

Depth distribution of benthic foraminifera in the middle and deeper sublittoral to uppermost bathyal zones northwest of Okinawa, Japan

WAN NURZALIA WAN SAELAN^{1,*} & JOHANN HOHENEGGER²

¹ School of Marine and Environmental Sciences, Universiti Malaysia Terengganu, 21030 Kuala Terengganu, Malaysia

² Department of Palaeontology, University of Vienna, Althanstrasse 14, A-1090 Vienna, Austria

*Corresponding author email address: wannurzalia@umt.edu.my

Abstract: Distribution of dominant species of porcelaneous foraminifera is related to depth in the sublittoral and uppermost bathyal around Okinawa, Japan. Depth is a composite factor that influences physical factors, i.e., temperature, salinity, substrate caused by hydrodynamics and illumination. Depth distribution of optimally preserved porcelaneous tests demonstrate optima in the middle sublittoral, deeper sublittoral and uppermost bathyal zones. Optimal depth distribution of the tests in the middle and deeper sublittoral zones is related to dependence on either coarse sand, medium sand or no dependence on specific substrate type. Optimal depth distribution of the tests in the uppermost bathyal zone is related to dependence on fine and very fine sand. Porcelaneous tests have shown partial agreement between the depth distribution and dependence on substrate type. Life position of the porcelaneous foraminifera is influenced by test dominance in percentages of silt and clay. Dominance in the high percentages of silt and clay is reflected in infaunal life position. Dominance in the low percentages of silt and clay is reflected on epifaunal life position. Dominance in medium percentages or no dominance reflects on either epifaunal or infaunal life position. Test dominance in percentages of silt and clay is related to its dependence on substrate type.

Keywords: Optimal tests, porcelaneous foraminifera, depth distribution, substrate dependence, life position

INTRODUCTION

The niches of benthic foraminifera are not satisfactorily defined due to ecological complexities (Murray, 2006). There are no two similar microenvironments, therefore it is difficult to make generalisations on which environmental factors control distribution. A species must be sufficiently adapted to survive and compete in a niche and not necessarily have to be perfectly adapted to it (Hallock *et al.*, 1991). Critical thresholds of environmental factors control species distribution (Murray, 2001). They are defined by the upper and lower limits of the distribution function. An organism is not able to survive outside of these limits. Distribution of benthic foraminifera is influenced by a wide array of abiotic and biotic factors (Jorissen *et al.*, 1995; Murray, 2006). Abiotic factors such as temperature, salinity, substrate, oxygen concentration and organic carbon content are related to changes in water depth (Annin, 2001; Hohenegger, 2000a).

Depth dependence distribution

Depth distribution of living larger symbiont bearing benthic foraminifera has been successfully investigated using rigorous statistical techniques (Hallock, 1984; Hohenegger, 1994, 2000b, 2004). Illumination and hydrodynamics are the two most important single factors influencing the depth distribution of living larger benthic foraminifera (Hallock *et al.*, 1991; Hohenegger, 2004; Hottinger, 1983). Larger foraminifera build specialised wall structures to adapt to illumination intensity and strengthen test structures to handle water movement in the euphotic zone (Hohenegger *et al.*, 1999). Functional morphologies of larger foraminiferal tests are understood better (Hallock *et al.*, 1991) than smaller

benthic foraminifera, thus depth distribution of larger benthic foraminifera can be used as a test case to investigate the depth distribution of smaller benthic foraminifera.

Distribution of smaller benthic foraminifera is primarily influenced by substrate type working as a nutrient and oxygen reservoir. Investigation on the substrate dependence of smaller benthic foraminifera in this study is performed based on their distribution in grain size classes. The density of living larger foraminifera is different between hard and soft substrate (Hohenegger, 1994). Community composition is controlled by substrate preference and competition for space (Hottinger, 1983). Different substrates produce different biosystems, which are inhabited by different species of benthic foraminifera. Grain size distribution is an indicator of water energy; coarse sand indicates high water energy and contrarily, distribution of fine sand indicates low water energy (Hohenegger *et al.*, 1999).

Life position of benthic foraminifera

There are two types of benthic foraminiferal microdistribution pattern, i.e., spatial and temporal (Murray, 2006). Spatial microdistribution of benthic foraminifera is characterised by lateral or vertical position in sediments (infaunal) and elevated position above the sediments (epifaunal). Temporal microdistribution pattern is related to reproduction cycle of benthic foraminifera. The main controls of microdistribution pattern are microenvironmental condition and reproduction (Murray, 2006). Studies have shown that microhabitat of benthic foraminifera is controlled by pore water oxygen concentration (Jorissen, 2002; Jorissen *et al.*, 1995) and food availability (Corliss

& Emerson, 1990; Hohenecker *et al.*, 1993; Jorissen *et al.*, 1992; Linke & Lutze, 1993). Vertical zonation within sediments strongly corresponds to depth related distribution of oxic respiration, nitrate and sulphate reductase (Jorissen *et al.*, 1994; Jorissen *et al.*, 1998). Even though there is no clear pattern of benthic foraminiferal depth distribution within sediments, studies have shown that there are different morphotypes corresponding to different depths within sediments (Corliss, 1985, 1991; Corliss & Emerson, 1990). Epifaunal foraminifera live on top of firm substrates or sediments and include foraminifera living in the top 1cm while infaunal foraminifera live in the top few centimetres of the sediments. Epifaunal foraminifera show attached, clinging or free living life modes.

Life positions of smaller benthic foraminifera in the present study, either on sediments (epifaunal) or within sediments (infaunal) are investigated based on their distributions in the silt and clay fraction. Silt and clay in the sediments can contain and stabilise organic matter such as carbon and nitrogen (Hassink, 1997). Organic rich fine sediments provide the best habitat for infaunal foraminifera (Kitazato, 1995). Coarse and medium sediments provide shelter and attachment for epifaunal foraminifera (Diz *et al.*, 2004). Preference to epifaunal or infaunal life position of the smaller benthic foraminifera in a shallow water region may be related to food availability. In the shallow water region, there is a relatively high organic carbon flux in the seafloor resulting in a shallow oxic layer (Corliss & Emerson, 1990) thus eliminating the control of porewater oxygen as a limiting factor. This paper aims to assess the depth distribution, substrate dependence and life position of porcelaneous benthic foraminifera.

METHODOLOGY

Location and environmental setting

Okinawa is the largest island of the Ryukyu Island Arc. The Ryukyus are located in the southwest of mainland Japan and consist of hundreds of islands and islets. These islands are arranged in a curve hence the name Ryukyu Island Arc. The Ryukyus extend from Tanega Island (30°44'N, 131°0'E) in the northeast to Yonaguni Island (24°27'N, 123°0'E) in the southwest. The area is bounded by the East China Sea on the northwest and by the Pacific Ocean on the northeast. The Okinawa Trough of 2000m depth in the south separates the Ryukyu Arc from the East China Sea shelf. The Kuroshio warm current flows through the trough (Hatta & Ujiie, 1992). The climate of the Ryukyus is subtropical with monthly mean seawater temperature of 21.5 - 29.0°C (at the surface) and 20.4 - 21.4°C (at 150m depth). Annual mean seawater temperature is 25.2°C (at the surface) and 20.7°C (at 150m depth). Annual mean salinity is 34.6ppt at the surface and 34.8ppt at ~200m depth. The area is rimmed by fringing coral reefs with two basic topographic zones that can be divided into the reef flat and reef slope. The reef slope zone starts with a steep drop from the reef flat and it extends from the surface to 50m depth. The shelf around Ryukyus is flat and slope gently seaward.

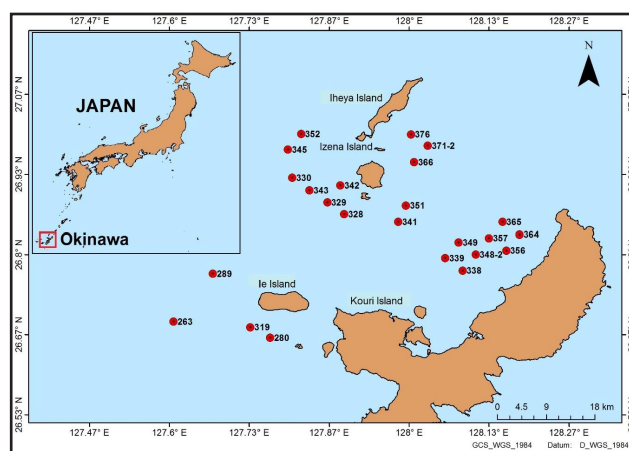


Figure 1: Map of the investigation area showing locations of sampling stations.

The seaward margin is located at the depth of 90m to 170m (Matsuda & Iryu, 2011). The width of the shelf is from 0 to 25km. Okinawa is subjected to several typhoon events per year thus the sediments were always transported from the beach and reef moat area to the upper fore reef area (Yordanova & Hohenecker, 2002).

The northern transects of the investigation area are located to the northwest of Okinawa with sampling stations located around the south of Izena Island (Figure 1). The southern transect is located to the west of Motobu Peninsula with sampling stations located in the south of Ie Island.

Sampling and preparation

Samples were collected using a grab sampler during a cruise of a Japanese research vessel investigating the seafloor around Okinawa. These samples were sent to the Department of Palaeontology, University of Vienna by Prof. Dr. Kazuhika Fujita from the University of the Ryukyus. The samples were collected between 64m and 275m depth. Parts of the surface sediments were stored in plastic jars, filled with seawater and formalin to fix the protoplasm of living organism. A set of sieves with mesh sizes of 63µm, 125µm and 250µm was used to wash and sieve the samples. Samples were dried at 60°C. A universal sample splitter was used to split samples of 250µm fraction. Microsplitter was used to split samples of 125µm fraction. Only optimally preserved foraminiferal specimens were picked and identified using Motic SMZ-168 Series microscope. Taxonomic identification was performed following Akimoto *et al.*, 2002; Hatta & Ujiie, 1992; Hohenecker, 2011; Loeblich & Tappan, 1994; Parker, 2009. Samples for grain size analysis were brought to the sedimentology laboratory of the Department of Sedimentology, University of Vienna for further analysis. Sediments that are < 63µm were analysed using the Micromeritics Sedigraph ET5100. Sediments that are > 63µm were analysed by sieving (Boggs, 2006; Cheetham *et al.*, 2008). A stack of sieves with mesh size diameters of 4mm, 2mm, 1mm, 0.5mm, 0.25mm, 0.125mm and 0.063mm were placed onto a sieve shaker with water running through the sieves that washed along the sediments. Sediments collected at each sieve were dried at 60°C.

Data analysis

Optimally preserved specimens (Yordanova & Hohenegger, 2002) were identified and counted. Normalization of the test abundance to a standard weight of 100g was conducted due to differences in sample weights. Depth distributions of porcelaneous benthic foraminiferal species presented in histograms were analysed in IBM SPSS Statistics 22 and Microsoft Excel 2013 for Windows. Frequency distributions are unimodal and can be fitted by power transformed normal distributions (Hohenegger, 2000a, 2000b, 2006; Hohenegger & Yordanova, 2001b). The formula is:

$$\varphi(x) = d \exp[-(x^y - \mu)^2 / 2\sigma^2]$$

In this equation, x is the metric environmental gradient, d represents the abundance optimum, μ the mean and σ^2 the distribution variance. The power factor y signalizes intensities of left ($y > 1$) or right side ($y < 1$) skewness. Values of the power factor higher than 1.5 or less than 0.1 indicate significant restriction by the gradient at higher scores in the former and lower scores in the latter. Distributions in grain size classes and percentages of silt and clay are depicted in circle graphs using Microsoft Excel.

RESULTS

Grain size distribution

Sediment samples collected in the south of Ie Island (Figure 2) were all poorly sorted. All were symmetrically distributed except at 189m where the sediments were strongly fine skewed. Sediments at 69m depth belong to the very fine sand class. Sediments at 148m belong to the medium sand class. Deeper sediments at 189m and 203m were distributed into very fine sand class. Bimodal distribution of the sediments was shown by the shallowest sample in this area at 69m depth. The bimodal pattern shows that the main component is composed of fine sand

and the second component belongs to the coarse sand. Sediments of the south of Ie Island were mainly composed of very fine sand.

Sediments sampled in the southeast of Izena Island (Figure 3) were all poorly sorted. At less than 100m depth, symmetric distributions were found at 64m, 79m and 94m except at 95m, where sediments were fine-skewed. Between 100m and 200m; symmetric distributions were found at 134m. Sediments at 105m and 139m were fine-skewed. The deepest sample in this area was located at 211m. Sediments were strongly fine-skewed at this depth. Shallowest sediments sampled at less than 100m belong to the medium sand class except at 64m, where sediments belong to the fine sand class. Between 100m and 200m; sediments fit into the medium sand class except at 105m, where sediments belong to the fine sand class. The deepest sample at 211m consisted of very fine sand. Bimodal distributions of the sediments were shown at samples 64m and 95m. These bimodal distributions show that the main components are composed of fine-grained sediments and second component consists of coarse grains. Sediments of the transect in the southeast of Izena Island were composed of mainly medium sand class.

Sediment samples collected in the south of Izena Island were all poorly sorted (Figure 4). The shallowest samples collected at 71m and 72m were nearly symmetrically distributed. A slightly deeper sample at 75m was strongly fine-skewed. Coarse-skewed sediments of the shallow depth were at 79m and 83m. Between 100m and 140m, sediments were nearly symmetrically distributed except at 117m, where sediments were fine-skewed. Sediment skewness of the deeper samples between 150m and 300m were as follows; strongly coarse-skewed at 168m, strongly fine-skewed at 227m and symmetrically distributed at 275m. Shallowest samples between 70m and 80m were distributed in different sand size classes; medium sand at 71m, coarse

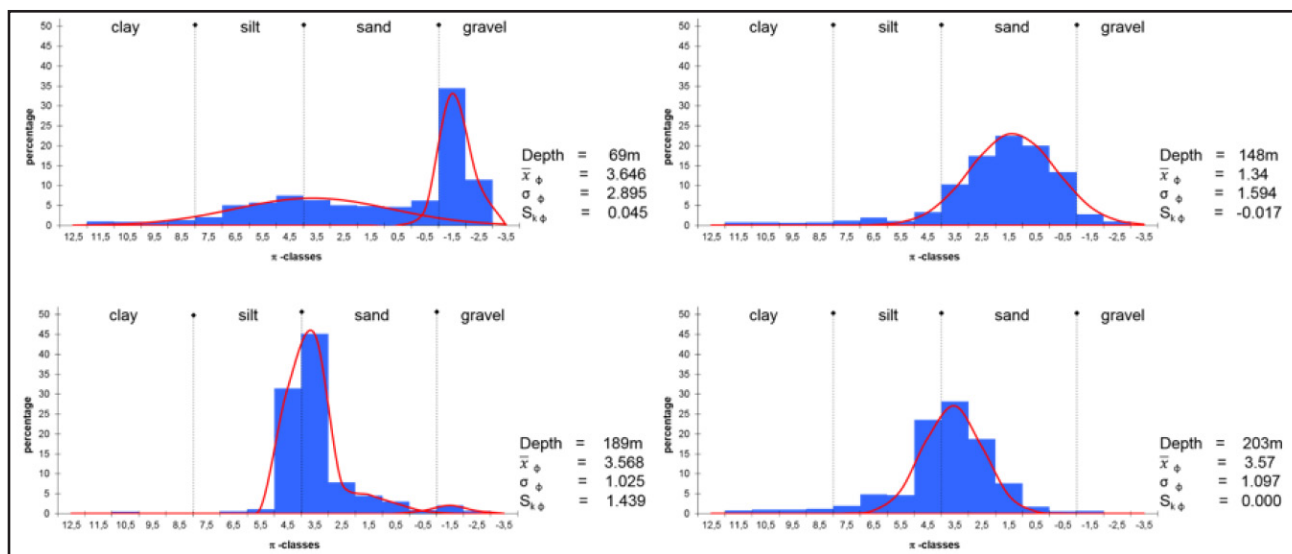


Figure 2: Grain size distribution of sediments sampled in the south of Ie Island. Decomposition of non-normal distributed frequencies into normal distributed components. All parameters (mean, sorting and skewness) in phi (ϕ) units.

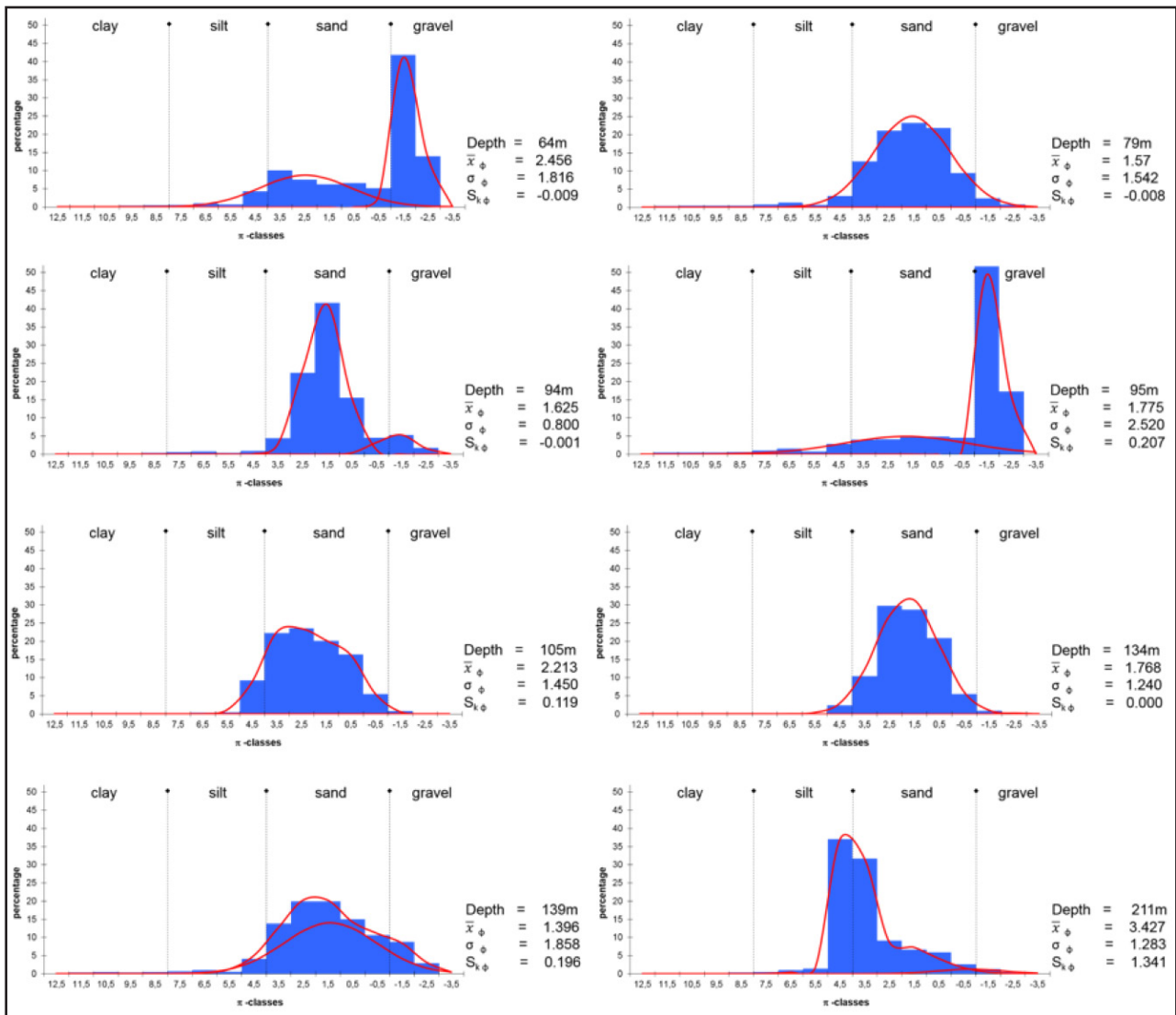


Figure 3: Grain size distribution of sediments sampled in the southeast of Izena Island. Decomposition of non-normal distributed frequencies into normal distributed components. All parameters (mean, sorting and skewness) in phi (ϕ) units.

sand at 72m and 79m and very fine sand at 75m. Sediments at 100 - 140m fit to the medium sand class. Sediments at depth range of 150 - 300m belong to different sand classes; coarse sand at 168m, very fine sand at 189m, medium sand at 227m and fine sand at 275m. Bimodal distributions of the sediments were shown in samples at 71m, 79m, 115m and 275m, with main components distributed in the fine grain size classes and the second components belong to the coarse grain size classes. Sediments of the transect in the south of Izena Island were composed of mainly medium to coarse sand class at less than 100m, medium sand class at 100 - 150m and fine to very fine sand class at 150 - 300m.

Depth distribution

Porcelaneous foraminifera are distributed from the middle sublittoral to uppermost bathyal zones (Figure 5). Table 1 shows the locations at which the porcelaneous foraminiferal species were found. Depth zonations are characterised based on the depth ranges; the middle sublittoral zone was located at less than 100m depth, the

deeper sublittoral zone was located between 100m to 200m depth and the uppermost bathyal zone was located at more than 200m to 300m depth. The shallowest depth distribution is shown by *Triloculina affinis*. The optimum is located in the middle sublittoral zone at 86m. *Triloculina affinis* is one of the three species showing depth distributions in the middle sublittoral zone. The other two species are *Quinqueloculina bicarinata* and *Quinqueloculina seminulum*. Both species show bimodal distribution patterns. *Quinqueloculina bicarinata* shows that the first component has an optimum at the 120m depth class, while the second component demonstrates an optimum at 270m depth class. *Quinqueloculina seminulum* shows that the first component has an optimum at the 90m depth class, while the second component demonstrates an optimum at 240m depth class.

Porcelaneous foraminifera showing distributions in the deeper sublittoral zone are *Triloculina tricarinata*, *Quinqueloculina lamarckiana*, *Spirosigmoilina speciosa*, *Miliolinella subrotunda*, *Miliolinella* cf. *M. chiastocytis*

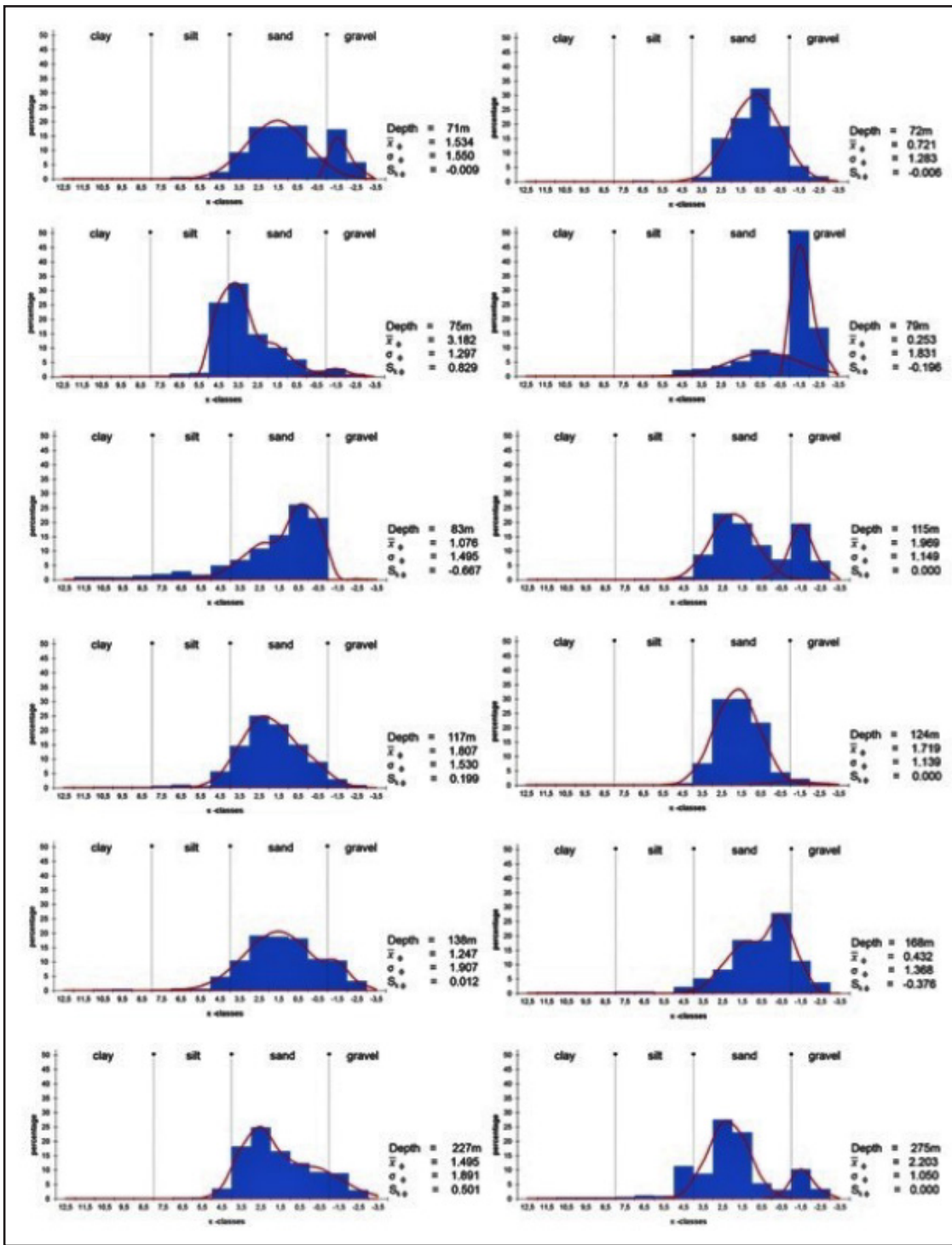


Figure 4: Grain size distribution of sediments sampled in the south of Izena Island. Decomposition of non-normal distributed frequencies into normal distributed components. All parameters (mean, sorting and skewness) in phi (ϕ) units.

and *Spiroloculina manifesta*. *Triloculina tricarinata* shows an optimum at 109m; *Quinqueloculina lamarckiana* and *Spirosigmoilina speciosa* show optima near to one another, occurring at 127m and 133m respectively. Optima of the distributions of *Miliolinella subrotunda* and *Miliolinella* cf. *M. chiastocyttis* are also located very near to each other at 160m and 166m respectively. The deepest distribution in the deeper sublittoral zone is shown by *S. manifesta*, which occurs at 175m.

Depth distributions occurring in the uppermost bathyal zone are shown by *Quinqueloculina venusta*, *Pyrgo sarsi*, *Pyrgo denticulata* and *Miliolinella circularis*. The optima of these four species in the uppermost bathyal zone are located near to each other. *Quinqueloculina venusta* shows that the optimum is located at 235m. *Pyrgo sarsi* shows an optimum of the depth distribution at 239m. Optima of the depth distributions of *Pyrgo denticulata* and *Miliolinella circularis* are located at 247m and 249m respectively.

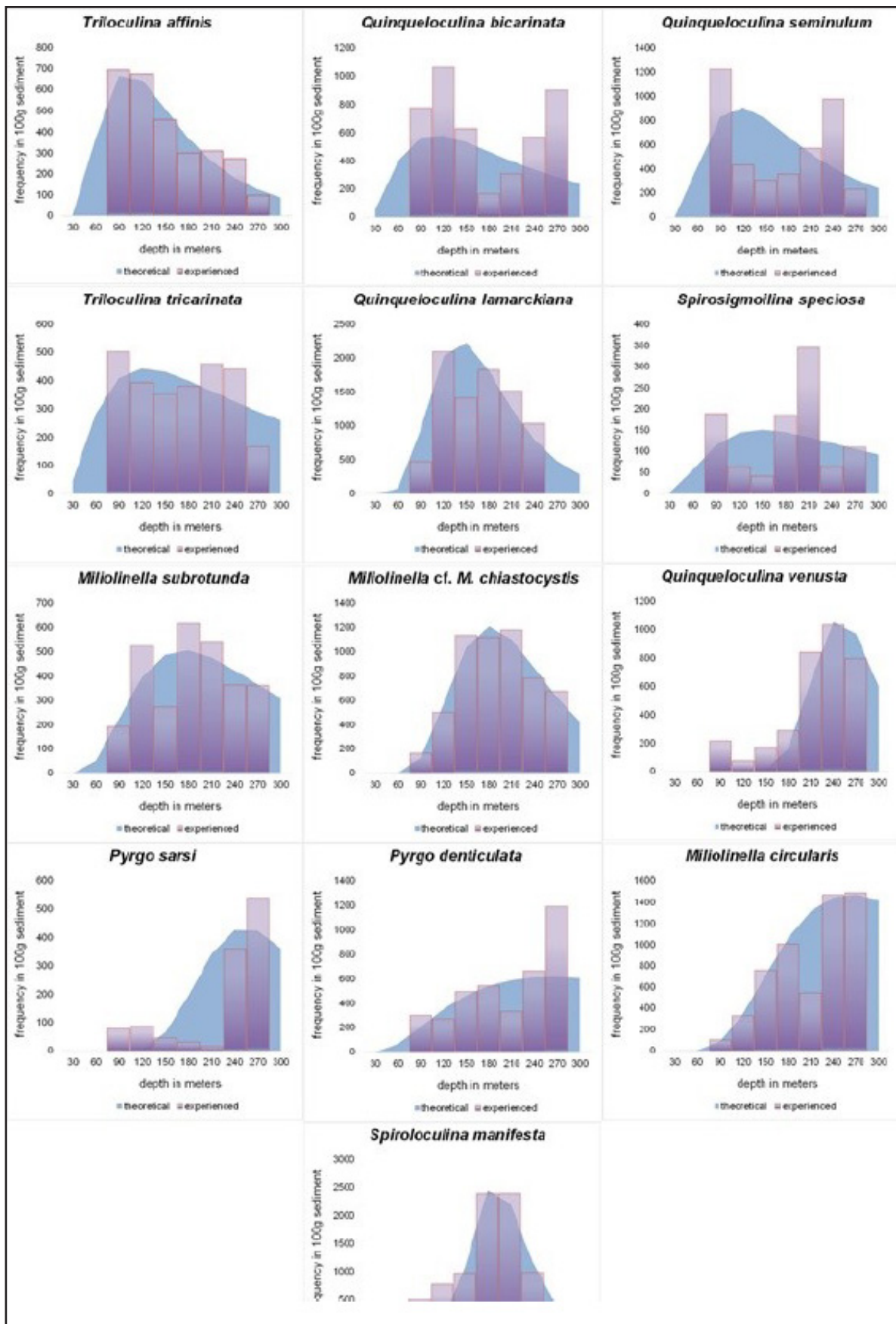


Figure 5: Experienced depth distributions (column) fitted by power transformed normal distributions. Abundances of porcelaneous benthic foraminifera are shown in frequency distributions.

Table 1: Locations of stations showing where the dominant porcelaneous foraminiferal species have been found.

Station	Depth (m)	<i>Milolinella cf. M. chiasocytis</i>	<i>Milolinella circularis</i>	<i>Milolinella subrotunda</i>	<i>Pyrgo denticulata</i>	<i>Pyrgo sarsi</i>	<i>Quinqueloculina bicarinata</i>	<i>Quinqueloculina tamarckiana</i>	<i>Quinqueloculina seminitum</i>	<i>Quinqueloculina venusta</i>	<i>Spiroloculina manifesta</i>	<i>Spirosmiolina speciosa</i>	<i>Triloculina affinis</i>	<i>Triloculina tricarinata</i>
338	64	102	34	68	186	0	423	102	119	34	271	119	17	339
319	69	0	98	74	246	0	197	98	74	25	418	74	74	172
376	71	22	0	65	151	86	411	65	259	173	151	108	930	0
352	72	4	2	0	127	32	16	0	0	4	32	0	32	96
342	75	129	203	0	74	18	129	481	1443	444	129	74	222	129
345	79	14	0	57	57	43	43	115	29	14	187	14	57	373
356	79	0	0	16	16	48	48	79	349	32	32	0	0	79
289	83	341	0	341	0	105	525	131	0	0	236	105	210	0
348	94	0	55	27	82	7	55	691	164	7	157	0	7	55
339	95	113	135	90	0	101	485	834	0	11	608	23	0	0
364	105	108	0	0	22	0	43	603	129	22	86	22	43	0
328	115	61	259	503	152	30	396	549	274	30	244	0	221	213
329	117	637	319	159	239	53	266	1036	0	106	292	27	80	345
366	124	312	293	156	351	0	156	839	0	59	176	0	39	78
357	134	340	321	25	76	0	31	309	145	13	340	6	0	63
343	138	582	240	34	137	68	342	205	103	171	308	34	34	68
349	139	409	303	91	152	0	121	334	0	15	288	0	0	76
263	148	168	905	268	335	0	0	670	134	67	1005	0	101	335
371	168	431	193	136	159	45	68	352	102	0	681	23	11	23
330	189	863	216	342	72	0	0	1240	36	575	1474	288	324	126
280	203	19	56	93	149	0	205	37	0	0	465	0	37	0
365	211	410	740	90	140	0	0	100	640	960	580	20	320	40
351	227	389	1092	216	173	519	216	811	0	11	173	11	54	86
341	275	109	246	27	711	0	246	191	109	656	137	55	0	0

Distribution in grain size classes

Distribution in grain size classes was investigated because depth distribution was related to substrate type. Results from the investigation are presented in circle graphs. The distribution of porcelaneous foraminifera in grain size classes are represented by 13 dominant species (Figure 6). Most of the species, i.e., *Triloculina tricarinata*, *Miliolinella subrotunda*, *Miliolinella* cf. *M. chiastocytis*, *Quinqueloculina bicarinata*, *Quinqueloculina lamarckiana* and *Pyrgo denticulata* do not show preferred distributions in any grain size classes. Distribution in the medium sand class are demonstrated by *M. circularis* (42% of the samples) and *P. sarsi* (58% of the samples). The remaining five species demonstrate abundant distribution in the very fine sand class, i.e., *Triloculina affinis* (43% of the samples), *Quinqueloculina seminulum* (45% of the samples), *Quinqueloculina venusta* (60% of the samples), *Spirosigmoilina speciosa* (45% of the samples) and *Spiroloculina manifesta* (43% of the samples).

Distribution in percentages of silt and clay

Distribution in percentages of silt and clay gives account into the life position of optimally preserved porcelaneous benthic foraminifera. Results from the investigation are presented in circle graphs. The distribution of porcelaneous

foraminifera in percentages of silt and clay is represented by 13 dominant species (Figure 7). Abundant distribution in the high percentages of silt and clay is demonstrated by *Quinqueloculina seminulum* (40%), *Spiroloculina manifesta* (33%), *Spirosigmoilina speciosa* (39%) and *Triloculina affinis* (29%). Abundant distribution in the highest percentages of silt and clay is demonstrated by *Quinqueloculina venusta* (38%). Abundant distribution in medium percentages of silt and clay is demonstrated by *Pyrgo denticulata* (37%). Abundant distribution in low percentages of silt and clay is demonstrated by *Quinqueloculina bicarinata*, with 30% of the samples. Abundant distribution in the lowest percentages of silt and clay is demonstrated by *Pyrgo sarsi* (47%). The remaining species, i.e., *Miliolinella subrotunda*, *Miliolinella* cf. *M. chiastocytis*, *Miliolinella circularis*, *Triloculina tricarinata* and *Quinqueloculina lamarckiana* do not show abundant distribution in percentages of silt and clay.

DISCUSSION

Optimally preserved tests

In the study by Yordanova & Hohenegger (2002), empty tests were categorised into three preservation states, i.e., optimal, good and poor. The categorisation separates taphonomic processes induced by water movement (abrasion

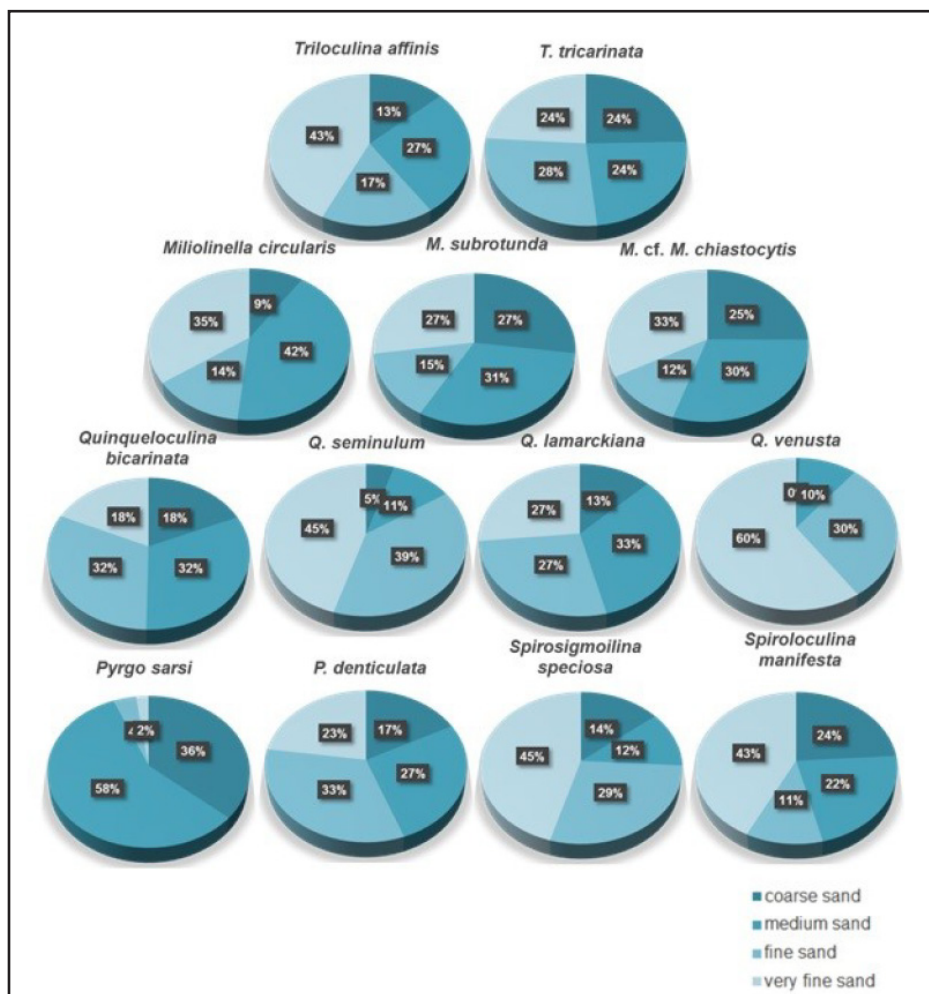


Figure 6: Distribution of porcelaneous benthic foraminifera in grain size classes.

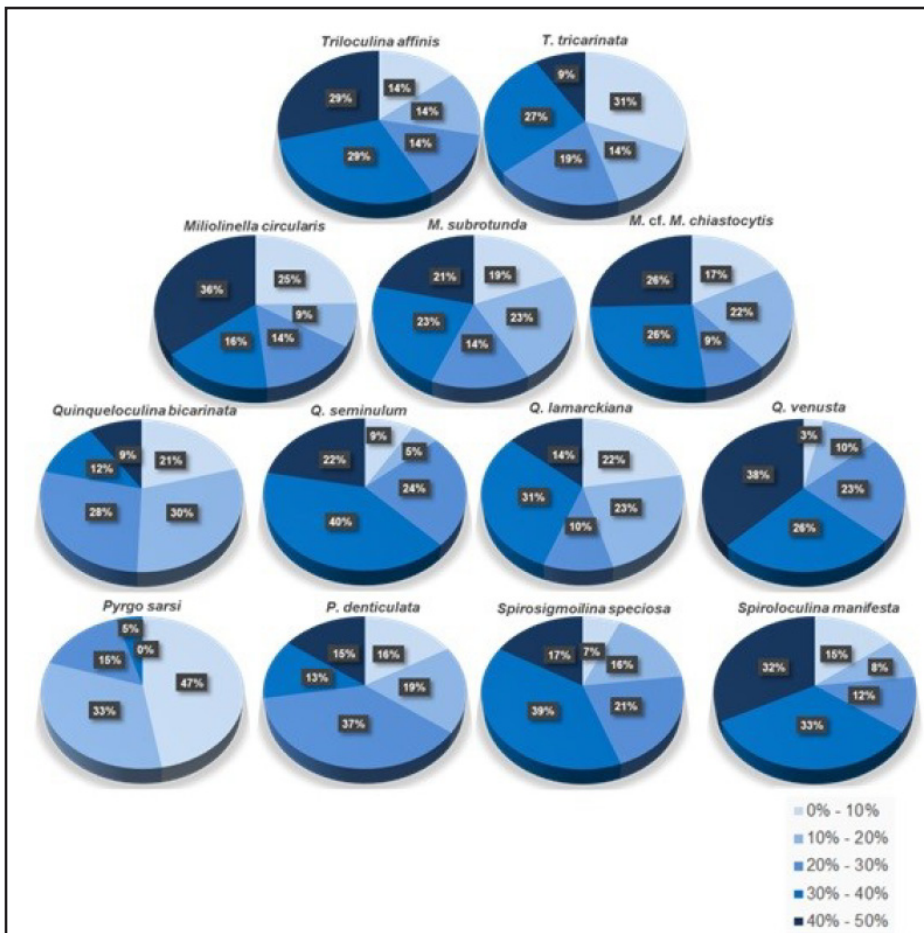


Figure 7: Distribution of porcelaneous benthic foraminifera in percentages of silt and clay.

and mechanical fragmentation) from non-transport related signals (corrosion, predation, dissolution, encrustation and colouring). Distributions of optimally preserved larger benthic foraminiferal tests have shown coincidence with the distributions of living individuals (Yordanova & Hohenegger, 2002). The sum of both distributions (empty tests and living individuals) indicates time-averaged biocoenosis. Distribution of tests with good preservation state signals time-averaged down-slope transport. Distribution of poorly preserved tests signals allochthonous material or reworking of relict sediments. Distribution of optimally preserved larger benthic foraminiferal tests from the same investigation area (unpublished data) has shown agreements on depth distribution and substrate dependence with previous studies by Hohenegger (1994); Hohenegger *et al.* (1999); Yordanova & Hohenegger (2002) conforming on the applicability of optimally preserved empty tests in investigating the distribution of smaller benthic foraminifera.

Depth distribution

The depth distribution of larger benthic foraminifera is well understood based on studies that have been conducted by Hallock & Hansen (1978); Hottinger (1983); Hallock (1984); Hallock *et al.* (1991); Hohenegger (1994); Hohenegger *et al.* (1999); Hohenegger (2000a); Hohenegger (2000b); Hohenegger & Yordanova (2001a); Yordanova & Hohenegger (2002); Hohenegger (2004). Smaller benthic foraminifera

constituting the majority of benthic foraminiferal species are underrepresented in depth distribution investigations. Depth distribution inferences of benthic foraminifera are crucial in paleodepth estimation. The inferences obtained from living to fossil foraminifera are required in many fields of earth sciences, i.e., sequence stratigraphy, paleoceanography and oil exploration. The depth distribution patterns of the porcelaneous benthic foraminifera are asymmetric (shallow-side and deep-side skewness) and bimodal (Figure 5). The distribution of porcelaneous benthic foraminifera show that the optima are located throughout the depth gradient, from the middle sublittoral to uppermost bathyal zones (Table 2).

Bimodal distribution

Quinqueloculina bicarinata and *Quinqueloculina seminulum* are the two species showing bimodal distribution pattern. *Quinqueloculina bicarinata* shows that the optima of the first and second components are located at the 120m and 270m depth classes respectively. *Quinqueloculina seminulum* shows that the optima of the first and second components are located at the 90m and 240m depth classes respectively. The first optima in the bimodality shows the depth distribution of benthic foraminifera found in autochthonous sediments. The second optima shows the distribution of benthic foraminifera in allochthonous sediments.

The bimodal distribution shown by the benthic foraminifera might have been caused by depth transport.

Depth transport was induced by traction in the seafloor that has been caused by currents and cyclones, steepness of the slope and different test buoyancies (Hohenegger & Yordanova, 2001b). Slope topography and exposure of coast to storms can lead to the deposition of allochthonous sediments from shallow water regions. Open shelf areas were more affected by tropical storms down to 150m depth (Hohenegger & Yordanova, 2001b). Correlation between depth and proportion of gravel indicates depth transport (Figure 8). The second order polynomial trendline shows that the proportion of gravel is the highest in the shallow water region. The proportion decreases between 50m and 150m depth before it increases again between 200m and 270m depth. The high proportion of gravel in the deeper region indicates that the sediments have been transported

from the surrounding shallow water region. The composition of dead foraminiferal assemblages is influenced by transport (Hohenegger & Yordanova, 2001b).

Grain size distribution in all samples demonstrate associations with depth and distance to the reef edge (Figure 9). Depth was more important than distance to the reef edge due to its position in the ordination. Depth is located close to axis 1, which has the highest eigenvalue of 99.6%. Distance to the reef edge is located much nearer to axis 2, which has much lower eigenvalue of 0.4%. There were four samples located in the top-left of the ordination showing close associations with increasing depth. These samples represent the dominance of silt and clay in the deeper region. Four samples located in bottom-left of the ordination were also showing correlations with increasing depth. These samples represent dominance of sandy sediments. One of the samples show bimodal distribution pattern indicating that the sediments were transported from the shallow region, with the main component distributed as sand and the second component shows low proportion of gravel. Most samples were located in the shallow water region, as demonstrated by the positions of nine samples in the bottom-right of the ordination. These samples have shown associations with decreasing water depth. Grain size distribution of these samples show strong dominance of coarser sediment grains, i.e., coarse sand and gravel. Four of these samples show bimodal pattern with the main component dominated by sand and the second component dominated by high proportion of gravel. The remaining seven samples located in the top-right show associations with increasing distance

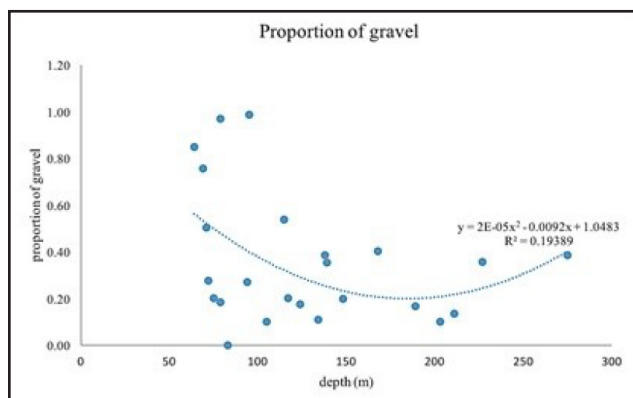


Figure 8: Correlation between depth and proportion of gravel.

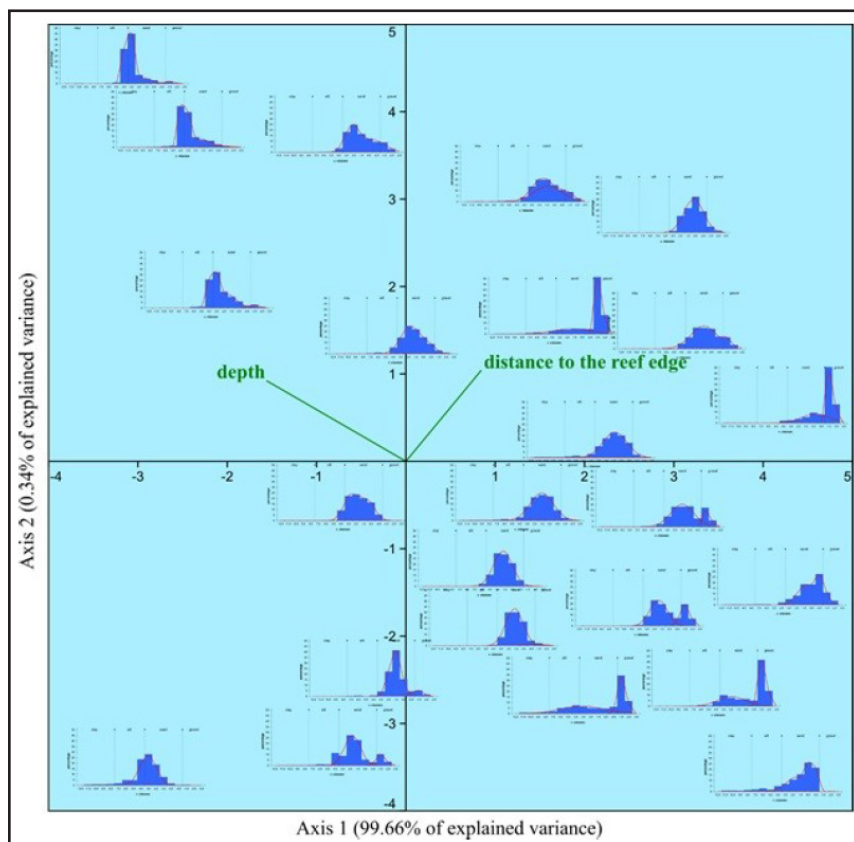


Figure 9: Ordination of canonical correspondence analysis of depth, distance to the reef edge and grain size distribution.

Table 2: Summary of depth distribution, dependence on substrate type, dominance in silt and clay fraction and life position of benthic foraminiferal species in the middle to deeper sublittoral and uppermost bathyal zones, Northwest of Okinawa, Japan.

Species	Optima (m)	Substrate type	Silt & clay fraction	Life position
<i>Miliolinella</i> cf. <i>M. chiastocytis</i>	166	No dependence	No dominance	Epi/ Infaunal
<i>Miliolinella circularis</i>	248	Medium sand	No dominance	Epi/ Infaunal
<i>Miliolinella subrotunda</i>	159	No dependence	No dominance	Epi/ Infaunal
<i>Pyrgo denticulata</i>	247	No dependence	Medium %	Epi/ Infaunal
<i>Pyrgo sarsi</i>	239	Medium sand	Lowest %	Epifaunal
<i>Triloculina affinis</i>	86	Very fine sand	High %	Infaunal
<i>Triloculina tricarinata</i>	109	No dependence	No dominance	Epi/ Infaunal
<i>Spirosigmoilina speciosa</i>	133	Very fine sand	High %	Infaunal
<i>Spiroloculina manifesta</i>	175	Very fine sand	High %	Infaunal
<i>Quinqueloculina bicarinata</i>	94	No dependence	Low %	Epifaunal
<i>Quinqueloculina lamarckiana</i>	127	No dependence	No dominance	Epi/ Infaunal
<i>Quinqueloculina seminulum</i>	99	Very fine sand	High %	Infaunal
<i>Quinqueloculina venusta</i>	235	Very fine sand	Highest %	Infaunal

to the reef edge and increasing water depth. These samples show dominance of sandy component except two of them which show dominance of gravel component in the bimodal distribution pattern. The main component in the bimodal distributions indicate autochthonous material and the second component represents allochthonous material.

Inferences of life position

The depth distribution of benthic foraminifera is crucial in paleodepth estimation. Depth distribution inferences using statistical technique (power transformed normal distribution) has never been conducted in this region. Besides depth distribution, dependence on substrate type is also analysed based on foraminiferal distribution in sediments. According to our data, foraminiferal dependence on substrate type is related to their dominance in the silt and clay fraction. The life position of smaller benthic foraminifera is inferred based on this relationship (Figure 7).

Triloculina affinis is distributed from the middle sublittoral to uppermost bathyal zones. The optimal depth distribution is located at 86m (Table 2). The

highest abundance (43%) is represented in very fine sand. Distributions in silt and clay shows highest abundance in the 40-50% and 30-40% classes. The proportions of samples decrease continuously with the decrease of silt and clay percentages thus no dominance in other classes is detected. Dependence on very fine sand substrate is in agreement with the dominance in high percentages of silt and clay thus reflecting the preference of infaunal life.

Quinqueloculina bicarinata is distributed from the middle sublittoral to uppermost bathyal zones. Optimal depth distribution is located at 94m (Table 2). Distribution in grain size classes does not show preference on substrate type due to similar distributions of 32% in each medium and fine sand class. Distribution in silt and clay demonstrates highest abundance (30%) in low percentages (10-20%) of silt and clay. Proportion of samples decreases continuously with the increasing percentages of silt and clay thus no dominance is detected in other classes. Independence on substrate type and dominance in low percentages of silt and clay does not allow the indication of life position.

Quinqueloculina seminulum is distributed from the middle sublittoral to uppermost bathyal zones with an optimum at 99m (Table 2). The highest abundance (45%) is in very fine sand. The silt and clay proportions demonstrate highest abundance (40% of the samples) in the high percentage (30-40%) class. The proportion of samples decreases continuously with decreasing silt and clay percentages, thus no dominance in other classes was detected. The dependence on very fine sand substrate is in agreement with the dominance in high percentages of silt and clay thus reflecting the preference of infaunal life. *Q. seminulum* is a dominant species in normal marine lagoon possessing epifaunal and infaunal life positions (Murray, 2006).

Miliolinella cf. *M. chiastocytis* is distributed from the middle sublittoral to uppermost bathyal zones with an optimum at 166m (Table 2). The distribution in grain size classes does not show preference on substrate type due to 33% of the samples is found in very fine sand and 30% in medium sand. Distribution in silt and clay does not demonstrate any dominance. The highest abundance (26% of the samples) is recorded in the highest percentages class of 40-50%. The decrease in the proportion of samples is not continuous with decreasing silt and clay percentages where the second highest sample proportion of 22% is located in the low percentages class (10-20%). This demonstrates dominance in the highest and low percentage classes. Independence on substrate type is in agreement with no dominance in silt and clay thus does not allow the indication of life position.

Miliolinella subrotunda is distributed from the middle sublittoral to uppermost bathyal zones with an optimum at 160m (Table 2). The distribution in grain size classes does not show preference on substrate type due to 31% of the samples in medium sand and 27% in coarse sand. The distribution in silt and clay does not demonstrate any high abundance in percentages classes. 19% of the samples is

located in the 0-10% class (lowest percentages), 14% in the 20-30% class (medium percentages), 21% in the 40-50% class (highest percentages) thus indicating no dominance. Thus, independence on substrate type and no dominance in percentages of silt and clay does not allow the indication of life position. In Murray (2006), *M. subrotunda* was identified as an epifaunal species.

Triloculina tricarinata is distributed from the middle sublittoral to uppermost bathyal zones with an optimum at 109m (Table 2). The distribution in grain size classes does not show preference on substrate type due to 28% of the samples is distributed in fine sand and the remaining sample proportion is distributed equally in the other grain size classes, with 24% of sample in each class. The distribution in silt and clay does not demonstrate any dominance in percentages. The highest abundance (31% of the samples) is found in the lowest percentages class (0-10%). The decrease in sample proportion is not continuous with the increasing silt and clay percentages where second highest abundance (27% of the samples) is recorded in the high percentages class of 30-40%. This demonstrates dominances in the high and lowest percentages classes. Independence on substrate type is in agreement with no dominance in silt and clay percentages thus does not allow the indication of life position.

Quinqueloculina lamarckiana is distributed from the middle sublittoral to uppermost bathyal zones with an optimum at 127m (Table 2). The distribution in grain size classes does not show preference on substrate type due to 33% of the samples is distributed in medium sand and the remaining sample proportion is distributed equally in the fine and very fine sand classes, with 27% of samples in each class. The distribution in silt and clay does not demonstrate any dominance in percentages classes. The highest abundance (31% of the samples) is recorded in the high percentages class of 30-40%. The decrease in sample proportion is not continuous with the decreasing silt and clay percentages where second highest abundance (23% of the samples) is recorded in the low percentages class of 10-20%. This demonstrates dominances in the high and low percentages classes. No dependence on substrate type is in agreement with no dominance in silt and clay percentages thus does not allow the indication of life position.

Spirosigmoilina speciosa is distributed from the middle sublittoral to uppermost bathyal zones with an optimum at 133m (Table 2). The highest abundance (45%) is in very fine sand. Silt and clay proportions demonstrate highest abundance (39%) in the high percentages (30-40%) class. The proportion of samples decreases continuously with decreasing silt and clay percentages, thus no dominance in other classes is detected. Dependence on very fine sand is in agreement with the dominance in high percentages of silt and clay, thus reflecting the infaunal life.

Spiroloculina manifesta is distributed from the middle sublittoral to uppermost bathyal zones with an optimum at 175m (Table 2). The highest abundance (43%) is in very fine sand. Silt and clay proportion show highest abundances in the 40-50% and 30-40% classes, with 32% of the

samples distributed similarly in each class. The proportion of samples decreases continuously with decreasing silt and clay percentages, thus no dominance in other classes is detected. Dependence on very fine sand substrate is in agreement with the dominance in high percentages of silt and clay, thus reflecting the infaunal life.

Miliolinella circularis is distributed from the middle sublittoral to uppermost bathyal zones with an optimum at 248m (Table 2). The highest abundance is in medium sand, with 42% of the samples located in this grain size class. Distribution in silt and clay demonstrates abundance optimum (36% of samples) in the highest percentages class of 40-50%. The decrease in the proportion of samples is not continuous with decreasing silt and clay percentages, where the second highest sample proportion of 25% is located in the lowest percentages class of 0-10%. This demonstrates another dominance in silt and clay percentages. The dependence on medium sand substrate is in agreement with no dominance in silt and clay percentages thus does not allow the indication of life position.

Pyrgo denticulata is distributed from the middle sublittoral to uppermost bathyal zones with an optimum at 247m (Table 2). The distribution in grain size classes does not show preference on substrate type due to 33% of the samples in fine sand and 27% in medium sand. The distribution in silt and clay demonstrates highest abundance (37% of the samples) in medium percentages (20-30%) of silt and clay. Independence on substrate type and dominance in medium percentages of silt and clay thus does not allow the indication of life position.

Pyrgo sarsi is distributed from the middle sublittoral to uppermost bathyal zones with an optimum at 239m (Table 2). The highest abundance (58%) is found in medium sand. The distribution in silt and clay demonstrates highest abundance (47% of the samples) in lowest percentages of silt and clay. The proportion of samples decreases continuously with the decrease of silt and clay percentages thus no dominance in other classes is detected. Dependence on medium sand substrate and dominance in lowest percentages of silt and clay does not allow the indication of life position.

Quinqueloculina venusta is distributed from the middle sublittoral to uppermost bathyal with an optimum at 235m (Table 2). The highest abundance (60%) is in very fine sand. Silt and clay proportions demonstrate highest abundance (38% of the samples) in the highest percentages class. The proportion of samples decreases continuously with decreasing silt and clay percentages, thus no dominance in other classes is detected. Dependence on very fine sand substrate is in agreement with the dominance in highest percentages of silt and clay thus reflecting infaunal life.

CONCLUSION

Relationship between depth distribution and dependence on substrate type

Benthic foraminifera demonstrate partial agreement between optima in the middle sublittoral zone and dependence on substrate type. Species showing optima in the

middle sublittoral zone demonstrate dependence on very fine sand or independence of specific substrate type. *Triloculina affinis* with an optimum at 86m shows dependence on very fine sand and *Quinqueloculina bicarinata* with an optimum at 94m does not demonstrate dependence on any specific substrate type. Foraminiferal species showing optima in the deeper sublittoral zone demonstrate dependence on very fine sand or independence of specific substrate type. *Spiroloculina manifesta* with an optimum at 175m shows dependence on very fine sand and *Quinqueloculina lamarckiana* with an optimum at 127m does not demonstrate dependence on any specific substrate type. Foraminiferal species showing optima in the uppermost bathyal zone demonstrate dependence on very fine sand, medium sand or independence of specific substrate type. *Quinqueloculina venusta* with an optimum at 235m shows dependence on very fine sand, *Miliolinella circularis* with an optimum at 248m shows dependence on medium sand and *Pyrgo denticulata* with an optimum at 247m does not demonstrate dependence on any specific substrate type.

Relationship between dependence on substrate type and dominance in silt and clay fraction

Relationships among the depth distribution, dependence on substrate type and dominance in silt and clay fraction are summarised in Table 2. The investigation shows that benthic foraminiferal distribution in the depth gradient is related to dependence on substrate type. Dependence on substrate type is related to dominance in silt and clay fraction which enabled inferences of life position to be made. The silt and clay fraction stabilises organic matter in the sediments (Hassink, 1997). Therefore, the distribution of benthic foraminiferal species in the middle and deeper sublittoral to uppermost bathyal zones are related to organic material in sediments.

- I. Dependence on fine or very fine sand is related to test dominance in the high or highest percentages of silt and clay. Dominance in the high or highest percentages of silt and clay is reflected on infaunal life position of the species.
- II. Dependence on coarse sand, medium sand or no dependence on any specific substrate type is related to test dominance in the low or lowest percentages of silt and clay. Dominance in the low or lowest percentages of silt and clay is reflected on epifaunal life position of the species.
- III. Dependence on coarse sand, medium sand or no dependence on any specific substrate type is related to no dominance in percentages of silt and clay. No dominance of the tests in percentages of silt and clay reflects on either epifaunal or infaunal life position of the species.

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