Below the MOW, North Atlantic deep water is present and shows only slow movements (Zenck, 1980). The bottom sediments pass from hemipelagic silty clays into foraminiferal oozes (Lebreiro et al., 1997).

Summer upwelling due to persistent northerly winds is a common feature of the entire western Iberian coast (Abrantes, 1988). Intensity maxima are recognised in the coastal regions off Galicia (42–44°N) and off Cape Sines at 38°N (Fiúza, 1983; Fiúza et al., 1982). In the Gulf of Cadiz, seasonal upwelling only takes place in the north-

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ern part, off the Algarve coast between Cape San Vincente and Faro. Satellite sea surface temperature images processed by the Plymouth Marine Laboratory Remote Sensing Group indicate that upwelling off the Algarve seldomly reaches intensities as off northern Iberia (e.g. http://www. npm.ac.uk/rsdas/composite/po comps/full size/ weekly_all/1998/). Satellite data reveal that ocean surface productivity ranges from 153 to 219 g C m^{-2} yr⁻¹ in the Gulf of Cadiz (Sathyendranath et al., 1995) while earlier compilations of primary productivity maps allow an estimate of 82 g C m^{-2} yr⁻¹ for the entire Cadiz region (Berger et al., 1987). Later approaches reckon 90-150 g C m⁻² yr⁻¹ from Coastal Zone Colour Scan remote sensing data (Antoine et al., 1996).

3. Material and methods

3.1. Foraminiferal studies

Twenty-seven sediment surface samples from the Gulf of Cadiz were used in this study. They were recovered with a large box corer with 50×50 cm surface area and a Van Veen grab sampler of 45×45 cm size during RV *Meteor* cruise M39 in April and May 1997 (Schott et al., 1999). One sample (GIK15809) from RV *Noroit* cruise KR 84 in 1984 was also analysed. That sample was also recovered with a large box corer.

Macrobenthos and other hard substrates like mollusc shells, ships clinker, deep-water corals, hydroids, and sponges were carefully removed from the sediment surface of box cores and conserved in methanol. These objects were later examined for attached epibenthic foraminifers. The maximum height of the substrates or points of attachment above the ambient surface was recorded. For massive objects as pebbles and shells that were partly embedded in the surface sediment, zero level for attachment height was assigned to a horizon from where below traces of fine sediment were still sticking to the object. For free-standing, delicate substrates as hydroids, Rhabdammina tubes or Pheronema sponges, a 'mudline' of fine, adherent sediment was commonly recognisable.

A volume-defined sample from the uppermost centimetre of the surface sediment was taken and immediately conserved and stained with a solution of 2 g Rose Bengal in 1 l methanol p.a. (Lutze and Altenbach, 1991). This sample was used to study the living, shallow epi- and endobenthic foraminifers, and the dead assemblage in the surface sediment. The surface area sampled was $173-260 \text{ cm}^2$ on box core surfaces and $87-150 \text{ cm}^2$ on grab sample surfaces. A representative coverage of different microenvironments on the sediment surface was attempted wherever possible.

The samples for foraminiferal studies were washed on a 63-µm mesh screen. They were first passed through a 2000-µm sieve to collect larger particles and fragile tubular arenaceous foraminifers which can be damaged if washed too long. The dried residues were further divided into the grain-size fractions 63-250 µm, and 250-2000 µm. Benthic foraminifers were analysed from the fraction $> 250 \,\mu\text{m}$ to exclude smaller forms which are often displaced by redeposition (Lohmann, 1978; Lutze, 1980), and to make the data comparable to previous benthic foraminiferal studies in adjacent areas (Lutze and Coulbourn, 1984; Schönfeld, 1997). The samples were then picked for wellstained benthic foraminifers that are considered to have been living at the time of sampling (Murray and Bowser, 2000). From sand-rich samples (e.g. M39009-1 and M39023-3), splits of up to 1/8 were made to facilitate microscopic work. Arenaceous, and thick-walled miliolid species were either soaked with water to make their staining pattern more visible or crushed to see whether the test contained protoplasm. After the living forms were sorted out, a further split was made and picked for dead foraminifers. Living and dead assemblages were collected in Plummer cell-slides, sorted at species level, fixed with glue, and counted.

Multivariate statistical analyses were applied to the faunal census data by using StatView 4.02© Abacus Concepts, Berkely, CA, USA, for Macintosh[®]. Species were grouped by factor analysis with principal component solution and varimax rotation.

4. Results and discussion

4.1. Foraminiferal assemblages in surface sediments

The foraminiferal fauna shows middle to upper bathyal characteristics and is very similar to assemblages previously described from other adjacent parts of the eastern North Atlantic (Calvez, 1958; Colom, 1952; Seiler, 1975; Lutze, 1980; Levy et al., 1995; Schönfeld, 1997). 192 different species are recognised, of which 74 are Textulariina, 30 are Miliolina and 88 are Rotaliina. To reduce the high species number to a practical size, only those species which occur in at least one sample among the first five ranked species were taken into consideration. This results in a reduction to 58 and 57 species which comprise 67.3-87.0% and 64.9-89.7% of the living and dead assemblage, respectively. Taxonomic references and the percentages of living and dead benthic foraminiferal taxa that are used for the multivariate analyses are given in Appendices 1-3.

Factor analyses were applied to the reduced data sets in order to obtain species associations with distinct depth distributions or demands to specific environmental conditions. Living and dead assemblages were not combined but analysed separately. Foraminiferal species were assigned to different associations following the analvsis of the living assemblage. The living fauna is considered to be in equilibrium with the ambient environmental parameters and not biased by redeposition, postmortal loss of arenaceous species, and degradation due to bioerosion (Murray et al., 1982; Schröder, 1986; Martin and Liddell, 1991). For 58 frequent benthic foraminiferal species from 21 samples where the living assemblage has been assessed, the analysis extracts 65 factors. The four first ranked factors are clearly separated from the others by their variance proportion, and they account for 46.7% of the total variability of the data set (Table 1). The best resolution of faunal groups is achieved between factors 1 and 2. Factor loading of species infer three main clusters that are assigned to Assemblages 1, 2 and 3 (Fig. 2). Assemblage 2 may be subdivided further into assemblages 2a and 2b.

Species of Assemblage 1 show high, positive factor 1 loading (>0.243) and only low factor 2 loading (-0.148-0.037). The cumulative percentages of this group show a successive increase with water depth from 0.3% at 103 m to 48.2%at 802 m (Fig. 3). Only a slight increase to 66.0% at 1917 m is achieved below. The interval between 901 and 945 m from where on percentages of Assemblage 1 do not increase substantially with depth is close to the upper boundary of the lower MOW core layer in distal settings (Zenk and Armi, 1990). Assemblage 1 from the Gulf of Cadiz contains several species that were previously grouped in the 'Lower Slope Association' off southern Portugal (Schönfeld, 1997), e.g. Cibicidoides kullenbergi, Cribostomoides subglobosum, Saccorhiza ramosa and Trochammina spp. There, the first significant increase of 'Lower Slope Association' percentages is recognised between 968 and 1103 m, which is only slightly deeper than the comparable change in the Gulf of Cadiz. The major shift to greater proportions of the 'Lower Slope Association' occurs off southern Portugal about 1000 m deeper, below the MOW. Although the lower MOW core layer is not very well covered by the present data set from the Gulf of Cadiz, all samples from that depth interval and the one below are dominated by Assemblage 1. They are located close to the margins of the area where the MOW flow impinges the sea floor and hence represent a deep and distal facies (Fig. 4).

Assemblage 2 is characterised by high negative to low positive factor 1 loading (-0.599-0.110)and negative to low positive factor 2 loading (-0.370-0.062). It may be subdivided into assemblage 2a (factor 1 < -0.233) and Assemblage 2b (factor 1 > -1.74) (Fig. 2, Table 1). Assemblage 2a contains typical shelf foraminifera, as Nonion asterizans and Ammonia beccarii, and species that were previously designated to the 'Shelf Edge Association' off southern Portugal (Amphicoryna scalaris, Globobulimina sp. 324, Uvigerina elongatastriata, and Uvigerina sp. 221; Schönfeld, 1997). The highest proportions of this subgroup are found in all samples from the shelf and uppermost slope at depths of 103-272 m (Figs. 3 and 4). Between 272 and 496 m, Assemblage 2a is gradually replaced by Assemblage 2b and further de-

Table 1 Factor loadings and resulting species groups of the living fauna

Assemblage I:		Factor 1	Factor 2	Factor 3	Factor 4
Bultmön stritat mexicana 0.599 0.005 -0.085 0.003 Cibiciabides kullenbergi 0.544 0.012 -0.015 0.114 Cibiciabides paculongerianus 0.750 0.037 0.092 0.161 Crithonina hispida 0.515 0.035 -0.024 0.021 Cyclammina cancellata 0.308 -0.043 -0.062 1.052 Glomospire chronitals 0.59 -0.043 0.000 0.091 Hyperammina laveigata 0.517 0.043 0.000 0.091 Rhizammina digaeformis 0.687 -0.043 0.000 0.091 Saccamina sphaerica 0.687 -0.067 0.266 0.114 Sphaeroidha bulloides 0.355 -0.067 0.266 -0.131 Tochamming dibigeriniformis 0.404 </td <td></td> <td></td> <td></td> <td></td> <td></td>					
Chickides kullenbergi 0.544 0.012 -0.015 0.114 Chickides subglobosum 0.382 0.002 0.056 0.106 Crithionin kipida 0.515 0.005 -0.024 0.021 Cyclammina curellata 0.382 -0.033 0.061 -0.029 Gionopira charoides 0.599 -0.032 0.135 -0.062 Hyperanmina laevigata 0.597 -0.038 0.006 0.091 Rhizammina algeformis 0.683 -0.067 0.266 0.114 Sacconiza ramosa 0.683 -0.067 0.266 0.114 Sphaeroidha hulloides 0.355 -0.062 0.155 0.158 Tochammina bellingshauseni 0.260 -0.026 -0.051 -0.031 Trochammina bellingshauseni 0.418 -0.068 0.026 -0.051 -0.031 Tochammina bellingshauseni 0.418 -0.068 0.026 -0.275 -0.236 Urigerina medita folder -0.530 -0.137 -0.491 0.220 <td< td=""><td>Ammolagena clavata</td><td></td><td></td><td></td><td></td></td<>	Ammolagena clavata				
Chrichides pseudoningerianus 0.882 0.002 0.056 0.066 Cribrostomoides subglobosum 0.750 0.037 0.092 0.161 Cribrostomoides subglobosum 0.515 0.005 -0.024 0.021 Cyclammina cancellata 0.308 -0.043 0.000 0.239 Hyperannina levigata 0.519 -0.043 0.000 0.091 Rhizammina levigata 0.587 -0.043 0.000 0.091 Rhizammina levigata 0.587 -0.063 0.183 Saccanita sphaerica 0.685 -0.067 0.266 0.114 Sphaeroidina buloides 0.355 -0.063 0.155 0.158 0.165 0.158 Tochammina sphaerica 0.404 0.249 0.180 0.766 -0.031 Virgerina gregrina para 0.242 0.349 0.180 17cohamina splotigerinformis 0.444 0.368 0.082 0.161 Tochamina splotigerinformis 0.444 0.348 0.082 0.178 Dot18 Virgerina mediterranea 0.243 -0.148	Bulimina striata mexicana		0.005		0.003
Cribrosimoides subglobasam 0.750 0.037 0.092 0.161 Cribinomia hispida 0.315 0.005 -0.024 0.021 Cyclammina cancellata 0.308 -0.043 0.061 -0.029 Glomospira charoides 0.249 -0.032 0.135 -0.062 Hyperannina levigata 0.519 -0.043 0.000 0.012 Saccamina sphaerica 0.689 -0.063 0.155 0.158 Saccarhia ramosa 0.685 -0.063 0.155 0.158 Tochammina belingshauseni 0.260 -0.026 -0.031 1.758 Tochammina globigerinformis 0.418 -0.068 0.276 -0.031 Trochammina belingshauseni 0.202 -0.063 0.155 0.158 Tochaminia globigerinformis 0.418 -0.068 0.276 -0.031 Viegerina machiterranea 0.232 -0.063 0.155 0.018 Viegerina machiterranea -0.330 -0.216 -0.031 -0.249 0.267 Annnosciala	Cibicidoides kullenbergi	0.544	0.012	-0.015	0.134
Crithinina hispida 0.515 0.005 -0.024 0.021 Glomospira charoides 0.549 -0.081 -0.010 0.239 Ihperannina clongata 0.230 -0.081 -0.010 0.239 Ihperannina lavigata 0.519 -0.043 0.000 0.091 Rhizaminia digaefornis 0.587 0.003 0.128 Saccanita spherica 0.689 -0.050 0.441 0.187 Saccanita spherica 0.685 -0.067 0.266 0.118 Saccanita spherica 0.404 0.024 0.349 0.180 Saccanita spherica 0.240 -0.026 -0.051 Tochamina segas 0.404 0.024 0.349 0.180 Tochamina boliogeratinomis 0.240 -0.042 -0.051 Tochamina segas 0.418 0.368 0.082 0.155 0.158 Uvigerina paregrina parva 0.230 -0.044 0.024 -0.031 Tochaminia segas 0.404 0.024 -0.031 Assemblage 2a: - - 0.307 -0.4	Cibicidoides pseudoungerianus	0.382	0.002	0.056	0.106
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Hyperammina languata 0.290 -0.032 0.135 -0.062 Hyperammina lavitgata 0.519 -0.043 0.000 0.091 Rhizammina adgacformis 0.587 -0.008 0.003 0.128 Sacconitia amosa 0.689 -0.067 0.256 0.114 Sphaerica 0.685 -0.063 0.155 0.158 Tolypammina vagans 0.404 0.024 0.349 0.180 Trochammina belingshasseni 0.200 -0.026 -0.031 Tochamina belingshasseni 0.404 0.368 0.082 Uvigerina mediterranea 0.243 -0.148 -0.066 0.276 -0.031 Assemblage 2a: - - - -0.041 0.260 -0.274 0.220 Ammonia becarii -0.504 -0.296 -0.754 0.267 - - -0.473 0.282 0.135 0.018 - - - - - - - - - - - - - -	Cyclammina cancellata	0.308	-0.043	0.061	-0.029
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	Vulvulina pennatula	0.079	0.000	0.291	0.027

Table 1 (Continued)

	Factor 1	Factor 2	Factor 3	Factor 4
Assemblage 3:				
Ammodiscus tenuis	-0.075	0.930	-0.153	0.033
Cibicides lobatulus	-0.104	0.955	-0.067	0.046
Cibicides refulgens	-0.075	0.932	-0.139	0.035
Cibicidoides sp.	-0.037	0.702	0.057	0.171
Deuterammina ochracea	-0.109	0.910	-0.153	-0.155
Discanomalina semipunctata	-0.026	0.830	0.060	0.077
Pyrgoella sphaera	-0.074	0.931	-0.148	0.034
Trifarina angulosa	-0.161	0.329	0.137	0.018
Variance proportion (%)	15.3	12.2	10.1	9.1

creases with depth below. The transition between both subgroups is recorded within that depth interval where the change of 'Shelf Edge Association' to 'Upper Slope Association' is recognised off southern Portugal (268–498 m). It is still deeper than off NW Africa (100–200 m; Lutze, 1980) or the Bay of Biskay (230–290 m; Pujos-Lamy, 1973).

Assemblage 2b is dominated by species previously assigned to the 'Upper Slope Association' off southern Portugal, in particular passive suspension-feeders (Jacuella obtusa, Marsipella elongata, Rhabdammina abyssorum) (Mackensen, 1987; Linke and Lutze, 1993; Thomsen, 1998) or elevated epibenthic species (Hanzawaia concentrica, Planulina ariminensis, Vulvulina pennatula) that pursue active suspension-feeding (Lutze and Thiel, 1989; Schönfeld, 1997). High proportions of Assemblage 2b are found in samples from the upper MOW core layer and the transition layer above. Most of them are located in distal settings including the top of Faro Drift (Fig. 4). The depth interval where this subgroup dominates the foraminiferal fauna is 396-901 m (Fig. 3).

Species of Assemblage 3 show low, negative factor 1 loading (-0.026 to -0.161) and high, positive factor 2 loading (> 0.329). The majority of species from this group is adapted to epibenthic habitats (*Cibicidoides* sp., *Cibicides lobatulus, Cibicides refulgens, Deuterammina ochracea, Discanomalina semipunctata*). Among the Assemblage 3, *Trifarina angulosa* shows a distinctively lower factor 2 loading than the other species (Fig. 2, Table 1). *Trifarina angulosa* is a cosmopolitan,

shallow infaunal species (De Stigter et al., 1998; Schönfeld, 2001), and occurs in low to moderate abundances from subtidal to middle bathyal depths (e.g. Seiler, 1975; Lutze, 1980; Jorissen, 1988). High percentages are recorded from current-swept passages (Hayward et al., 1994), coarse, biogenic sands on the inner shelf (McGann, 1996), and deep, high-energy environments on the outer shelf and upper slope (Mackensen et al., 1985; Violanti, 1996). It is often associated with *C. lobatulus, C. refulgens*, and *Planulina exorna* (=*Planulina ariminensis*). Apparently, *T. angulosa* is adapted to strong water turbulences of varying intensity (Mackensen,

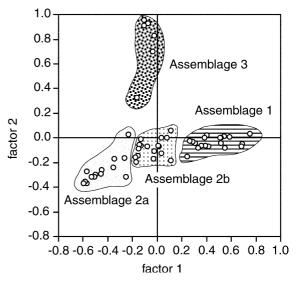


Fig. 2. Orthogonal plot of factor loading from 58 first five ranked species of the living fauna (Table 1).

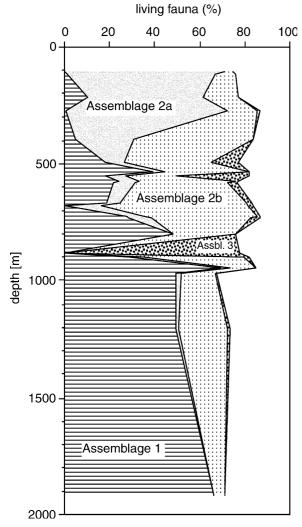


Fig. 3. Depth distribution of cumulative percentages of Assemblages 1, 2a, 2b and 3.

1987). As observations of living specimens attached to large particles have not been reported to date, the species seemingly occupies interstitial microhabitats in the coarse-grained sediments where it may withstand water turbulence. *Trifarina angulosa* is assigned to Assemblage 3 because of their adaptation to similar environments as the other, though epibenthic members of this group.

The highest proportions of Assemblage 3 are found in three samples (M3910-2, M39018-1 and

M39028-3) from 496 to 881 m water depth (Fig. 3). They are located in the immediate flow paths of the upper MOW (Fig. 4). Sample M39010-2 was taken from the centre of a slopeperpendicular channel wherein a current ribbon flows down to the lower MOW core layer (Nelson et al., 1993). The bottom sediment is a coarse sand rich in pebbles and biodetritus from bivalves, gastropods, balanids, bryozoans, and deep-water corals ('valley floor facies' after Nelson et al., 1999). A current velocity of 50 cm s⁻¹ has been recorded 15 m above the seabed 9 km further downstream in that channel (Howe, 1982: Station 21104), whereas 26 cm s^{-1} has been measured at an adjacent mooring outside the main flow path (Madelain, 1970: Station C6). Samples M39018-1 and M39028-3 were taken from the centre of the northernmost, slope-parallel channel (locally named 'Fossa Alvarez Cabral'; Faugères et al., 1984). The bottom sediment is a silty fine sand (M39018-1) and medium sand (M39028-3). Flow velocities of up to 40 and 80 cm s⁻¹ are reported from this channel (Stow et al., 1986), and 20 cm s⁻¹ from adjacent sites outside the main flow (Madelain, 1970; Howe, 1982). Assemblage 3 therefore characterises proximal settings under the influence of strong and persistent near-bottom currents.

Factor analysis of the dead assemblage only allows the recognition of three species groups, that resemble to a large extent Assemblages 1, 2a and 2b from the living fauna. Index species from Assemblage 3 of the living fauna are grouped together with those of Assemblage 2b. As such, the dead assemblages only display shelf edge conditions, MOW influence, and the environmental conditions of the lower MOW core layer, even though this depth interval is not well represented by the present sample set. The living assemblages trace, however, the top and bottom of the upper MOW core layer and allow separation of environments of high and low hydrodynamic energy.

4.2. Colonisation structures

Samples from locations with a proximal highenergy facies in the eastern Gulf of Cadiz retrieved sand with pebbles, gravel lag and outcrop

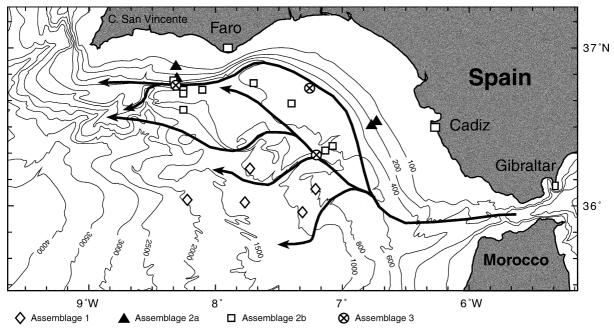


Fig. 4. Location of samples dominated by the foraminiferal assemblages. The area where the immediate MOW undercurrent sweeps along the bottom with salinities > 36.40 PSU is marked in light grey (after Heezen and Johnson, 1969; Madelain, 1970; Thorpe, 1976; Ambar and Howe, 1979a,b). Arrows indicate the main MOW flow paths (after Howe, 1982). The bathymetry in metres is given for comparison. Note that the MOW flow may detach from the sea floor at depths below 1200 m.

slabs. Even megacurrent ripples migrating on an omission surface were recovered with a box core on station M39009-1 from a small terrace about 200 m above the valley floor of a slope-perpendicular channel. The standing stock of the entire benthic foraminiferal fauna is with 2.4 living specimens per 10 cm³ rather low at this location. The epibenthic population density is also low (0.5)specimens per 10 cm²). In the neighbouring sample M39010-2 from the channel centre, attached forms are with 2.0 specimens per 10 cm² more frequent than free-living species (1.4 specimens per 10 cm²) but they are not observed on pebbles smaller than 5-7 mm in diameter. Large blocks, however, are densely stocked by epibenthic foraminifers. Discanomalina semipunctata, Cibicides lobatulus, and Cibicides refulgens are most frequent, whereas Placopsilina confusa, Deuterammina ochracea, Gavelinopsis translucens, Trochammina squammata and others occur in moderate abundances (Fig. 5, Appendix 4). These species even inhabit ships clinker (sample M39014-1) that is typically avoided elsewhere (Schönfeld,

1997). The blocks are squattered only in the upper part, preferentially above 20 mm (sample M39014-1). Large numbers of foraminifers were found attached to free-standing hydroids collected from the top of an outcrop slab (sample M39010-1). The attachment point of the hydroids is about 140 mm high. Up to 67 foraminifers were found on one hydroid colony (Fig. 5). The average epibenthic population density on the outcrop slabs is with 2.1 specimens per 10 cm² very similar to that of the adjacent surface sediment sample M39010-2 (2.0 specimens per 10 cm^2) where smaller pebbles are inhabited, preferentially fragments of coral stems. On the flat and shallow outcrop slab (15 mm high) retrieved at the adjacent station M39013-1, where no prominent hydroid colony or other elevated point is available, the average population density is with 0.5 specimens per 10 cm² substantially lower. Nonetheless, only large and heavy objects seem to provide a sufficient substrate stability for epibenthic foraminifers in this environment. Sands and small pebbles are permanently reworked, and only specialised endo-

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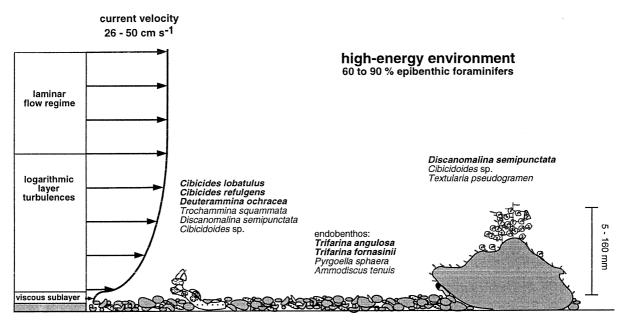


Fig. 5. Epibenthic colonisation structures in high-energy environments in the Gulf of Cadiz (samples M39010-1, M39010-2). A schematic current strength section with distance from the sea bed (not to scale) indicates the different hydrodynamic environments. Frequent species are marked in bold. Epibenthic foraminifers prefer elevated positions on hydroids (grey lines) or large fragments of deep-water corals (stippled).

benthic forms, as for instance *Trifarina angulosa*, could keep pace with erosion and redeposition. Current meter moorings in this area recorded near-bottom velocities ranging from 26 to 50 cm s⁻¹ (Madelain, 1970; Zenk, 1975b). Epibenthic foraminifers that thrive on suspension-feeding may find even higher food particle fluxes if they settle on more elevated substrates at high current velocities (Muschenheim, 1987; Altenbach et al., 1993; Auffret et al., 1994; Thomsen, 1998). This may explain why the large blocks are only inhabited on the top, and why the population density is lower on shallower objects.

The hydrodynamic environment leaves also an impact in the faunal composition. *Cibicides refulgens* and *Deuterammina ochracea* are frequent in the epibenthic associations in proximal areas. They co-occur with *Quinqueloculina aspera*, *Quinqueloculina intricata* and *Spiroloculina excavata* in the dead assemblage. These species are common in boreal high-energy shelf environments in the Channel area (Calvez, 1958; Rosset-Moulinier, 1986; own data), Irish Sea (Dobson and Haynes, 1973), Rockall Plateau (own data), and off northern Norway (Mackensen et al., 1985; own data), and they were not recorded off south-western Iberia to date.

The situation is quite different in distal settings to the west where the bottom sediment is sandy silt to silty clay (M39020-1 to M39023-3). The standing stock varies between 14 and 39 living specimens per 10 cm³. The near-bottom current velocities are in the range of $4-25 \text{ cm s}^{-1}$ (Heezen and Johnson, 1969; Madelain, 1970; Zenk, 1975b), and hence distinctively lower than in proximal settings. The dominant constituent of the foraminiferal fauna are tubular arenaceous species, mostly Rhabdammina abyssorum, that make up to 60% of the living assemblage. The tubes again provide substrates for a diverse epibenthic assemblage of Crithionina pisum, Trochammina squammata, Saccammina sphaerica, Rosalina anomala and others (Fig. 6). They also use other objects as colonising substrates, in particular haleciid hydroids, pteropods, mollusc shells, echinoid spines, and sponges. Not all potential objects are colonised, only one of five and one of six in samples M39021-2 and M39022-1 (Ap-

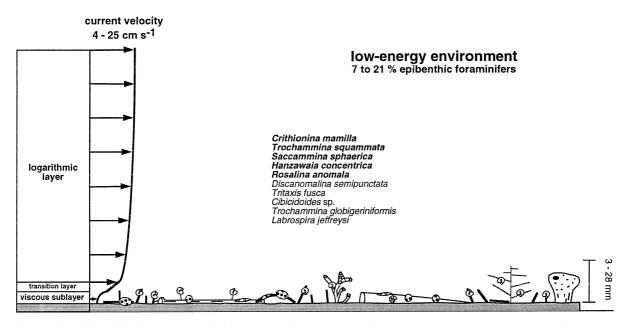


Fig. 6. Epibenthic colonisation structures in low-energy environments (samples M39020-1, M39021-5, M39022-1 and M39023-3). A schematic current strength section with distance from the sea bed (not to scale) indicates the different hydrodynamic environments and the transition layer, where suspended particles are concentrated. Frequent species are marked in bold. Epibenthic foraminifers (stippled: *Crithionina* spp.) use a wide variety of substrates as *Rhabdammina* tubes (thick lines), haleciid hydroids (branched and curved tubes), other hydroids (grey lines), pteropods, mollusc shells, and echinoid spines. They concentrate on a distance of 3–28 mm above the sea bed.

pendix 4). The elevation of the attached foraminifers above the ambient sediment surface typically does not exceed 28 mm, though more elevated substrates are available. This level at about 3 cm height is related to the transition layer between the viscous sublayer close to the sea floor, where a laminar flow regime dominates, and the turbulent logarithmic layer above. The transition layer forms a hydrologic boundary and entraps suspended particles (Altenbach et al., 1988; Rahm and Svensson, 1989). Particle concentration and lateral flux decrease again with distance from the sediment surface and would not provide a substantial higher yield of food particles for epibenthic foraminifers at more elevated positions (Thomsen, 1998).

4.3. Epibenthic assemblages

A compilation of occurrence and settling height above the ambient sediment surface shows that substrates elevated higher than 0.5 cm above the

sea floor are inhabited by epibenthic foraminifera only below 550 m water depth (Fig. 7). There is one exception, sample M39018-1 from the northernmost, slope-parallel channel. In particular Cibicidoides sp., Cibicides lobatulus, Discanomalina semipunctata, Planulina ariminensis, Textularia pseudogramen, Trochammina squammata, and Vulvulina pennatula change their settling height between 550 and 576 m. At shallower water depths, they only use low objects even though more elevated substrates are still available. Cibicides refulgens, Cibicides sp., Deuterammina ochracea, Epistominella rugosa, Gavelinopsis translucens, Guttulina sp. (fistulous variety), Placopsilina confusa, and Spiroplectinella sagittula may also use elevated microhabitats.

The capability of dynamic, elevated microhabitat selection in order to optimise food acquisition under near-bottom currents has been suggested as competitive advantage for selected species forming the 'Epibenthos Group' off southern Portugal (Schönfeld, 1997; Schönfeld and Zahn, 2000).

sample	depth [m]	Ammodiscus anguillae	Cibicidoides sp.	Cibicides lobatulus	Cibicides refulgens	Cibicides sp.	Crithionina hispida	Crithionina mamilla	Deuterammina ochracea	Discanomalina semipunctata	Epistominella rugosa	Gavelinopsis praegeri	Gavelinopsis translucens	Guttulina sp. (fistulous variety)	Hanzawaia concentrica	Hanzawaia rhodiensis	Labrospira jeffreysii	Placopsilina confusa	Planulina ariminensis	Rosalina anomala	Rosalina obtusa	Saccammina sphaerica	Saccorhiza ramosa	Spiroplectinella sagittula	Textularia pseudogramen	Tritaxis fusca	Trochammina bellingshauseni	Trochammina earlandi	Trochammina globigeriniformis	Trochammina squammata	Vulvulina pennatula	elevated substrates
M39024-2	103		0	0	0																			0	۲							
M39005-3	118			0													٠								0							
M39006-1	214							٠														◙			0			0				Ø
M39025-1	272		٠							ο														۲	0							
M39027-1	396			0		0													0		٠	0		Θ								
M39007-1	454		0	0															0					ο	0							
M39018-1	496																		ο				٠		۲							Ø
M39017-5	532		0	0											0	0			0				۲						•		0	٥
M39028-3	550		0		0											0			0	0			٠	ο	0							
M39008-4	576	0	0				•																۲	0					•			٥
M39016-1	581	•			0	0												•	0			Θ	0	0								٥
M39022-1	667	◉		۲	•	٠	•								0	0							0						•			Ø
M39009-1	681		ο	0						0					0				0			0		0	0							
M39020-1	726	•		0			٠						٠			0			۲			۲		0					٠			٥
M39023-3	730	•														0								0			٠					٥
M39003-1	802			0			•																0									٥
M39011-1	846		0	<u> </u>	<u>°</u>	0				<u>°</u>			_						•	0				0	0							_
M39014-1	850																															٥
M39013-1	871																														600000	٥
M39012-1	873		0	0	0	0				0									0	0				0			Ν	Л(W	1	
M39010-1	878																															٥
M39010-2	881																		0	0				0	0							٥
M39021-5	901	1	0		0										0		•		0				0								0	٥
GIK15809	945	•		ο			•												0				0		•		0		0		0	
M39004-1	966														۲							۲	۲									٥
M39002-2	1208	0		0			•					•			1. Mar 200								۲			0		-			0	٥
M39029-3	1917						•																0				0	0	•			٥
Foraminife		rence	e	• i			-	ass			-						lead	d as	sen	nbla				-		-						lages
Living spec	imens				atta	ache	ed to	o sh	allo	ws	ubs	trate	es (< 0,	5 cr	n)				a	ttac	hed	l to	elev	ate	d su	ıbst	rate	s (≥	:0,5	cm)	

Fig. 7. Depth distribution and attachment elevation of epibenthic foraminifers in the Gulf of Cadiz. Elevated substrates are preferentially occupied in the depth interval of the Mediterranean outflow (grey box).

This association is slightly different in the Gulf of Cadiz area under higher current velocities. With 15 out of 192 species recognised, the elevated epibenthic assemblage comprises 7.8% of the entire faunal spectrum which is more than double their

proportion off southern Portugal (3.6%) where the current strength is lower on average. *Cibicides refulgens*, *Cibicides* sp., *Cibicidoides* sp., *Deuterammina ochracea*, *Discanomalina semipunctata*, *Epistominella rugosa*, *Gavelinopsis translucens*, Guttulina sp. (fistulous variety), Placopsilina confusa, Spiroplectinella sagittula, Textularia pseudogramen, and Trochammina squammata supervene to the elevated epibenthic assemblage whereas Discanomalina coronata and Epistominella exigua were not recorded in the Gulf of Cadiz. Hanzawaia concentrica apparently prefers low substrates here even though elevated positions were available in the samples studied.

The majority of species from Assemblage 3, as described above, show elevated microhabitat preferences. Highest proportions of this group were recorded in samples from the immediate MOW flow paths. The depth limit from where below epibenthic species change their settling height and use elevated substrates is in good agreement with the upper boundary of the MOW. Elevated epibenthic foraminifers are therefore considered as reliable indicators for the impact of the MOW contour current in the Gulf of Cadiz, and further downstream off southern Portugal (Schönfeld, 1997).

5. Summary and conclusions

The impact of the MOW contour current on recent benthic foraminiferal assemblages is studied in the Gulf of Cadiz, Spain. Factor analyses of living and dead assemblages allows the recognition of four and three different faunal groups. Factor analysis of the dead assemblage displays the shelf edge, upper, and lower MOW environments. The four groups obtained from the living assemblages trace the upper boundaries of MOW core layers, and they discern different biofacies under weak and strong near-bottom currents.

Epibenthic foraminiferal assemblages are dominated by *Discanomalina semipunctata*, *Cibicides lobatulus*, and *Cibicides refulgens* under high near-bottom flow velocities of 26–50 cm s⁻¹ in the eastern Gulf of Cadiz. The species prefer objects larger than 5–7 mm in diameter that provide a certain microenvironment stability and attach at prominent points. This may be explained by a higher yield of advected food particles with distance from the sediment surface at high current velocities. In the western Gulf of Cadiz, epibenthic foraminifers such as *Crithionina pisum*, *Trochammina* squammata, Saccammina sphaerica, and Rosalina anomala use Rhabdammina abyssorum tubes and other small objects, but their elevation does not exceed 28 mm. This level is related to the transition layer with high concentrations of suspended particles. Abundance and lateral flux of particles decreases again with distance from the sediment. More elevated positions do therefore not provide a better food yield at low current velocities of 4– 25 cm s⁻¹.

Colonisation structures, standing stock, and assemblage composition under high versus low current velocities reveals that substrate stability may be a confining environmental variable for benthic foraminifers. Only a few specialised endobenthic species, such as boreal high-energy shelf miliolids and Trifarina angulosa, seemingly can withstand permanent winnowing and redeposition. The settling height of epibenthic foraminifera above the ambient sediment is related in proximal and distal settings to the highest lateral flux of suspended food particles within reach from the sea floor. In general, epibenthic foraminifers only use elevated substrates under the influence of near-bottom flow. This pattern may provide a sensitive biotic indicator for the upper depth limit of the MOW current.

The dynamic selection of elevated microhabitats is used as strategy to optimise food acquisition only by a few specialised foraminiferal species. They comprise only 7.8% of all species recognised. Nonetheless this proportion is twice as high as off southern Portugal (3.6%) where the MOW flow is less intense. *Cibicides lobatulus*, *Planulina ariminensis*, and *Vulvulina pennatula* occur in the elevated habitats in both areas. Hence it is justified to assume, that a co-occurrence of these species could serve as indicator of a nearbottom flow regime also in areas outside the MOW flow.

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Appendix 1. Benthic foraminiferal species which are considered in this paper

Note: Taxonomic references were given by Barker (1960), Ellis and Messina (1940–1978), Schiebel (1992), Timm (1992), and Jones (1994). They are not included in the reference list.

Ammodiscus anguillae Höglund 1947 Ammodiscus tenuis Brady 1881 Ammolagena clavata (Jones and Parker) = Trochammina irregularis var. clavata Jones and Parker 1860 Ammonia beccarii (Linné) = Nautilus beccarii Linné 1758 Ammoscalaria foliacea (Brady) = Haplophragmium foliaceum Brady 1881 Ammoscalaria tenuimargo (Brady) = Haplophragmium tenuimargo Brady 1882 Amphicoryna scalaris (Batsch) = Nautilus (Orthoceras) scalaris Batsch 1791 Bigenerina nodosaria d'Orbigny 1826 Bolivina subaenariensis Cushman 1922 Bulimina acanthia Costa 1856 Bulimina striata mexicana Cushman = Bulimina inflata var. mexicana Cushman 1922 Cibicides lobatulus (Walker and Jakob) = Nautilus lobatulus Walker and Jakob 1798 Cibicides refulgens Montfort 1808 Cibicides sp. Note: Cibicide sp. differs from Cibicides lobatulus by the greater number of chambers in the final coil (8-11), by a distinct umbo on the umbilical side formed by the earlier whorls, and by the nacreous shine of the chamber wall which is recognised in particular in living specimens. Cibicidoides kullenbergi (Parker) = Cibicides kullenbergi Parker 1953 Cibicidoides pseudoungerianus (Cushman) = Truncatulina pseudoungeriana Cushman 1922 Cibicidoides sp. Note: This taxon has been determined as Cibicidoides pseudoungerianus by Dobson and Haynes (1973), Rosset-Moulinier (1986), and Levy et al. (1995). The tests are planoconvex to slightly biconvex, and the periphery is broadly rounded. It is missing the peripheral carina with circular gutter on the umbilical side, however, as it is typically developed in Cibicidoides pseudoungerianus. Clavulina mexicana Cushman 1922 Cribrostomoides scitulum (Brady) = Haplophragmium scitulum Brady 1881 Cribrostomoides subglobosum (Sars) = Lituola subglobosa Sars 1868 Crithionina hispida Flint 1899 Crithionina mamilla Goës 1894 Crithionina pisum Goës 1896 Cyclammina cancellata Brady 1879 Deuterammina ochracea (Williamson) = Rotalina ochracea Williamson 1858 Discanomalina coronata (Parker and Jones) = Anomalina coronata Parker and Jones 1857 Discanomalina semipunctata (Bailey) = Rotalina semipunctata Bailey 1851 Elphidium crispum (Linné) = Nautilus crispus Linné 1758 Epistominella exigua (Brady) = Pulvinulina exigua Brady 1884 Epistominella rugosa (Phleger and Parker) = Pseudoparella (?) rugosa Phleger and Parker 1951 Gavelinopsis praegeri (Heron-Allen and Earland) = Discorbina praegeri Heron-Allen and Earland 1913 Gavelinopsis translucens(Phleger and Parker) = Rotalia translucens Phleger and Parker 1951 Globobulimina sp. 324 Lutze 1980 1995 Globobulimina auriculata (Bailey 1851) Levy et al., p. 36, pl. 8, fig. 3. Globobulimina turgida (Bailey) = Bulimina turgida Bailey 1851 Glomospira charoides (Jones and Parker) = Trochammina squamata var. charoides Jones and Parker 1860

Guttulina sp. (fistulous variety) Note: The capability of polymorphinid species to anchor in small cavities by using fistulous extensions of their last chamber has been described by Giese (1991) from the Channel off Brittany. Gyroidina orbicularis d'Orbigny 1826 Hanzawaia concentrica (Cushman) = Truncatulina concentrica Cushman 1918 Note: Discorbinella bertheloti (d'Orbigny 1839) of authors. Hanzawaia rhodiensis (Terquem) = Truncatulina rhodiensis Terquem 1878 Hoeglundina elegans (d'Orbigny) = Rotalia (Turbinulina) elegans d'Orbigny 1826 Hyalinea balthica (Schröter) = Nautilus balthicus Schröter 1783 Hyperammina elongata Brady 1884 Hyperammina laevigata Wright 1891 Jacuella obtusa Brady 1882 Labrospira jeffreysii (Williamson) = Nonionina jeffreysii Williamson 1858 Lenticulina rotulata (Lamarck) = Cristellaria rotulata Lamarck 1804 Marsipella elongata Norman 1878 Melonis barleeanum (Williamson) = Nonionina barleeana Williamson 1858 Nonion asterizans (Fichtel and Moll) = Nautilus asterizans Fichtel and Moll 1798 Nummoloculina contraria (d'Orbigny) = Biloculina contraria d'Orbigny 1846 Placopsilina confusa Cushman 1920 Planulina ariminensis d'Orbigny 1826 Pyrgo oblonga (d'Orbigny) = Biloculina oblonga d'Orbigny 1839 Pyrgoella sphaera d'Orbigny 1839 Quinqueloculina aspera d'Orbigny 1826 Quinqueloculina intricata Terquem 1878 Reophax bilocularis Flint 1899 Reophax scorpiurus Montfort 1808 Reophax subfusiformis Earland 1933 Rhabdammina abvssorum Sars 1868 Rhizammina algaeformis Brady 1879 Rosalina anomala Terquem 1875 Rosalina obtusa d'Orbigny 1846 Saccamina sphaerica Sars 1868 Saccorhiza ramosa (Brady) = Hyperammina ramosa Brady 1879 Sigmoilopsis woodi Atkinson 1968 Sphaeroidina bulloides d'Orbigny 1826 Spiroloculina excavata d'Orbigny 1846 Spiroplectinella sagittula d'France 1824 Textularia pseudogramen Chapman and Parr 1937 Tolypammina vagans Brady 1819 Trifarina angulosa (Williamson) = Uvigerina angulosa Williamson 1858 Trifarina fornasinii (Selli) = Angulogerina fornasinii Selli 1948 Tritaxis fusca (Williamson) = Rotalina fusca Williamson 1858 Trochammina bellingshauseni (Brönnimann and Whittaker) = Globotrochamminopsis bellingshauseni Brönnimann and Whittaker 1988 Trochammina earlandi (Brönnimann and Whittaker) = Paratrochammina (Paratrochammina) earlandi Brönnimann and Whittaker 1988 Trochammina globigeriniformis (Parker and Jones) = Lituola nautiloidea var. globigeriniformis Parker and Jones 1865 Trochammina squammata Jones and Parker 1860 Uvigerina elongatastriata (Colom) = Angulogerina elongatastriata Colom 1952 Uvigerina mediterranea Hofker 1932 Uvigerina peregrina Cushman 1923 Uvigerina peregrina parva Lutze = Uvigerina peregrina forma parva Lutze 1986 Note: Uvigerina bradyana (Cushman 1923) of authors. Uvigerina sp. 221 Lutze 1986 1995 Uvigerina peregrina (Cushman 1923) Levy et al., p. 38, pl. 8, fig. 11. Vulvulina pennatula (Batsch) = Nautilus (Orthoceras) pennatula Batsch 1791

Appendix 2. Formaminiferal census data of the living assemblage

sample	latitude			Ammoscalaria foliacea	Ammoscalaria tenuimargo	Ammodiscus tenuis	Ammolagena clavata	Ammonia beccarii	Amphicoryna scalaris	Bigenerina nodosaria	Bulimina striata mexicana	Cibicidoides sp.	Cibicidoides kullenbergi	Cibicidoides pseudoungerianus	Cibicides lobatulus	Cibicides refulgens	Clavulina mexicana	Cribrostomoides scitulum	Cribrostomoides subglabosum	Crithionina hispida	Crithionina mamilla	Cyclammina cancellata	Deuterammina ochracea	Discanomalina semipunctata	Globobulimina sp. 324	Globobulimina turgida	Glomospira charoides	Gyroidina orbicularis	Hanzawala concentrica	Hanzawaia rhođiensis	Hoeglundina elegans	Hyalinea balthica
M39024-2 M39005-3 M39025-1 M39027-1 M39027-1 M39018-1 M39018-1 M39018-1 M39008-4 M39008-4 M39008-1 M39008-1 M39008-1 M39002-1 M39002-1 M39001-2 GIK15809 M39004-1 M39004-1 M39004-1	36.882 36.535 36.512 36.803 36.782 36.753 36.650 36.771 36.381 36.779 36.712 36.350 36.738 36.736 36.111 36.321 36.962 36.962 36.237		(m) 103 118 214 272 396 496 532 576 581 667 681 726 802 881 901 945 966 1208 1917	1.7 8.1 0.8 0.9 4.2 - - - - - - - - - - -	4.2 3.4 1.9 6.5 2.7		0.8 3.6 18.9 7.5 2.1 0.9 2.0 - 2.9 14.3 5.1 - 9.2 3.2 7.6 7.6 3.9	3.8 1.2 0.4 3.6 0.4 - - -	6.4 10.5 3.2 0.9 3.8 - - - 1.6 - - - - - - - - - - - -	2.3 2.4 9.2 - 0.4 5.9 15.5 2.8 3.3 3.6 2.4 - 3.5 3.5 2.6 - 1.3 - 0.8	- - - - - - - - - - - - - - - - - - -	- 0.9 2.7 - 1.8 0.5 - 0.9 0.9 2.5 - - 0.8		0.8	0.1 2.1 2.4 0.6 1.3 0.4 - 0.9 - 17.5 1.0	0.4	- 0.8 - 0.4 0.8 - 0.9 0.3 1.3 0.4 - - - - - - - - - -	1.2 6.5 2.0 0.9 0.8 - - - 0.4 0.8 - 1.2 0.7 - 1.3 3.8 0.3 1.5 -	2.1 - - 1.2 2.1 0.3 - 1.2 2.1 0.9 - 1.5 1.0 3.0 7.7	- - - 1.2 - - - - - - - - - - - - - - - - - - -	0.6 0.1 0.4 1.3 2.1 7.1 3.3 1.3 4.2 2.1 5.2 1.5 10.2 2.9 0.2 0.2	0.8 0.9 0.3 1.3 1.2 2.1 4.3 2.6 2.6 2.0.6 2.3 1.0	- - - - - - - - - - - - - - - - - - -	- 4.4 - 0.9 0.8 - 5.0 1.3 - 0.8	13.1 10.1 8.0 12.5 1.3 - - - - - - - - - - - -	3.8 3.2 1.2 28.6	0.3 0.4 0.4 0.4 0.8 - - 0.9 - - 2.4 - 1.9	0.4	- - - - - - - - - - - - - - - - - - -	5.0 2.5 2.4 - - 0.6 0.9 - - - - - - - - - - - - - -	- 0.8 0.8 - 0.9 0.9 - 16.3 - - 0.9 - - 4.0 2.3 -	0.3 1.2
																							Ē	nis								
sample	Hyperammina elongata	Hyperammina laevigata	Jacuella obtusa	Lenticulina rotulata	Marsipella elongata	Melonis barlceanum	Nonion asterizans	Nummoloculina contraria	Planulina ariminensis	Pyrgoella sphaera	Pyrgo oblonga	Reophax bilocularis	Reophax scorpiurus	Reophax subfusiformis	Rhabdammina abyssorum	Rhizammina algaeformis	Saccamina sphaerica	Saccorhiza ramosa	Sigmoilopsis woodi	Sphaeroidina bulloides	Tolypammina vagans	Trifarina angulosa	Trochammina bellingshauseni	Trochammina globigeriniformis	Uvigerina elongatastriata	Uvigerina mediterranea	Uvigerina peregrina parva	Uvigerina sp. 221	Vulvulina pennatula	counted specim.	standing stock (#/10 cm3	\ \

Only those species are considered which occur in at least one sample among the first five ranked species of the living assemblage.

Only those species are considered which occur in at least one sample among the first five ranked species of the dead assemblage.

sample			depth	Ammoscalaria foliacea	Ammolagena clavata	Ammonia beccarii	Amphiconyna scaiaris	Bigenerina nodosaria	Bolivina subaenariensis	Bulimina acanthia	Bulimina striata mexicana	Cibicidoides sp.	Cibicidoides kullenbergi	Cibicidoides pseudoungerianus	Cibicides lobatulus	Cibicides refulgens	Clavulina mexicana	Cribrostomoides scitulum	Cribrostomoides subglobosum (Cyclammina cancellata	Discanomalina semipunctata	Elphidium crispum	Globobulimina sp. 324	Globobulimina turgida	Glomospira charoides	egyroidina orbicularis	Hanzawaia concentrica	Hanzawaia rhodiensis	Hoeglundina elegans	Hyalinea batthica	Hyperammina elongata
M39024-2 M39005-3 M39006-1 M39025-1 M39027-1 M39017-5 M39008-4 M39008-4 M39028-3 M39008-4 M39028-3 M39008-4 M39022-1 M39022-1 M39022-1 M39023-3 M39011-1 M39012-1 M39011-2 M39011-2 M39021-2 M39021-2 M39021-2 M39024-3 M39024-2 M39024-3 M39044-3 M39044-3 M39044-3 M39044-3 M39044-3 M39044-3 M39044-3 M39044-3 M39044-3 M39044-3 M39044-3 M39044-3 M39044-3 M39044-3 M3904-3 M39044-3 M3904-3 M3904-3 M3904-3 M3904-3 M39044-3 M39044-3 M39044-3 M39044-3	(*N) 36.882 36.535 36.512 36.535 36.782 36.782 36.753 36.6381 36.771 36.381 36.779 36.771 36.381 36.779 36.771 36.321 36.271 36.221 36.321 36.722 36.321 36.722 36.321 36.722 36.321 36.722 36.321 36.722 36.321 36.722 36.321 36.722 36.321 36.722 36.321 36.721 36.722 36.721 36.221	('W) 8 313 6.736 6.774 8.312 8.317 6.916 7.252 7.410 8.318 7.076 7.706 8.254 7.208 8.253 7.220 7.208 8.253 7.314 7.732 7.314 7.775 8.233	(m) 103 118 214 272 396 530 550 576 581 726 681 726 681 726 802 846 873 802 846 873 881 901 945 1208 1917	0.7 0.4 0.3 - - - - - - - - - - - - - - - - - - -	- - - - - - - - - - - - - - - - - - -	7.4 12.9 14.4 0.7 - - - 0.5 0.5 0.5 0.5 0.5 0.5 0.5 0.5 0.5 - - - - - - - - - - - - - - - - - - -	8.8 10.3 4.5 6.4 7.2 0.8 11.0 0.5 3.9 9.8 9.8 9.8 9.8 9.8 9.8 9.8 9.5 0.5 3.4 0.5 0.5 1.3	3.5 3.4 2.5 0.7 4.6 1.9 6.7 22.5 3.9 7.6 16.7 8.7 1.5 6.0 7.2 3.5 0.4 0.9 5.4 4.4 1.3	0.4 5.1	1.4 3.4 1.3 6.7 0.3 - 0.9 -	- - - - - - - - - - - - - - - - - - -	1.8 - - - - - - - - - - - - - - - - - - -		2.8 4.3 7.7 3.1 3.8 0.4 2.2 3.2 3.8 5.1 1.6 0.3 1.5 1.4 2.3 5.5 6.0 3.8 0.4 2.5 6.0 3.8 0.4	2.1 4.6 2.0 5.7 3.1 5.5 2.3 5.7 5.1 2.3 2.3 2.1 6.6 6.1 0.5 30.7 15.5 30.7 15.8 2.0 0.4	1.4 - - - - - - - - - - - - - - - - - - -	1.4 1.0 0.8 0.6 4.7 0.9 6.2 3.0 1.6 3.4 3.0 1.6 3.4 3.0 0.9 1.1	0.4 - - - - - - - - - - - - - - - - - - -	1.1 0.4 2.6	1.1 0.4 0.4 - - - - - - - - - - - - - - - - - - -	0.7 	1.8 0.4 - - 2.7 - - - 0.5 0.5 0.5 0.5 0.5 0.5 - - - - - - - - - - - - - - - - - - -	3.2 8.7 2.5 1.4 1.0 - - - - - - - - - - - - - - - - - - -	0.4 1.5 0.3 7.1 9.3 1.9 - - 0.4 - - 0.4 - - -	0.7 - - - - - - - - - - - - - - - - - - -	- - - - - - - - - - - - - - - - - - -	- - - - - - - - - - - - - - - - - - -	2.5 1.9 2.1 0.5 1.3 0.7 0.2 0.4	3.5 2.1 5.7 1.8 - 4.4 - 0.6 0.8 8.2 4.9 1.0 2.5 1.4 1.9 0.9 3.7 3.3 0.9 4.0	6.7 13.7 27.7 5.0 3.1 10.0 7.4 8.0 2.6 0.6 0.8 - 6.6 4.4 0.5 1.8 1.9 - 0.6 - 2.1 - 2.1	- - - - - - - - - - - - - - - - - - -
	igata		Ę	ta	unu	su	contraria	sisis	~		<u>y</u> ı	SI	imis	abyssorum	aeformis	ġ		Ţ,	bulloides	vagans	a a	bellingshauseni	globigeriniformis	elongatastriata	rranea	a parva	g		ıla		
sample	Hyperammina laevigata	Jacuella obtusa	Lenticulina rotulata	Marsipella elongata	Melonis barleean	Nonion asterizar	Nummoloculina c	Planulina ariminensis	Pyrgoella sphaera	Pyrgo oblonga	Reophax bilocularis	Reophax scorpiurus	Reophax subfusiformis	Rhabdammina aby	Rhizammina algaefo	Saccamina sphaerica	Saccorhiza ramosa	Sigmoilopsis woodi	Sphaeroidina bu	Tolypammina va	Trifarina angulosa	Trochammina be	Trochammina gle	Uvigerina elonga	Uvigerina mediterranea	Uvigerina peregrina	Uvigerina peregrina	Uvigerina sp. 221	Vulvulina pennatula	counted specim.	abundance (#/10 cm ³)

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Appendix 4. Recordings of the living epibenthic foraminiferal species

Once the height above the ambient sediment is recognised, the maximum attachment elevation in mm is added. Abbreviation of substrate types: br, bryozoans; co, coral fragments; cr, crinoids; ech, echinoid spines; hy, hydroids; mo, mollusk fragments; pch, polychaet tubes; pt, pteropods; py, pyrite nodules; qz, quarz; sc, scaphopods; sk, ship's klinker; sp, sponges; taf, tubular arenaceous foraminifers. *, settling on other epizoans (mostly hydroids) on the large objects, attachment elevation is given in mm above the base of the host, and the squattering density refers to one single colony. s, specimens squatter small cavities in the slab surface. Note that the smaller surface area in the size fraction 250–2000 μ m is due to splits been made to reduce the sample to a practical size.

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sample	latitude (°N)	longitude (°W)	depth (m)	grainsize fractions, no. of other objects	substrate types	Ammodiscus anguillae	Cibicidoides sp.	Cibicides lobatulus	Cibicides refulgens	Cibicides sp.	Crithionina hispida	Crithionina mamilla	Deuterammina ochracea	Discanomalina semipunctata	Epistominella rugosa	Gavelinopsis praegeri	Gavelinopsis translucens	<i>Guttulina</i> sp. (fistulous variety)	Hanzawaia concentrica
M39024-2	36.882		103	250-2000 µm		- 1	-	-	-	1	-	1	-	-	-	-	-	-	:
M39005-3	36.535	6.736	118		taf, mo	-		-	-			-	-	-				-	-
100006 1	00 510	6 774	014	>2000 µm			-	-	-	-	-	1	•	-	-	-	-	-	-
M39006-1	36.512	6.774	214	250-2000 μm >2000 μm		-	•	2	-	-	-	·	-	-	•	2	•	-	-
					hv]		-	-		-	-	2						- 1
M39027-1	36.782	8.317	396	250-2000 µm		1 -	-	-	-	-	-	2		-	-			-	-
M39007-1	36.455	6.916	454	>2000 µm		-	-	-	-	-	-	1	2	-	-	-		-	-
M39018-1	36.753	7.252	496		mo, hy, taf	-	З	4	-	-	-	-	-	5	-	-	-	•	-
					hy, br, taf, pt, mo	·	7/3	2	-	-	-	4	-	11/3	-	•	4	•	-
M39017-5	36.650	7.410	532	250-2000 µm		•	-	-	-	-	-	1	-	-	-	•	-	•	-
	1			>2000 µm	pt pch			-	-	-	-	2	-	-	-			-	
M39028-3	36.771	8.318	550	250-2000 µm		1		2	-	1	2	7							1
		0.070			mo			1	-		-	1	-	-				-	
M39008-4	36.381	7.076	576	250-2000 µm		1 -	4	2	-	-	-	6	1	-	-	-		-	5
				>2000 µm	pt, mo, taf, br	-	4	-	-	-	-	10	-	1	-	•	•		2
				9	co, taf, cr, sc	•	-	1/6	-	·	•	2	•	•	•	•	•	•	-
M39016-1	36.779	7.706	581	250-2000 µm		-	3	2	-	-	-	1	-	1	-		•	-	1
1					mo, pt, taf, br, hy hy, taf, pch	· ·	3/4	-	-	•	-	2	1	1/10 1	1/10	1		-	1
M39022-1	36 712	8.260	667	250-2000 µm		1 .			-	1		9		2				-	
MODULL 1	00.7 12	0.200	007	>2000 µm		-	1	-	-		-	2/2	-	-	-		-	-	
				6 (1 colonized)		-	1/23	-	-		-	-	-	26/28	-		-	-	-
M39009-1	36.350	7.142	681	250-2000 µm	mo] -	•	-	-	-	-	-	-	-	•	•	-	-	-
				>2000 µm		-	•	-	-	•	-	-	1	-	-	-	-	-	-
M39020-1	36.738	8.106	726		taf, mo, pt	-	:	-	-	•	-	3	-	-	-	•	•	-	1
				>2000 µm 3		-	1	•	-	•	-	4	-	-	-	•	-	-	2
M39023-3	36 736	8.254	730	and the second se	taf, sp mo, taf	1]			1		:	6	:				:		:
1000020-0	00.700	0.204	100		mo, pt, taf, hy, br		2/9	2	-			11	-	1/10	-	1		-	1
				3	ech, sk, sp	- 1		-	-	-		-	-	-	-	-		-	-
M39003-1	36.111	7.223	802	250-2000 µm	pt, mo	1	-	-	-	-	•	1	-	-	-	-	•	-	-
					pt, taf, mo	-	•	-	-	-	-	3	-	-	1	•	•	-	2
	00.070			1	komokiacea	-	•	-	-	•	•	-	-	-	-	-	- 3/40	-	•
M39014-1 M39013-1			850 871		sp, slag		•	17/40 5/15	10/30 7/15	-	•	•	-	4/20 6/15	-	-	3/40	- 3/15 ^{\$}	•
M39010-1		7.207	878		hy, sp, sandstone hy*, sp*	1]	- 2/9	5/15			:	:	-	83/3-18			1	1	
M39010-2		7.208	881		co, mo, ech	1.	1/6	7/10	5/5	2/5		-	4/6	2/5	-		2	-	-
M39021-5			901	250-2000 µm		1 -	-	-	•	-	-	6	-		-	-	-	-	-
				>2000 µm	py, pt, mo, hy	-	-	3	•	1	•	з	-	4/11	-	1	1/6	-	-
				5 (1 colonized)	py*, co	- 1	-	1	-	-	-	1	-	-	-	-	•	-	-
GIK15809	35.962	7.314	945	250-1000 µm		-	-	•	-	-	-	-	-	•	-	-	-	-	-
	00.00-			1000-2000 µm		1 .	-	-	-	-	2	-	-	-	-	-	-	-	-
M39004-1	36.237	7.732	966	250-2000 μm			-	-	-	-	5	7	-	-	-	-	-	•	-
M39002-2	36 027	7.775	1208	>2000 µm 250-2000 µm	pt, tar, pcn pt, hy, taf	1]	-	-		-	10	6	2	- 1	2	-	1/7		
	00.021		.200		hy, pt, mo	1.		-		-		1	-	-		-	-		-
				5	sp, taf	-	-	-	-	-		-	-	-	-	-	-	-	-
M39029-3	36.041	8.233	1917	250-2000 µm		1 -	-					-	-	-	-	-	-		-
1	1			>2000 µm		1 -	-	-	-	-	-	2	-				-	-	

sample	grainsize fractions, no. of other objects	Hanzawaia rhodiensis	Labrospira jeffreysii	Placopsilina confusa	Planulina ariminensis	Rosalina anomala	Rosalina obtusa	Saccamina sphaerica	Saccorhiza ramosa	Spiroplectinella sagittula	Textularia pseudogramen	Tritaxis fusca	Trochammina bellingshauseni	Trochammina earlandi	Trochammina globigeriniformis	Trochammina squammata	Vulvulina pennatula	others, indet. sp.	total number of specimens	examined surface area (cm₂)	average population density (#/10 cm₂)	maximum squattering density (#/object)
M39024-2	250-2000 µm	10	1	•	-	-	1	•	-	•	•	-	-	-	•	•		-	14	87	2,42	1
1100005.0	>2000 µm	7	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	7	87		6
M39005-3	250-2000 μm >2000 μm	6 1		:	:	4	-		-	-	-	-	-	-	-	-	-	-	10 3	41 260	2,53	
M39006-1	250-2000 µm	3	-		-	1	-	-	-		-	-	-	-					6	42	1,66	2
	>2000 µm	-	-	-	-	1	-	-	-	3	-	-	-	-	-	-	-	-	6	260		6
M39027-1	2 250-2000 μm	- 1	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	0			
M39027-1 M39007-1	>2000 µm	-	-	-	2		2		-			-		2		2		-	7	44	1,59 0,26	1
M39018-1	250-2000 µm	-	1	-	-		-	9	-	5/3	-	-	-	-				5	32	95	5,28	2
	>2000 µm	•	2	-	-	-	-	-	-	2/12	-	-	-	-	-	•	-	1	33	173		4
M39017-5	250-2000 μm >2000 μm	-	•	-	-	•	•	5	-	-	-	-	-	-	-	1	-	-	7	81	0,94	1
	>2000 µm 1	-	-				:	-	:	:	:		:			:	:	:	2 0	260		- 1
M39028-3	250-2000 µm	-	-	-	-	-	-	1	-		-	-	-	-	-	з	•	-	15	47	3,49	1
	>2000 µm	-	•	-	-	-	•	-	-	•	-	-	-	-	-	1	•	-	3	93		1
M39008-4	250-2000 μm >2000 μm	2	8	-	2 1/2	1	-	-	-	•	•	6	-	1	-	1	-	1	40	135	3,86	1
	>2000 µm	:			1/2	:	:	1	-	:	:	-	:	:	:	1 1/6	:	2	23 8	260		<u>4</u> 5
M39016-1	250-2000 µm	2	-	-	-	1	-	-	-			-		-	-	-		-	11	122	1,36	2
	>2000 µm	•	1	-	-	2	-	-	-	•	-	1	•	•	-	-	1/10	-	12	260		9
M39022-1	3 250-2000 um	•	-	-	-	-	-	-	-	•	•	- 2	-	- 2	-	- 3	-	•	4 25	68	0.01	2
10139022-1	>2000 µm	- 1	1	2	-	-	-	4	-	:		-		-		-	2	:	25 6	260	3,91	1 2
	6 (1 colonized)	-	-	-	1/14		-	-	-	1/20	-	-	-		-	-	-	-	29			29*
M39009-1	250-2000 μm	1/2	-	-	•	-	-	-	-	-	-	-	•	-	-	-	-	•	1	22	0,52	1
M39020-1	>2000 µm 250-2000 µm		-	-	-	- 2	-	-	•	•	-	-	•	-	-	- 2	•	-	1 9	<u>173</u> 68	1,51	1
100020-1	>2000 µm		1		-	-			1	:		2			-	2			11	65	1,51	4
	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0			-
M39023-3	250-2000 µm	-	-	-	-	-	-	3	-	•	-	-	-	-	-	1	-	-	11	36	2,11	1
	>2000 µm 3		1	2	1	-	-	1	1	•	2/6	-	-	-	1	4	-	1	30	260		1
M39003-1	250-2000 µm	-	2	-	2			-	:	:		4		-	- 5	2	:	2 2	4 15	62	3,29	3
	>2000 µm	-	•	-	2	-	-	з			-	8	-	-	-	2		2	23	260	0,20	4
11000444	1	-	-	-	-	•	•	-	-	-	-	-	-	-	-	-	-	-	1			-
M39014-1 M39013-1	1 ship's clinker 1 outcrop slab	-	-	12/20	1/30	•	-	-		-	•	-	-	-	-	- 1/15	-	:	47 22	<u>190</u> 434	2,48	
	3 outcrop slabs	-	-	-				-			1/15	-		2	2	-			88	434	2,07	33*
M39010-2	>2000 µm	-	•	1/5	-	-	-	-			•	-	-	-	-	2/6	-	-	24	120	2,00	9
M39021-5	250-2000 μm	-	-	-	-	•	-	1	-	•	•	-	·	-	1	2	•	-	10	68	2,37	1
	>2000 µm 5 (1 colonized)		-	4 12	-	1	-	-	-	•	-	1	-	-	2	2	•	-	23	260		2
GIK15809	250-1000 µm	1		-	-		-	-	:			1	:	:	:	:		:	16 1	125	0,12	16*
	1000-2000 µm	-	-	-		-	-	2	-	-		-	-	-	-	-	-	-	2	500	3,12	1
M39004-1	250-2000 µm	·	-	-	-	-	-	-	-		-	-	-	-	-	-	•	-	12	63	2,64	1
M39002-2	>2000 μm 250-2000 μm	-	-	-	•	1/7	-	•	-	•	-	-	-	-	1	-	•	-	19	260		2
1103002-2	250-2000 μm >2000 μm	2		:	-	2	-	- 5/2-5	-		-	-	2	1	3	-	:	1 2	9 10	62 260	1,83	1 6
	5			-	1/8		-	-	-		-	-	-	-	-	-	-	-	1	200		1
M39029-3	250-2000 μm	•	-	5	-	-	-	5	-	-	•	-			-	-	-		10	52	2,10	1
L	>2000 µm	· ·	•	<u>.</u>	-	· ·	-	2	•	•	-	-			· ·	-	-	1	5	260		2

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