Diversity and Taxonomy Of Recent Benthic Foraminifera In The Northeast Atlantic Ocean

Dissertation

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Kiel, 2014

Diversity and taxonomy of Recent benthic foraminifera in the Northeast Atlantic Ocean

Dissertation

zur Erlangung des Doktorgrades

Dr. rer. nat.

der Mathematisch-Naturwissenschaftlichen Fakultät

der Christian-Albrechts-Universität zu Kiel

vorgelegt von

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Kiel, 2014

Erster Gutachter: Prof. Dr. Wolf-Christian Dullo

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Eingereicht am: 23.09.2014

Datum der Disputation: 10.11.2014

Zum Druck genehmigt: 10.11.2014

gez. Prof. Dr.Wolfgang J. Duschl, Dekan

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Kiel, den 23.09.2014

Sabine Dorst

Contents

Abstract

This study is focusing on the diversity and taxonomy of Recent benthic foraminifera on the shelf and continental slope of the northeast Atlantic Ocean between 43° and 58° N. To get an overview about previous foraminiferal studies from this area, qualitative and quantitative published data of foraminiferal occurrences and abundances at 2902 stations were retrieved and analyzed. These investigations revealed a compiled total of 1486 species, of which 379 species were synonymous and 241 species had an uncertain identity. Therefore, the significant minimum species number of benthic foraminifera in the study area was 866. A common distribution of a hyaline test structure and a free mode of life, as well as an increase of diversity (Fisher α index) from the shelf to the slope and of mean species number on the shelf from N to S, are distinctive for the whole area. In addition, two mid-slope diversity maxima were found. One is located on the Basque continental margin at 550 – 850 m water depth and the other one is located west of Ireland between 700 and 1100 m. Analyses of the latitude-depth-distribution of six dominant species showed an oak leaf-shaped distribution pattern for the shelf areas and similar patterns for all six species on the continental slope, which suggests that these species have the same ecohabitat throughout their depth range. Comparing different datasets and recording general biodiversity patterns was difficult because of inconsistencies in foraminiferal taxonomy and sample preparation, absence of essential metadata and gaps in data coverage. These difficulties influenced the diversity calculations, and in some cases, made rough estimates impossible.

An influence on a benthic faunal composition by the time and methods of sampling was detected during analyses of Recent benthic foraminifera from the shelf and slope of the Celtic Sea. A total number of 294 species was recorded at 13 stations in a range from 100 to 500 m water depth. While the distribution pattern of the living species revealed a bisection in a distal and proximal fauna on the shelf, the living fauna on the slope changed within small depth intervals and geographic position. This structured slope is probably caused by along-slope currents of varying strengths, different topography and bottom sediments. High population densities were determined along the shelf edge and at one slope station, as well as an increasing diversity with water depth. These higher densities and diversities were likely promoted by a higher food supply, in response to the timing of

the spring bloom. *Trifarina angulosa* and *Gavelinopsis praegeri* were the most frequent species in the living fauna on the shelf and uppermost slope, whereas *Cibicides lobatulus* and *Spiroplectinella sagittula* were the most frequent species at almost all stations in the dead assemblages. A comparison with corresponding stations from earlier studies in the same area yields major differences in diversity, population density and dominant species, which is more likely due to the time and method of sampling than forced by environmental parameters.

Analyses of the distribution and ecology of benthic foraminiferal assemblages from the Celtic Sea yield 31 taxa of the family Trochamminidae. Eighteen of these 31 taxa could be determined at species level, which comprise about 9 % of all species of this taxonomic group that were described from Recent sediments. In the frame of this study, 19 taxa of the Trochamminidae were described and illustrated. Several taxonomic concepts exist, which differs from each other in their systematic classification. These concepts were assessed with respect to their applicability. All concepts used the morphology of the test, internal structures and apertural features for the systematic subdivision of the Trochamminidae. Especially the position of the aperture plays an important role for genera definition and differentiation. Using apertural features for a sound taxonomic designation of species in this study was proven difficult. A combination of morphological and molecular phylogenetic studies is required to verify the relevance of apertural features.

Kurzfassung

Diese Studie beschäftigt sich mit der Diversität und Taxonomie rezenter benthischer Foraminiferen vom Schelf und Kontinentalhang des Nordostatlantiks zwischen dem 43. und 58. nördlichen Breitengrad. Um sich eine Überblick über bisherige Foraminiferenarbeiten aus diesem Gebiet zu verschaffen, wurden bereits veröffentlichte qualitative und quantitative Daten über das Vorkommen und die Häufigkeit benthischer Foraminiferen von 2902 Stationen zusammengetragen und ausgewertet. Diese Erhebung ergab eine Gesamtartenzahl von 1486. Davon wurden 379 Arten als Synonyme identifiziert und 241 Arten konnten nicht eindeutig bestimmt werden. Damit liegt die als gesichert zu erachtende Mindestartenzahl in diesem Untersuchungsgebiet bei 866. Foraminiferen mit einer hyalinen Gehäusestruktur und einer freien Lebensweise sind am häufigsten vertreten. Weiterhin ist für das untersuchte Gebiet ein Diversitätsanstieg (Fisher α Index) vom Schelf zum Hang, sowie eine Zunahme der durchschnittlichen Artenzahl auf dem Schelf von Nord nach Süd charakteristisch. Es wurden zwei Diversitätsmaxima im Bereich des mittleren Kontinentalhanges gefunden. Das eine befindet sich am baskischen Kontinentalrand in 550 – 850 m Wassertiefe, das andere liegt westlich von Irland in 700 – 1100 m Tiefe. Die Ermittlung einer Breiten-Tiefen-Verteilung von sechs dominanten Arten ergab ein eichenblattartiges Verbreitungsmuster für die Schelfgebiete und ein ähnliches Verbreitungsmuster für alle sechs Arten auf dem Kontinentalhang. Dies lässt vermuten, dass diese Arten dasselbe Ökohabitat besitzen. Ein Vergleich der unterschiedlichen Literaturdaten und die Bestimmung eines generellen Diversitätsmusters hat sich aufgrund der Unterschiede in der Foraminiferentaxonomie und Probenbearbeitung, dem Fehlen wichtiger Metadaten, sowie größeren Lücken in der Datenabdeckung als schwierig erwiesen. Diese Unterschiede beeinflussten die Berechnungen und machten in einigen Fällen eine Bewertung unmöglich.

Untersuchungen an rezenten benthischen Foraminiferen vom Schelf und Kontinentalhang der keltischen See zeigten, das der Zeitpunkt und die Art der Probennahme die Zusammensetzung der Fauna beeinflusst. An den beprobten 13 Stationen aus einem Tiefenbereich zwischen 100 und 500 m wurden insgesamt 294 Arten ermittelt. Während die Verbreitungsmuster der lebenden Arten auf dem Schelf eine Zweiteilung in eine distale und proximale Fauna erkennen ließen, variierte die

Lebendfauna am Hang sowohl innerhalb kurzer Tiefenintervalle als auch bezüglich der geographischen Entfernung zwischen den Stationen. Gründe für diese starke Faunenstrukturierung am oberen Kontinentalhang könnten die unterschiedlichen, an der Schelfkante entlang fließenden Strömungen, als auch die differenzierte Hangtopographie und Sedimentzusammensetzung sein. Die höchsten Siedlungsdichten wurden entlang der Schelfkante und an einer Hangstation ermittelt. Außerdem konnte eine Zunahme der Diversität mit zunehmender Wassertiefe festgestellt werden. Diese höheren Siedlungsdichten, als auch die Diversitätszunahme wurden wahrscheinlich durch ein höheres Nährstoffangebot, aufgrund der Frühjahrsblüte begünstigt. Für den Schelf und obersten Kontinentalhang wurden *Trifarina angulosa* und *Gavelinopsis praegeri* als häufigste Arten der Lebendfauna ermittelt, während innerhalb der Totfauna *Cibicides lobatulus* und *Spiroplectinella sagittula* im gesamten Untersuchungsgebiet am häufigsten vertreten waren. Ein Vergleich mit früheren Studien aus demselben Gebiet ergab deutliche Unterschiede hinsichtlich der ermittelten Diversitäten, Siedlungsdichten und häufigsten Arten. Diese Unterschiede scheinen vor allem mit dem Zeitpunkt und der Art der Probennahme zusammenzuhängen, als durch Umwelteinflüsse bedingt zu sein.

Im Rahmen von Untersuchungen zur Verbreitung und Ökologie benthischer Foraminiferenfaunen aus der keltischen See wurden insgesamt 31 Arten ermittelt, die zur Familie der Trochamminidae gezählt werden. Von diesen 31 Taxa konnten 18 Arten eindeutig bestimmt werden, was einem Anteil von etwa 9 % an allen bisher aus rezenten Sedimenten beschriebenen Arten dieser Familie entspricht. In dieser Studie haben wir 19 Taxa aus der Familie der Trochamminidae ausführlich beschrieben und abgebildet. Zu dieser Foraminiferengruppe existieren mehrere taxonomische Konzepte mit unterschiedlicher Systematik, welche bezüglich ihrer Anwendbarkeit bewertet wurden. Für eine systematische Klassifizierung der Gattungen und Arten innerhalb der Trochamminidae, wurden in allen Konzepten die Gehäusemorphologie, innere Gehäusestrukturen sowie die verschiedenen Mündungsmerkmale herangezogen. Insbesondere die Lage der Mündung scheint eine entscheidende Rolle für die Definition und Unterscheidung der Gattungen zu spielen. Die Verwendung der Mündungsmerkmale für die Bestimmung der Arten aus der keltischen See erwies sich allerdings als schwierig. Eine Kombination von morphologischen und molekular-phylogenetische Untersuchungen wird benötigt, um die taxonomische Bedeutung der Mündungsmerkmale belegen zu können.

Introduction

Benthic foraminifera are unicellular protistans, mostly covered by a hard-shelled test which consists either of secreted calcite (rotaliids and milioliids), agglutinated sediment particles (textulariids) or organic material (allogromiids). They are generally small (<1 mm), occur in all marine environments, and their tests may be preserved in the fossil record (Murray, 2006). Due to these attributes and their ability to respond quickly to changing environmental conditions, benthic foraminifera play an important role in Recent as well as paleo-oceanographic and paleo-climatic research. There are two features which allow a reconstruction of environmental conditions in a benthic foraminiferal habitat. On one hand, the chemical composition of calcite tests provides information about the surrounding seawater. On the other hand, foraminiferal assemblage compositions, diversity, mode of life, test morphology and their adaptation to extreme habitat niches give information about Recent and paleo-environmental conditions. For both features, a precise determination of foraminiferal species is essential. At present, benthic foraminiferal species are defined primarily on wall structure, chamber and test shape, and the position of the aperture. Therefore, foraminiferal ecology is based entirely on morphospecies (Murray, 2006).

Benthic foraminifera are distributed everywhere in the ocean, from marginal marine environments (marsh, lagoons, estuaries, fjords and deltas) down to the abyssal plain (Murray, 2006, 2007). Extensive biogeographic provinces of benthic foraminifera have been recognized on various continental shelves and slopes (Sen Gupta, 1999). Many studies on the distribution of benthic foraminiferal assemblages on the shelf and slope of the Northeast Atlantic Ocean (NE Atlantic) exist. Over 40 benthic foraminiferal studies from the western European margin between the Basque shelf and continental slope north of Spain and the Hebrides north of Ireland were analyzed in this thesis. Most of these studies are located on the shelf. The shelves are broad and irregular; their width varies between 10 – 60 km off northern Spain and approximately 500 km in the Celtic Sea (Huthnance et al., 2009). The continental slope is steep from the north of Spain to northwest Scotland, and characterized by spurs and canyons organized in submarine drainage basins (Bourillet et al., 2006; Huthnance et al., 2009).

The general hydrography in the studied area is characterized by different intermediate and deep water masses as well as surface currents. The two major components of the NE Atlantic circulation are the Mediterranean Outflow Water (MOW) and the Eastern North Atlantic Water (ENAW). The MOW flows northward along the European continental margin through the Porcupine Seabight underlying the ENAW at depth between 750 and 1250 m (van Aken and Becker, 1996; van Rooji et al., 2003). Eastern North Atlantic Water is found to depths of 600 to 750 m (Huvenne et al., 2002; White, 2007) and being formed during the winter month in the Bay of Biscay (Pollard and Pu, 1985; van Aken, 2000). A north-flowing surface current (= North Atlantic Current, NAC) is present along the continental slope, transports warm subtropical water from the Iberian margin to high latitudes (Pingree and Le Cann, 1989; Rice et al., 1991). One branch of the NAC flows northwards to the Norwegian Sea, the other branch flows southwards into the Bay of Biscay to joins the subtropical gyre (Pingree, 1993; van Aken and Becker, 1996). This slope current is also important for physical exchange processes at the shelf break and hence cross-shelf fluxes (Huthnance, 1995; White and Bowyer, 1997).

Intensified currents, either contour, tidal or slope currents, as well as storm induced waves, and wind and density driven flows account for sediment transport and therefore influence the microhabitats of benthic foraminiferal assemblages (Murray et al., 1982). Depending on the substrate and preferred mode of life, benthic foraminifera can live epifaunal, on the surface of the substrate, or infaunal, in the sediment. Epifaunal, as well as infaunal individuals may live free, attached (= attached immobile of Sturrock and Murray, 1981) or opportunistic/free and attached (= attached mobile of Sturrock and Murray, 1981). Especially under high current velocities, some attached living species preferred elevated substrates such as shell debris, sponges, hydroids, rocks and plants to maximize the acquisition of suspended organic matter (Schönfeld, 1997, 2002a, 2002b). The hydrographic conditions together with a coarse shell detritus-rich sandy substrate were found on the Celtic Sea shelf and the western English Channel. The continental slopes of the study area are mostly covered by mud or silt.

The availability of food supply seems to be the fundamental limiting factor controlling benthic foraminiferal distribution patterns. Especially phytoplankton blooms, which are patchy in occurrence, may be a prime cause of spatial patchiness in the abundance of benthic foraminifera (Lee et al., 1977; Murray, 2006). Spring phytoplankton blooms are a prominent seasonal feature of the NE Atlantic, and can be initiated by certain

weather conditions and promoted by internal tides (Henson et al., 2006; Ji et al., 2010; Van Oostende et al., 2012). The bloom usually starts at the end of March, propagates northward following surface warming and stratification (Robinson et al., 1993; Leblanc et al., 2009), and involves a rapid diatom growth and their dominance in the phytoplankton in April. This "diatom bloom" is followed by a more diverse community bloom of prymnesiophytes (mainly composed of coccolithophores, Van Oostende et al., 2012), cynobacteria, dinoflagellates and green algae in the later seasons (Sieracki et al., 1993; Leblanc et al., 2009).

The main objective of this thesis is the determination of benthic foraminiferal diversity from the northwest European shelf and continental slope, and the generation of a standardized foraminiferal taxonomy. The thesis is based on three chapters.

In Chapter 1, I reviewed the distribution of benthic foraminiferal species in the NE Atlantic based on over 40 publications and unpublished information. In this context, a synonymy matrix and an associated standardized taxonomy of benthic foraminifera of the western European continental margin was proposed. Foraminiferal diversity and distribution patterns of dominant species were determined and compared with data from the Gulf of Mexico.

In Chapter 2, samples from a transect perpendicular to the hydrographic front in the outer English Channel (South Western Approaches) were analyzed to constrain the influencing environmental parameters on a benthic foraminiferal fauna. Analyses indicated a greater importance of shelf upwelling and food availability than the impact of a hydrographic front for the composition of a foraminiferal assemblage. In addition, dead foraminiferal assemblages could demonstrate the influences of a high-energy environment on a faunal composition.

Benthic foraminiferal assemblages from the shelf and upper continental slope of the Celtic Sea showed a rich variety of Trochamminidae species. In Chapter 3, I assessed the applicability of hitherto proposed systematic concepts on the family Trochamminidae, and described and illustrated 19 common species of this family. In addition, emphasis was given on how far morphological criteria were suitable for a taxonomic classification.

Declaration

Declaration of my contribution to the following chapters:

CHAPTER 1 − Diversity of benthic foraminifera on the shelf and slope of the NE Atlantic: Analysis of datasets (published in: Journal of Foraminiferal Research, vol. 43, p. 238−254)

Statement:
I compiled the data from the literature and wrote the manuscript. The co-author helped by determining the foraminifera and by discussing the taxonomy. The co-author, the JFR editors P. Brenckle, J. Pawlowski and three reviewers helped improving and revising the manuscript.

CHAPTER 2 − Recent benthic foraminiferal assemblages from the Celtic Sea (South Western Approaches, NE Atlantic) (published in: Paläontologische Zeitschrift, doi 10.1007/s12542-014-0240-6)

Statement:
The foraminiferal samples were collected by André Freiwald, Beate Bader and Julia Langenbacher. Sampling preparation and picking of benthic foraminifera were done by myself, the second and the third author. Living foraminifera from two stations were picked by a student assistant (Lea Wiser). I analyzed the data set and wrote the manuscript. All co-authors helped improving the quality of the manuscript by discussing the data and their interpretation and proofreading. The second author and two reviewers helped improving and revising the manuscript.

CHAPTER 3 − Taxonomic notes on Recent benthic foraminiferal species of the family Trochamminidae from the Celtic Sea (resubmitted in: Journal of Foraminiferal Research)

Statement:
I determined the foraminiferal species of the family Trochamminidae and discussed the taxonomy with Joachim Schönfeld and Lilli Walter. I wrote the manuscript. The co-author, the JFR editors P. Brenckle, A. Holbourn and three reviewers helped improving and revising the manuscript.

CHAPTER 1 – Diversity of benthic foraminifera on the shelf and slope of the NE Atlantic: Analysis of datasets

Abstract

The objective of this work was to review the distribution of benthic foraminiferal species at the western European continental margin from 43 – 58° N, determine their diversity and generate a standardized taxonomy based on 44 publications (1913 – 2010) and unpublished information. Qualitative and quantitative data based upon foraminiferal occurrences and species abundances were included together with supplementary sedimentological and hydrographical data. From the species inventory, as well as from differences in morphological, physical and hydrographic conditions in the study area, we defined six regions. The investigation of 2902 stations revealed 1486 species, of which 26 % are synonymous. Most of the species have a hyaline test and live free, on or in the sediment. We recorded 608 species whose distributions were confined only to one of the six regions. Quantitative faunal data showed a general diversity increase from shelf to slope and two mid-slope diversity maxima, one located on the Basque continental margin at 550 – 850 m water depth and the other west of Ireland at 700 – 1100 m. In addition, the number of living species on the shelf generally increased from N – S. The latitudinal vs. depth distribution of six dominant species showed an irregular lobate distribution pattern for the shelf regions. These species displayed similar distribution patterns on the continental slope, despite different modes of life, and different food and substrate preferences. This suggests that they have the same ecohabitat throughout their depth range. The faunal distribution pattern revealed close relationships between the different

regions despite their varying hydrologic regimes. A delineation of one or two regions based on faunal criteria has not been attempted to date. There were no major distinctions in diversity among the six regions of the NE Atlantic, but the whole area exhibits an interregional diversity (γ-diversity of 16), similar in magnitude to that of the Gulf of Mexico. In some parts of the study area, gaps in data coverage and differences in foraminiferal taxonomy and hydrographic conditions prevented the calculation of diversity indices.

1.1 Introduction

Biodiversity describes the variety of life on all scales (Wilson and Peter, 1988). Marine biodiversity accounts for approximately 15 % of global biodiversity (Bouchet, 2006; Storch and Wehe, 2007). Taxonomy and classification of species are the basis of any biodiversity assessment. There is great uncertainty concerning the number of described marine species (Murray, 2007; Mora et al., 2011) with numbers ranging from 200,000 − 500,000 (Heip, 2003; Bouchet, 2006; Jaume and Duarte, 2006). Therefore, the "Census of Marine Life" project was initiated to create an oceanic inventory from 2000 – 2010. In this collaborative project, 250,000 established species of marine organisms were registered and made public (Yarincik, 2010). Accompanying projects, like HERMIONE, have investigated the species records, as well as the interaction between biota and ecological parameters. A precise estimation of the total number of living species requires an adequate number of data sources (Murray, 2007). The reliability of these sources in accurately recording the number of species and their synonyms turns out to be a major concern. Benthic foraminifera have been investigated since the mid-20th century and a large number of publications on their ecology and distribution are available. But inconsistencies in taxonomy and inadequate sampling in tropical and abyssal regions lead to major problems in estimating the total species number (see figs. 1 and 2 in Murray, 2007). In recording the diversity of benthic foraminifera, as well as all other organisms, it is important to generate a standardized taxonomy and to consider all marine environments in a balanced way.

Only a few studies to date have used a regional-synoptic approach to analyze the benthic foraminiferal diversity in certain regions (Murray, 1971, 2000; Culver and Buzas, 1980, 1981, 1985, 1986, 1987; Hayward et al., 1999; Saidova, 2008; Sen Gupta and

Smith, 2010). In particular, Murray (1971, 2000) analyzed several sources of previously published and his own foraminiferal data from the NE Atlantic and the Barents Sea together with multi-regional environmental information. He differentiated between living and dead individuals and indicated the mode of life of the common species. However, detailed quantitative information about the species at every station was not given in his publications.

Culver and Buzas (cited above) used specific computer programs to compile the first comprehensive reports on latitude and depth distribution of foraminifera from the North American Atlantic coast. Later, programs with faster converting processes (e.g., multivariate analyses) improved handling and examination of huge quantities of data. Because distinct and standardized identification of foraminiferal species is essential for analysis of species distribution and richness, Culver and Buzas (cited above) revised the species lists regarding synonymised taxa in all their five publications. Therefore, they limited their foraminiferal interpretations with reference to water depth, distribution, and test structure to the most commonly recorded species, due to inconsistencies in taxonomy and data recording. Furthermore, new morphological and molecular analyses of different species led to other emendations, especially in the last 20 years. For these reasons, Murray (2000) published a revised taxonomy of his 1971 report.

Hayward et al. (1999) used their earlier published data for a census report on benthic foraminifera around New Zealand. They determined different faunal associations based on diversity indices and cluster analyses, and divided the study area into six biogeographical provinces. Sen Gupta and Smith (2010) also divided the Gulf of Mexico into different sectors, but their division was based only on geographic coordinates, and not justified by faunal composition. Over 30 foraminiferal communities were distinguished by Saidova (2008) for the NE Atlantic shelf and slope. She limited the faunal information regarding distribution and depth to the dominant species, following an earlier approach in the Culver and Buzas papers. She also listed hydrological (temperature, salinity) and sedimentological data for all investigated areas, but detailed quantitative information about species occurrences at every station was not given.

In this study, we integrated benthic foraminiferal abundance and distribution data from 44 publications and some unpublished data to describe foraminiferal diversity in the NE Atlantic. For biodiversity investigations, we attempted to standardize taxonomy and identify synonyms. In our taxonomic reference list, we included new morphometric

concepts and genetic characteristics for some species (e.g., Ertan et al., 2004; Hayward et al., 2004; Schweizer et al., 2011) in addition to earlier morphological descriptions (e.g., Cushman, 1936; Buzas, 1966; Feyling-Hanssen, 1972). The aims of the present study are: 1) to create a synonymy matrix and an associated standardized taxonomy of benthic foraminifera of the NE Atlantic, 2) to determine foraminiferal diversity on the shelf and continental slope for comparison with Gulf of Mexico studies 3) to constrain the distribution patterns of dominant species, and 4) to determine the driving environmental parameters.

1.2 Materials and Methods

Within the framework of the EU-HERMIONE Project (Hotspot Ecosystem Research and Man's Impact on European Seas), we compiled all reliable data on the taxonomy and distribution of benthic foraminifera at the European continental margin between 43 – 58° N, published in 44 papers from 1913 – 2010 (Fig. 1.1; Table 1.1; Appendix 1.1). For 2902 sampling stations, the metadata together with qualitative and quantitative information regarding occurrence and abundance of foraminiferal species were retrieved. Supplementary oceanographic and sedimentological information, such as currents, waves and tides, primary production rates, and surface sediment composition, was also included.

During the compilation of the foraminiferal species, definite discrepancies in taxonomy and classification of numerous species emerged. Hence, we created a synonymy matrix and a standardized reference list (Appendix 1.2) by first generating a species list for every publication. Then, we compared all species names through their original reference and illustrations, as well as descriptions and illustrations from Ellis and Messina (1940), Murray (1971, 2006), Loeblich and Tappan (1987), and Jones (1994). For some genera (e.g., *Ammonia*, *Bolivina*), morphological and molecular data were taken into consideration. Furthermore, the second author of this paper checked his species identifications with the foraminiferal collections in the British Museum of Natural History, University of Aberystwyth, University of Utrecht and University of Kiel. This knowledge was integrated with our standardized taxonomy.

In order to facilitate regional comparisons, the study area was divided into six regions: A, Basque shelf and continental slope north of Spain; B, Bay of Biscay; C, Celtic

Sea; D, English Channel; E, Irish Sea; and F, the area west and north of Ireland consisting of the Rockall Trough, Porcupine Seabight, Malin Sea, and the Hebrides (Fig. 1.1). The regional divisions were based upon benthic foraminiferal assemblages and different physical-oceanographic parameters, including annual means of temperature, salinity, and dissolved oxygen of the near-bottom water, total species richness, richness of species confined to only one region, test structure, mode of life, dominant species, and Fisher α diversity index.

The Fisher α index (Fisher et al., 1943) was first described as a method of assessing species diversity. Under the assumption of an underlying logarithmical distribution of species vs. individuals, the Fisher α index is calculate from the number of species and individuals in a sample, and describes the gradient of the log relationship between these two factors (see fig. 8 in Fisher et al., 1943). Another index commonly used to measure species diversity is the information function H(S), also called the Shannon-Wiener index (Buzas and Gibson, 1969; Gibson and Buzas, 1973). This index is based upon the number of species and their relative proportions, but does not depend on any particular mathematical model (Buzas and Gibson, 1969). However, it is strongly influenced by the species frequency, resulting in a higher index value if there is one or a few dominant species. We, therefore, used the Fisher α index to avoid the effects of incomplete census data on the Shannon-Wiener index. In addition, the Fisher α index has been used in many other regional foraminiferal studies, so a comparison of diversity between regions is possible.

Hydrographical and sedimentological parameters from every station were retrieved from literature data or from the International Council for the Exploration of the Seas online database (ICES, 2009 for temperature, salinity and dissolved oxygen). The foraminiferal test structure was identified by our own observations or after Loeblich and Tappan (1987) when there was some uncertainty. While previous approaches used relational databases, we collected, processed, and stored the data as Microsoft Excel spreadsheets (Murray, 2006). This facilitates easier data handling and ensures instant visibility in table format. Statistical analyses and calculations of diversity indices were made with Microsoft Excel 2003 and PAST (Hammer et al., 2001). Distributional charts were created with Microsoft Excel and Ocean Data View (ODV; Schlitzer, 2011).
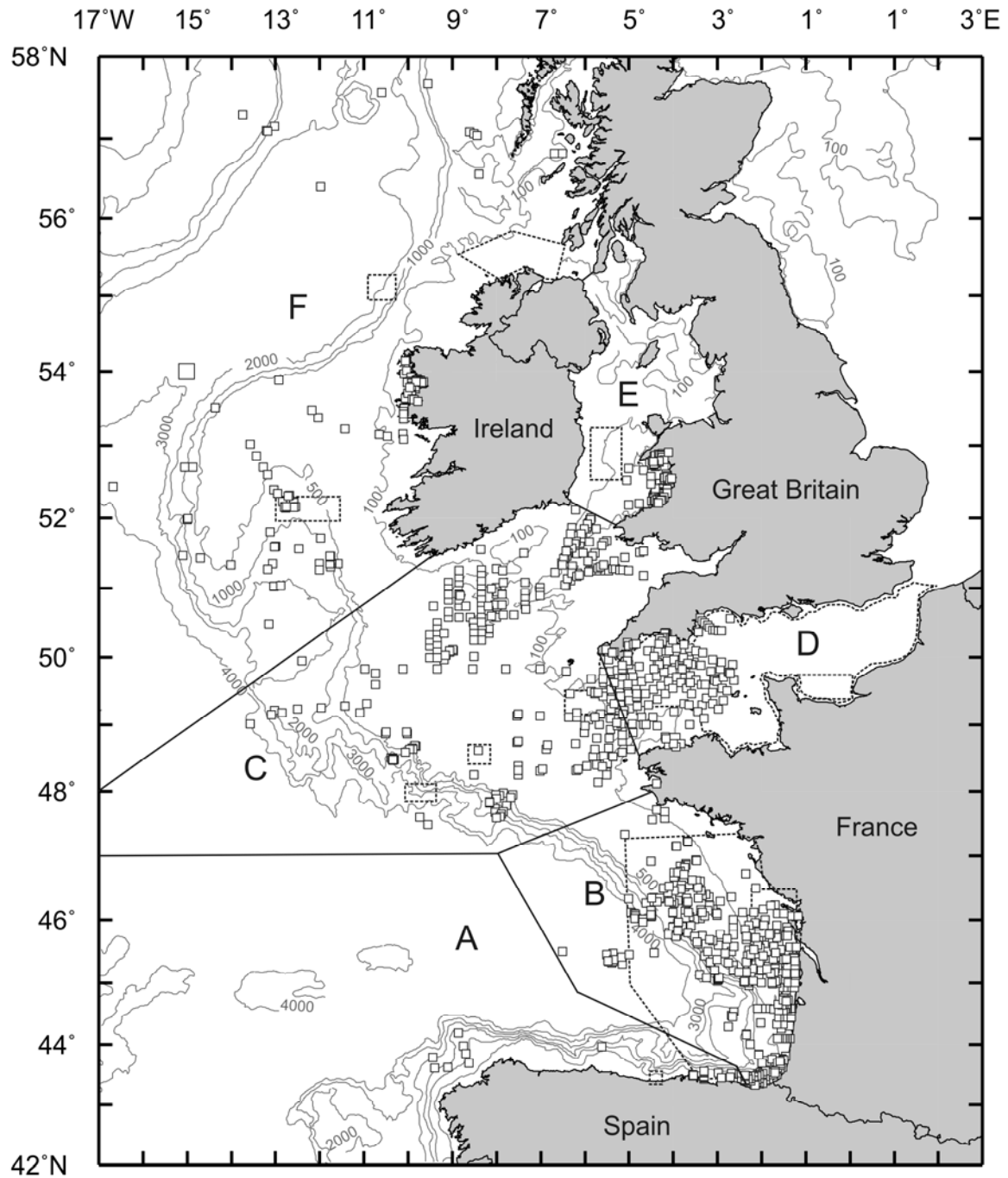
Figure 1.1 European continental margin showing 2902 stations (squares and dashed areas) from multiple studies within the context of six different environmental regions: **A** = Basque shelf and slope; **B** = Bay of Biscay; **C** = Celtic Sea; **D** = English Channel; **E** = Irish Sea; **F** = Porcupine Seabight, Rockall Trough, Malin Sea and the Hebrides. Polygons with dashed lines display areas where faunal information was available, but station coordinates were not reported (Rosset-Moulinier, 1986; Saidova, 2008).

Table 1.1 List of all publications from which data are used in this paper.

First author	Year	Region	Range (°N/°W)	Depth (m)	Assemblage	Stations
Heron-Allen	1913	W Ireland (F)	53-54/9-10	0-43	not specified	35
Douvillé	1936	Roscoff (D)	48-49/3-4	0-25	living+dead	7
Le Calvez	1958	Bay of Biscay+Celtic Sea+English Channel (B+C+D)	47-50/4-11	15-210	total	19
Le Calvez	1967	English Channel (C+D)	48-50/2-6	max. 200	dead	121
Lees	1969	W Ireland (F)	53-54/10	0-60	living+dead	72
Schnitker	1969	Gulf of Gascogne (B)	46-47/3-4	110-145	dead	42
Caralp	1970	Gulf of Gascogne (B)	45-46/3-4	135-3200	total	21
Murray	1970	Celtic Sea+English Channel (C+D)	48-51/4-11	13-1002	living+dead	38
Pujos	1972	Gulf of Gascogne (B)	45-46/1-2	4-106	not specified	72
Haynes	1973	Cardigan Bay (E)	52-53/4-5	0-80	total	125
Pujos-Lamy	1973	Gulf of Gascogne (B)	45-46/3-5	135-4450	living	57
Pujos	1976	Bay of Biscay (B)	43-47/1-5	8-220	total	216
Murray	1979	Celtic Sea (C)	50-52/8-10	75-135	living+dead	56
Sturrock	1981	Celtic Sea+English Channel (C+D)	48-52/4-9	44-176	living+dead	61
Murray	1982	Celtic Sea+English Channel (C+D)	48-50/3-8	0-152	total	25
Weston	1985	Porcupine Seabight+Western Approaches (C+F)	48-52/8-14	255-1600	living+dead	44
Murray	1986	Lyme Bay (D)	50/2-3	max. 50	living+dead	14
Rosset-M.	1986	English Channel (D)	48-51/2°E-6°W	2-89	living	907
Gooday	1989	Porcupine Seabight (F)	51/13	1320-1361	living	8
Lambshead	1990	Porcupine Seabight (F)	51/13	1320-1361	living	8
Giese	1991	Roscoff (D)	49/4	0.5-40	living+dead	77
Murray	1994	Celtic Sea+Porcupine Seabight (C+F)	47-52/8-12	160-4262	total	10
Coles	1996	Porcupine Basin (F)	52/12-13	610-800	total	4
Castignetti	1998	Plymouth Sound (D)	50-51/4	2.8-7	living	4
Debenay	2001	Île d'Yeu (B)	47/2	4-8	total	28
Fontanier	2002	Bay of Biscay (B)	43-44/1-3	140-1993	living	5
Fontanier	2003	Bay of Biscay (B)	44/2	550	living	1
Murray	2003a	Hebrides (F)	56-57/6-9	134-218	living+dead	6
Murray	2003b	Hebrides (F)	56-57/6-9	134-218	living+dead	6
Scott	2003	Celtic Sea (C)	51-52/4-7	41-116	living+dead	53
Ernst	2004	Bay of Biscay (B)	44/2	550	living	1
Sejrup	2004	W Ireland (F)	53-54/10-12	104-336	total	6
Duchemin	2005	Grande Vasiere (B)	47/3-4	100-130	living	4
Schönfeld	2005	Basque Shelf-Rockall Bank (A,C,D,F)	43-58/4-17	82-3889	living+dead	41
Panieri	2005	Rockall Trough (F)	54/15	800-1000	dead	7
Langezaal	2006	Bay of Biscay (B)	44/2	140	living	1
Pascual	2006	N Spain (A)	43/3	max. 3.5	total	18
Duchemin	2007	Bay of Biscay (B)	43-44+47/2-4	80-2000	living	11
Rüggeberg	2007	Porcupine Seabight (F)	52/13	704-820	dead	2
Pascual	2008	Basque Shelf+Bay of Biscay (A+B)	43-44/1-3	47-152	total	49
Saidova	2008	N Spain-Malin Sea (A-F)	43-56/0-13	1-4450	total	590
Margreth	2009	Porcupine Seabight+Rockall Bank (F)	51-54/11-15	202-982	total	20
Mojtahid	2010	Bay of Biscay (B)	43-46/2-7	320-4800	living	5
Schönfeld	2010	Porcupine Seabight (F)	51-52/11-13	696-982	living+dead	19

1.3 Results

1.3.1 Geographical subdivision

Changes in faunal assemblages and sedimentary environments (Pujos, 1976; Fontanier et al., 2002; Duchemin et al., 2007; Pascual et al., 2008) have been used for local differentiation of the Basque shelf (Region A) and the Bay of Biscay (Region B). Facies conditions change from an organic-rich sandy silt at 50 m depth in the east to a silty sand at 150 m in the west between 2°22' NW and 2°25' NW (see fig. 1 in Pascual et al., 2008). These sediment changes were associated with different foraminiferal assemblages. For instance, the most commonly recorded species in the western edge of Region B are *Uvigerina peregrina*, *Cassidulina laevigata* and *Gaudryina rudis*. In contrast, Region A supports dominant species such as *Gyroidina soldanii*, *Eponides repandus* and *Spiroloculina depressa*.

The Celtic Sea (Region C) adjoins the northern borders of Regions A and B (Fig. 1.1). Its boundary with the latter region is based on the faunal assemblages of Le Calvez (1958) and Duchemin et al. (2007) in the border area of Region B and of Le Calvez (1958), Weston (1985) and Murray and Alve (1994) in the border area of Region C. Comparing the presence/absence data of benthic foraminifera of Le Calvez's (1958) six stations bordering both regions, the species inventory matched by <50 %, indicating a mix of distinct and dissimilar assemblages. Furthermore, the dominant species of Region B (Duchemin et al., 2007) were completely different from those of Region C (Weston, 1985; Murray and Alve, 1994). The boundary between Regions A + B and C is almost the same as the boundary between the "South European Atlantic Shelf" and the "Celtic Sea" ecoregions of Spalding et al. (2007); a similar position is given for the line between Regions C and D (Fig. 1.1) and between the "Celtic Sea" and the "North Sea" ecoregions (see fig. 3 in Spalding et al., 2007). The demarcation based on foraminiferal assemblages has apparently led to similar divisions such as biogeographic division based on macro-organisms (Spalding et al., 2007).

The boundary between Region C (western approaches of Celtic Sea) and F (Porcupine Seabight) was based on differing topographical, sedimentological, and hydrographic properties (Weston, 1985). The continental slope of the Celtic Sea is comparatively steep (average inclination of 5 – 9°) and exhibits several submarine canyon

systems, with dendritic patterns imposed by numerous secondary valleys and side gullies (Day, 1959; Kenyon et al., 1978). In contrast, the Porcupine Seabight is a very wide valley with a significantly lower slope angle of $0.5 – 2°$ and only at its eastern margin is the slope cut by short canyons (Day, 1959; Kenyon et al., 1978). In Region F, brown silty muds were deposited predominantly at abyssal depths, whereas the proportion of sand and silt increased at shallower water depths (Weston, 1985). Sediments on the continental slope of the Celtic Sea (Region C) are composed of unconsolidated fine muds–gravel and consolidated clasts of Cenozoic and Mesozoic marl and chalk (Mart et al., 1979). Seasonal cascading of shelf water and seasonal upwelling of deep water on the continental slope (Cooper and Vaux, 1949; Heaps, 1980), as well as the occurrence of turbidity currents in submarine canyons (Shepard et al., 1979), are typical in the Celtic Sea. In Region F, northward-flowing boundary currents follow the local topography. Current-meter data from NW and S of the Porcupine Seabight showed dominant along-slope transport consistent with these currents (Rice et al., 1991). On the other hand, no consistent transport was recorded from intermediate depths in the center of the Seabight. In addition, nepheloid layers have been found at $700 – 800$ m depths along with a permanent, gradual thermocline ranging from $\sim600 – 1400$ m (Rice et al., 1991).

The borders of the Irish Sea (Region E) are based on illustrations from Huthnance et al. (2009, fig. 1). The position of the north and south boundaries is defined by the stratification and tidal-mixing fronts within the sea.

Delineating Regions C (Celtic Sea) and D (English Channel) was difficult because there was no distinct faunal change. However, the number of species did continuously increase from the English Channel to the Celtic Sea (Le Calvez, 1958; Le Calvez and Boillot, 1967; Fig. 1.2A). Furthermore, mode-of-life analyses (free or attached) showed variations in the border area between SW Cornwall and NNW of Brittany. An increase in the minimum abundance of free and attached living species was centered around $5°$ W (Fig. 1.2B and 1.2C). The position of this transition, hereby recognized as our borderline, coincides with the hydrographic boundary drawn by other authors based on currents and patterns of seasonal stratification (see fig. 1 in Murray et al., 1982; Hardisty, 1990; Huthnance et al., 2009). However a corresponding change in substrate properties is not recognized from the sediment distribution (Le Calvez and Boillot, 1967; Pingree, 1980).
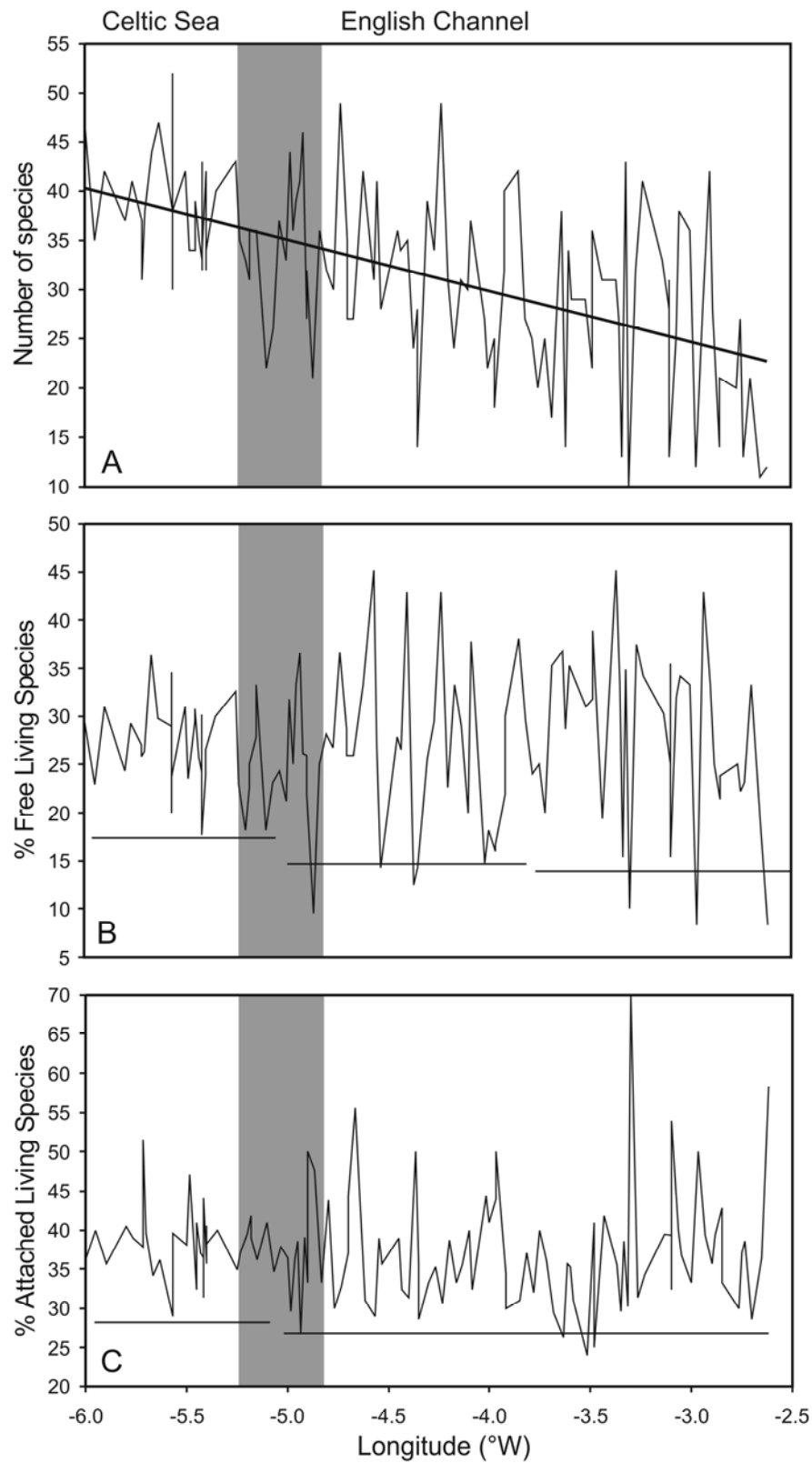
Figure 1.2 A Number of species, **B** relative abundance of free-living species, and **C** relative abundance of attached-living species in the English Channel at all stations from Le Calvez and Boillot (1967); black lines: linear regression line in A, minimum levels in B and C; vertical gray bars: longitudinal range of changes.

1.3.2 Taxonomy and synonymy

A standardized species list of the shelf and slope areas in the NE Atlantic was completed first before proceeding with biodiversity investigations. Our literature investigation revealed a compiled total of 1486 species. However, our taxonomic analysis concluded that 379 of these species (26 %) were synonymous, which is at the upper limit of the range given by Murray (2007) at 10 – 25 %. Thus, the number of benthic foraminiferal species at the European continental margin was reduced to 1107 (Appendix 1.2). To obtain a benthic fauna record as complete as possible, the original species list included 241 species of uncertain identity (cf., aff., gr., ex gr., sp.). These taxa are likely to include more than one species, reducing the significant minimum species number to 866.

In this context, the identification of potential synonyms was essential to quantify the total number of foraminiferal species. Species of the following genera were found to be represented by synonymous names (listed in Appendix 1.2): *Ammoglobigerina*, *Asterigerinata*, *Bolivina*, *Cassidulina*, *Cibicides*, *Cibicidoides*, *Cribrostomoides*, *Eggerelloides*, *Elphidium*, *Fissurina*, *Labrospira*, *Lagena*, *Miliolinella*, *Mississippina*, *Neoconorbina*, *Oolina*, *Polymorphina*, *Rosalina*, *Spiroplectinella* and *Stainforthia*. For example, many authors relate some species of *Bolivina* to the genus *Brizalina* (e.g., Murray, 1970, 1971, 1979, 1986; Murray et al., 1982; Weston, 1985; Giese, 1991; Debenay et al., 2001; Panieri, 2005; Murray, 2006; Pascual et al., 2006; Pascual et al., 2008; Saidova, 2008). Morphologic and genetic investigations of both these genera revealed that a separation is not justified (e.g., Hofker, 1967; Lutze, 1974; Mehrnusch, 1993; Ertan et al., 2004).

For the genus *Ammonia*, an attempt was made to assign different literature species to the molecular types of Hayward et al. (2004). The species distribution was compared to the geographical position of the known occurrences of molecular types in the NE Atlantic. In many cases an assignment to these types was not possible, so we continued to use the morphologically defined taxa (Appendix 1.2).

Taxa or genera that were listed as "spp.-taxa" in the literature belong mostly to the Bolivinidae, Fissurinidae and Miliolidae, although species of Nodosaridae, Trochamminidae and Saccamminidae were also often included in such a category (e.g., Lees et al., 1969; Caralp et al., 1970; Pujos-Lamy, 1973; Weston, 1985; Murray and Alve, 1994; Coles et al., 1996; Debenay et al., 2001; Fontanier et al., 2003; Duchemin et al.,

2007). The occurrences of these "spp.-taxa" were noted at the particular stations, but were not included in our taxonomic list and further statistical analyses. These taxa contain a number of different species of a particular genus; hence, information about their total number in the study area is strongly biased. As a result, both the total number of species and the synonymy rate were possibly higher in places.

1.3.3 Species distribution and test composition

Most of the species (31 % of 1107 taxa) occur in the Bay of Biscay (B), with the second largest proportion of species richness (26 %) found in Region F (Table 1.2). The Celtic Sea (C) and the English Channel (D) were similar with 12 – 13 % of all species present. Abundance was lower in Regions A and E, where only 7 % of all species occurred. We recorded 608 species that were found in only one region and were termed "unique species". Most of them (46 %) were found in the Bay of Biscay (Table 1.3), while Region F showed the second largest abundance of unique species at 36 %. Lower percentages of unique species were recorded in Regions D and E (7 – 9 %), and Regions A and C (~1 %). The ratio of total to unique species for each region indicates almost identical values for Regions A and C and the same ratio for Regions B and F (Table 1.4).

Table 1.2 Percent of 1107 NE Atlantic species by region and test structure. For 62 species (3.1 %) an assignment to a region was not possible, because their occurrence was not specified in publications belonging to more than one region.

Region	Percent of total species represented	Hyaline	Agglutinated	Porcelaneous	Unknown
A	7.3	65.5	16.2	17.6	0.7
B	31.0	61.6	23.1	15.0	0.3
C	12.4	58.6	29.1	12.0	0.4
D	12.6	64.7	15.7	19.2	0.4
E	7.1	66.4	18.2	14.0	1.4
F	26.4	62.2	26.0	11.6	0.2
No data	3.1	56.5	22.6	21.0	0.0
Total	100.0	62.2	22.8	14.6	0.4

Twenty-three percent of all species have agglutinated tests, 15 % have calcareous tests with a porcelaneous structure, and 62 % have a calcareous hyaline test (Table 1.2). The latter are most frequent in all regions, except among the unique species in Regions A

and C. In the English Channel (D), however, porcelaneous species are more common than arenaceous ones in both total and unique species. The same situation is recorded in the Irish Sea (E) for unique species and for all species on the Basque shelf (A) and continental slope (Tables 1.2 and 1.3). Furthermore, no unique porcelaneous species were found in the Celtic Sea (C).

Table 1.3 Percent of 608 unique species for all regions by test structure.

Region	Percent unique species	Hyaline	Agglutinated	Porcelaneous
A	0.7	25.0	50.0	25.0
B	45.7	63.3	21.9	14.8
C	1.2	42.9	57.1	0
D	7.1	58.1	18.6	23.3
E	9.1	61.8	14.6	23.6
F	36.4	65.6	24.0	10.4
Total	100.0	63.2	22.4	14.5

Table 1.4 Ratio of total to unique species by region.

Region	Species Total	Unique Species	Ratio (Rounded)
A	148	4	37:1
B	627	278	2:1
C	251	7	36:1
D	255	43	6:1
E	143	55	3:1
F	534	221	2:1

1.3.4 Diversity

We used the Fisher α index to investigate the diversity of benthic foraminifera in the NE Atlantic. Some publications did not provide quantitative data, hence only 18 of 44 publications could be used to calculate the Fisher α index. We also counted and illustrated the number of species from 27 of the publications, where complete species lists but no census data were provided. Note that the number of species depends on the sample size, which differs at different stations. The separation of living and dead faunas is essential to obtain significant results on diversity and the diversity response to changing

environments. For this reason, we only could use 13 publications for the Fisher α index and 12 papers for species number (Figs. 1.3, 1.4; Table 1.5; Appendix 1.3).
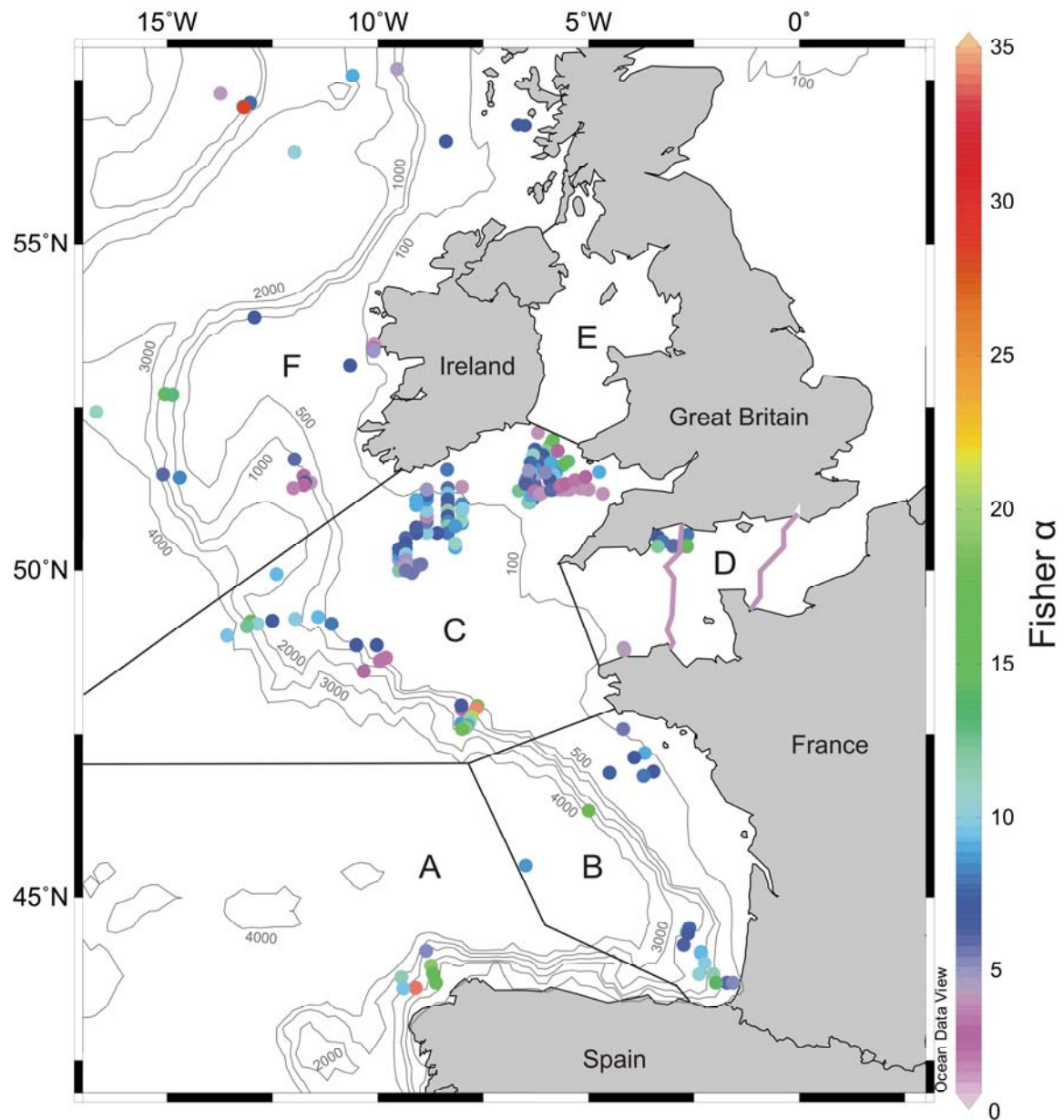
Figure 1.3 Distribution of the Fisher α indices of foraminiferal assemblages in the NE Atlantic (based on data from Appendix 1.3). A mean value of the Fisher α index was given for the two transect lines in the English Channel, as calculated from the data of Rosset-Moulinier (1986).
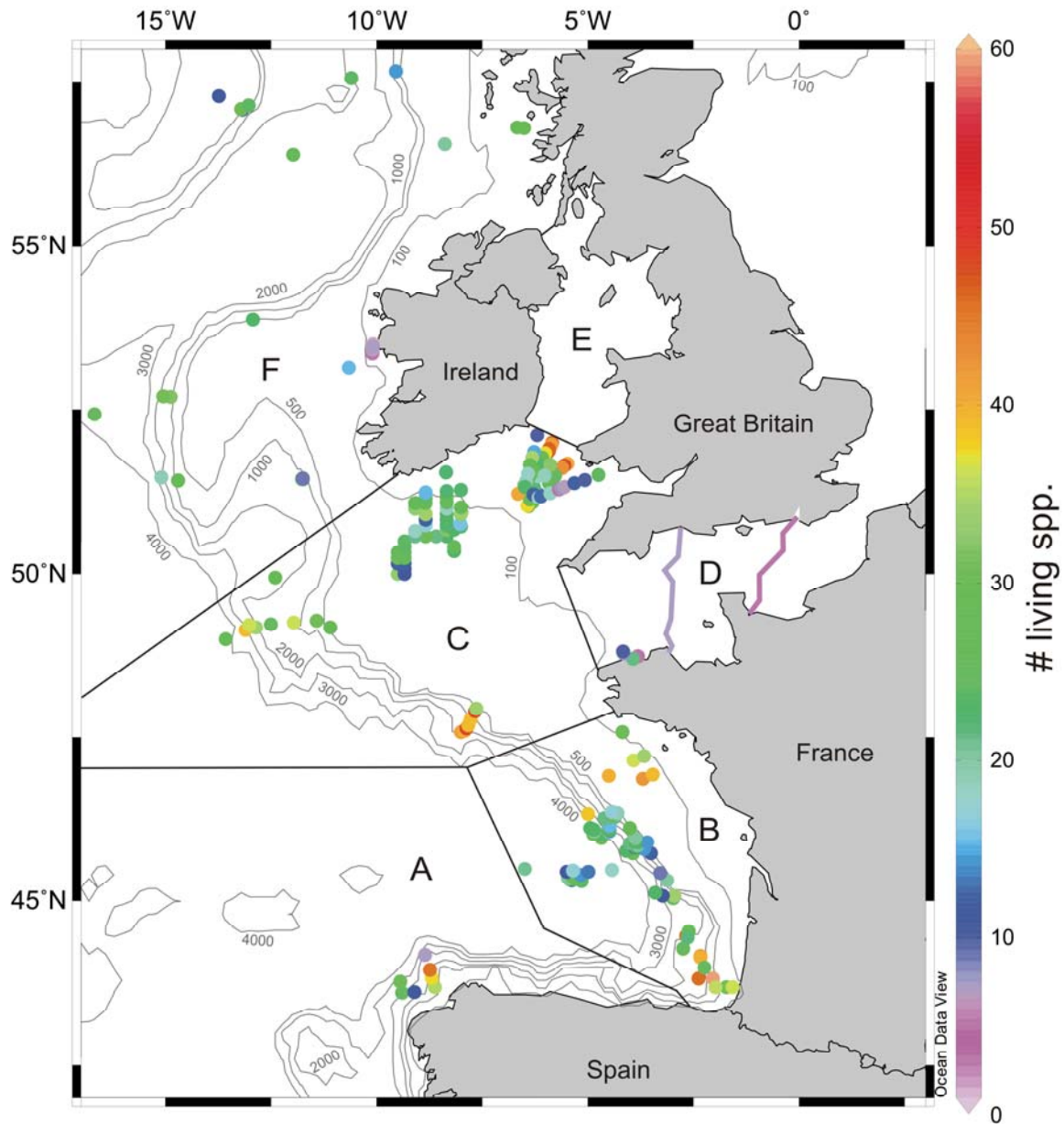
Figure 1.4 Distribution of the number of living species in the NE Atlantic (based on data from Appendix 1.3). A mean value of the species number was given for the two transect lines in the English Channel, as calculated from the data of Rosset-Moulinier (1986).

Region A showed the highest diversity, even though it only comprises seven stations. Highest Fisher α values were found between 550 − 850 m on the Basque continental slope (Fig. 1.5, left). Whereas the average number of species encountered is almost the same in Regions A, B and C, the average Fisher α index in Regions B and C is lower by half as compared to Region A (Table 1.5). An increase in diversity from the shelf to the slope was recorded in Regions B, C, and F (Figs. 1.5 and 1.6). The mean indices (seven on the shelf, 10 on the slope) were identical between the Bay of Biscay (B) and the

Celtic Sea (C), but these regions did not have mid-slope diversity maximum as in Region A. Region F showed lower average Fisher α values (four on the shelf, nine on the slope). The highest diversity was found at depths ranging from 700 − 1100 m (Fig. 1.6, right). Schönfeld et al. (2010) illustrated the Fisher α index of benthic foraminifera at the Irish and Armorican margin (parts of Regions C and F in the present paper) and constrained a diversity maximum between 500 − 1200 m. In addition they included unpublished data of Weston (1982) and Schönfeld (2006). The separation of the two regions and the use of other data sources may have led to this discrepancy in the diversity-maximum depth range. In region F, the mean species number was lower than in Regions A, B and C (Table 1.5), but this may result from the depth range of the samples. The uppermost 20 m showed only low species numbers. After exclusion of these data, the mean species number rose from 13 to 21 (from six to 19 on the shelf), a value closer to those recorded in other areas. The mean indices and species numbers would potentially be marginally lower if we had suitable data available from the first 20 m of water depth in Regions A, B, and C. The diversity of benthic foraminifera was markedly lower in the English Channel. Over the entire area, the average number of living species on the shelf increased from north (six species in Region F) to south (35 in Region A). However on the slope, no relationship between latitude and species number was found. Nevertheless, the highest mean species number (37) was recorded on the continental slope of the Celtic Sea.

Table 1.5 Summary of data sources, Fisher α index, and number of living species (based on data from Appendix 1.3).

Region	Parameter	Publications	Stations	Depth (m)	Range (total)	Average	Ø shelf	Ø slope
A		1	7	188-2170	5-34	16	16	16
B		3	20	85-4800	5-17	9	7	10
C	Fisher α	5	134	24-3889	1-34	8	7	10
D	index	4	55	2-89	0-17	5	5	—
E		2	210	—	—	—	—	—
F		5	38	1-3653	1-28	7	4	9
A		1	7	188-2170	7-45	27	35	26
B		4	76	85-4800	9-59	25	27	24
C	Number of	4	110	49-3889	4-48	26	24	37
D	species	4	53	2-89	1-21	6	6	—
E		2	210	—	—	—	—	—
F		5	48	1-3653	1-33	13	6	22
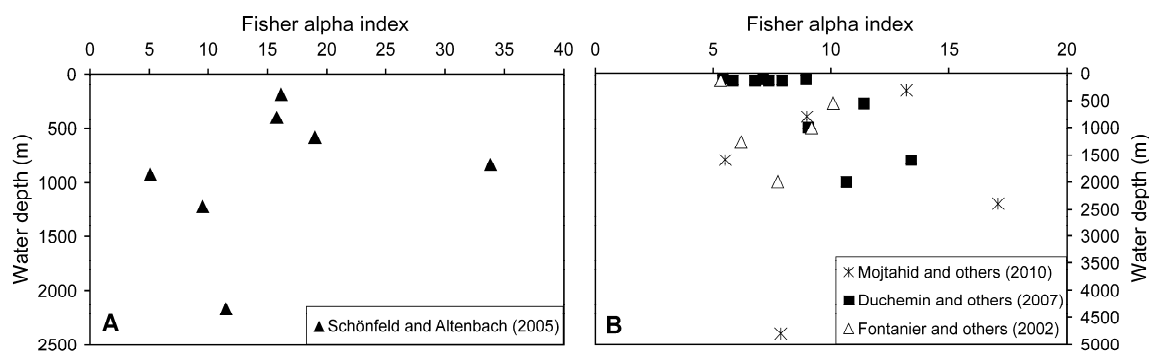
Figure 1.5 Diversity of benthic foraminifera vs. water depth from Regions A (left) and B (right). Note the different scales on the axes.
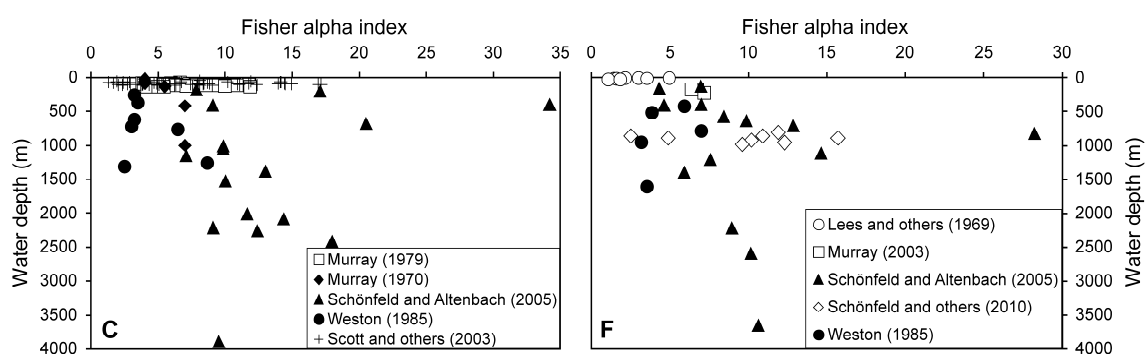
Figure 1.6 Diversity of benthic foraminifera vs. water depth from Regions C (left) and F (right).

1.3.5 Dominant species

The most abundant species were identified in 31 of the 44 publications (Table 1.1). The first and second most abundant species at each station were marked in each of the 31 publications. However, 143 species (13 % of 1107) were dominant and subdominant over the whole study area, except in Region E. About 64 % of these 143 species were dominant in one region only. The first and second ranked most abundant species in the majority of the 31 publications are *C. laevigata*, *Cibicides lobatulus*, *Bulimina marginata*, *Gavelinopsis praegeri* and *S. sagittula*. They were dominant or subdominant on the shelf and slope, except *G. praegeri* which was dominant only on the shelf.

The dominant species in most stations was designated as the most frequently occurring species in a particular region. Consequently, 51 of the 143 most frequently recorded species (5 % of 1107) were the first or the second most frequently recorded in one or more publications. Listed in seven publications, the first-ranked species, *C. laevigata* occurred most frequently in Regions B, C, and F. The second-ranked species

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from five publications were *Uvigerina mediterranea*, frequent on the slope in Regions B and F, and *Stainforthia fusiformis*, common in the English Channel (D) and the shelf adjacent to the Celtic Sea (C). To determine the distribution patterns of the six dominant species *Cassidulina laevigata*, *Cibicides lobatulus*, *Spiroplectinella sagittula*, *Bulimina marginata*, *Bolivina dilatata*, and *Trifarina angulosa*, which have the largest data coverage, we plotted their latitudinal vs. depth distribution for the study area from literature data and unpublished information from the localities of Schönfeld and Altenbach (2005). Because of the large number of data points, the distribution was plotted separately for the shelf (0 – 200 m) and slope (201 – 2500 m). Stations with living individuals were highlighted to visualize the distribution patterns (Fig. 1.7A-F).

Cibicides lobatulus, *S. sagittula* and *T. angulosa* showed similar distribution patterns on the shelf. In contrast to the other five dominant species, *C. laevigata* was found above 80 m with the exception of one station in the English Channel (Murray, 1970; Fig. 1.7A left), and *B. dilatata* was recorded living north of 55° N in only one station (Fig. 1.7E left). Most of the living individuals of all six species were found in the Celtic Sea (C) and the English Channel (D), whereas the fewest living individuals were recorded in Regions E and F. Examination of both the living and total assemblages showed that all six species exhibit a lobate, "oak-leaf" distribution pattern on the shelf (Fig. 1.7, left figures).

On the continental slope, five of the dominant species showed similar distribution patterns with the exception of *B. dilatata*, as no living individuals were recorded north of 52° N (Fig. 1.7E right). *Trifarina angulosa* also showed a slightly different pattern, because it was living in the Bay of Biscay below 2000 m. In addition, no living specimens of *C. laevigata* and *B. marginata* were found between 45 − 47°30' N (Figs. 1.7A, 1.7D, both right). The sample coverage was substantially lower in Regions E and F, as well as on the shelf. With all six dominant species, we found a surprising correlation between the distribution patterns in Regions A and B (shelf) and the mode of life (free or attached). The distribution patterns of attached-living species *C. lobatulus* and *S. sagittula* were similar to each other in lower latitudes. The free-living species (*B. dilatata*, *B. marginata*, *C. laevigata*, *T. angulosa*) also have a similar distribution to each other on the shelf. In the other regions (C – F) there is no correlation between the distribution patterns, mode of life, and environmental parameters. Although *C. lobatulus*, *B. marginata*, and *T. angulosa* prefer to colonize areas influenced by bottom currents, their respective distribution

patterns are different. *Bulimina marginata* and *B. dilatata* thrive in fine-grained sediments, whereas the other four species have a positive correlation to coarse-grained material, but none of these "groups" shows a similar distribution within the living fauna on the shelf or slope.
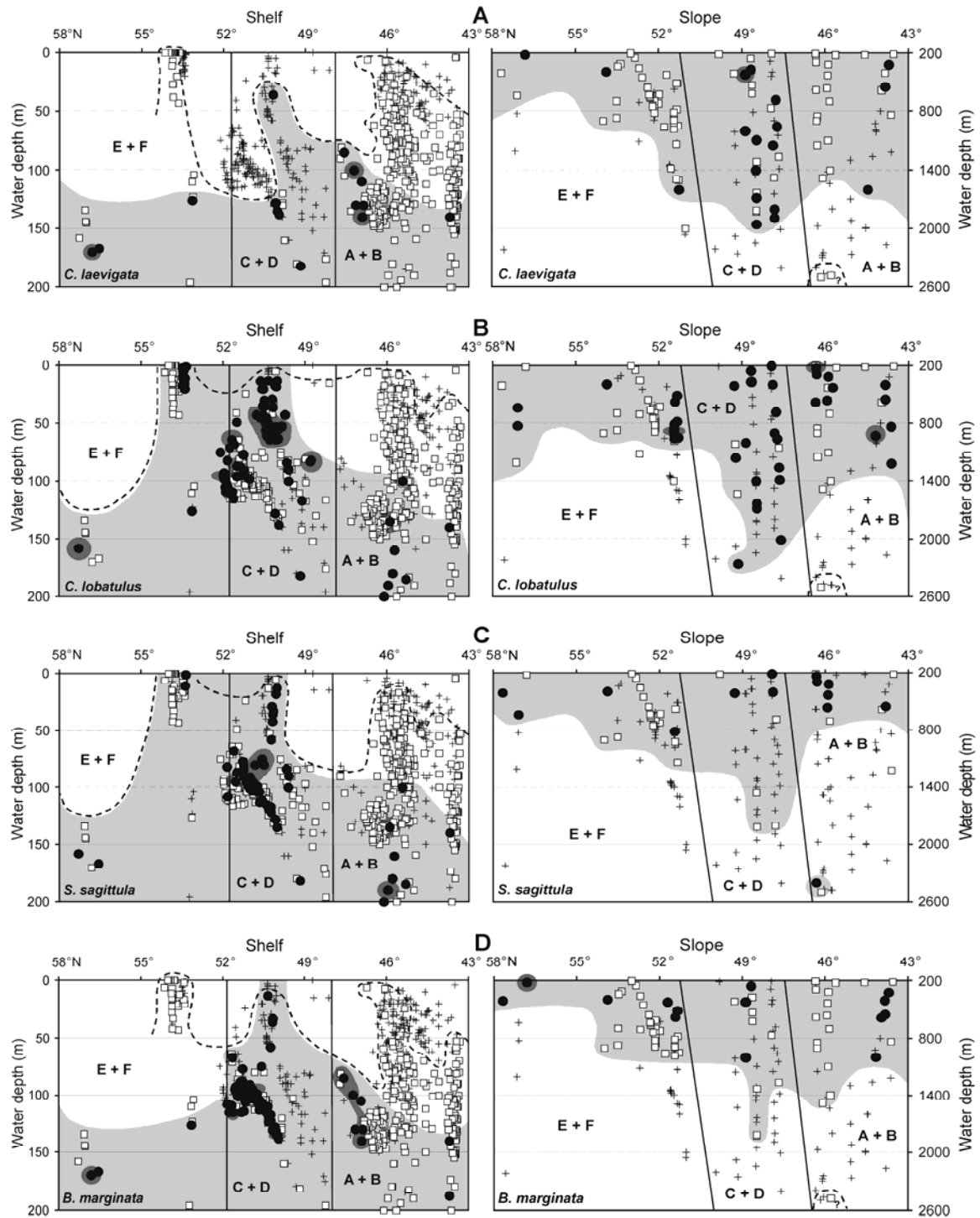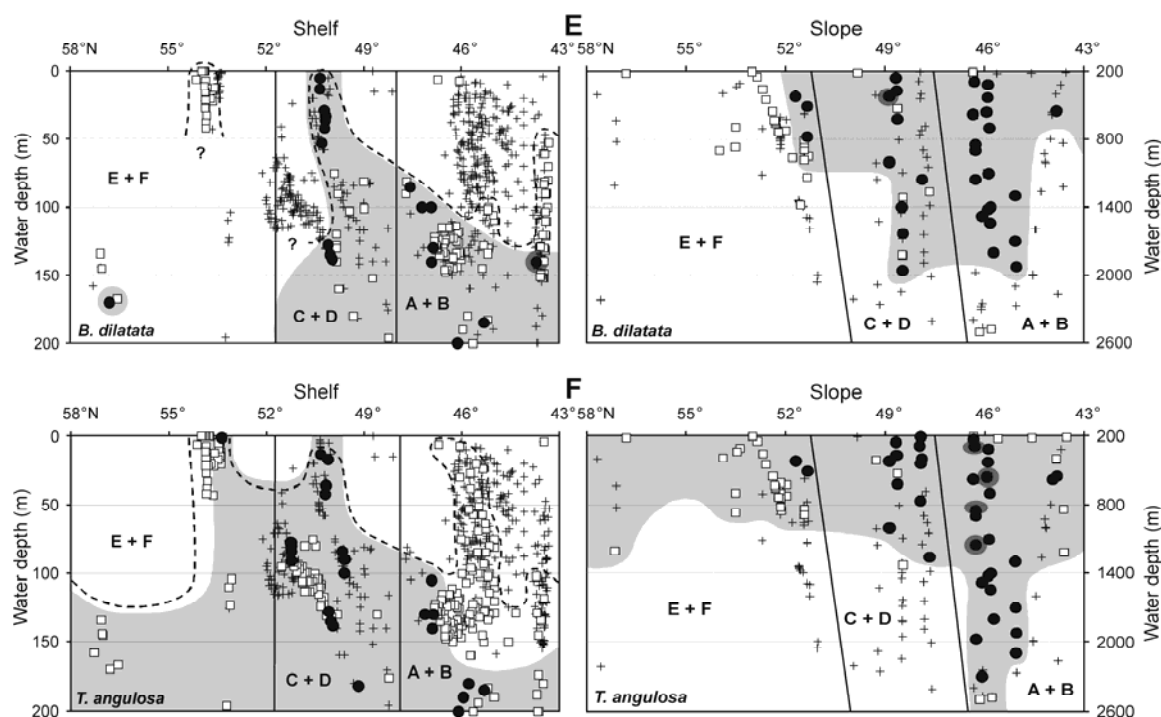
Figure 1.7 A−F Latitudinal vs. depth distribution of six dominant foraminiferal species on the shelf (left) and slope (right) of the NE Atlantic; black dots: living individuals; white squares: dead or total fauna; crosses: all other stations without these taxa; vertical lines: boundary between two regions (A+B, C+D, and E+F); black dashed lines: distribution of dead/total assemblages; light gray polygon: distribution of living assemblages; dark gray patches: abundance maxima of ≥10 % in the living fauna.

1.3.6 Mode of life

Sixty percent of the species in this study lived free on or in the sediment (Table 1.6). The second-ranked mode of life is for species that lived free or attached (20 %). The percentages of attached living foraminifera increased from S − N in both shelf and slope areas. For Regions D, E, and F, the proportion of species with attached, and free and attached modes of life was almost identical.

The proportions of free and attached living specimens on the shelf and slope were compared for Regions B, C, and F (Table 1.7). In the Bay of Biscay (B), about twice as many species live free or attached on the slope as compared to the shelf. In the Celtic Sea (C), the number of attached species was almost the same on the shelf and slope, whereas the number of free-living species was about 10 % higher on the shelf. In Region F, over twice as many attached species lived on the continental slope, whereas ~16 % more free-living species occurred on the shelf (Table 1.7). Note that only 435 of 2902 stations were

used for these calculations. In Region B (85 stations), there are three times more slope stations than shelf ones. In Regions C (224 stations) and F (126), however, the number of shelf stations is three times higher and two times higher than the number of slope stations, respectively. This discrepancy could also lead to a higher species number on the slope of the Bay of Biscay for both modes of life.

Table 1.6 Percent of living and dead species related to their mode of life. For 62 species (3.1 %) an assignment to a region was not possible, because their occurrence was not specified in publications belonging to more than one region.

Region	Percent total species	Free	Attached	Free and attached	Unknown
A	7.3	60.8	12.8	23.7	2.7
B	31.0	62.4	14.4	19.8	3.5
C	12.4	60.2	15.9	20.3	3.6
D	12.6	52.6	21.2	22.0	4.3
E	7.1	55.9	21.0	21.7	1.4
F	26.4	59.6	18.2	18.7	3.6
No data	3.1	59.7	12.9	24.2	3.2
Total	100.0	59.5	16.7	20.4	3.4

Table 1.7 Relationship of free and attached living species between shelf and slope (relative abundances of living fauna).

Region	Free	Attached	Unknown	
B	30.7	3.6	2.7	Shelf
	53.9	9.0		Slope
C	46.0	9.0	2.0	Shelf
	35.0	8.0		Slope
F	41.7	10.0	0.8	Shelf
	25.8	21.7		Slope

An increase in species with a free mode of life on the shelf from S to N was recognizable. In the Bay of Biscay (B), more species occurred on the slope than on the shelf. However, in the Celtic Sea (C) 11 % more species lived on the shelf than on the slope, and ~16 % more lived on the shelf than on the slope in Region F. For attached living species, no N − S trend was visible. In Regions B and F, more than twice as many attached living species occurred on the slope, whereas in Region C 1 % more species lived on the shelf than on the slope (Table 1.7).

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1.4 Discussion

1.4.1 Data and inconsistencies

The analysis of qualitative and quantitative data in this study demonstrated the difficulties in comparing different datasets and recording general biodiversity patterns. Often, essential metadata, such as station coordinates, water depth, sediment grain-size fraction, differentiation between living and dead fauna, complete species lists, and census data were not available in the literature we examined. Furthermore, methods and instruments for sampling and preparation were not as evolved in earlier studies. For example, species now routinely identified from the >63 μm sieve fraction were usually overlooked at the beginning of the 20th century, and a reliable means for differentiating living and dead individuals was not developed until the 1950s. The preparation and identification of benthic foraminifera also differed among scientists, making it difficult to compare faunas and determine realistic estimates of biodiversity indices.

In addition, the six regions within our study area encompass varying morphological, physical, hydrographical, and sedimentological conditions, which complicate comparison of the foraminiferal assemblages that also change markedly with depth. Two of the six regions (D and E) are confined to the shelf, while the others extend down to the abyssal plain. Even when comparing similar depositional regimes, inconsistencies result from unequal sample coverage, as is the case for shelf areas in Regions B, C, and D that were investigated much more extensively than those in Regions A, E, and F. Thus, a much smaller database is available for sound comparisons. These inconsistencies probably influenced the diversity calculations, and in some cases, made rough estimates impossible (e.g., the number of species and diversity in Region E).

1.4.2 Taxonomy, synonymy, and comparison with Gulf of Mexico

The 44 publications included in our analyses provided valuable distribution data, but they also demonstrate how data acquisition and species concepts have changed over the past century. Most of these publications drew conclusions about ecological and environmental conditions from faunal assemblages and overlooked taxonomic considerations. We synonymised 26 % of the foraminiferal species on the European

continental margin, which is the same rate also found by Culver and Buzas (1980 – 1987) for the Atlantic (Newfoundland to the Gulf of Mexico) and Pacific (Alaska to Panama) coasts of North and Central America. Recently, Sen Gupta and Smith (2010) merged data from the census report of Culver and Buzas (1981) with those from 157 older and newer papers from the Gulf of Mexico to generate a comprehensive list of 987 foraminiferal species, of which 382 were also found in the NE Atlantic. Comparing these taxa with our synonymy matrix, we obtained a synonymy rate of 2 % between our approach and the Gulf of Mexico project. Using our species concepts, *Cancris oblongus*, *Cassidulina carinata*, *Chilostomella oolina*, *Cibicides kullenbergi*, *Cibicidoides pseudoungerianus*, *Melonis affinis* and *Neouvigerina ampullacea* could be included as synonyms of other species, thus reducing the total Gulf of Mexico species number to 980. In the NE Atlantic, we positively identified 866 species from the literature we examined, while excluding 241 species with uncertain designation, thus implying that diversity in the Gulf of Mexico is higher. Using the number of stations and positively identified species, we calculated the γ-diversity for both areas. Although there are many more sampled stations in the Gulf of Mexico (8299), both areas have a similar number of species and a γ-diversity of 16, expressed as a Fisher α index. This challenges the recognition of the Gulf of Mexico as a biodiversity hotspot (Chassignet, 2012), or implies that the NE Atlantic should also be regarded as a region of exceptional diversity.

1.4.3 Integration of morphotypes and molecular species

While assessing synonymies, we questioned whether results of recent genetic studies could be integrated into our investigation. In particular, the molecular type of different *Ammonia* species (Hayward et al., 2004) demonstrated that some forms assigned to "*Ammonia beccarii*" (Linné) most likely did not belong to this species. In fact, the illustrated *A. beccarii* species of Murray (1970), Pujos (1976), Rosset-Moulinier (1986), Giese (1991), Debenay et al. (2001) and Pascual et al. (2008) are more similar to the molecular type T3S [*Ammonia batavus* type] or T3V. Hence, *A. beccarii* from the Bay of Biscay, the Celtic Sea and the English Channel are most likely *A. batavus* or the T3V "Vendeé type". Also Rosset-Moulinier's (1986) species *Pseudoeponides falsobeccarii* (*Ammonia falsobeccarii* herein) was considered to be related to the molecular type T3S. In contrast, morphometric and molecular-phylogenetic analyses of *A. falsobeccarii* classified

this species as a new phylotype, different from the T3 molecular types (Schweizer et al., 2011). There is no clear taxonomic consensus for the species reported by Rosset-Moulinier (1986). We emphasize that the applicability of molecular types is limited, as our assumptions were only based on comparing illustrated specimens. To confirm the above species assignments, the original *Ammonia* material from different regions must be analyzed with the same morphological and genetic approaches.

1.4.4 Test composition, diversity, and mode of life

Regions A and E have the lowest number of species (living and dead), while Regions B and F have the highest. In contrast, when calculating the mean number of living species, Regions D and F have the lowest species number and Regions A and C have the highest. These variable results indicate the importance of distinguishing living and dead individuals for biodiversity assessment. The transport of empty tests, especially in areas with high bottom currents, can lead to a bias in dead assemblage composition (Murray, 1982; Schönfeld, 2002). Furthermore, total assemblages (living and dead) reveal no significant correlation to any environmental parameters (see figs. 4 and 5 in Morvan et al., 2006). For this reason, we only used the living fauna to calculate diversity, thereby finding two mid-slope diversity maxima in the Galicia area of Region A and to the west of Ireland in Region F. However, the mid-slope diversity maximum for Region A is based on only two data points, because only one publication could be used to calculate Fisher α indices for the living fauna. No mid-slope diversity maximum was found in any of the other regions. Nevertheless, an increase in shelf to slope diversity was also recorded in the Bay of Biscay (B) and the Celtic Sea (C). Despite the identical range of Fisher α indices (Table 1.5), the mean values in Region A were twice as high as in Region C. This is most likely an effect of data coverage. For instance, on the Basque continental slope between 400 − 2220 m only one station had an index <9, whereas in the Celtic Sea eight stations showed such values in that respective depth interval. For some stations in the Celtic Sea, the Fisher α index did not correspond with the "real" diversity, because the index could only be calculated from dominant species. Thus, we obtained very low values resulting in a lower mean Fisher α index for the Celtic Sea.

The English Channel (D) and the Irish Sea (E) are the only completely shelf regions and have different regimes compared to the other four. In both regions, there are

more unique porcelaneous species than agglutinated ones and the frequency of attached specimens commonly exceeds 20 %. The lower diversity in the English Channel indicates that only a few species are adapted to the specific ecological and physical conditions in this sea strait. Comparing the biodiversity of both regions was not possible, because no data for the living fauna were available. Despite these regional differences, most taxa have a hyaline test and a free mode of life throughout the study area.

1.4.5 Dominant species

The latitudinal vs. depth distribution of the six dominant species (*Cassidulina laevigata*, *Cibicides lobatulus*, *Spiroplectinella sagittula*, *Bulimina marginata*, *Bolivina dilatata* and *Trifarina angulosa*) showed the highest frequency in the living fauna on the shelf (C and D) between 40 − 150 m. In the total fauna, these species were more common in Regions A and B. Living individuals of these species occurred between 80 − 200 m in the south of the study area, whereas in Regions C and D the species shoaled in that they were confined to depths <150 m. On the slope, the distribution patterns are quite similar for all six species, except *B. dilatata*. *Trifarina angulosa* showed a somewhat different distribution in the Bay of Biscay (B), where it was also found living at greater depths. One reason for this distribution could be the small grain-size fraction that was analyzed in this region as *Trifarina angulosa* was mainly found in the <250 μm fraction. While they have different modes of life, as well as different food and substrate preferences, the six species occurred in wide latitudinal and depth ranges. We thus conclude that they have the same ecohabitat. Especially on the shelf, the individual distribution of these species showed an outline similar in shape to an oak leaf. One reason for this pattern could be the species' reaction to a patchy nutrient supply. This irregular, patchy distribution pattern was also described off NW Africa as a reaction of the foraminiferal community to higher primary production and downward organic flux (Lutze, 1980; Morigi et al., 2001). In some cases, stations with living individuals of a particular species were located close to stations where this species was not found. Causes for the absence of a species according to our analyses, in order of frequency, are: 1) the distribution of the species could not be plotted on the diagram, because no coordinates and/or water-depth values exist (or only an interval was given) at particular stations; 2) the particular species was ignored in the analyses because of its low abundance (e.g., <1 %) or size; 3) the species was not relevant for the aims of

the study and thus was not collected; 4) species of the same genus were not differentiated; or 5) the species was not properly identified. The incompleteness of published data strongly affected the results of the foraminiferal distribution. Hence, the occurrence of our six dominant species could not be illustrated from the data by Douvillé (1936), Le Calvez and Boillot (1967), Haynes (1973), Sturrock and Murray (1981), Giese (1991) and Saidova (2008). Because other workers listed quantitative data only for abundant species, the particular species we considered in this paper was unrepresented their stations (e.g., Castignetti and Manley, 1998), or some species were recorded only in stations where they occurred frequently (e.g., Murray, 1970; Murray, 1979; Coles et al., 1996). The analyzed size fraction also greatly affected our results. The benthic fauna was commonly collected from grain-size fractions of >100, >125, or >250 μm (e.g., Weston, 1985; Rosset-Moulinier, 1986; Schönfeld and Altenbach, 2005; Rüggeberg et al., 2007; Schönfeld et al., 2010). Because of this, several species limited to the <125 μm or smaller grain-size fraction were not recorded at some stations.

1.4.6 Latitudinal diversity gradient and comparison with other taxa

An increase in species numbers in the total assemblages on the shelf from N to S was first described by Saidova (2008). Our data show the same trend for the living fauna. A similar, southward increase in species richness was recognized in the NE Atlantic (20° W) down to depths of 2000 m along with fish, ostracods and other crustaceans (Angel, 1993). The continuous increase in macrofaunal species richness was mainly recognized at greater water depths (>800 m). Species diversity analyses of bivalves, gastropods and isopods from the E and W Atlantic by Rex et al. (1993) showed clear latitudinal diversity gradients in the N Atlantic. A continuous increase in species diversity in the deep-sea benthos (500 − 4000 m) was visible from 80 − 10° N. However, no increase in foraminiferal species numbers from N to S at the same water-depth range was recognized in our study. Possible reasons may be inconsistency in the available data, which hampers the comparison of species numbers (e.g., the "nematode example" in Rex et al., 2001). In contrast, when comparing the mean Fisher α indices of the different regions, a diversity increase was recorded from N to S on the shelf and slope areas. The diversity of gastropods on the shelf in the eastern Pacific and western Atlantic from the tropics to the Arctic Ocean also revealed an increase in species richness from N to S (Roy et al., 1998).

This increase had a steep gradient between 12 − 35° N. Compared with our latitudinal range (43 − 58° N), the number of gastropod species increased slightly from N to S. Only mean sea-surface temperature showed a significant relationship with gastropod diversity, which was higher in warmer temperatures. The bottom-water temperature of the NE Atlantic shelf showed an average increase from the N to the S of approximately 3° C (ICES, 2009) in our study area. The salinity increased only slightly from 34 to 35.5 psu and the concentration of dissolved oxygen decreases from 6.5 ml/l to 5 ml/l (ICES, 2009). These latter variations do not influence the living conditions of benthic foraminifera, though.

1.4.7 Regional differentiation

Our data analyses have provided new insights into the biodiversity of the NE Atlantic. Complex relationships exist between the six regions, depending on test structure, mode of life, and diversity of benthic foraminiferal faunas. A distinct differentiation of one or two areas based on faunal criteria alone is initially not possible. The six regions in our study are not easily comparable due to inconsistent data, variable sample coverage, and different hydrographic conditions, particularly in the English Channel and the Irish Sea. Although every area is characterized by specific morphological, ecological and hydrographical conditions, the faunal data corroborate that benthic foraminiferal assemblages from all regions are connected with one another. We could locate neither one hot spot area nor large differences in biodiversity between the regions. Hence, there is only a low interregional diversity (γ-diversity) of Regions A − F in the NE Atlantic.

1.5 Summary

The data analyses of 44 publications on the distribution of benthic foraminifera from the NW European shelf and continental slope revealed an interregional diversity pattern. A comparison of faunal assemblages by region showed close linkages between the areas despite different hydrographical, sedimentological and morphological boundary conditions. The common distribution of a hyaline test structure and of a free mode of life, as well as increases of the Fisher α index from the shelf to the slope and of mean species number on the shelf from N to S, is distinctive for all six regions.

The latitudinal distribution of six dominant species exhibits an oak leaf-shaped distribution pattern for the shelf areas. At present, it is difficult to judge whether this pattern reflects the real distribution or if it is artificially created by heterogeneous sample coverage. For example, the distribution patterns of living individuals on the Regions E and F shelves were based only on three publications (20 stations). A more representative distribution pattern requires more faunal information from these regions and from adjacent boundaries. However, available data display similar distribution patterns for a particular species on the continental slope. Especially in the English Channel and the Celtic Sea, the dominant species, except *Trifarina angulosa*, were found nearly throughout the whole depth range (0 − 2000 m). This suggests that favorable environmental and substrate conditions were the same for most species, supporting the contention that the "oak leaf" distribution pattern displays a mega-patchiness, as has already been described for the NW-African margin.

Determination of foraminiferal diversity requires a standardized taxonomy as well as standard protocols for sampling and preparation. The integration of published data has shown significant variation in taxonomy and sampling and preparation methods among different working groups. The main obstacles impeding sound diversity analyses of existing data are data availability, such as station coordinates, grain size, water depth, and incomplete faunal reference lists. Thus, compilation studies, such as ours, that standardize data are essential in creating a composite picture of benthic foraminiferal distribution and assemblage change over time.

1.6 Acknowledgements

CHAPTER 2 – Recent benthic foraminiferal assemblages from the Celtic Sea (South Western Approaches, NE Atlantic)

Abstract

The faunal composition and diversity pattern of Recent benthic foraminifera from the shelf and slope of the South Western Approaches (Celtic Sea) were assessed. The sampling stations cover a depth range from 100 to 500 m. A total number of 294 species was recorded, of which 89 were found exclusively in the living fauna and 118 only in the dead assemblage, whereas 87 species were found in both assemblages. The faunal composition revealed a distinct bisection of the living fauna on the shelf. While certain distribution patterns of living dominant species were recognized along a NE – SW trending transect towards the shelf edge, the living fauna changed within small depth intervals and geographic position on the slope. Causes for this structured slope assemblages were probably along-slope currents of varying strengths, as well as variations in topography and bottom sediments. Analyses of population densities and diversity patterns determined high densities along the shelf edge and at one slope station, as well as an increasing diversity with water depth. A comparison with literature data from the same area yields distinct differences in faunal composition on the shelf and slope. The diversity was similar on the shelf, but higher at corresponding stations on the slope. We conclude that the faunal composition was highly influenced by the time and methods of sampling. In order to obtain consistent results in regional studies, all samples should be taken in a short time interval and by using the same sampling device. In addition, we depicted the

influences of environmental parameters on dead faunal assemblages and their consequences for paleoenvironmental interpretations of fossil foraminiferal assemblages.

2.1 Introduction

2.1.1 Geomorphology

The study area is located at the South Western Approaches, a region of the Celtic Sea. This shallow marginal sea is situated to the south of Ireland and southwesterly of Great Britain and covers an area of 75000 km² up to 200 m water depth (Hardisty, 1990). The outer western English Channel and the southern Celtic Sea are known generally as the South Western Approaches (Hamilton, 1979). The sea floor of the Celtic Sea shelf is characterized by an extensive field of SW – NE trending linear tidal sand ridges between a water depth of 130 m and the shelf break (Bouysse et al., 1979; Pantin and Evans, 1984; Scourse et al., 2009). These ridges are 40 – 200 km long and 4 – 15 km wide. They are discrete sedimentary bodies resting on a sub-horizontal erosional surface cut across Lower Pleistocene to Devonian-Carboniferous marine formations (Pantin and Evans, 1984; Scourse et al., 2009). Below the shelf break at about 200 m depth, the 1° - 4° steep continental slope leads down to the abyssal plain in water depths ranging from 4200 – 4400 m (Hamilton, 1979; Bourillet et al., 2003). The western continental slope is characterized by terraces with a low gradient (e.g., Goban spur), whereas the southern part of the slope consists of more than 30 NE-SW running submarine canyons in a dendritic pattern (e.g., Shamrock canyon, Blackmud canyon; Hamilton, 1979; Bourillet et al., 2003; van Rooij et al., 2007).

2.1.2 Bottom sediments

Recent sea-floor sediments of the Celtic Sea consist mainly of Pleistocene gravels, sands and clays, as well as biogenous components (skeletal and shell fragments) from organisms living on the shelf (Banner and Culver, 1979; Hamilton, 1979). In areas affected by strong bottom currents, these sediments move over a pavement of immobile pebbles and shells (Stride, 1963; Pantin and Evans, 1984). Especially in the South Western Approaches, sediments are successively transported towards the shelf edge,

where they may travel down submarine canyons as a grain flow (Stride, 1963; Hamilton, 1979).

2.1.3 Hydrography

Sediment transport on the Celtic shelf is characterized mainly by wind and density driven flows, as well as tidal currents and seasonal storm induced waves (Murray et al., 1982; Pingree and LeCann, 1989; Huthnance, 1995). Because of low water depths, the shelf is characterized by a seasonal thermal stratification of the water column (Austin et al., 2006). During the winter months the water column is well mixed to a depth of 300 m, whereas from April to October it is strongly stratified (Joint et al., 2001). A slope current flows in northward direction alongside the shelf edge and the upper slope (< 1000 m; Huthnance, 1995; White, 2007). This slope current occurs together with a wind and density driven cross current on the shelf (White and Bowyer, 1997). Contour currents, in depth ranges of 100 – 450 m and 450 – 1000 m, transport northeastern Atlantic water masses to the Norwegian Sea. They reach the highest current velocity in the winter months (Pingree et al., 1999; Friocourt et al., 2007).

2.1.4 Productivity

The development of the spring bloom in the Celtic Sea depends strongly on the mixing of the water column (Joint et al., 2001). This bloom occurs mainly between the middle of April and the beginning of May (Gowen et al., 1999; Rees et al., 1999; Joint et al., 2001). Over the shelf, phytoplankton production is influenced by changes in nutrient advection at the shelf edge (Pingree et al., 1981, 1982). The phytoplankton species composition varies both annually and geographically and it is influenced by dissolved nutrient ratios as well as vertical mixing events (Martin-Jézéquel and Videau, 1992; Van Oostende et al., 2012). The annual surface ocean phytoplankton production at the South Western Approaches is 245 g C m^{-2} a^{-1}. During spring bloom, it may reach 1.4 g C m^{-2} d^{-1} (= 511 g C m^{-2} a^{-1} for bloom times; Joint et al., 2001). Phytodetritus is rapidly deposited on the sea floor immediately after the bloom (Rees et al., 1999). On the shelf, it is swept by currents, moves towards the shelf break, and forms intermediate and near-bottom nepheloid layers. They spread along density interfaces at mid depth, or descend the

continental slope, partially funneled in canyons (Heussner et al., 1999; Van Weering et al., 2001).

2.1.5 Previous work

Early studies of benthic foraminifera from the Celtic Sea and western English Channel depicted a correlation between the faunal variations and water depth, sediment type, and tidal and current regimes (Le Calvez, 1958; Le Calvez and Boillot, 1967; Murray, 1970; Murray, 1979; Sturrock and Murray, 1981; Murray et al., 1982; Weston, 1985; Scott et al., 2003). Further investigations of suspended sediment samples showed that small, dead foraminiferal tests (<200 μm) were suspended and transported from areas with powerful vertical turbulences and mixing (e.g., English Channel) to areas with a thermally stratified water column (e.g., South Western Approaches; Murray, 1970; Murray, 1979). Particularly strong bottom currents in the southern Celtic Sea pass over the shelf and lead to deposition of transported tests on the slope (Murray et al., 1982). The intensity of the current systems influences the seasonal stratification on the Celtic shelf. Environmental parameters such as food supply and oxygen concentrations in pore and bottom waters are linked to seasonal stratification and vary from mixed to stratified waters. These parameters are the primary controlling factors on the distribution of benthic foraminiferal assemblages (Weston, 1985; Scott et al., 2003).

In a recent compilation study, distribution patterns of common benthic foraminiferal species depicted "oak leaf" shaped mega patchiness on the shelf, suggesting lateral variations in environmental conditions on a 100 km scale or mirroring non-random sample distribution. A transect through the English Channel suggested an indistinct increase in species richness towards the Celtic Sea. This trend was blurred by large differences in taxonomy, sampling and preparation methods as reported in the literature (Dorst and Schönfeld, 2013).

The aim of our study was to revisit and extend the Channel transect across the shelf to the uppermost slope of the South Western Approaches. For this purpose, samples were taken on a transect perpendicular to the hydrographic front in the outer Channel separating mixed and thermally stratified waters. This will allow us to assess the effect of depth and distance from the Channel entrance on benthic fauna, and to constrain which environmental parameters influence these changes. Samples from other cruises, lying

close to the transect were also considered in order to improve the spatial sample resolution of the transect. During the course of the study, it turned out that the influence of the hydrographic front was less distinct and that shelf upwelling and food availability were of greater importance for the benthic faunal assemblages. Following these results, we extended our study and took samples underneath the shelf upwelling zone during the spring bloom in May 2008. Integrating both sample sets will allow describing the foraminiferal response to multiple environmental influences. Such insights should contribute to a better understanding of fossil assemblages and their paleoenvironmental implications. Sample preparation, faunal analyses and taxonomy followed current concepts, facilitating a higher data consistency as among earlier studies (Schönfeld et al., 2012, 2013).

2.2 Materials and Methods

2.2.1 Sample and data sources

The study area is located in the South Western Approaches of the Celtic Sea, southwest of the English Channel between 47° and 50° N (Fig. 2.1). We investigated 13 surface samples from the shelf and uppermost continental slope between 115 and 467 m water depth. The samples are broadly aligned along a NE – SW transect, with several samples situated along the NW – SE directed shelf break. Faunal data of five adjacent shelf stations of Sturrock and Murray (1981) and Murray et al. (1982) were also considered in our analyses (Fig. 2.1). For these two studies only, the metadata (coordinates, water depth, size fraction, discernation of live and dead specimens, complete quantitative faunal data) were available, and thus allow a comparison with the results of our study. Census data of the living fauna were published as Excel web files (WA-118) by Murray (2006). For the continental slope, faunal data from three stations of Schönfeld and Altenbach (2005) were considered too. The census data were partially published in 2005 (living *Uvigerina* species only). Herein, we used the complete dataset of living and dead foraminiferal species. Foraminiferal data from Le Calvez (1958), Le Calvez and Boillot (1967), Murray (1970) and Weston (1985) from this area were also considered (Fig. 2.1).
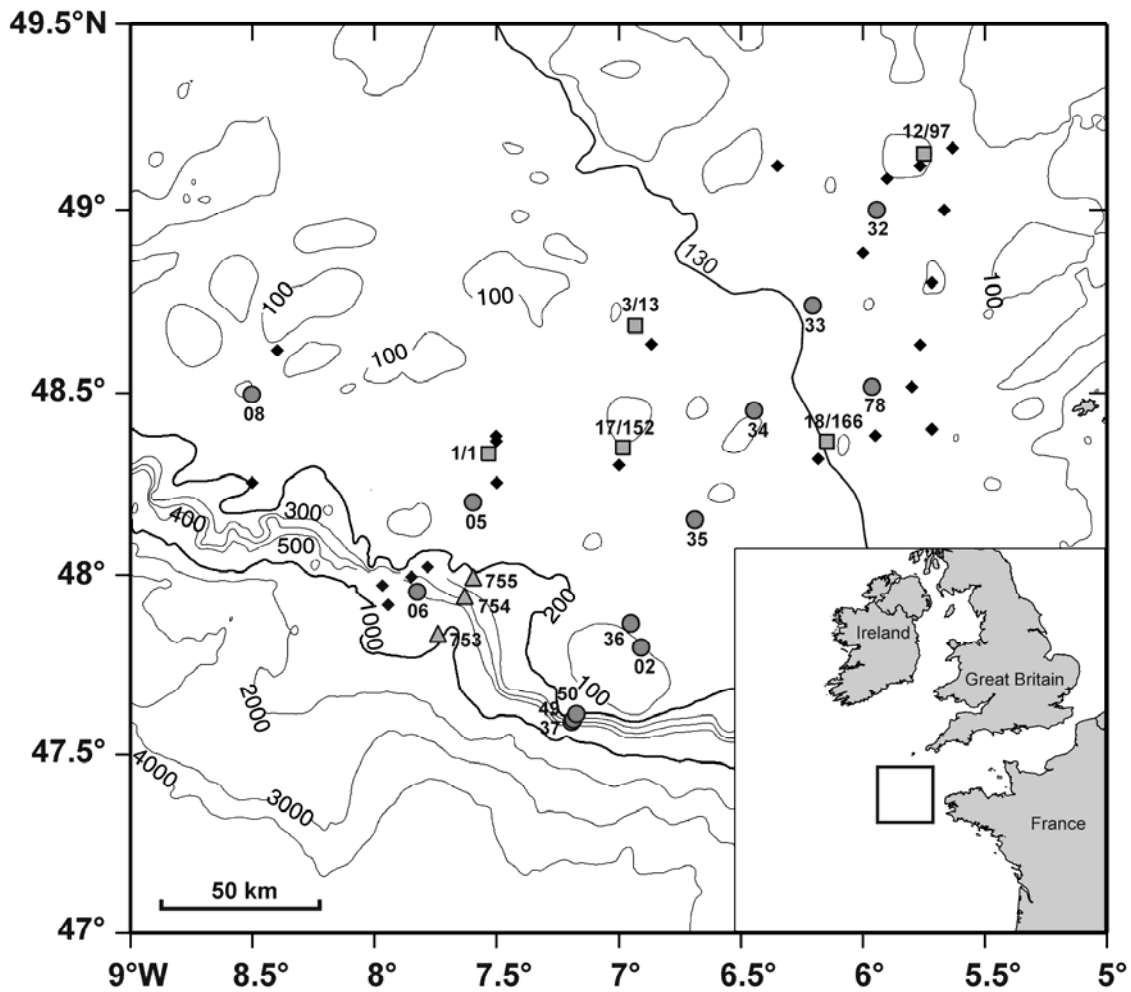
Figure 2.1 Geographical position of our stations (circles) and corresponding stations of other authors; squares: stations of Sturrock and Murray (1981) and Murray et al. (1982), triangles: stations of Schönfeld and Altenbach (2005), diamonds: stations of Le Calvez (1958), Le Calvez and Boillot (1967), Murray (1970) and Weston (1985).

2.2.2 Methods of sampling

Samples were taken on three separate cruises in 1995 (FS Thalia), 1997 (R/V Victor Hensen) and 2008 (R/V Belgica; Tab. 2.1). During the R/V Victor Hensen cruise, a Van Veen grab sampler was used. Samples were preserved and stained in a Rose Bengal/ethanol solution in order to recognize foraminifers living at the time of sampling (Lutze and Altenbach, 1991; Murray and Bowser, 2000). Samples from the R/V Belgica cruise and the FS Thalia cruise were taken with a NIOZ Haja box corer, also preserved, and stained in ethanol and Rose Bengal (Tab. 2.1). All samples were taken from the uppermost centimeter of the surface sediment.

Samples of Sturrock and Murray (1981) and Murray et al. (1982) were taken with a Shipek grab sampler (modified to prevent washing of the sample) and preserved in methanol. Samples of Schönfeld and Altenbach (2005) were recovered with a USNEL box corer. Foraminiferal samples were taken from the 0 to 1 cm interval of the surface sediment, and preserved and stained with a methanol/Rose Bengal solution on collection (Tab. 2.1).

Table 2.1 Metadata of stations from this study and Sturrock and Murray (1981), Murray et al. (1982), and Schönfeld and Altenbach (2005). Bold numbers were used as abbreviations of the station numbers in the text and figures.

Studies	Cruise	Station	Sampling date	Latitude	Longitude	Depth (m)	Device
This study	R/V Victor Hensen	VH-97-**32**D	04.04.1997	49°00.03' N	5°56.55' W	115	Van Veen grab
		VH-97-**33**D	04.04.1997	48°44.33' N	6°12.33' W	131	Van Veen grab
		VH-97-**34**	04.04.1997	48°27.05' N	6°26.82' W	116	Van Veen grab
		VH-97-**35**	04.04.1997	48°09.23' N	6°41.29' W	150	Van Veen grab
		VH-97-**36**	04.04.1997	47°51.95' N	6°57.05' W	170	Van Veen grab
		VH-97-**37**	04.04.1997	47°32.94' N	7°14.99' W	467	Van Veen grab
		VH-97-**49**	05.04.1997	47°33.21' N	7°14.45' W	340	Van Veen grab
		VH-97-**50**	05.04.1997	47°34.43' N	7°13.10' W	191	Van Veen grab
	RV Belgica 2008/12a	BG0812a-**02**	08.05.2008	47°47.94' N	6°54.48' W	128	NIOZ Haja box corer
		BG0812a-**05**	10.05.2008	48°12.06' N	7°35.88' W	177	NIOZ Haja box corer
		BG0812a-**06**	09.05.2008	47°53.94' N	7°53.88' W	450	NIOZ Haja box corer
		BG0812a-**08**	11.05.2008	48°29.76' N	8°30.18' W	151	NIOZ Haja box corer
	FS Thalia	D**78**/95	29.10.1995	48°30.97' N	5°57.81' W	119	Van Veen grab
Murray et al. (1982)	unknown	12/97	08.-13.10.1979	49°10' N	6°59' W	122	Shipek grab
Sturrock and Murray (1981)	unknown	3/13	spring/ autumn 1977-1979	48°41' N	6°56' W	145	Shipek grab
		18/166		48°22' N	6°09' W	145	Shipek grab
		17/152		48°21' N	6°59' W	176	Shipek grab
		1/1		48°20' N	7°32' W	170	Shipek grab
Schönfeld and Altenbach (2005)	FS Poseidon 201	PO201/10-**753**	04.07.1994	47°47.04' N	7°45.90' W	684	USNEL box corer
		PO201/10-**754**	04.07.1994	47°54.18' N	7°39.90' W	398	USNEL box corer
		PO201/10-**755**	04.07.1994	47°56.64' N	7°37.92' W	207	USNEL box corer

2.2.3 Sample preparation

Samples were carefully washed through stacked 2000 µm and 63 µm sieves. Residues were dried at 60° C. In cases when residues were very rich in foraminifers, samples were split with an Otto microsplitter to manageable subsets with a target number of 300 to 400 specimens per census. Splits or residues were further subdivided into different grain-size fractions (63 – 125 µm, 125 – 250 µm, 250 – 400 µm and 400 – 2000 µm) to facilitate microscopic work. The >2000 µm fraction, consisting of pebbles, sand, and skeletal and shell fragments was examined for attached living foraminifers. Samples were routinely picked dry. Some detritus-rich samples were picked wet in order to facilitate microscopic work. Living and dead individuals were recorded separately. All specimens were collected in Plummer cell-slides, sorted at species level, fixed with glue, and counted. The samples and Plummer cells were stored at GEOMAR Helmholtz Centre for Ocean Research Kiel.

Samples of Sturrock and Murray (1981) were reported to have been washed on a 63 µm sieve, stained with rose Bengal, washed again on a 63 µm sieve and dried at 80° C. Afterwards the foraminiferids were floated off in trichloroethylene and over 100 living (stained) individuals were counted. All substrates >4 mm were examined for attached species. Samples of Murray et al. (1982) were reported to have been stained in a Rose Bengal solution of at least 30 minutes and then were washed on a 76 µm sieve. Residues were examined wet for all stained foraminifers.

Samples of Schönfeld and Altenbach (2005) were washed by the second author of the present paper through stacked 2000 µm and 63 µm sieves. The >2000 µm fraction was examined for attached living foraminifers. Residues were further divided into the 63 – 250 µm and 250 – 2000 µm grain-size fractions. Both, the living (stained) and dead foraminiferal specimens were analyzed from the >250 µm fraction by the second author. Their samples and Plummer cells were stored at GEOMAR Helmholtz Centre for Ocean Research Kiel, too.

2.2.4 Taxonomic identification of foraminiferal species

Foraminiferal species were determined after Phleger and Parker (1951), Parker (1954), Murray (1971), Haynes (1973), and Jones (1994). They were cross-checked with

type descriptions of Ellis and Messina (1940) catalogue. Certain arenaceous species were determined after Brönnimann and Whittaker (1983), Brönnimann and Zaninetti (1984), and Brönnimann and Whittaker (1988, 1990). *Ammonia* species were assigned to their molecular types after Hayward et al. (2004).

2.3 Results

2.3.1 Faunal distribution pattern and abundant species

A total number of 294 species were recorded, of which 89 were found exclusively in the living fauna and 118 only in the dead assemblage, whereas 87 species were found in both assemblages. These figures are based on an overall census of 4419 living and 5948 dead specimens. Fifty-nine percent of all species belong to the suborder Rotaliina, 33 % to the suborder Textulariina and 9 % to the suborder Miliolina.

The distribution pattern of living species revealed a bisection in shelf and slope. The shelf is also structured by a proximal and a distal fauna (Fig. 2.2). The faunal composition was largely consistent within these shelf groups, whereas a strong variation in the living faunas between the individual stations was found on the slope. Dead assemblages showed differences in composition as compared to the living fauna, but the variability in dead assemblages between individual stations was lower. In particular, the number of species of the living fauna (28 dominant species) was nearly twice the number of the dead assemblage (15 dominant species). A bisection was recorded between a shelf assemblage (stations 32 – 36, 02 and 78) and a mainly slope assemblage (stations 37, 49, 50, 06, and 05 and 08; Fig. 2.3). *Trifarina angulosa* and *Gavelinopsis praegeri* were the most frequent species in the living fauna (Fig. 2.2, Pl. 1, 2). They were recorded as dominant species (one of the five most abundant species in a station) at nine and ten stations, respectively, with a frequency of 5 – 28 %. *Trifarina angulosa* was recorded up to 340 m water depth, whereas *Gavelinopsis praegeri* was found frequently only to the shelf edge at 191 m. *Bolivina difformis* and *Cassidulina obtusa* showed distinct distribution pattern on the shelf (Fig. 2.2, Pl. 1, 2). *Bolivina difformis* was recorded as a frequent species only at stations that were located inside the tidal sand ridges system (Fig. 2.2). *Cassidulina obtusa* was recorded as an abundant species at stations situated along the shelf edge (Fig. 2.2). In addition, *Cibicides lobatulus* (Pl. 1, 2) was with 36 % the most

abundant species only at one station close to Brittany, and its frequency was markedly low (<5 %) at all other stations. *Epistominella vitrea* was the most abundant species (23 %) at the westernmost shelf edge (Fig. 2.2). This species was also found living at other shelf and slope stations, but with much lower proportions (≤2 %).
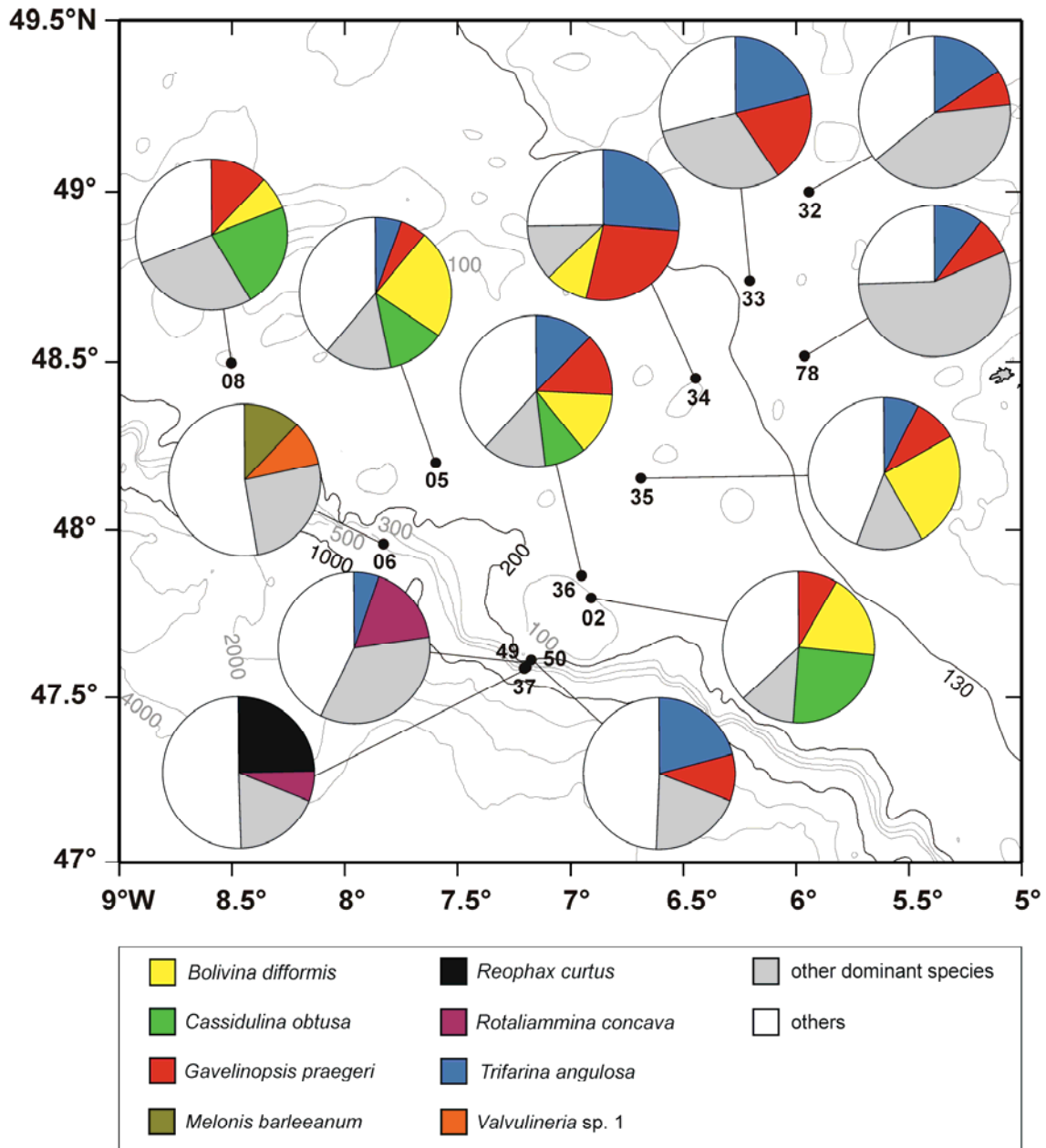
Figure 2.2 Station map with proportions of dominant living species.

The living fauna was different at the slope stations, changing substantially with increasing depth and geographical distance between the stations. In particular, *Trifarina*

angulosa and *G. praegeri* were the first and second ranked species on the shelf edge (station 50), whereas *Rotaliammina concava*, *Reophax curtus*, *Placopsilina* sp., *Valvulineria* sp. and *Melonis barleeanum* were the first and second ranked species at the deeper stations (Fig. 2.2, Pl. 1, 2). We used the similarity index of Sanders (1960) to identify the similarities between the living faunal assemblages of the slope stations. Therefore, we compared the relative abundance of taxa between stations 50 and 49, 49 and 37, 37 and 06, and 49 and 06. The similarity index decreased from 38 % to 4 %, which means that the faunal differences changed significantly with increasing depth and geographical distance between the stations.

We compared the inventory of our most abundant living species at six shelf stations (32 – 35, 05 and 78) with those from adjacent stations reported by Sturrock and Murray (1981) and Murray et al. (1982). They recorded a total number of 61 living species and 587 specimens from five stations. In contrast, the total number of living species at our six stations was 98 and based on an overall census of 2371 specimens. The γ-diversity was with a Fisher α index of 17 in the literature data and about 21 in our data, not substantially different (Schönfeld et al., 2013). Comparing the dominant species inventory of adjacent stations, we found a match of the same four dominant species (*T. angulosa*, *G. praegeri*, *C. lobatulus* and *Spirillina vivipara*) for our station 78 and their station 18/166 (Fig. 2.1). At all other stations, only two species were the same as in our corresponding samples. These species were *T. angulosa*, *G. praegeri*, *Portatrochammina murrayi* or *C. obtusa*, each at respective stations. In addition, *S. vivipara* was recorded as a frequent species in four samples of Sturrock and Murray (1981) and Murray et al. (1982). This species was abundant only in the above-mentioned station 78, but less frequent (<2 %) at the other five stations.

The living fauna at the slope stations 37, 49, 50 and 06 were compared with the living fauna from three adjacent stations of Schönfeld and Altenbach (2005). They analyzed the benthic foraminiferal fauna from the >250 μm fraction. No further foraminiferal analyses of the <250 μm fraction was made, in order to preserve the authenticity of the reference material of Schönfeld and Altenbach (2005). Therefore, we extracted the faunal data of the >250 μm fraction from our census for the four slope stations. A total number of 38 living species and 172 specimens were recorded. In contrast, 88 living species and 330 specimens were recorded by the other authors. Hence their γ-diversity with a Fisher α index of 39 was markedly higher than that of 15 in our

samples. A consistent species distribution pattern was not found in either sample set. The faunal composition changed significantly with increasing depth. However, species of the genus *Reophax* were recorded dominant at the stations of Schönfeld and Altenbach (2005). On the other hand, *R. concava* was one of the dominant species at our stations. Comparing the dominant species from similar water depths, only one living species was the same at every station.

Cibicides lobatulus and *Spiroplectinella sagittula* were the most frequent species in the dead assemblages (Fig. 2.3, Pl. 1, 2). They occurred as dominant with a frequency of 6 – 39 %. Distinct distribution patterns were distinguished for other dominant species. *Textularia pseudogramen* was recorded as a frequent species only up to 150 m water depth, whereas it was less abundant (<5 %) in all other stations (Fig. 2.3, Pl. 1, 2). *Bolivina difformis* and *C. obtusa* were found in all stations, but were only recorded as a dominant species along the shelf edge and at station 06. *Globocassidulina subglobosa* was found to be frequent at all slope stations and at station 05 (Fig. 2.3, Pl. 1).

The dead assemblage of the >250 µm fraction from slope stations 37, 49, 50 and 06 was compared with the dead assemblage of Schönfeld and Altenbach (2005). We determined a total number of 59 dead species, based on 432 specimens, whereas a total number of 73 dead species and 954 specimens were recorded by Schönfeld and Altenbach (2005). The γ-diversities were with an index of 18 in each case the same. *Cibicides lobatulus*, *Cibicides refulgens* and *Cibicidoides* sp. were recorded as a dominant species at our stations 49 and 50 and their stations 754 and 755, respectively. At deeper stations, the inventory of the five most abundant species changed completely. Only one dominant species from our station 06 matched with one dominant species from their station 753.
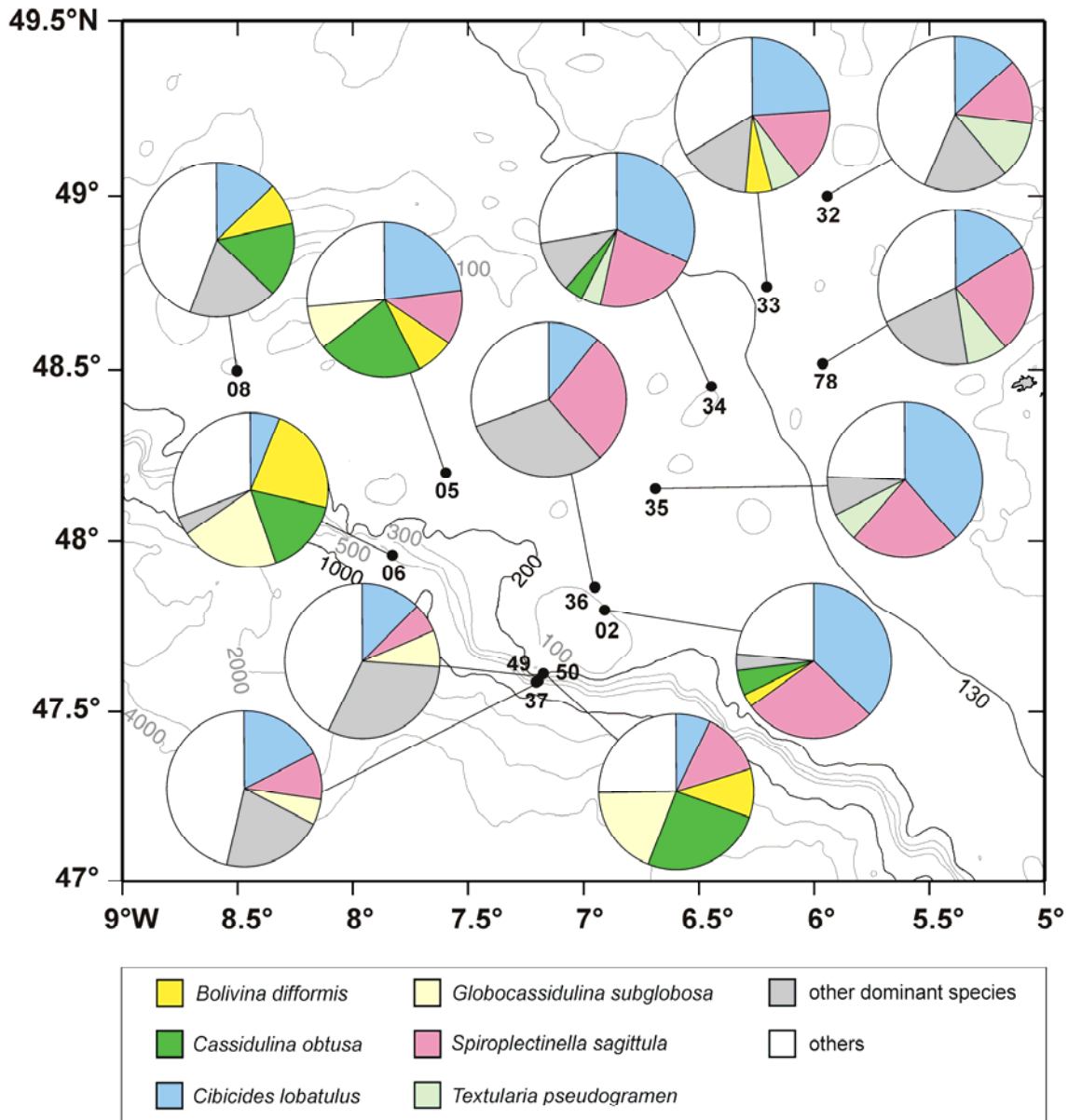
Figure 2.3 Station map with proportions of dominant dead species.

2.3.2 Population density and faunal diversity (Fisher α index)

In the living fauna, population densities ranged from 12 specimens per 10 cm³ (station 37) to 522 specimens per 10 cm³ (station 08). The population density was generally highest between 130 – 180 m depth (Fig. 2.4). The number of individuals per 10 cm³ decreased successively on the slope, with exception of station 06. The number of tests per 10 cm³ in the dead assemblage was highest at station 06, and the lowest number was found at station 49 (Fig. 2.5). Overall, the number of tests per 10 cm³ was highest along the shelf edge and lowest along the transect on the slope.
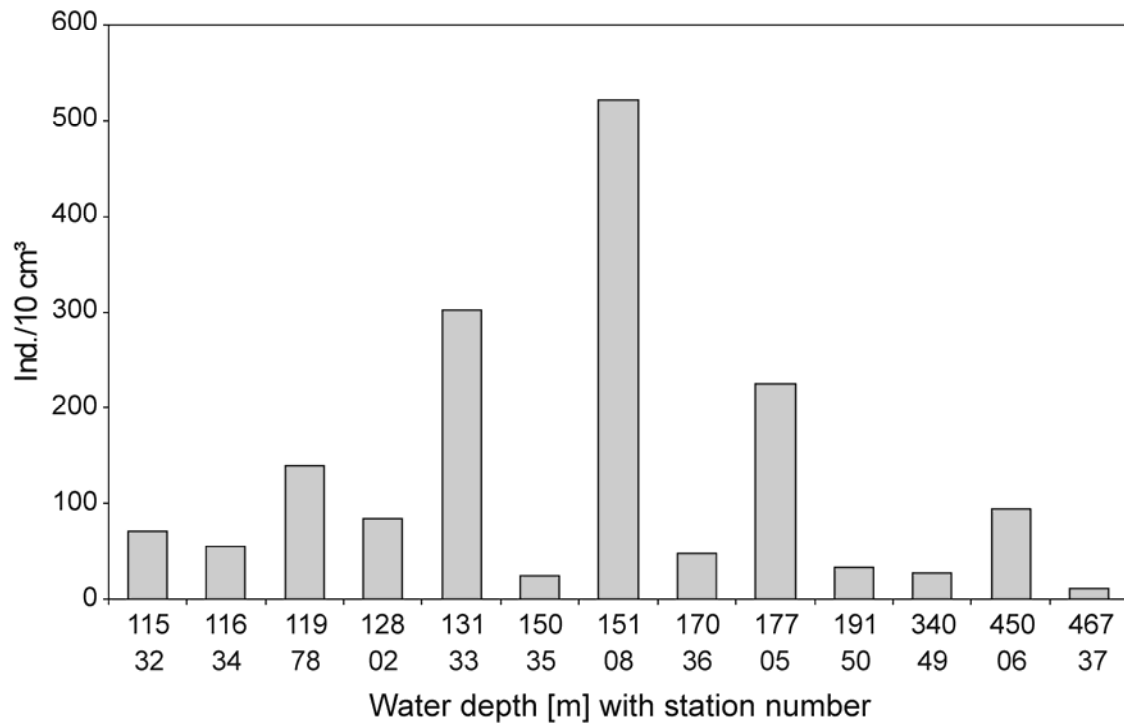
Figure 2.4 Population densities of the living fauna per 10 cm³.
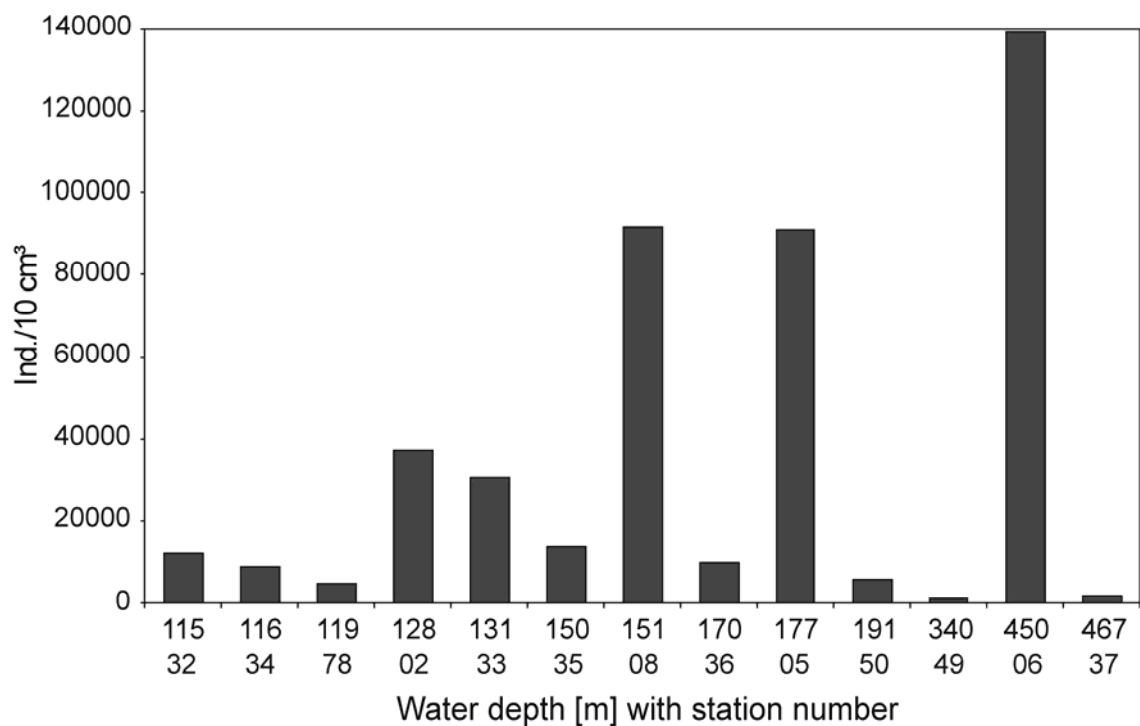
Figure 2.5 Number of individuals per 10 cm³ of the dead assemblages. Please note the different scale at the y-axis compared to Fig. 2.4.

Population densities of six stations were compared with densities from adjacent stations of Sturrock and Murray (1981) and Murray et al. (1982; Fig. 2.1). They found population densities between 60 and 80 individuals per 10 cm³ in their samples, whilst we recorded population densities between 25 and 300 individuals per 10 cm³. We additionally compared the number of living individuals per 10 cm³ (>250 µm) from three stations of Schönfeld and Altenbach (2005), with data from stations 37, 49, 50 and 06 in this study. Population densities were with 11 and 23 individuals per 10 cm³ higher in the samples of Schönfeld and Altenbach (2005) than in samples from this study, where 4 – 12 individuals per 10 cm³ were recorded.

To describe and compare the diversity of benthic foraminifera in the study area, we used the Fisher α index, in order to retain consistency with other publications from the NE Atlantic (Fisher et al., 1943; Hayek and Buzas, 2013). A distinct bisection of Fisher α indices and water depth was found (Fig. 2.6). The index of the living fauna showed values between 6 and 15 up to the shelf break. At the deepest stations on the slope, the Fisher α index of the living fauna ranged from 17 to 19. Similar indices for the living fauna were found at most stations, when comparing our data with diversity measures as reported by Sturrock and Murray (1981) and Murray et al. (1982). Therefore, the diversity can be considered as being rather uniform in this area (Fig. 2.6). In contrast, the diversity on the slope was significantly different between our stations and the stations of Schönfeld and Altenbach (2005). With indices between 20 and 40, the diversity of the living fauna was much higher in the aforementioned study than in our study (<10).
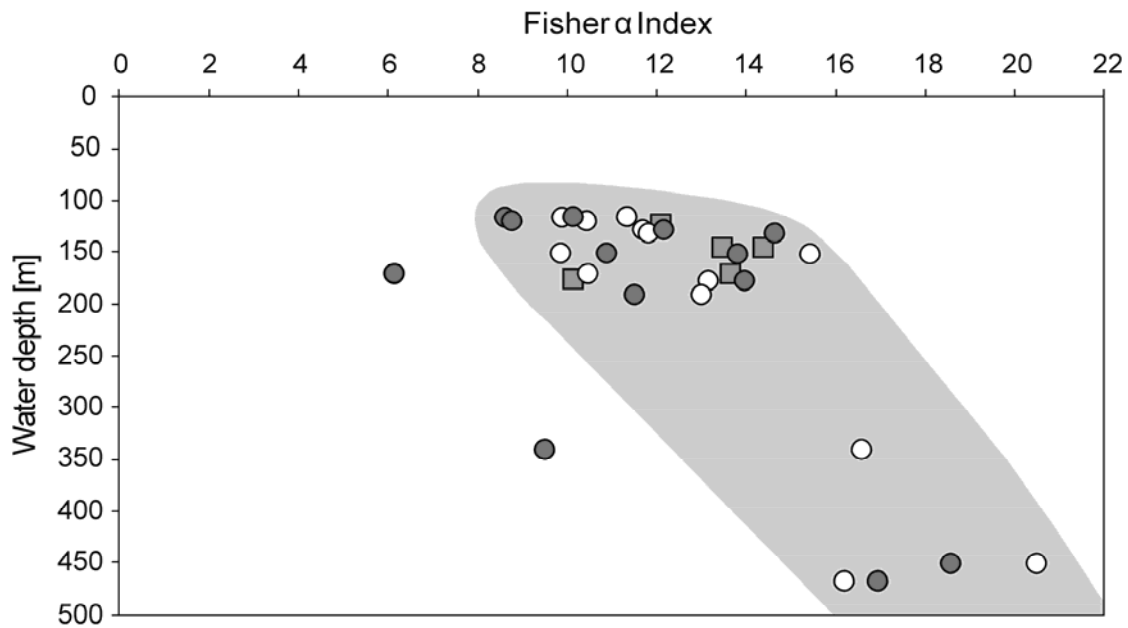
Figure 2.6 Fisher α index of the living fauna (gray circles) and dead assemblages (white circles) as a function of water depth; gray squares: Fisher α index of the living fauna of Sturrock and Murray (1981) and Murray et al. (1982).

2.3.3 Correspondence analysis

Correspondence analysis (CA) is one of the eigenvector methods for exploring large and complex data sets. The analysis produces scatter plots where data with the same or similar properties are shown in a cloud of points in an ordination plot (Hennebert and Lees, 1991; Hammer et al., 2001). We applied CA for our samples together with the data of Sturrock and Murray (1981), Murray et al. (1982), and Schönfeld and Altenbach (2005) to identify relationships between samples or faunal assemblages.

CA was undertaken for the dominant living species, which comprise the five ranked species from every station, and which produced the most significant results. Because station 06 had a complete different faunal assemblage, we eliminated this station from the CA. The analysis extracted 11 axes for 23 dominant species from 12 samples. The best discernation of faunal groups was displayed between the two first ranked axes representing 44 % of the total data variability. The station scores inferred three clusters, where stations 37 and 49 from the slope were separated from the other stations by an axis 1 score of 1.2, and by each other by axis 2 scores (Fig. 2.7). All other samples derived from the shelf and grouped at axis 2 in a score range from 0.6 to -0.7. It is therefore

conceivable that axis 1 can be interpreted as reflecting water depth. At axis 2, station 08 was situated at the positive score end, whereas station 78 was situated at the negative score end. Thus, axis 2 can be interpreted as reflecting the proximal and distal distribution at the shelf. The species scores inferred to a top left open parabola-like structure (Fig. 2.8). One or three species were situated at the endpoint and right edge of the parabola. They were dominant in only one station. These species were *Epistominella vitrea* at station 08, *Textularia skagerakensis* and *Placopsilina* sp. at station 49, as well as *Bolivina variabilis*, *Reophax curtus* and *Trochammina squamata* at station 37 (Pl. 1, 2). All above mentioned species occurred with low frequencies in other stations, except *Reophax curtus*. We also carried out CA for all living species and for the living species with a frequency ≥2 % and ≥5 %, together with the data of Sturrock and Murray (1981), Murray et al. (1982), and Schönfeld and Altenbach (2005). No other results were obtained from the CA as compared to the analyses described above.
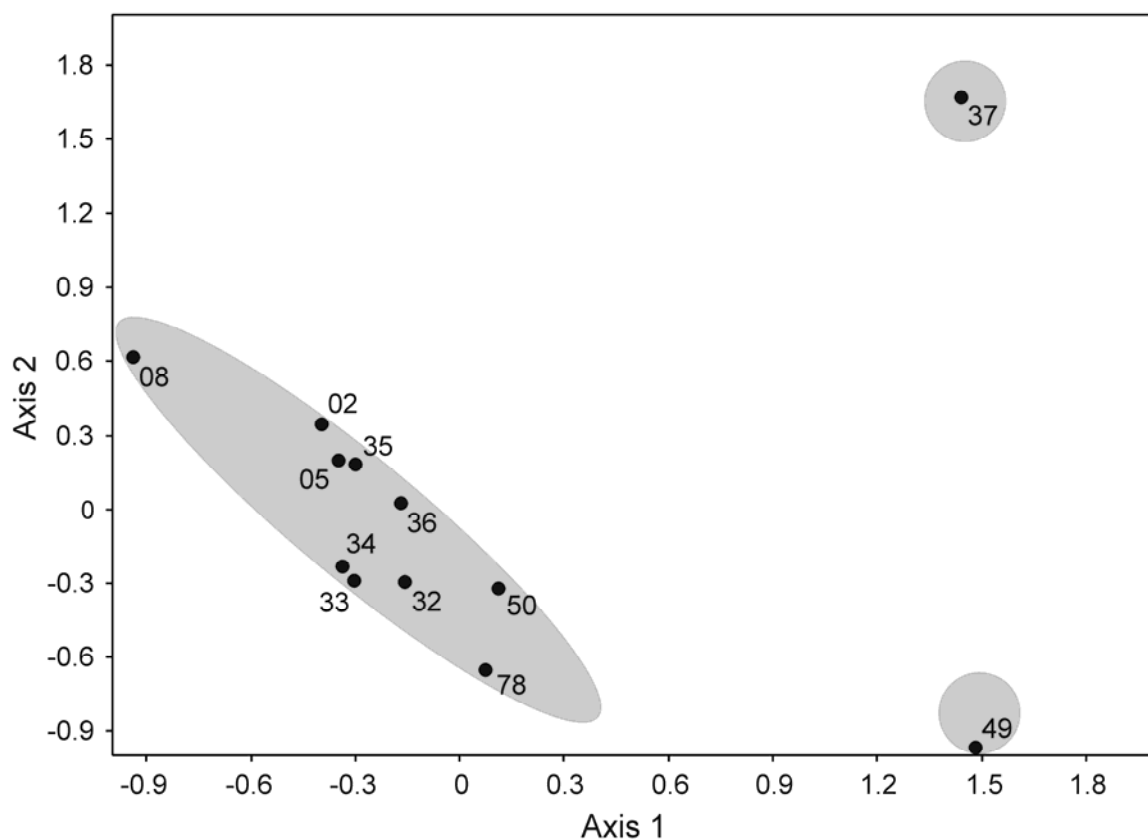
Figure 2.7 Correspondence analysis of the living dominant species without station 06; sample distribution.
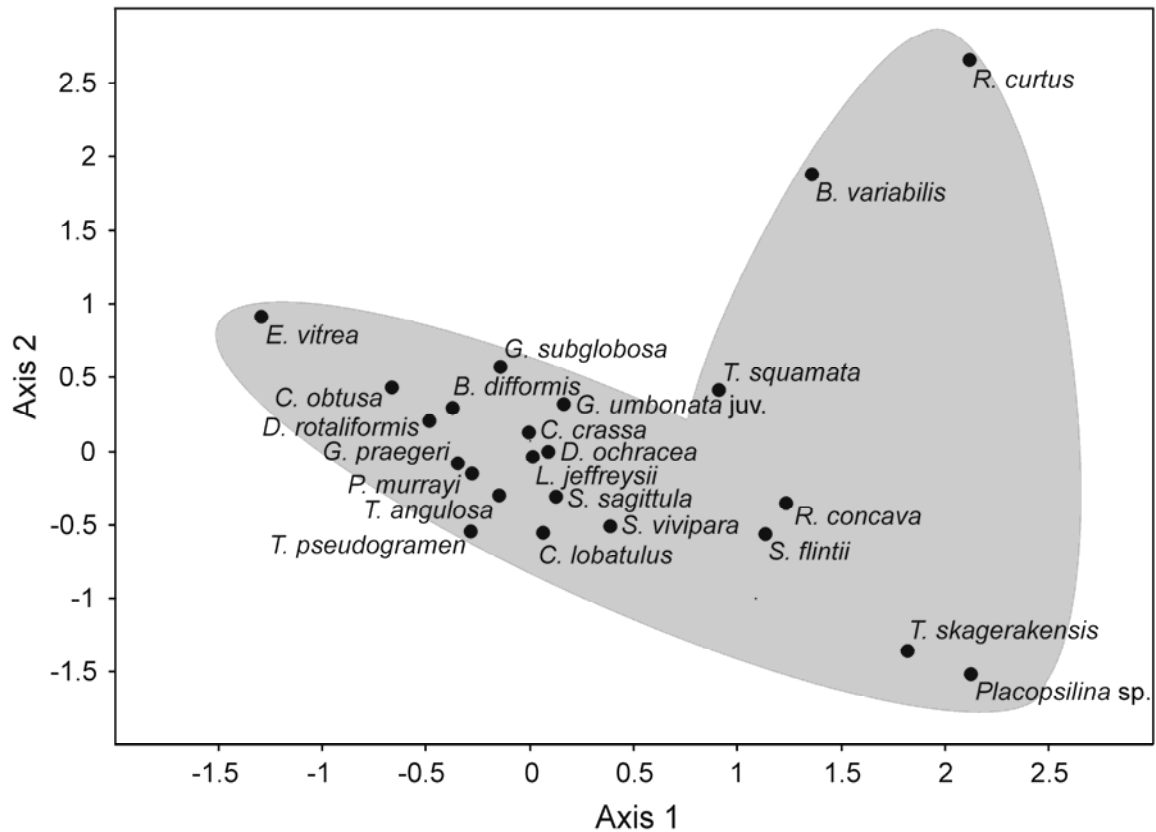
Figure 2.8 Correspondence analysis of the living dominant species without station 06; species distribution.

2.4 Discussion

2.4.1 Distribution pattern of abundant species in the living fauna

The species distribution pattern revealed a bisection in shelf and slope, and a structured shelf with a proximal and distal faunal assemblage. *Trifarina angulosa* and *Gavelinopsis praegeri* were the most common species on the shelf and uppermost continental slope. *Trifarina angulosa* is an epifaunal to shallow infaunal (0 – 1.5 cm sediment depth) free living species and occurs in coarse to gravelly biogenic sands on the shelf and upper slope, where the sediment is under the influence of bottom currents, and where oxic conditions prevail (Mackensen et al., 1993, 1995; Harloff and Mackensen, 1997; De Stigter et al., 1998; Schönfeld, 2001, 2002; Murray, 2006, 2013). *Gavelinopsis praegeri* is an epifaunal opportunistic (free or attached) living species that is most frequent in coarse pebbly sands of the inner and middle shelf influenced by tidal currents and storm

waves (Sturrock and Murray, 1981; Murray, 2006). In contrast, other abundant species showed distinct distribution patterns. *Bolivina difformis* was recorded as a frequent species only on the shelf within the tidal sand ridges (130 – 200 m, Fig. 2.9). Different hydrographic conditions inside and outside of the tidal sand ridge field may therefore influence the abundance of this species. *Cassidulina obtusa* was frequent only at stations along the shelf edge. Water masses from the Bay of Biscay run alongside the shelf edge in a NNW direction. This flow is connected with a higher supply of food particles (New, 1988; Wollast and Chou, 2001) by enhanced primary production (Joint et al., 2001; Van Oostende et al., 2012). This process seems to favor the abundance of *C. obtusa*. Besides a higher food supply, the quality and composition of organic matter could influence the faunal assemblages. For example, *Epistominella vitrea* was only abundant at station 08, sampled immediately after the spring bloom (Van Oostende et al., 2012). *Epistominella vitrea* is an infaunal opportunistic species that prefers a muddy to sandy substrate and which responds to high food availability (Jorissen et al., 1992; Murray, 2006; Mendes et al., 2012). Concentration of surface water chlorophyll a was 15 mg/m² at station 08 at the time of sampling, whereas chlorophyll a concentration ranged between 30 and 40 mg/m² at stations 02, 05 and 06 (Van Oostende et al., 2012). In addition, the phytoplankton community was dominated by coccolithophores and dinoflagellates at station 08, whereas diatoms were most abundant at the other three stations (fig. 9 in Van Oostende et al., 2012). This pattern suggests that *Epistominella vitrea* being better adapted to feed on coccolithophores and dinoflagellates. Different substrates also had an influence on species distribution pattern. Most of the shelf stations were dominated by gravel sands, whereas larger pebbles and shell fragments were retrieved at station 78. Species like *Cibicides lobatulus* and *Spirillina vivipara*, which preferred to live epibenthic on different substrates (Sturrock and Murray, 1981; Schönfeld, 2002; Murray, 2006), were frequent at this station. These two species were also found abundant at the adjacent station 18 /166 of Sturrock and Murray (1981). *Cassidulina obtusa* was found frequently by the aforementioned authors inside the tidal sand ridge system at stations 3/13, 17/152 and 1/1, although these stations were not situated along the shelf edge (Fig. 2.9). A reason for this pattern could be the time of sampling combined with a higher food supply. The growth of some species was favored during the summer months, when under a stratified water column a higher organic carbon concentration in the sediment prevailed (Scott et al., 2003). Samples of Sturrock and Murray (1981) were taken before the vertical mixing of

the water column in autumn. This would offer an explanation for the higher proportion of *C. obtusa* in their samples from the sand ridges.
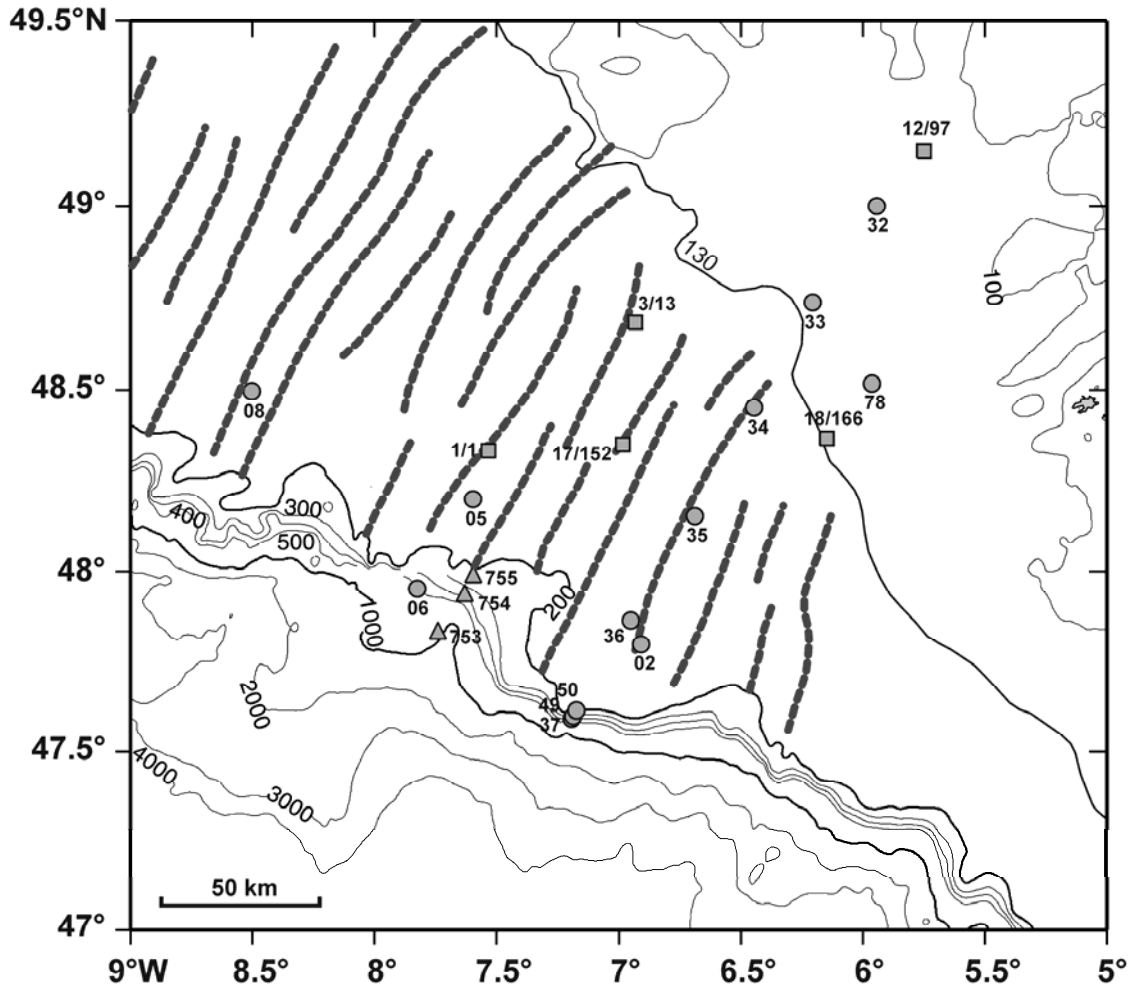
Figure 2.9 Location map showing Celtic Sea linear tidal sand ridges; circles: stations of this study, squares: stations of Sturrock and Murray (1981) and Murray et al. (1982), triangles: stations of Schönfeld and Altenbach (2005); modified from Scourse et al. (2009).

The living faunas on the slope were significantly different to those on the shelf. Abundant species changed within small depth intervals. Even though our data set is rather sparse in seasonal and spatial coverage, the living fauna evidently showed a high degree of partitioning on the uppermost slope in comparison to the shelf. In this context, different water masses on the continental slope gain relevance. Whilst the North Atlantic Current moves in a SE direction along the shelf edge, underlying water masses of the slope current flow in a northward direction (Van Aken, 2001; Friocourt et al., 2007). Nutrient inputs

variable by lateral advection, timing, and composition at specific depth intervals are therefore important in establishing habitats for different species on the upper slope. As on the shelf, different substrates probably also influenced the occurrence of certain species. At station 06, the sediment was a very fine quartz-rich sand, whereas a coarser sand with abundant shell detritus was found at the other stations. Completely different species were abundant at station 06, and were found neither living nor dead at the other stations (e.g. *Melonis barleeanum*). Besides the influence of different slope currents at different depths, the time of sampling could influence the faunal assemblages. Samples of Schönfeld and Altenbach (2005) were taken in July, whereas our samples were taken at the beginning of April and May (Tab. 2.1). Only one positive match of a frequent species >250 μm was recognized between the three stations of Schönfeld and Altenbach (2005) and our four slope stations. Most of these abundant species lived epifaunal and attached onto hard substrates (*Cibicides lobatulus*, *Placopsilina* sp. and *Trochammina squamata*).

2.4.2 Distribution pattern of abundant species in the dead assemblage

The abundant species of the dead assemblage were significantly different from the living fauna, but occurrence patterns were more consistent within the dead assemblages. A distinct distribution pattern as seen in the living fauna on the shelf was not recognized. However, *Bolivina difformis* and *Cassidulina obtusa* were only common on and along the shelf edge, as well as at station 06. Total foraminiferal assemblages were analyzed by Le Calvez (1958) close to stations 05 and 08 from this study. *Bolivina difformis* and *C. obtusa* were not observed, but *C. crassa* and *C. laevigata* were found in this area. It is conceivable that a taxonomic misidentification of *C. crassa* and *C. laevigata* accounts for this difference. In particular, shape and size of *C. crassa* and *C. obtusa* are very similar. High percentages of *Cibicides lobatulus* and *Spiroplectinella sagittula* were found in almost all samples. Both species were also recorded in the living fauna, but with a frequency of <10 %. They were also reported from adjacent stations of Le Calvez (1958) and Le Calvez and Boillot (1967) from the outer western English Channel, as well as along the shelf break in samples of Le Calvez (1958) and Murray (1970). Both species were recorded as frequent species (>10 %) in dead assemblages of the English Channel, Bristol Channel and the northern Celtic Sea (Murray, 1970; Murray, 1979). The high abundance of *S. sagittula* in the dead assemblage is due to concentration over a long

period of time, as the tests are robust and withstand destruction (Sturrock and Murray, 1981; Murray et al., 1982). In addition, mixing of assemblages and postmortem transport of small foraminiferal tests from the English Channel and Bristol Channel to the W and SW of the Western Approaches resulted from near-bottom residual flows of suspended sediment (Murray, 1970; Murray, 1979; Sturrock and Murray, 1981; Murray et al., 1982). Together with gale-force winds in the late autumn and winter, the sediment suspension may pass over the shelf and lead to deposition of transported tests on the slope (Murray et al., 1982). These hydrographic processes could explain the distribution of *C. lobatulus* and *S. sagittula* from the shelf to the slope. Furthermore, a decrease in abundance from the shelf to the slope samples was observed for both species. This decrease is maybe linked with the test size (generally >125 μm) and thus reflects a decline in transport over long distances.

The dead assemblages from the slope differed less among each other in terms of the abundant species. Species of the suborder Textulariina were not frequent on the slope, except *S. sagittula*. Most Textulariina species had a large test size and were maybe too heavy to be thrown into suspension and transported over the shelf edge. There were fewer differences in frequent species at the slope stations, in comparison to the living fauna. The distribution pattern of the dominant slope species in the dead assemblages were similar, especially between stations 50 and 06, and 37 and 49. Much more consistency in the dead assemblages in comparison to the living one was noted between our dominant species and dominant species of Schönfeld and Altenbach (2005). Mainly species of the genera *Cibicides* and *Cibicidoides* of a size fraction >250 μm were recorded dominant up to 500 m water depth at our stations and at two stations of the aforementioned authors. At greater depths (station 753, 684 m), the dead assemblage changed completely, even though frequent species of the dead assemblage were similar to frequent species of the living fauna.

2.4.3 Paleoenvironmental implications

In this study, we demonstrated the influences of hydrographic processes on dead foraminiferal assemblages. As such, the question about the significance of fossil assemblages for sound paleoenvironmental interpretations arises. For instance, analyses of Eocene benthic foraminiferal assemblages of the western English Channel showed

likewise a homogeneous distribution pattern (Wright and Murray, 1972; Murray and Wright, 1974). Species with a porcelaneous and hyaline test structure were most frequent, whereas species with an agglutinated test were rare. This assemblage composition suggested an environment ranging from a shallow, nearshore hyposaline shelf sea to a hypersaline lagoon (Wright and Murray, 1972). In our samples, however, abundances of agglutinated species were about 20 % lower in the dead assemblages as compared to the living fauna, probably due to destruction during transport processes. In addition, 89 of 294 species were only found in the living fauna. Most of these species had an agglutinated test, and their proportion in a sample was between 4 % and 54 %. Fossil foraminiferal assemblages from the western English Channel were generally dominated by robust taxa of Rotaliina and Miliolina. A similar spectrum of abundant, robust Rotaliina and Miliolina was reported from Oligocene deposits of northern Germany. This faunal composition provided evidences for a high-energy costal depositional environment (Nuglisch and Spiegler, 1991). Generally, it has been recognized that fossil foraminifera showed no significant lateral variability. Homogenization by sediment redistribution and bioturbation were considered as main attenuated processes. This view has been challenged by an inhomogeneous lateral distribution pattern in fossil foraminiferal assemblages, similar to meter-scale patchiness documented from the living fauna (Scott, 1958; Smith and Buzas, 1986).

2.4.4 Population density and diversity

Analysis of the population density and diversity patterns of the living fauna revealed distinct regional differences on the shelf and slope. The outer shelf of the Celtic Sea is covered by SW – NE trending linear tidal sand ridges. Most of our shelf stations were located in this area and some stations were likely situated on these sand ridges (Fig. 2.9), as reflected by a lower water depth at stations 34 and 02 (Tab. 2.1). The ridges are 20 – 50 m high (Bouysse et al., 1976; Belderson et al., 1986) and stations 34 and 02 had a 20 – 50 m lower water depth as in the vicinity, as inferred from bathymetrical charts. In addition, samples 34, 02 and 08 had the same sediment composition with a high proportion of rounded quartz grains and pebbles, whereas station 08 was likely situated at the fold side of a sand ridge as stations 35 and 36, and not on the top of the ridge (Fig. 2.9). On the other hand, the sand-fraction of samples 35 and 36 was dominated by shell

fragments. Comparing the population density of the living fauna on the shelf, densities were highest at stations 33, 05, 08 and 78 with over 100 individuals/10 cm³. Lowest population densities on the shelf were observed in the transect samples, with the exception of sample 33. Possible reasons appeared to be not the sediment composition or the position of the station with reference to water turbulence, but the time and method of sampling. Transect samples were collected with a grab sampler at the beginning of April, whereas samples 02, 05, 08 and 78 were collected with a box corer at the beginning of May and at the end of October, respectively (Tab. 2.1). A box corer is designed to retrieve a well-preserved sediment surface, whereas a grab sampler is not intended to maintain the integrity of near-surface sediments accurately. Some sediment may be washed out when the grab does not close correctly (Schönfeld, 2012). The transect samples were collected before the spring bloom, which was constrained for the adjacent Irish Sea to have developed in the middle of April (Gowen et al., 1999), and therefore at a time of lower food supply. The 2008 samples of the Belgica cruise were collected during times of high primary production immediately after the spring bloom, as indicated by satellite data and chlorophyll a measurements (Van Oostende et al., 2012). Therefore, population densities were higher at the 2008 stations.

The Fisher α index yields a similar pattern of the living fauna on the shelf. The diversity was higher at the 2008 stations than at the 1997 stations, except station 33. Possible reasons for higher diversity could be the same as reasons given for population densities above. For example, stations 36 and 02 were situated close together at a tidal sand ridge near the shelf edge, but diversity was twice as high at station 02 compared to station 36. A comparison with samples of Sturrock and Murray (1981) and Murray et al. (1982) showed different results for the population density and the Fisher α index. While the diversity was almost the same, the population density in our six adjacent stations was higher than in the stations of aforementioned authors. In addition, the faunal similarity was under 50 % between corresponding samples. The time of sampling could be a reason for the lower population densities in the samples of Sturrock and Murray (1981). The samples may have been collected at a time of lower food supply. Additionally, the time period between their sample collection and the collection of our samples represents 20 – 30 years. In this time period, it is probable that long-time changes in faunal assemblage composition occurred in this area. The development of trawling at the end of the 1990s could have led to a change in benthic faunal composition. High trawling activity affects the oxygen

content in surface bottom sediments and disturbs benthic foraminiferal habitats (Trimmer et al., 2005). This does not appear to have reduced the species number (similar indices), but could have left an impact in the faunal composition.

The upper slope established various habitats in different depth intervals probably induced by different slope currents. Favorable conditions could have led to stronger reproduction and a rich benthic foraminiferal fauna at station 06. This case is also confirmed by the highest Fisher α index at station 06. Comparing the diversity pattern of our four slope stations (37, 49, 50 and 06) and the three stations (753, 754 and 755) of Schönfeld and Altenbach (2005) revealed differences in the population densities, as well as the Fisher α index. Causes for the higher population densities and Fisher α indices of the aforementioned authors could be a higher nutrient supply, due to the station location and the time of sampling. Stations of Schönfeld and Altenbach (2005) were located between two canyons, where it is possible that food particles from intermediate nepheloid layers were trapped. In addition, their samples were taken in beginning of July when a higher phytodetritus supply prevailed due to the spring bloom two months previously.

2.5 Conclusion

Analysis and comparison of benthic foraminiferal assemblages from the shelf and slope of the Celtic Sea revealed an increase in diversity from the shelf to the continental slope. Highest diversities were determined at the slope and at those shelf stations, which were sampled in May. Such higher diversities were likely promoted by a higher food supply, in response to the timing of the spring bloom. Faunal assemblages on the shelf were more consistent than on the slope, indicating extensive sediment redeposition. The slope fauna was more structured due to the different topography, bottom sediments and specific hydrographical conditions. The faunal composition therefore changed within small depth intervals and geographic position. The comparison of our stations with corresponding stations from earlier studies in the same area revealed major differences in the benthic foraminiferal assemblages, both on the shelf and on the slope. These differences were more likely due to the time and method of sampling than forced by environmental parameters. This leads to the conclusive recommendation that once consistent results in regional studies are required, all samples should be taken within a short period and with the same sampling device. In addition, our analyses of Recent dead

foraminiferal assemblages could demonstrate the influences of a high-energy environment on a faunal composition, e.g., loss of arenaceous species, increase of robust miliolids, and a lateral homogenization in assemblage compositions. These constraints may facilitate a better interpretation of palaeoenvironments from fossil foraminiferal assemblages.

2.6 Acknowledgements

CHAPTER 3 – Taxonomic notes on Recent benthic foraminiferal species of the family Trochamminidae from the Celtic Sea

Abstract

Benthic foraminiferal faunas from the shelf and upper continental slope of the Celtic Sea (NE Atlantic) show a rich variety of Trochamminidae species. We recognize 31 taxa, of which 18 could be determined at species level. These 18 species comprise about 9 % of all species of the family Trochamminidae that are describe from Recent sediments worldwide. For species determination and generic classification, we use existing taxonomic concepts and assess their applicability. Beside the morphology of the test and internal structures, different apertural features are considered playing a fundamental role in the systematic subdivision of the Trochamminidae. The position of the aperture controls the chamber arrangement and therefore the final shape of the test. However, we found no relationship between the apertural features and shape of the chambers as well as between apertural features and mode of life. Using apertural features for a sound taxonomic designation of our specimens proves difficult, because apertures are often obscured. Further, combined morphological and molecular-phylogenetic studies are required to constrain the taxonomic relevance of apertural characteristics.

3.1 Introduction

Describing benthic foraminiferal diversities in a given area requires a distinct taxonomic identification of all species. The determination of many species (usually calcareous) is generally deemed an easy task. Agglutinated species, however, in particular those of the family Trochamminidae Schwager, 1877 are sometimes very difficult. Therefore, these taxa were often listed as *"Trochammina* sp. or spp."* in foraminiferal publications. Different classification concepts on the family Trochamminidae were proposed in the past five decades (e.g., Rhumbler, 1938; Loeblich and Tappan, 1964; Saidova, 1981; Loeblich and Tappan, 1982; Brönnimann et al., 1983; Brönnimann and Zaninetti, 1984; Loeblich and Tappan, 1987; Brönnimann and Whittaker, 1988a; Kaminski, 2004; Mikhalevich, 2004). These classifications were based on test morphology, internal structures and apertural features (Loeblich and Tappan, 1987; Brönnimann et al., 1983). Another concept to study the phylogenetic relationships among different taxa is the molecular approach, which uses similarities between DNA, RNA, or proteins (Pawlowski, 2000). These different concepts were linked by the theoretical morphospace model (Tyszka, 2006). The morphospace model is based on principal morphogenetic rules deduced from the geometry of foraminiferal tests. This model revealed the fundamental role of apertures controlling the chamber position and hence for the development of the final test shape (Labaj et al., 2003; Tyszka et al., 2005).

Already in the mid 20th century, Rhumbler (1938) developed a diagram formula for spiral coiled foraminiferal tests, which allow the description of the chamber arrangement, and thus facilitating the designation of species. By this geometric concept, Rhumbler (1938) distinguished several species of the family Trochamminidae in sediment samples from Helgoland (North Sea). The most comprehensive studies of the Trochamminidae were given by Brönnimann and Whittaker (1990, *cum lit.*). They subdivided this family in several subfamilies and genera, as distinguished by the overall apertural features and test morphologies.

The goal of the present paper is to assess the applicability of hitherto proposed systematic concepts. Emphasis is given on how far morphological criteria are suitable for a taxonomic classification. In order to achieve these goals, a study area was chosen where as many Trochamminidae as possible were found. During a previous study on the ecology

and distribution of Recent benthic foraminifera of the Celtic Sea and Amorican margin, we found 31 different species of the Trochamminidae on the shelf and uppermost continental slope (Dorst et al., 2014), of which 18 taxa could determined at species level. They resemble 9 % of all Recent Trochamminidae as described in the literature (Ellis and Messina, 1940). In order to provide a balanced state of information, we re-described and illustrated these taxa in the present paper.

3.2 Materials and Methods

We used 13 surface samples from the shelf and uppermost continental slope of the Celtic Sea between 100 and 500 m water depth (Table 3.1). The samples were preserved and stained in a Rose Bengal/ethanol solution in order to recognize foraminifers living at the time of sampling (Lutze and Altenbach, 1991; Murray and Bowser, 2000). Specimens were picked from the size fraction of >63 μm and subfractions. Large-sized pebbles, shell fragments and other objects from the size fraction >2000 μm were examined for attached Trochamminidae specimens, which were isolated if possible. Living and dead individuals were recorded separately. All specimens were collected in Plummer cell-slides, sorted at species level, fixed with glue, and counted. Illustrations of selected specimens were carried out with a CamScan 44/EDX scanning electron microscope and a Keyence VHX – 700 FD digital camera. The illustrated specimens, samples and Plummer cells were stored at GEOMAR Helmholtz Centre for Ocean Research Kiel.

Table 3.1 Metadata of sampling stations.

Cruise	Station	Sampling date	Latitude	Longitude	Depth (m)
	VH-97-32D	04.04.1997	49°00.03' N	5°56.55' W	115
	VH-97-33D	04.04.1997	48°44.33' N	6°12.33' W	131
	VH-97-34	04.04.1997	48°27.05' N	6°26.82' W	116
R/V Victor	VH-97-35	04.04.1997	48°09.23' N	6°41.29' W	150
Hensen	VH-97-36	04.04.1997	47°51.95' N	6°57.05' W	170
	VH-97-37	04.04.1997	47°32.94' N	7°14.99' W	467
	VH-97-49	05.04.1997	47°33.21' N	7°14.45' W	340
	VH-97-50	05.04.1997	47°34.43' N	7°13.10' W	191
	BG0812a-02	08.05.2008	47°47.94' N	6°54.48' W	128
RV Belgica	BG0812a-05	10.05.2008	48°12.06' N	7°35.88' W	177
2008/12a	BG0812a-06	09.05.2008	47°53.94' N	7°53.88' W	450
	BG0812a-08	11.05.2008	48°29.76' N	8°30.18' W	151
FS Thalia	D78/95	29.10.1995	48°30.97' N	5°57.81' W	119

3.3 Systematics

Classification of the investigated species was carried out after Brönnimann and Zaninetti (1984), Brönnimann and Whittaker (1988a), and Brönnimann and Whittaker (1990).

Family TROCHAMMINIDAE Schwager, 1877

Subfamily TROCHAMMININAE Schwager, 1877

Genus *Trochammina* Parker and Jones, 1859, emend. Brönnimann and Whittaker, 1988a

Description: Test free or attached, trochospiral, spiral side convex, umbilical side concave, with four or more chambers in the final whorl. Wall agglutinated and imperforate. A single, interiomarginal aperture situated on the ultimate chamber of final whorl between the umbilicus and the periphery of the test (umbilical-extraumbilical). *Trochammina* differs from *Paratrochammina* Brönnimann, 1979 and *Trochamminopsis* Brönnimann, 1976 by its apertural position, which rests completely on the ultimate chamber. In *Paratrochammina* and *Trochamminopsis* it rests on the ultimate and penultimate chamber of the final whorl. It differs from *Tritaxis* Schubert, 1920 by the

number of chambers in the final whorl, which is three in *Tritaxis*, and by its test shape, which is plano-convex in *Tritaxis*.

<div align="center">

Trochammina advena Cushman, 1922

Pl. 3, Fig. 2a, b; Pl. 11, Fig. 10; Pl. 12, Fig. 1

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Trochammina advena Cushman, 1922, p. 20, pl. 1, figs. 2−4; Phleger and Parker, 1951, p. 9, pl. 4, fig. 15; Todd and Brönnimann, 1957, p. 30, pl. 4, fig. 16.

Material: Six living specimens, free, from stations VH-97-50 and BG0812a-08, size fraction 63 − 125 μm.

Description: Test small (<100 μm) and rounded, moderately convex on the spiral side, composed of three volutions. Final whorl with four chambers, moderately inflated. Sutures are straight on both sides and slightly depressed. Wall composed of quartz grains of equal size.

Remarks: All specimens were probably juvenile individuals, because they were four times smaller than the type material of Cushman (1922). Brönnimann (1979) examined the holotype of *T. advena* and recognized an accumulation of secondary agglutinate (cyst formation), which covers the apertural feature. Therefore, he suggested to consider the name of *T. advena* as a nomen non conservandum, because the generic position of the holotype cannot be determined. Furthermore, Brönnimann (1979) examined other foraminiferal slides of Cushman, curated in the U.S. National Museum collection, from the Atlantic shelf of N America containing trochamminas referred to *T. advena* by Cushman. These trochamminas were reassigned to *Paratrochammina simplissima* (Cushman and McCulloch, 1948) by Brönnimann (1979). Our specimens differ from *P. simplissima* in the number of chambers in the final whorl (never more than four), the number of whorls and the straight sutures on the umbilical side (sinusoid in *P. simplissima*). Therefore, we decided to retain the name *T. advena*. However, the apertural features are not clearly visible, which hampers a clear distinction with *P. simplissima*.

<div align="center">

Trochammina astrifica (Rhumbler, 1938)

Pl. 4, Fig. 2a, b; Pl. 11, Fig. 7

</div>

<div align="center">63</div>

Trochammina squamata Jones and Parker forma *astrifica* Rhumbler, 1938, p. 188, figs.
29−31.

Trochammina astrifica (Rhumbler). Höglund, 1947, p. 206, 208, text-fig. 186, pl. 15, fig.
2; Haynes, 1973, p. 34, pl. 4, figs. 18−20.

Material: Two specimens from station VH-97-32 and VH-97-35, one free living specimen from size fraction 63 − 125 μm, and one dead, attached specimen from size fraction >2000 μm.

Description: Test flat to low convex on the spiral side and flat to slightly concave on the umbilical side. Chambers arranged in a low, trochoid spiral of about two and a half whorls, six chambers in the final whorl, slightly crescent-shaped on the umbilical side. Sutures impressed, radial on umbilical side, incised towards the open umbilicus creating a regular, star-shaped figure. Attached test was surrounded by a "Puffermasse" in the sense of Rhumbler (1938) of agglutinated, white material. Our free specimen more resembles the specimens figured by Höglund (1947) than Rhumbler's type specimens.

Remarks: Brönnimann and Whittaker (1990) suspected that Rhumbler's (1938) "Ternärform" *Trochammina squamata astrifica* is very similar to their new described species *Deuterammina (Lepidodeuterammina) plymouthensis* Brönnimann and Whittaker, 1990 and *Deuterammina (Lepidodeuterammina)? celtica* Brönnimann and Whittaker, 1990. They also suspected that *T. astrifica* could also be a junior synonym of *Deuterammina (Deuterammina) rotaliformis* (Heron-Allen and Earland, 1911). A distinct classification of Rhumbler's (1938) species was not possible, because Brönnimann and Whittaker (1990) could not photograph the type specimens with a scanning electron microscope and the apertures were not visible. Comparing our free specimen with the figures of *D. (L.) plymouthensis* in Brönnimann and Whittaker (1990), we found a high morphological similarity with the holotype of *D. (L.) plymouthensis* (pl. 3, figs. 11−14). Therefore, it is possible that our two specimens could be determined as *D. (L.) plymouthensis*. A classification to *D. (L.)? celtica* or a juvenile *D. (D.) rotaliformis* could be excluded. However, even Brönnimann and Whittaker (1990) could not definitely determine Rhumbler's (1938) *T. astrifica*; we decided to retain Rhumbler's (1938) designation.

Trochammina squamata Jones and Parker, 1860

Pl. 5, Fig. 4a, b; Pl. 6, Fig. 4a, b; Pl. 10, Fig. 8; Pl. 12, Fig. 2

Trochammina squamata Jones and Parker, 1860, p. 304, type figure not given; Hedley et
 al., 1964, p. 419, figs. 1, 1a, b; 3, 1a, b, 3a−c.

?*Trochammina squamata* Jones and Parker. Heron-Allen and Earland, 1913 p. 50, pl. 3,
 figs. 7−10; Heron-Allen and Earland, 1930, p. 70, 71.

Trochammina squamata squamata (Jones and Parker). Rhumbler, 1938 p. 181, fig. 18.

Material: 49 specimens from stations VH-97-32, -35, -36, -37, -49, BG0812a-02, -
05, -06, -08, and D78/95, size fraction >63 µm; thereof 20 free living and two free, dead
specimens, as well as 15 attached living and 12 attached dead specimens.

Description: Tests of juvenile specimens are free and rounded, or adult specimens
are attached and more oval, with a low trochoid spire, composed of two or sometimes
three volutions. Attached tests are mostly surrounded by a "Puffermasse" of agglutinated
whitish material. Eight to nine chambers, with four chambers in the final whorl and a slit-
like aperture at the inner margin of the flat umbilical side of the ultimate chamber.
Chambers in juvenile specimens inflated, in adult specimens flattened. Last chamber
occupying about a quarter of the final whorl. Sutures slightly depressed and darker than
the test shell on the spiral side. Wall finely agglutinated with occasional larger grains,
smoothly finished.

Remarks: According to Brönnimann and Whittaker (1990), *Trochammina
squamata* of Jones and Parker (1860) from the Mediterranean Sea is a *Tritaxis*. However,
their morphological description of *T. squamata* as well as the re-description and
illustration by Hedley et al. (1964) of the original material of Jones and Parker (1860)
disagrees with the genotype description of *Tritaxis* by Brönnimann et al. (1983),
Brönnimann and Whittaker (1984), Brönnimann and Whittaker (1988a), and Brönnimann
and Whittaker (1988b). Therefore, we kept the genus *Trochammina* for this species.

Genus *Paratrochammina* Brönnimann, 1979 (emend. Brönnimann and Whittaker, 1988a)

Description: Test free or attached, axial compression variable, from subglobular conical tests to flattened watchglass-like tests. Wall single layered and imperforate. Aperture single and interiomarginal, without an umbilical flap, remains open into the umbilicus and rests with its border on the wall of the ultimate chamber and on the penultimate chamber. *Paratrochammina* differs from *Trochammina*, *Tritaxis*, *Trochamminopsis*, *Deuterammina* Brönnimann, 1976 and *Rotaliammina* Cushman, 1924 by its apertural features. The single aperture of *Trochammina* and *Tritaxis* rests only on the ultimate chamber of the final whorl. *Trochamminopsis* has a symmetric aperture with respect to the axis of coiling (umbilical position). *Deuterammina* has a double aperture, and in *Rotaliammina* has an axially directed apertural opening on each chamber. The single aperture of *Portatrochammina* Echols, 1971 is covered by an umbilical flap. Brönnimann and Whittaker (1986) divided this genus in two subgenera, based on the degree of axial depression: *Paratrochammina (Paratrochammina)* Brönnimann, 1979 and *Paratrochammina (Lepidoparatrochammina)* Brönnimann and Whittaker, 1986. *P. (Paratrochammina)* has more or less inflated chambers, moderately high to high spires and lives mostly free. *P. (Lepidoparatrochammina)* is characterized by axially strongly compressed adult chambers and watchglass-like tests. With its flattened and flexible umbilical walls, it is better adapted to fixation and lives mostly attached.

Paratrochammina (Paratrochammina) tricamerata (Earland, 1934)

Pl. 3, Fig. 1a, b; Pl. 11, Fig. 2; Pl. 12, Fig. 3

Trochammina tricamerata Earland, 1934, p. 103, pl. 3, figs. 50−52; Echols, 1971, p. 149, pl. 8, figs. 3a−c.

Paratrochammina (Paratrochammina) tricamerata (Earland). Brönnimann and Whittaker, 1988a, p. 51, figs. 19A−K, p. 53, figs. 20A−D; Brönnimann and Whittaker, 1988b, p. 35, pl. 1, figs. 2−3.

Material: Five living specimens from stations VH-97-33, BG0812a-05, and -08, thereof four free living specimens of size fraction 63 − 250 μm and one attached living specimen from the size fraction 63 − 125 μm.

Description: Test small and probably juvenile, broadly rounded with a moderately compressed trochospire, consists of 14 chambers, arranged in two and a half whorls with

three chambers in the final whorl. Chambers of final whorl very inflated and rapidly increasing in size. Sutures slightly depressed on the spiral side and moderately depressed on the umbilical side. Aperture interiomarginal with a small lip, under which the aperture opens as a narrow slit. Wall thin, composed of quartz grains.

Remarks: The final whorl of our specimens consists of only three chambers, like the type specimen in Earland (1934), but they differ from the genus *Tritaxis* essentially by the apertural features, which are typical for *Paratrochammina-*, rather than for *Trochammina*. The species name *tricamerata* is a misnomer, because the final whorl consists of four chambers, in which the fourth chamber is sometimes covered (Figs. 19C and 20C in Brönnimann and Whittaker, 1988a).

Paratrochammina (Lepidoparatrochammina) haynesi (Atkinson, 1969)

Pl. 4, Fig. 1a, b; Pl. 11, Fig. 5; Pl. 12, Fig. 4

?*Trochammina squamata* Jones and Parker. Heron-Allen and Earland, 1913, p. 50, pl. 3, figs. 7−8.

Trochammina squamata Jones and Parker. Heron-Allen and Earland, 1930, p. 70, 71 (*pars*).

Trochammina haynesi Atkinson, 1969, p. 529, pl. 6, figs. 1a−c; Haynes, 1973, p. 35, text-fig. 6.

Paratrochammina (Lepidoparatrochammina) haynesi (Atkinson). Brönnimann and Whittaker, 1986, p. 119, pl. 2, figs. A−I; Brönnimann and Whittaker, 1990, p. 129, pl. 2, figs. 5−8 (original material of Heron-Allen and Earland, 1930); Murray and Alve, 1993, p. 34, figs. 1−3; Alve and Murray, 1994, p. 20, pl. 1, figs. 15, 16; Murray and Alve, 2011, p. 26, figs. 15.13, 15.14.

Material: Eight specimens from stations VH-97-32 and BG0812a-02, thereof five free living specimens from size fraction 63 − 125 μm, and three attached specimens (one living, two dead) from size fraction >2000 μm.

Description: Test probably juvenile, composed of 14 chambers arranged in two and a half volutions, six chambers in the final whorl. Chambers tangentially crescentic on umbilical side and half-moon shaped on spiral side. Sutures slightly sinuous on the

umbilical side. Umbilicus is deep and stellate in outline. Wall surface texture granular on the spiral side with some interspersed larger flakes, on the umbilical side slightly smoother and more uniform in grain size. Aperture single, interiomarginal, a thin arched slit, which extends from the penultimate to the ultimate chamber of the final whorl (*Paratrochammina* type).

Genus *Portatrochammina* Echols, 1971

Description: Test free and low to moderately high-spired. Wall imperforate and single-layered. Aperture as in *Paratrochammina* − a single interiomarginal arch, which rests on the ultimate and penultimate chamber of the final whorl. *Portatrochammina* differs from all other trochamminid genera by the presence of an umbilical septal flap covering the axial depression. One flap derived from each chamber and these flaps forms a lamellar structure in the axial cavity.

Portatrochammina murrayi Brönnimann and Zaninetti, 1984
Pl. 5, Fig. 3a, b; Pl. 6, Fig. 3a, b; Pl. 10, Fig. 6; Pl. 12, Fig. 5
?*Trochammina rotaliformis* Heron-Allen and Earland. Heron-Allen and Earland, 1913, p. 52, pl. 3, fig. 12.
Trochammina globigeriniformis (Parker and Jones) var. *pygmaea* Höglund. Murray, 1970 p. 485, pl. 1, figs. 4, 8; Murray, 1971, p. 35, pl. 10, figs. 1, 2; Haynes, 1973, p. 36, pl. 4, fig. 14; Rosset-Moulinier, 1986, p. 437, pl. 3, figs. 3, 6; Giese, 1991, p. 31, pl. 1, fig. 10.
Portatrochammina murrayi Brönnimann and Zaninetti, 1984, p. 72−74, pl. 5, figs. 7, 12−15; Gooday, 1986, p. 1363, figs. 10O, P; Debenay, 2001, p. 86, pl. 1, figs. 22−24; Murray, 2003, p. 13, figs. 3.6, 3.7.

Material: 148 specimens from almost all stations, size fraction >63 μm, thereof 144 free specimens (141 living, three dead), and four attached specimens (three living, one dead).

Description: Test with subglobular chambers in two whorls, with four chambers in the final whorl. The test is virtually flat on the spiral side and very shallow-concave on the

umbilical side, chambers increase rapidly in size in the final whorl. Axial depression on the umbilical side is covered by a flap. Aperture interiomarginal, an arch-like slit, which extends below the umbilical flap. Wall consists of quartz grains of different size embedded in a fine agglutinated matrix.

Portatrochammina pacifica (Cushman, 1925)

Pl. 3, Fig. 3a, b; Pl. 11, Fig. 9

Trochammina pacifica Cushman, 1925, p. 39, pl. 6, fig. 3a−c; Le Campion, 1968, p. 265,
pl. 6, fig. 3, pl. 12, fig. 11, pl. 13, fig. 2b; Murray, 2006, p. 123, fig. 5.2.16.

Portatrochammina pacifica (Cushman). Brönnimann, 1979, p. 12, fig. 10D, H−J.

Material: Six free living specimens from stations BG0812a-02, -05, and -08, size fraction 63 − 125 μm.

Description: Test composed of 18 chambers in three and a half volutions, with four to five chambers in the final whorl, periphery rounded. Spiral side with a moderately elevated trochospire, umbilical side with a flap extending over the axial depression. Sutures more depressed on the umbilical side. Wall slightly coarser agglutinated on the spiral than on the umbilical side.

Remarks: Brönnimann (1979) examined Cushman's holotype of *Trochammina pacifica* from British Columbia. This specimen showed apertural features with a large umbilical flap covering the axial cavity similar to those found in *Portatrochammina eltaninae* Echols, 1971, type species of the genus *Portatrochammina*.

Genus *Rotaliammina* Cushman, 1924 (emend. Brönnimann and Zaninetti, 1984)

Description: Test compressed, watchglass-like, with a low or moderate trochospire, with a peripheral flange, attached and often surrounded by a "Puffermasse" in the sense of Rhumbler (1938). Generally more than seven chambers per whorl, chambers have umbilically a mushroom-like outline. Sutures sigmoid on the umbilical side. Aperture single, interiomarginal, at the axial end of each chamber and facing the umbilicus. Wall thin, flexible, chamber walls of umbilical side rich in sulphur and

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magnesium-bearing organic compounds; agglutinant-rich spiral surface contains largely calcium carbonate. *Rotaliammina* differs from *Trochammina* in its flexible test and the apertural features.

Remarks: The genera *Rotaliammina*, *Siphotrochammina* Saunders, 1957 and *Tiphotrocha* Saunders, 1957 were placed by Loeblich and Tappan (1987) and Kaminski (2004) to the subfamily Rotaliammininae Saidova, 1981, and by Mikhalevich (2004) to the family Rotaliamminidae.

<p align="center">*Rotaliammina concava* (Seiglie, 1964)</p>

<p align="center">Pl. 7, Fig. 2a−c; Pl. 8, Fig. 2a, b; Pl. 10, Fig. 3; Pl. 12, Fig. 6</p>

Tiphotrocha concava Seiglie, 1964, p. 500, pl. 1, figs. 4a−b, 5a−c.

Rotaliammina concava (Seiglie). Brönnimann and Zaninetti, 1984, p. 76, pl. 4, figs. 11, 13−16, figs. U 1−3, V 1−3.

Material: 85 living specimens from stations VH-97-35, -36, -37, -49, and -50, BG0812a-02 and -05, and D78/95, thereof 54 attached and 31 free specimens, size fraction >63 μm.

Description: Test shape watchglass-like, composed of four volutions with 28 chambers, seven chambers in the final whorl, chambers strongly compressed on the spiral side and mushroom-like on the umbilical side. Sutures slightly curved on the spiral side and sinuous on the umbilical side Aperture single, interiomarginal, open at the pointed umbilical end of each chamber, umbilicus small with star-shaped outline. Wall thin, flexible and smooth.

Remarks: These are the first specimens of *R. concava* recorded in the Celtic Sea. Living and dead specimens of *Rotaliammina* sp. were found at Lyme Bay, southern England (Murray, 1986, listed only).

<p align="center">*Rotaliammina siphonata* (Seiglie, 1964)</p>

<p align="center">Pl. 3, Fig. 5a, b; Pl. 12, Fig. 7</p>

Polysiphotrocha siphonata Seiglie, 1964, p. 500, pl. 1, figs. 9a−c, pl. 2, figs. 1−6; Hofker, 1979, p. 3−5, fig. 2.

Rotaliammina siphonata (Seiglie). Brönnimann et al., 1983, p. 209, pl. 1, figs. 1−3, 6, 12, p. 210, pl. 2, figs. 1, 2, 5−7, p. 212, pl. 3, figs. 1, 3−8; Brönnimann and Zaninetti, 1984, p. 79, pl. 4, figs. 4, 10, 17, figs. Y 1, 2, Z 1, AA 1, 2.

Material: Two free living specimens from station VH-97-33, size fraction 63 − 125 μm.

Description: Test watchglass-like, outline elongate-oval to subcircular, loosely coiled low trochospire. Seven to eight chambers in the final whorl gradually increasing in size, mushroom-like with narrow tubular extensions towards the axial depression. A single interiomarginal aperture is situated at the end of each extension, directed into the axial cavity. Wall thin, flexible and smoothly finished on spiral side.

Genus *Tritaxis* Schubert, 1920 (emend. Brönnimann and Whittaker, 1988a)

Description: Test free or attached, plano-convex or conical, trochospiral, with three crescentic chambers in the final whorl. Ultimate chamber of the final whorl making up about one-half of the almost flat umbilical side. Wall imperforate and single layered. Aperture single, with a thin lip, interiomarginal, resting completely on the ultimate chamber of the final whorl (*Trochammina* type). Attached specimens surrounded by a "Puffermasse" in the sense of Rhumber (1938). *Tritaxis* differs from *Trochammina* by the number of chambers in the final whorl, which is pluriserial (four or more chambers) in *Trochammina*, and by its test shape, which is concave-convex in *Trochammina*. It differs from the triserial *Trochamminella* Cushman, 1943 by its apertural features. *Trochamminella* has an areal aperture near and parallel to the base of the ultimate chamber.

Tritaxis conica (Parker and Jones, 1865)
Pl. 9, Fig. 3a, b; Pl. 10, Fig. 1; Pl. 12, Fig. 8

Valvulina triangularis d'Orbigny var. *conica* Parker and Jones, 1865, p. 406, pl. 15, figs. 27a, b.

Valvulina conica (Parker and Jones). Höglund, 1947, p. 187, figs. 170−172, pl. 14, figs. 1a−c.

Tritaxis conica (Parker and Jones). Gabel, 1971, p. 34, pl. 5, figs. 13, 14; Schiebel, 1992, p. 63, pl. 7, fig. 6; Murray and Alve, 2011, p. 32, fig. 18.31.

Trochamminella conica (Parker and Jones). Jones, 1994, p.54, pl. 49, figs. 15b, 16.

Material: 218 free, dead specimens from stations VH-97-32, -33, -34, -35, -36, -37, and -49, BG0812a-02, -05, and -08, and D78/95, size fraction >63 µm.

Description: Test attached (living individuals), conical, five volutions with triserial arrangement of chambers. Ultimate chamber occupying about one-half of the final whorl. Sutures distinct and strongly curved. Wall smooth or rough with much cement. Aperture single, interiomarginal, an elongate opening at the inner margin of the ultimate chamber.

Genus *Trochamminopsis* Brönnimann, 1976 (emend. Brönnimann and Whittaker, 1988a)

Description: Test free, conical to subconical with axially slightly compressed chambers. Aperture single, interiomarginal, umbilically situated, resting on the wall of the ultimate chamber and of the penultimate chamber of the final whorl. Wall thin, imperforate and single layered. *Trochamminopsis* differs from the genus *Paratrochammina* by its apertural position to the axis of enrolment.

Trochamminopsis pusilla (Höglund, 1947)

Pl. 9, Fig. 4a, b; Pl. 11, Fig. 1

Trochammina pusilla Höglund, 1947, p. 200, figs. 183, 184, p. 201, pl. 17, figs. 4a−c; Gabel, 1971, p. 41, pl. 8, figs. 36−38.

Trochamminopsis quadriloba (Höglund). Loeblich and Tappan, 1987, p. 33, pl. 129, figs. 1−3; Murray and Alve, 2011, p. 31, figs. 18.36−18.39.

Material: Two attached living specimens from stations VH-97-37 and D78/95, size fraction 250 − 400 µm.

Description: Test attached, conical, composed of three and a half volutions. Chambers subglobular, inflated, four in the final whorl. Wall coarsely arenaceous, consisting of comparatively large quartz grains; therefore sutures indistinct.

Remarks: Höglund (1948) renamed his species *T. pusilla* Höglund, 1947 as *T. quadriloba*, because it was a junior secondary homonym of the Permian species *Serpula pusilla* Geinitz, 1848 which was thought at the time to be a *Trochammina*. Because Geinitz's taxon is not a Trochamminacea but a Miliolina, Höglund's new name was unnecessary (Brönnimann and Whittaker, 1988a). As *T. quadriloba* was proposed before 1961, the name *T. pusilla* is permanently invalid (Article 59 (b) of the International Commission on Zoological Nomenclature = ICZN) and cannot automatically be reinstated (Brönnimann and Whittaker, 1988a; Kaminski, 2004). To this end, an application has been made to the ICZN by Brönnimann and Whittaker (1988a) for the conservation of *T. pusilla* Höglund. An opinion of the ICZN to this application was not issued until today. Until a decline is made by the ICZN we retain the name *pusilla*.

Genus *Ammoglobigerina* Eimer and Fickert, 1899

Description: Test free, trochospiral and subglobose. Chambers subglobular to globular, increase rapidly in size as added. Wall thin, imperforate, single layered and finely to coarsely agglutinated. Aperture single, an interiomarginal slit on the umbilical side, which rests on the ultimate and penultimate chamber of the final whorl. *Ammoglobigerina* differs from *Trochamminopsis* by its subglobular to globular chambers arranged in a low trochospire (conical growth form in *Trochamminopsis*). The genus *Globotrochamminopsis* Brönnimann and Zaninetti, 1984 was regarded as synonymous with *Ammoglobigerina* by Loeblich and Tappan (1987).

Ammoglobigerina shannoni (Brönnimann and Whittaker, 1988a)
Pl. 9, Fig. 2a, b; Pl. 10, Fig. 5

Trochammina globigeriniformis (Parker and Jones). Haake, 1980, p. 8, pl. 1, fig. 18.

Globotrochamminopsis shannoni Brönnimann and Whittaker, 1988a, p. 38, figs. 15A−H.

Trochammina shannoni (Brönnimann and Whittaker). Schiebel, 1992, p. 27, pl. 7, fig. 10a, b.

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Material: Five free living specimens from station BG0812a-06, size fraction 63 −
250 μm.

Description: Test free, with a low trochospire, consists of 12 globular chambers
arranged in two and a half volutions with four chambers in the final whorl. Periphery
broadly rounded. A tight coiling with a bluntly pointed apex of spire. Umbilical
depression narrow and deep. Sutures slightly depressed and slightly curved on both sides.
Wall single layered, imperforate, composed of planar quartz grains, different in size,
giving a smooth surface mosaic. Aperture single and interiomarginal, a low crescent slit in
a lateral position.

Subfamily POLYSTOMAMMININAE Brönnimann and Beurlen, 1977 (emend.
Brönnimann and Whittaker, 1988a)
Genus *Polystomammina* Seiglie, 1965 (emend. Brönnimann and Whittaker, 1988a)

Description: Test free or attached, with a low trochospire and a rounded
periphery. Chambers increase rapidly in size as added. Sutures straight or gently curved.
Wall thin and fragile, single layered, imperforate. Aperture double, primary opening in
form of a narrow slit or hook beginning in an interiomarginal position then entering
deeply onto the umbilical side, secondary arch-like opening at umbilical tip of each
chamber, opens posteriorly rather than directly into the umbilicus. *Polystomammina*
differs from the genus *Deuterammina* Brönnimann, 1976 (and its subgenera) in the type
and position of the primary opening, which is "interio-areal" in *Polystomammina* and
wholly interiomarginal in *Deuterammina*.

Polystomammina nitida (Brady, 1881)
Pl. 9, Fig. 1a, b; Pl. 10, Fig. 2; Pl. 12, Fig. 9
Trochammina nitida Brady, 1881, p. 52, pl. 41, figs. 5a−c, 6; Cushman and McCulloch,
1939, p. 105, pl. 11, figs. 7−9.
Polystomammina nitida (Brady). Loeblich and Tappan, 1987, p. 127, pl. 135, figs. 6−9, pl.
136, figs. 5−8; Jones, 1994, p. 46, pl. 41, figs. 5, 6 (same figures as in Brady,
1881).

Material: 51 specimens, thereof 48 free living specimens (47 living, one dead) and three attached living specimens from stations VH-97-33, - 34, -35, -36, -37, -49, and -50, BG0812a-02, -05, - 06, and -08, size fraction 63 − 400 μm and >2000 μm.

Description: Test free or attached, low trochospire, composed of three volutions with nine chambers in the final whorl. Chambers increase rapidly in size as added. Sutures straight and slightly depressed on spiral and umbilical side. Wall finely agglutinated, smooth and appears sometimes as being polished. Aperture double, with an interiomarginal arched slit curving slightly upward on the umbilical side, and a secondary opening at the inner tips of the chambers.

Genus *Deuterammina* Brönnimann, 1976 (emend. Brönnimann and Whittaker, 1988a)

Description: Test free or attached, variable axial compression from subglobular to watchglass- and scale-like tests. Sutures radial. Wall thin, single layered and imperforate. Primary aperture interiomarginal, crescent-like slit, secondary aperture at the umbilical tip of the ultimate chamber and opening posteriorly directed or centrally directed into the umbilicus. *Deuterammina* is divided into the subgenera *D. (Deuterammina)* Brönnimann, 1976 and *D. (Lepidodeuterammina)* Brönnimann and Whittaker, 1983a, based on the degree of axial depression: species with subglobular chambers are placed in *D. (Deuterammina)*, species with strongly compressed watchglass-like tests referred to *D. (Lepidodeuterammina). D. (Lepidodeuterammina)* differs from *Rotaliammina* in apertural characters: *D. (Lepidodeuterammina)* has a double *Deuterammina*-type aperture; *Rotaliammina* possesses a single, umbilically directed apertural opening on each chamber.

Remarks: In the classificatory scheme of Brönnimann and Whittaker (1988a), the axial compression is considered to be only of subgeneric significance, because it is a gradational feature. Both subgenera *D. (Deuterammina)* and *D. (Lepidodeuterammina)* were elevated to generic status by Loeblich and Tappan (1987), Kaminski (2004), and Mikhalevich (2004). An ecological distinction between these two subgenera was assessed by Brönnimann and Whittaker (1983a and 1990). Species of the subgenus *D. (Deuterammina)* occur in relatively deeper water and in the deep sea, whereas species of the subgenus *D. (Lepidodeuterammina)* are restricted to inner shelf and marginal marine

environments. An opposite situation is given for species of these subgenera in our samples from the Celtic Sea. *D. (Deuterammina)* species were only found on the shelf (up to 177 m water depth), and living *D. (Lepidodeuterammina)* species were found on the shelf and upper slope (up to 467 m).

Deuterammina (Deuterammina) balkwilli Brönnimann and Whittaker, 1983

Pl. 4, Figs. 4a, b; Pl. 10, Fig. 7; Pl. 12, Fig. 10

Trochammina inflata (Montagu) var. Balkwill and Wright, 1885, p. 331, pl. 13, fig. 12a only.

Trochammina rotaliformis Heron-Allen and Earland. Cushman, 1920, p. 77, pl. 16, fig. 1 (left only).

?*Trochammina rotaliformis* Heron-Allen and Earland. Murray, 1971, p. 39, pl. 12, fig. 5 only.

Deuterammina (Deuterammina) balkwilli Brönnimann and Whittaker, 1983b, p. 352, figs. 13−16, 26.

Material: One attached, dead specimen from station VH-97-36, size fraction >2000 μm.

Description: Test consists of 13 chambers arranged in two and a half whorls with six chambers in the final whorl; low trochospire, slightly oval. Shape of chambers nearly triangular on the umbilical side and elongate on the spiral side. Sutures umbilically almost straight and curved on the spiral side. Umbilical depression open and deep. Aperture double, primary aperture interiomarginal, border resting completely on the ultimate chamber of the final whorl. Secondary aperture not visible, because of remains of adhered sediment used for attachment (Puffermasse) on the umbilical depression. Wall imperforate, smooth and single-layered, finely granular with some larger grain flakes.

Remarks: *D. (D.) balkwilli* differs from *D. (D.) rotaliformis* in the apertural features, the number of chambers in the final whorl (six instead of five chambers in *D. (D.) rotaliformis*) and the shape of chambers on the spiral side.

Deuterammina (Deuterammina) rotaliformis (Heron-Allen and Earland, 1911)

Pl. 7, Fig. 1a, b; Pl. 8, Fig. 1a, b; Pl. 10, Fig. 4; Pl. 12, Fig. 11

Trochammina inflata (Montagu) var. Balkwill and Wright, 1885, p. 331, pl. 13, figs. 11a,
12b.

Trochammina rotaliformis Heron-Allen and Earland, 1911, p. 309; Heron-Allen and
Earland, 1930, p. 71 (*pars*); Lévy et al., 1974, p. 128, pl. 1, figs. 4−5.

Deuterammina (Deuterammina) rotaliformis (Heron-Allen and Earland). Brönnimann and
Whittaker, 1983b, p. 348-352, figs. 1−12, 25; Murray, 2003, p. 11, figs. 2.7, 2.8.

Material: 35 living specimens from stations VH-97-32, -33, -34, -35 and -36, and
BG0812a-05 and -08, size fraction >63 μm, thereof two attached specimens.

Description: Test free or attached, moderately high trochospire, composed of 19
chambers arranged in four volutions with five chambers in the final whorl, periphery
rounded. Shape of chambers depressed and elongate on the spiral side, broadly triangular
on the umbilical side. Sutures indistinct, slightly curved spirally and almost straight
umbilically. Umbilical depression forms a five-arm star, open and deep. Wall single-
layered and imperforate. Two separate openings form the *Deuterammina*-type aperture: a
single interiomarginal extra-umbilical, arch-like primary aperture and a secondary opening
in posteriorly directing position.

Deuterammina (Lepidodeuterammina) mourai Brönnimann and Zaninetti, 1984
Pl. 3, Fig. 4a, b; Pl. 11, Fig. 6; Pl. 12, Fig. 12

Deuterammina (Lepidodeuterammina) mourai Brönnimann and Zaninetti, 1984, p. 85−87,
pl. 4, figs. 5−7, figs. M 1−4, N 1−3, O 1−4; Bender, 1995, p. 43, pl. 5, fig. 11.

Material: Two free living specimens from station BG0812a-05, size fraction 63 −
125 μm.

Description: Test watchglass-like, shallow-concave umbilically, composed of 17
compressed, arc-like chambers arranged in three and a half whorls, six chambers in the
final whorl. Chambers umbilically triangular to slightly mushroom-like in shape. Sutures
whitish and well defined on both sides, almost straight on the spiral side and slightly

incurved on the umbilical side. Small axial depression, star-shaped. Wall thin, single-layered and imperforate, agglutination uniformly fine-grained.

Deuterammina (Lepidodeuterammina) ochracea (Williamson, 1858)

Pl. 5, Fig. 2a−c; Pl. 6, Fig. 2a, b; Pl. 11, Fig. 4; Pl. 12, Fig. 13

Rotalina ochracea Williamson, 1858, p. 55, pl. 4, fig. 112, pl. 5, fig. 113.

Trochammina ochracea (Williamson). Höglund, 1947, p. 209, text-fig. 190, p. 211, pl. 16, figs. 2a−c; Hedley et al., 1964, p. 420, 421, figs. 2, 2A−C, 3, 2; Murray, 1970, p. 481, pl. 1, figs. 2, 3; Murray, 1971, p. 37, pl. 11, figs. 1−5; Haynes, 1973, p. 40, pl. 5, figs. 15−18.

Deuterammina (Lepidodeuterammina) ochracea (Williamson). Brönnimann and Whittaker, 1983a, p. 233−235, figs. 1−8, 10; Brönnimann and Whittaker, 1988a, p. 119, figs. 52A−F; Murray and Alve, 2011, p. 29, figs. 17.10, 17.11.

Deuterammina (Lepidodeuterammina) ochracea ochracea (Williamson). Brönnimann and Zaninetti, 1984, p. 87, pl. 2, figs. 1, 3, fig. AD 2.

Deuterammina ochracea (Williamson). Rosset-Moulinier. 1986, p. 437, pl. 3, fig. 5.

Lepidodeuterammina ochracea (Williamson). Debenay, 2001, p. 86, pl. 1, figs. 12, 13, 21.

Material: 94 living specimens from stations VH-97-33, -34, -35, -36, -37, -49, -50, BG0812a-02, -05, -08 and D78/95, size fraction >63 μm, thereof 21 attached and 73 free specimens.

Description: Test watchglass-shaped, strongly compressed, composed of 32 chambers arranged in three an a half volutions with nine chambers in the final whorl. Attached mostly with "Toga" in the sense of Rhumbler (1938). Chambers compressed, arc-like, increase rapidly in size, umbilically chambers overlapping with inflated proximal margins. Sutures curved and weakly depressed in the last whorl on the spiral side, on the umbilical side sinuous. Axial depression narrow, open and star-shaped. Wall thin, single-layered, flexible and imperforate, spiral side with mosaic of well-cemented quartz flakes, umbilical side more smooth. Aperture double, of *Deuterammina*-type.

Deuterammina (Lepidodeuterammina) sinuosa (Brönnimann, 1978)

Pl. 5, Fig. 1a−c; Pl. 6, Fig. 1a, b; Pl. 11, Fig. 3; Pl. 12, Fig. 14

Trochammina ochracea (Williamson). Heron-Allen and Earland, 1930, p. 71 (*pars*).

Asterotrochammina sinuosa Brönnimann, 1978, p. 6, text-fig. 3, pl. 2, figs. 1, 2, 6−8.

Deuterammina (Lepidodeuterammina) ochracea (Williamson) *sinuosa* (Brönnimann). Brönnimann and Zaninetti, 1984, p. 87, figs. AD 1, AE 1−3, AF 1−3; Brönnimann and Whittaker, 1990, p. 116, pl. 1, figs. 9−12.

Material: Six free living specimens from stations VH-97-33 and BG0812a-05, size fraction 63 − 125 μm.

Description: Test watchglass-like, low trochospire, compressed, periphery rounded. Made of up to 19 chambers arranged in two and a half volutions, final whorl consists of nine chambers. Each chamber overlaps the preceding one on the umbilical side. Sutures whitish, distinct and slightly curved on the spiral side, sinuous on the umbilical side. Axial depression deep, star-shape with nine branches. Aperture double, of *Deuterammina*-type. Wall single-layered, imperforate, smooth, of uniform quartz grains, only a few larger quartz flakes on the umbilical side.

Remarks: Due to the morphological differences between *D. (L.) ochracea* and *D. (L.) sinuosa*, we decided to keep *sinuosa* as a separate species.

Deuterammina (Lepidodeuterammina) sp. 2
Pl. 4, Fig. 3a, b; Pl. 11, Fig. 8; Pl. 12, Fig. 15

Material: 15 attached specimens from station D78/95, size fraction 250 − >2000 μm, thereof four living and 11 dead specimens.

Description: Test watchglass-like, strongly compressed, attached with "Puffermasse" in the sense of Rhumbler (1938), composed of 21 chambers arranged in three volutions with nine chambers in the final whorl. Chambers sustained and arc-like on the spiral side, umbilically slightly collapsed. Sutures strongly curved on spiral side and sinuous on umbilical side. Shallow axial depression, star-shaped. Wall thin, single-layered and flexible.

Remarks: This species differs from the other *D. (Lepidodeuterammina)* species in the shape of the chambers and the shallow axial depression. Furthermore, it differs from *D. (L.) mourai* and *D. (L.) ochracea* in the outline of the test (rounded in *mourai* and *ochracea*, slightly ovate in this species) and the character of the sutures on the spiral side.

3.4 Results

3.4.1 Abundance and diversity pattern of the Trochamminidae

In 13 surface sediment samples from the Celtic Sea, 31 Recent species of the family Trochamminidae were found (Table 3.2). They comprise between 5 and 32 % of the living fauna, and up to 12 % of the dead assemblages (Table 3.2). Therefore, the trochamminid species are a subdominant faunal element of the total living fauna. Population densities ranged from two to 40 specimens per 10 cm³. The number of tests per 10 cm³ in the dead assemblages ranged from 10 to 1758 individuals, except of station 50, where no trochamminids were found (Table 3.2). *Portatrochammina murrayi* was the most abundant species in the living fauna (144 specimens), whereas *Tritaxis conica* was the dominant species in the dead assemblages (218 specimens).

From our 31 trochamminids, 18 taxa could be determined at species level. In order to relate this assemblage to the global species number of Recent Trochamminidae, we counted all species that were initially described from Recent sediments as listed in the Ellis and Messina (1940) catalogue. A total number of 202 species was recorded, of which 18 species were found in the Celtic Sea. They resemble 9 % of the worldwide species number. In addition, analyses of published occurrences of benthic foraminiferal species from the NE Atlantic (Dorst and Schönfeld, 2013), and the records of trochamminid species in the Ellis and Messina (1940) catalogue showed that the total species number (202) could be reduced by synonymous taxa. If we apply a synonymy rate of 26 % (Dorst and Schönfeld, 2013), our 18 species would comprise about 12 % of all Recent species of the family Trochamminidae.

Table 3.2 Distribution table of all species of the family Trochamminidae (absolute frequency) recognized at 13 stations.

Station	VH-97-32D		VH-97-33D		VH-97-34		VH-97-35		VH-97-36		VH-97-37		VH-97-49		VH-97-50	
Living/dead	living	dead	living	dead	living	dead	living	dead	living	dead	living	dead	living	dead	living	dead
Species																
Ammoglobigerina shannoni																
Deuterammina (Deut.) balkwilli									1							
Deuterammina (Deut.) rotaliformis	2		1		1		14		1							
Deuterammina (Deut.) sp. 1		1														
Deuterammina (Deut.) sp. 2			1													
Deuterammina (Lepidodeut.) mourai																
Deuterammina (Lepidodeut.) ochracea			2		9		19		9		1		10		1	
Deuterammina (Lepidodeut.) sinuosa			5													
Deuterammina (Lepidodeut.) sp. 1									1							
Deuterammina (Lepidodeut.) sp. 2																
Deuterammina (Lepidodeut.) sp. 3																
Paratrochammina (Lepidopara.) haynesi	3															
Paratrochammina (Para.) tricamerata			1													
?Paratrochammina (Para.) wrighti	1															
Polystomammina nitida			1		1		1		12		1		3		4	
Polystomammina sp. juv.																
Portatrochammina murrayi	22	2	30	1	10		14		11			1	3		4	
Portatrochammina pacifica juv.																
Rotaliammina concava							2		11		5		27		7	
Rotaliammina siphonata			2													
Tritaxis conica		30		17		19		17		42		1		3		
Trochammina advena juv.															1	
Trochammina astrifica	1							1								
Trochammina squamata	6	1					3		2		4		5			
Trochammina sp. 1						1										
Trochammina sp. 2							1									
Trochammina sp. 3		2									1					
Trochammina sp. 4							1								1	
Trochammina sp. 5																
Trochammina sp. 6			1													
Trochamminopsis pusilla juv.											1					
Proportion of trochamminids of total fauna (%)	21.4	12.2	16.1	5.4	12.9	4.7	23.5	5.1	31.8	5.4	17.2	4	18.5	2	18.2	0
Population density (Ind./10 cm³)	16	1223	20	1758	4	229	6	467	10	1177	2	10	9	9	3	0

Table 3.2 Continued.

Station	BG0812a-02		BG0812a-05		BG0812a-06		BG0812a-08		D78/95	
Living/dead	living	dead	living	dead	living	dead	living	dead	living	dead
Species										
Ammoglobigerina shannoni					5					
Deuterammina (Deut.) balkwilli										
Deuterammina (Deut.) rotaliformis			10				6			
Deuterammina (Deut.) sp. 1										
Deuterammina (Deut.) sp. 2									1	1
Deuterammina (Lepidodeut.) mourai			2							
Deuterammina (Lepidodeut.) ochracea	10		26				4		3	
Deuterammina (Lepidodeut.) sinuosa			1							
Deuterammina (Lepidodeut.) sp. 1										
Deuterammina (Lepidodeut.) sp. 2									4	11
Deuterammina (Lepidodeut.) sp. 3									1	
Paratrochammina (Lepidopara.) haynesi	3	2								
Paratrochammina (Para.) tricamerata			1				3			
?Paratrochammina (Para.) wrighti										
Polystomammina nitida	8		1		14	1	4			
Polystomammina sp. juv.									1	
Portatrochammina murrayi	5		23				18		4	
Portatrochammina pacifica juv.	1		3				2			
Rotaliammina concava	2		6						15	
Rotaliammina siphonata										
Tritaxis conica		7		3				2		77
Trochammina advena juv.							5			
Trochammina astrifica										
Trochammina squamata	1	2	1			2	4	1	5	11
Trochammina sp. 1										
Trochammina sp. 2										
Trochammina sp. 3										
Trochammina sp. 4										
Trochammina sp. 5									2	
Trochammina sp. 6	1		1							
Trochamminopsis pusilla juv.									1	
Proportion of trochamminids of total fauna (%)	19.7	2.2	18.2	0.9	5.2	0.1	5.5	0.7	8.2	12.3
Population density (Ind./10 cm³)	14	824	40	817	5	12	28	633	9	589

3.4.2 Development of systematics of the Trochamminidae

Our species were assigned to the subfamilies Trochammininae and Polystomammininae. According to several classification concepts (Saidova, 1981; Loeblich and Tappan, 1982, 1987; Brönnimann and Whittaker, 1990, *cum lit.*; Kaminski, 2004; Mikhalevich, 2004), the family Trochamminidae contains five to ten subfamilies. The subfamilies Trochammininae and Polystomammininae, which were described in this paper, were included in all above mentioned classification concepts, except for the scheme of Saidova (1981). This author used as a first-order criterion for the definition of her subfamilies the opened or closed umbilical depression, which has only taxonomic significance at species level (Brönnimann et al., 1983). Brönnimann and Whittaker (1990, *cum lit.*) proposed the following six subfamilies defined on overall apertural features: Trochammininae, Polystomammininae, Trochamminellinae Brönnimann et al., 1983, Arenoparrellinae Saidova, 1981, Carterininae Loeblich and Tappan, 1955, and Zavodovskininae Brönnimann and Whittaker, 1988a. These subfamilies were also defined in the reclassification of agglutinated foraminifera by Kaminski (2004), to which he added four more subfamilies. Within the subfamily Polystomammininae, Brönnimann and Whittaker (1988a) defined two subgenera (*Deuterammina* and *Lepidodeuterammina*) under the genus *Deuterammina*. Both subgenera were elevated to generic status by Loeblich and Tappan (1987), Kaminski (2004) and Mikhalevich (2004). Saidova (1981) placed the subfamily Polystomammininae as a genus under the subfamily Trochammininae. For the genus *Paratrochammina* (under the subfamily Trochammininae), two subgenera were defined by Brönnimann and Whittaker (1986): *Paratrochammina* and *Lepidoparatrochammina*, which were also elevated to generic status by Kaminski (2004) and Mikhalevich (2004). Furthermore, the new introduced subfamily Rotaliammininae by Saidova (1981) were placed as genus *Rotaliammina* under the subfamily Trochammininae by Brönnimann et al. (1983).

In this study we described and illustrated 19 trochamminids (18 species and one taxon in open nomenclature), classified in nine genera. Their differential diagnoses are partially or exclusively based on six different aperture types (Table 3.3, Fig. 3.1). After Brönnimann and Whittaker (1988a), these six apertural types are the *Trochammina*-type (type 1), the *Paratrochammina*-type (type 2), the *Trochamminopsis*-type (type 3), the *Deuterammina*-type (type 5), the *Polystomammina*-type (type 6), and the *Rotaliammina*-

type (type 8). The various types were named after genera in which the particular aperture has been recognized first (Brönnimann et al., 1983; Brönnimann and Whittaker, 1988a).

3.5 Discussion

Designation of species of the family Trochamminidae and evaluation of earlier taxonomic concepts revealed that a consistent classification of this foraminiferal group does not exist. To date, molecular phylogenetic studies on specimens of the family Trochamminidae are not available to verify or reject the morphology-based systematics. At present, molecular phylogenetic studies could not address this problem, because only *Trochammina hadai* Uchio, 1962 and *Trochammina* sp. were sequenced to date (Pawlowski et al., 2013). Both species indicated a close phylogenetic relationship to species of *Eggerella* Cushman, 1933. Hence, they were assigned to the order Textulariida Delage and Herouard, 1896 (Pawlowski et al., 2013). However, according to morphological criteria, for instance wall structure, the suborder Trochamminina Saidova, 1981 was separated from the suborder Textulariina Delage and Herouard, 1896 (Brönnimann and Whittaker, 1988c), and assigned to the order Lituolida Lankester, 1885 (Kaminski, 2004; Mikhalevich, 2004).

To date, the systematics of Brönnimann and Whittaker (1990, *cum lit.*) exhibits the most comprehensive described and illustrated compendium of the Trochamminidae. How far their taxonomic concept has priority over other concepts was not considered by subsequent studies. In particular, no statements whether the determination of subfamilies, genera and species of the Trochamminidae were justified were provided by Saidova (1981), Loeblich and Tappan (1987), Kaminski (2004), and Mikhalevich (2004). Additional, the morphospace model indicated the fundamental role of apertures in the morphogenesis of foraminifera (Tyszka, 2006). After the principal morphogenetic rules revealed from the geometry of foraminiferal tests, the position of the aperture controls the geometry of chamber arrangement and the final shape of the test (Labaj et al., 2003; Tyszka et al., 2005). The position of the apertures is based on minimization of the distance between the foramina and aperture (Tyszka et al., 2005; Tyszka and Topa, 2005). However, this model could not include some morphological features, such as multiple apertures, complex chamber shapes and chamber internal structures (Tyszka, 2006). Even the chamber formation in polythalamous foraminifera is not very well known, because the

chamber itself does not define an aperture (Tyszka and Topa, 2005). As such, the morphospace model corroborates the initial classification concept of Brönnimann and Whittaker (1990, *cum lit.*).

Six different apertural types (after Brönnimann and Whittaker, 1988a) were distinguished within the species described in this paper. We tried to establish a relationship between these apertural types and the mode of life (free, attached, and opportunistic). For example, the genera *Deuterammina* and *Rotaliammina* exhibit different apertural types, although species of these genera preferred an attached mode of life. The preferred mode of life seems rather associated with the shape of the test and the chambers (flat, conical or globular). However, the position of an aperture has no influence on the chamber shape (Tyszka and Topa, 2005). Furthermore, some of the described species had an opportunistic mode of life despite having different apertural features. These species could live free or attached depending on environmental parameters. Our analyses with respect to the relation between the apertural features and the mode of life revealed no matches.

The applicability of the taxonomic concept of Brönnimann and Whittaker (1988a) poses another problem. Secure definition of a genus only based on apertural features is usually not possible, because the aperture is often covered or damaged. Nonetheless, we could designate our species after their concept, due to the fact of the comprehensive descriptions and illustrations of many Trochamminidae species. In addition, morphological characteristics such as the shape of the tests and chambers were also used by Brönnimann and Whittaker (1990, *cum lit.*) for determination between genera, subgenera and species. Finally, and despite the apertural problem, we consider their concept as valid and applicable unless forthcoming genetic investigations provide other evidence.

Table 3.3 Summarized observations of morphological features and mode of life of the 19 described trochamminid species. The numbers in parentheses indicate the apertural type after Brönnimann and Whittaker (1988a). p: primary aperture, s: secondary aperture.

Species	Test shape	Chambers final whorl	Whorls	Aperture type	Aperture position	Mode of life
Ammoglobigerina shannoni	low trochospire, globular chambers	4	2.5	(3) single, symmetric, umbilical	rests on ultimate and penultimate chamber	free
Deuterammina (Deut.) balkwilli	low trochospire, periphery rounded	6	2.5	(5) double, umbilical-extraumbilical	p: ultimate chamber; s: umbilical tip of chamber	attached
Deuterammina (Deut.) rotaliformis	moderate trochospire, periphery rounded	5	4	(5) double, umbilical-extraumbilical	p: ultimate chamber; s: umbilical tip of chamber	opportunistic
Deuterammina (Lepidodeut.) mourai	watchglass-like, periphery rounded	6	3.5	(5) double, umbilical-extraumbilical	p: ultimate chamber; s: umbilical tip of chamber	attached
Deuterammina (Lepidodeut.) ochracea	watchglass-like, strongly compressed	9	3.5	(5) double, umbilical-extraumbilical	p: ultimate chamber; s: umbilical tip of chamber	attached
Deuterammina (Lepidodeut.) sinuosa	watchglass-like, periphery rounded	9	2.5	(5) double, umbilical-extraumbilical	p: ultimate chamber; s: umbilical tip of chamber	attached
Deuterammina (Lepidodeut.) sp.	watchglass-like	9	3	(5) double, umbilical-extraumbilical	p: ultimate chamber; s: umbilical tip of chamber	attached
Paratrochammina (Lepidopara.) haynesi	watchglass-like outline subcircular	6	2.5	(2a) single, asymmetric, umbilical-extraumbil.	rests on ultimate and penultimate chamber	opportunistic
Paratrochammina (Para.) tricamerata	moderately compressed trochospire	3	2.5	(2a) single, asymmetric, umbilical-extraumbil.	rests on ultimate and penultimate chamber	mostly free
Polystomammina nitida	low trochospire	9	3	(6) double, interio-areal	p: ultimate chamber; s: umbilical tip of chamber	opportunistic
Portatrochammina murrayi	spiral flat, umbilical shallow-concave	4	2	(2b) single, asymmetric, with umbilical flap	rests on ultimate and penultimate chamber	mostly free
Portatrochammina pacifica juv.	moderate trochospire, periphery rounded	4-5	3.5	(2b) single, asymmetric, with umbilical flap	rests on ultimate and penultimate chamber	free
Rotaliammina concava	watchglass-like, periphery sharpened	7	4	(8) single, visible at each chamber	umbilical, axial end of each chamber	attached
Rotaliammina siphonata	watchglass-like, periphery subcarinate	7-8	2	(8) single, visible at each chamber	umbilical, axial end of each chamber	attached

Table 3.3 Continued.

Species	Test shape	Chambers final whorl	Whorls	Aperture type	Aperture position	Mode of life
Tritaxis conica	conical	3	5	(1) single, umbilical-extraumbilical	rests completely on ultimate chamber	attached
Trochammina advena juv.	low trochospire, periphery rounded	4	3	(1) single, umbilical-extraumbilical	rests completely on ultimate chamber	free
Trochammina astrifica	low trochospire, periphery rounded	6	2.5	(1) single, umbilical-extraumbilical	rests completely on ultimate chamber	opportunistic
Trochammina squamata	low trochospire, outline oval	4	2	(1) single, umbilical-extraumbilical	rests completely on ultimate chamber	opportunistic
Trochamminopsis pusilla juv.	conical	4	3.5	(3) single, symmetric, umbilical	rests on ultimate and penultimate chamber	attached
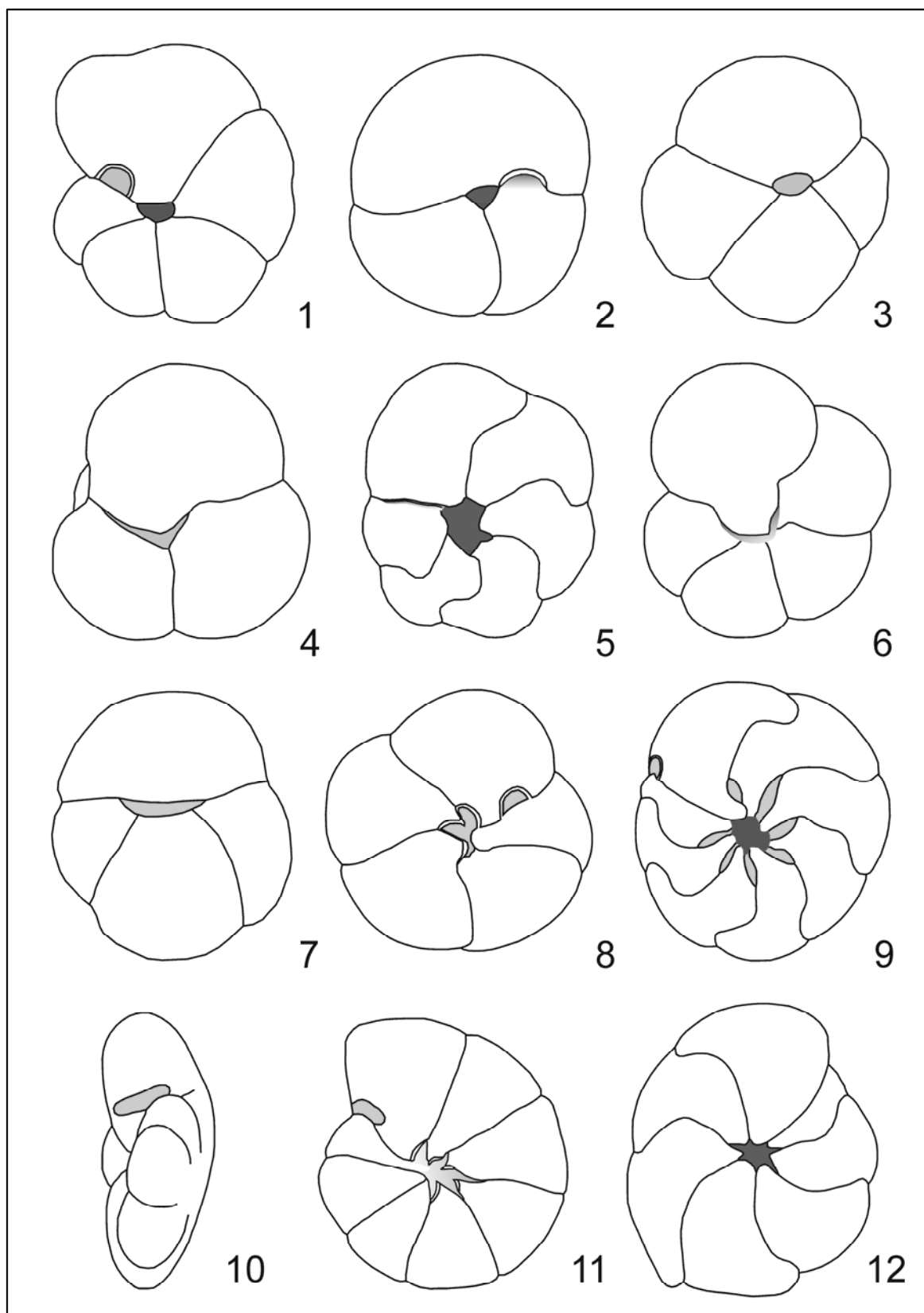
Fig. 3.1 Summary illustration of apertural types and test morphologies discussed in this paper. Light gray: apertures, dark gray: umbilical area. **1:** *Trochammina*, type 1; **2:** *Tritaxis*, type 1; **3:** *Trochamminopsis*, type 3; **4:** *Paratrochammina (Paratrochammina)*, type 2; **5:** *Paratrochammina (Lepidoparatrochammina)*, type 2; **6:** *Portatrochammina*, type 2; **7:** *Ammoglobigerina*, type 3; **8:**

Deuterammina (Deuterammina), type 5; **9:** *Deuterammina (Lepidodeuterammina),* type 5; **10 and 11:** *Polystomammina,* type 6; **12:** *Rotaliammina,* type 8. Figure 1, 2, 6, 8, 10 and 11 were redrawn from Brönnimann and Whittaker (1988a). Figure 4 and 7 were redrawn and modified from Brönnimann and Whittaker (1988a). Figure 5 was redrawn from Brönnimann and Whittaker (1986, 1988a). Figure 9 was redrawn from Brönnimann and Zaninetti (1984) and Brönnimann and Whittaker (1988a), and figure 12 was redrawn from Brönnimann and Zaninetti (1984).

3.6 Conclusion

Determination of Recent species of the family Trochamminidae from the shelf and upper slope of the Celtic Sea was very difficult, because many of these species were not found or described and illustrated from this area so far. To date, several taxonomic concepts exist, which differ from each other in their systematic classification within the Trochamminidae. The best applicable concept was proven that of Brönnimann and Whittaker (1990, *cum lit.*). Molecular phylogenetic studies on specimens of the family Trochamminidae are required to verify the existing morphological concepts. In addition, the formation of apertures and the causes of multiple apertures are still unknown. Clarifying these problems could depict the previously considered relevance of an aperture is justified as an important taxonomic criterion.

3.7 Acknowledgements

Summary and Conclusions

The objective of this study was to analyze the ecology, diversity, and distribution pattern of Recent benthic foraminiferal species from the shelf and slope of the NE Atlantic (43 – 58° N). Not less than 44 publications from 1913 – 2010 were analyzed to review the distribution and diversity pattern of benthic foraminifera in this area. In addition, a synonymy matrix and standardized taxonomy of benthic foraminifera was created. The study area was subdivided in six regions due to differences in species inventory, as well as morphological, physical and hydrographic conditions. The analyses revealed an interregional diversity pattern and close linkages of the faunal assemblages between the regions. Most of the species have a hyaline test structure and a free mode of life in all six regions. The diversity (Fisher α index) increases from the shelf to the slope and the mean species number on the shelf increases from N – S. The latitudinal distribution of six dominant species was analyzed and exhibits an "oak leaf" distribution pattern for the shelf areas. Heterogeneous sample coverage and inconsistencies in data documentation hamper to judge, whether this pattern reflects the real distribution or wether it is an artifact due to gaps in data coverage. Foraminiferal diversities as calculated from published data has shown, that standardized data as, for instance standard protocols for sampling and preparation or a standardized taxonomy are essential for compilation studies.

Analyses of Recent benthic foraminiferal assemblages from surface sediment samples from the shelf and slope of the South Western Approaches (Celtic Sea) revealed highest diversities on the slope and at those shelf stations, which were sampled immediately after the spring bloom. The living fauna showed a bisection on the shelf. On the slope, however, significant changes were recorded within small depth intervals and geographic position due to differences in topography, bottom sediments and hydrographical conditions. The Recent dead assemblages revealed the influences of a high-energy environment by loss of arenaceous species, higher proportions of robust miliolids, and a lateral homogenisation in the faunal assemblages. These results may facilitate a better interpretation of palaeoenvironments from fossil assemblages. A comparison with corresponding stations from earlier studies from the same area yields distinct differences in the benthic foraminiferal assemblages on the shelf and slope. These differences were presumably highly influenced by the time and methods of sampling than

by environmental changes. Therefore, and to obtain consistent results in regional studies, samples should be taken within a short period and by using the same sampling device.

Recent benthic foraminiferal assemblages from the Celtic Sea showed a rich variety of species of the family Trochamminidae. Many of these species were not described and illustrated from this area so far. Thirty-one taxa of this family were recorded, of which 19 taxa were described in detail. Several taxonomic concepts for a systematic classification within the Trochamminidae exist. All concepts were based on test morphology, internal structures and apertural features. A detailed assessment of the classification schemes revealed that the concept of Brönnimann and Whittaker (1990, *cum lit.*) is the best for application in comparative taxonomic studies. However, the formation of an aperture and the cause of multiple apertures are not yet sufficiently constrained. Hence, combined morphological and molecular phylogenetic analyses are required to verify the existing taxonomic concepts and to justify the fundamental role of apertural features in the systematic subdivision of the Trochamminidae.

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Danksagung

Zuallererst möchte ich mich bei Dr. Joachim Schönfeld für die fachliche Betreuung, intensive Unterstützung, und wertvollen Diskussionen herzlich bedanken.

Herrn Prof. Dr. Wolf-Christian Dullo und Frau Prof. Dr. Priska Schäfer möchte ich an dieser Stelle für die Bereitschaft zur Begutachtung dieser Arbeit danken.

Weiterhin danke ich Prof. Wolfgang Kuhnt für die Bereitstellung seiner digitalen Mikroskopkamera und seiner Hilfe bei der Erstellung der Foraminiferenaufnahmen, sowie Dr. Sebastian Meier und Birgit Mohr für die Durchführung der REM-Aufnahmen.

Außerdem möchte ich Nicholas Fraser für das Korrekturlesen der ersten beiden Kapitel meiner Arbeit danken.

Bei Nico, Jutta und Nadine möchte ich mich für ihre Hilfe, Ratschläge und das Ausleihen diverser Arbeitsutensilien bedanken.

Mein Dank gilt auch meiner Praktikantin Lea für ihre Hilfe beim Picken der Foraminiferen, und im Besonderen meiner „Hiwin" Lilli für ihre Unterstützung bei der Probenaufbereitung, dem Picken und Bestimmen der Arten, sowie die insgesamt schöne Zeit im Büro und in Berlin.

Meinen Mitstreitern Anna, Zeynep und dem „verpeilten Planungshörnchen" Silke danke ich für ihre Unterstützung, den Ideenaustausch, den Spaß und die gegenseitige Motivation. In diesem Zusammenhang möchte ich auch Almuth, Agnes, Steffi und Jürgen für ihre Hilfe und Ratschläge danken.

Mein größter Dank gilt natürlich meinen Eltern, Verwandten (besonders dem Zinkpferd) und Freunden (besonders Urmel) für ihren Rückhalt, Unterstützung und Ermutigungen während meines Studiums und der Doktorandenzeit.

Appendix 1 (Chapter 1)

1.1 Publication data

This appendix contains 42 tables as MS Excel spreadsheets, which can be found on the Cushman Foundation website in the JFR Article Data Repository (http://www.cushmanfoundation.org/jfr/index.html) as item number JFR_DR2013006 and at OceanRep (GEOMAR_Publications Database; http://oceanrep.geomar.de/14216/).

1.2 Taxonomic list of benthic foraminiferal species

This appendix contains list of 1107 foraminiferal species, which can be found on the Cushman Foundation website in the JFR Article Data Repository (http://www.cushmanfoundation.org/jfr/index.html) as item number JFR_DR2013006 and at OceanRep (GEOMAR_Publications Database; http://oceanrep.geomar.de/14216/).

1.3 Diversity and species numbers

This table contains the Fisher α indices of 13 publications and the species numbers of 12 publications, which were used to investigate the diversity of benthic foraminifera in the NE Atlantic. Numbers with an asterisk are mean values. Longitude "A" and "B" of Rosset-Moulinier (1986) are transects.

Publication	Region	Station	Latitude (°N)	Longitude (°W)	Depth (m)	Fisher α index	Species number
Douvillé (1936)	D	3	48.667	3.933	15		21
		1	48.717	3.817	1		5
Lees et al. (1969)	F	C493	53.363	10.091	1	4.94	8
		C494	53.363	10.091	2		3
		C492	53.385	10.091	1	3.00	7
		C446	53.397	10.093	11	1.59	4
		C453	53.407	10.092	20	1.06	3
		C434	53.418	10.092	20	1.81	5
		C433	53.419	10.093	15		1
		C502	53.425	10.090	2	2.13	7
		C561	53.429	10.089	1		1
		C454	53.429	10.092	16		1
		C455	53.435	10.092	14		1
		C457	53.439	10.090	4		2
		C456	53.450	10.092	4		1
		C470	53.463	10.092	9	1.41	6
		C408	53.469	10.088	9	3.54	7
		C520	53.470	10.098	5		2
		C414	53.479	10.091	9		1
		C522	53.481	10.095	6		1
		C523	53.483	10.095	5		2
		C479	53.486	10.093	11		3
		C501	53.497	10.091	2		1
		C458	53.503	10.086	17		1
Murray (1970)	C	1437	48.867	10.50	420	7	
		1438	48.867	10.017	1002	7	
		1440	49.967	9.183	138	5.5*	
		1441	50.033	9.133	135	5.5*	
		1442	50.083	9.05	128	5.5*	
		1443	50.10	8.97	128	5.5*	
		1454	51.183	4.667	24	4*	
		1453	51.25	5.00	57	4*	
		1448	51.25	5.45	77	4*	
		1447	51.25	5.533	80	4*	
		1446	51.25	5.667	84	4*	
		1444	51.25	5.883	91	4*	
		1445	51.25	5.80	95	4*	
		1452	51.267	5.133	67	4*	
		1451	51.267	5.20	77	4*	
		1450	51.283	5.30	77	4*	
		1449	51.283	5.35	77	4*	
Pujos-Lamy (1973)	B	C6940	45.041	2.98	2270		26
		C6941	45.052	2.973	1920		26
		C6944	45.063	2.963	2100		24
		C6945	45.074	2.955	1700		21
		C6950	45.078	2.955	1700		34
		C6406	45.083	3.233	1300		11
		C6305	45.133	3.40	4000		23
		C6931	45.305	5.14	4130		24
		C6302	45.317	3.133	185		20
		C6926	45.320	5.388	4280		12
		C6924	45.337	5.447	4230		25
		C6927	45.338	5.35	4058		*26*
		C6929	45.352	5.465	4100		20

Publication	Region	Station	Latitude (°N)	Longitude (°W)	Depth (m)	Fisher α index	Species number
		C6928	45.368	5.347	3920		27
		C6932	45.407	5.163	4300		14
		C6403	45.433	3.283	100		9
		C6922	45.453	5.497	4260		11
		C6933	45.453	4.983	4450		13
		C6707	45.467	5.35	4175		17
		C6714	45.477	4.425	4220		18
		D65119	45.733	3.50	160		12
		C6719	45.735	3.934	1800		28
		D6718	45.767	4.10	2480		23
		D65108	45.80	3.667	180		14
		D6723	45.822	3.883	1400		11
		C6717	45.834	3.867	1540		23
		D6720	45.853	3.817	700		20
		D6595	45.883	4.00	1100		21
		D6722	45.90	3.783	315		24
		C6711	45.900	3.833	1420		22
		D6721	45.903	3.592	135		14
		D6719	45.913	3.88	430		23
		D6592	45.942	3.883	560		24
		D6591	45.967	3.867	190		20
Pujos-Lamy (1973)	B	C6914	45.967	4.673	3275		27
		C6913	46.013	4.675	3050		30
		C6912	46.017	4.686	2850		23
		C6906	46.025	4.867	3800		28
		C6917	46.057	4.497	2470		28
		C6935	46.062	4.483	2250		16
		C6904	46.067	4.85	3375		19
		D6709	46.083	4.483	1480		13
		C6934	46.087	4.498	2278		25
		C6938	46.087	4.492	2300		23
		C6903	46.09	4.853	3190		25
		C6902	46.10	4.87	2870		22
		D6642	46.117	4.00	200		29
		C6901	46.117	4.947	3450		23
		D6712	46.151	4.495	2500		15
		C6709	46.268	4.601	1975		21
		D6706	46.283	4.367	850		20
		D6707	46.283	4.467	1150		21
		D6716	46.285	4.35	900		21
		D6704	46.317	4.40	290		27
		D6710	46.342	4.301	230		19
		D6702	46.358	4.433	580		17
		2217	50.00	9.333	132	5.40	11
		2207	50.00	9.50	135	11.85	33
		2216	50.083	9.333	131	4.14	11
		2215	50.167	9.333	130	4.73	12
		2208	50.167	9.50	131	5.01	12
Murray (1979)	C	2209	50.250	9.50	117	8.56	30
		2214	50.250	9.333	122	9.94	26
		2210	50.333	9.50	119	7.42	26
		2213	50.333	9.333	123	7.10	25
		2574	50.350	8.167	110	9.00	23
		2575	50.417	8.167	110	10.84	27

Publication	Region	Station	Latitude (°N)	Longitude (°W)	Depth (m)	Fisher α index	Species number
Murray (1979)	C	2212	50.417	9.333	115	6.66	24
		2211	50.50	9.333	80	5.93	24
		2090	50.583	9.083	75	6.59	21
		2077	50.583	8.333	106	7.83	23
		2078	50.583	8.583	110	6.87	21
		2079	50.583	8.833	111	9.97	30
		2091	50.667	9.083	113	6.25	18
		2076	50.683	8.333	104	11.72	32
		2577	50.683	8.167	106	8.65	23
		2570	50.733	8.00	106	8.72	22
		2075	50.750	8.333	99	8.19	22
		2080	50.750	8.833	104	5.41	17
		2571	50.767	8.017	102	10.71	16
		2081	50.833	8.833	80	3.77	12
		2074	50.833	8.333	99	6.29	23
		2073	50.917	8.333	95	11.44	23
		2572	50.917	8.00	100	11.79	34
		2082	50.917	8.833	100	9.94	33
		2573	50.950	7.983	103	9.82	34
		2072	51.00	8.333	95	6.09	18
		2089	51.00	9.083	97	8.83	33
		2567	51.017	8.00	91	8.21	27
		2084	51.083	8.833	95	8.58	28
		2088	51.083	9.083	99	8.88	26
		2071	51.10	8.333	95	7.31	25
		2085	51.167	8.833	95	7.77	24
		2070	51.183	8.333	92	9.51	27
		2086	51.250	8.833	91	4.73	15
		2069	51.267	8.333	88	5.74	22
		2568	51.283	8.00	91	3.90	22
		2068	51.550	8.350	95	7.90	22
Weston (1985)	C	107	47.675	8.017	1260	8.64	
		49	47.887	8.00	725	3.02	
		111	47.948	8.012	765	6.46	
		52	48.475	10.328	1310	2.50	
		48	48.633	9.957	620	3.19	
		106	48.652	9.90	370	3.47	
		46	48.682	9.807	255	3.21	
	F	29	51.267	12.00	1600	3.54	
		26	51.308	11.750	950	3.15	
		28	51.350	11.583	510	3.83	
		27	51.350	11.717	780	6.97	
		30	51.708	11.975	422	5.90	
Murray (1986)	D	3147	50.367	3.425	54	12	
		3359	50.383	2.967	49	4	
		3360	50.383	2.90	51	4	
		3150	50.383	2.90	55	17	
		3358	50.392	3.042	48	4.5	
		3357	50.40	3.10	50	5	
		3151	50.40	3.10	53	5	
		3355	50.467	3.217	35	6	
		3354	50.50	3.275	30	7	
		3353	50.533	3.333	20	8	
		3149	50.567	2.70	35	8	

Publication	Region	Station	Latitude (°N)	Longitude (°W)	Depth (m)	Fisher α index	Species number
Murray (1986)	D	3148	50.575	3.383	20	4.5	
		3352	50.575	3.383	20	7	
		B618			14	3.85	9
		G390			19	8.54	4
		B605			26	1.55	4
		G401			27	3.31	7
		B596			41	1.04	5
		G371			43	13.90	4
		B583			47	2.49	7
		B572			51	2.14	7
		B659			58	1.79	9
		1120			58	8.51	7
		1113		A	59	4.35	6
		B668			60	10.36	3
		B974			61	2.77	8
		B957			62	2.63	8
		1091			65	1.36	8
		G404			65	3.68	9
		G513			65	3.92	6
		1114			65	5.52	9
		1097			66	3.84	10
		1118			66	4.32	15
		B970			68	3.38	6
		1090			89	3.71	10
Rosset-Moulinier (1986)	D	F120			2	0.43	2
		F111			6	2.06	6
		B902			9	3.98	5
		F142			9		1
		F122			13	1.87	4
		F154			18		1
		F133			18	1.22	5
		B910			23		2
		F203			23	6.73	10
		B907			28		2
		F200			31	2.72	7
		F345			33	1.45	3
		F382			37	4.45	7
		F336		B	38		1
		F381			42	6.92	11
		B854			43		5
		B832			43		1
		B810			43	3.65	8
		F379			46	1.55	4
		B812			47	1.97	5
		F376			47	2.43	7
		B804			48	3.99	10
		F373			48		4
		F375			48	5.90	8
		F377			53	8.29	7
		B946			56	3.98	6
		B870			57		3
Fontanier et al. (2002)	B	D	43.699	1.568	140	5.32	36
		B	43.833	2.384	553	10.09	46
		A	44.151	2.338	1012	9.18	40

Publication	Region	Station	Latitude (°N)	Longitude (°W)	Depth (m)	Fisher α index	Species number
Fontanier (2002)	B	F	44.285	2.749	1264	6.19	25
		H	44.533	2.617	1993	7.74	27
Murray (2003b)	F	SN6b	56.563	8.383	167	6.72*	20*
		MD7a+b	56.813	6.503	218	7.18*	29*
		MD6a+b	56.815	6.675	170	6.35*	28*
Scott	C	T8S20	51.51	4.75	49	8.11	23
		T1S01	51.68	5.49	64	11.90	40
		T8S16	51.44	5.08	64	1.91	9
		T1S02	51.65	5.56	67	14.18	47
		T1S03	51.61	5.61	68	14.10	42
		T6S08	51.77	6.32	71	10.17	34
		T6S10	51.66	6.37	71	6.73	28
		T8S13	51.39	5.32	71	2.42	11
		T6S02	52.11	6.20	75	2.89	9
		T8S10	51.33	5.56	76	1.31	6
		T8S09	51.31	5.63	79	2.40	7
		T6S12	51.42	6.47	81	4.70	18
		T6S06	51.86	6.28	82	6.64	14
		T8S08	51.29	5.69	82	1.65	4
		T1S07	51.46	5.82	86	8.69	24
		T1S06	51.50	5.77	87	7.93	29
		T3S19	51.36	6.51	88	8.39	32
		T8S05	51.24	5.90	90	4.89	17
		T1S09	51.39	5.92	91	6.34	26
		T3S23	51.23	6.66	92	11.75	40
		T2S22	51.97	5.87	93	13.93	39
		T6S14	51.53	6.42	93	4.06	17
		T6S16	51.33	6.50	93	5.28	22
		T2S23	52.00	5.85	95	14.40	46
		T3S13	51.57	6.29	96	7.96	25
		T3S15	51.50	6.37	96	8.82	30
		T3S17	51.43	6.44	96	6.64	26
		T2S01	51.05	6.44	98	10.90	37
		T3S01	51.97	5.86	98	14.46	41
		T3S11	51.63	6.22	99	5.40	22
		T1S19	51.04	6.41	101	8.36	29
		T3S16	51.46	6.40	101	5.54	23
		T1S17	51.11	6.31	102	5.87	23
		T2S20	51.88	5.93	102	14.97	47
		T1S14	51.22	6.16	103	2.71	13
		T2S03	51.14	6.38	104	7.99	29
		T8S02	51.19	6.11	104	2.92	12
		T2S19	51.84	5.96	105	7.44	27
		T2S21	51.93	5.90	105	17.16	41
		T8S01	51.17	6.17	106	3.87	17
		T3S05	51.84	6.01	108	16.94	46
		T3S03	51.91	5.93	109	11.07	37
		T3S10	51.67	6.19	109	5.09	22
		T7S10	51.50	6.03	110	4.35	18
		T2S16	51.71	6.04	111	12.36	33
		T7S02	51.84	5.74	111	2.03	6
		T7S16	51.22	6.29	114	2.32	11
		T2S07	51.32	6.27	115	4.96	21
		T2S11	51.49	6.18	115	3.83	17

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Publication	Region	Station	Latitude (°N)	Longitude (°W)	Depth (m)	Fisher α index	Species number
		T2S14	51.63	6.10	115	9.05	16
Scott	C	T3S07	51.77	6.08	115	6.30	29
		T7S06	51.66	5.89	116	8.12	32
		M39070-1	43.618	9.392	1220	9.52	25
		M39074-1	43.625	9.097	837	33.82	11
		PO201/10-701	43.700	8.617	188	16.14	35
	A	M39072-1	43.787	9.435	2170	11.49	30
		PO201/10-702	43.844	8.689	402	15.77	37
		PO201/10-703	43.967	8.737	583	19.00	45
		PO201/10-704	44.187	8.858	929	5.11	7
		PO201/10-747	47.590	8.000	2410	17.97	41
		PO201/10-749	47.609	7.915	2011	11.65	40
		PO201/10-750	47.647	7.876	1387	12.99	48
		PO201/10-752	47.691	7.833	1050	9.87	39
		PO201/10-753	47.784	7.765	684	20.49	39
		PO201/10-754	47.903	7.665	398	34.19	48
		PO201/10-755	47.944	7.632	207	17.07	34
		GIK16906	49.010	13.567	3889	9.51	28
	C	M30/1 428	49.150	13.093	2260	12.39	39
		GIK16900	49.182	11.088	182	7.85	29
		M30/1 430	49.185	12.848	1529	10.02	34
		GIK16904	49.222	13.010	2084	14.35	36
Schönfeld		M30/1 433	49.237	12.493	1158	7.09	25
and		GIK16902	49.257	11.953	1013	9.85	36
Altenbach		GIK16901	49.285	11.416	410	9.07	31
(2005)		OMEX P2	49.948	12.396	2213	9.10	29
	D	D35/94	48.793	4.155	82	4.20	8
		D37/94	48.815	4.170	83	4.77	10
		GIK16222	51.430	14.695	576	8.43	28
		GIK16221	51.469	15.088	1398	5.91	19
		GIK17045	52.431	16.671	3653	10.63	25
		GIK16220	52.699	14.868	709	12.86	32
		GIK16219	52.704	15.050	1114	14.64	31
		GIK16218	53.148	10.646	126	6.97	15
	F	GIK16217	53.887	12.920	393	7.00	23
		GIK16216	56.404	11.974	2590	10.15	27
		GIK16215	57.094	13.177	825	28.23	10
		GIK16214	57.105	13.200	638	9.88	30
		GIK16213	57.158	13.019	1207	7.57	24
		GIK16212	57.301	13.733	158	4.31	11
		GIK16210	57.571	10.595	2220	8.94	24
		GIK16209	57.675	9.541	407	4.62	14
		2FP-D	43.70	1.717	140	5.83	31
		2FP-B	43.833	2.050	550	11.39	59
		2FP-A	44.167	2.333	1000	9.02	42
		2FP-11	44.467	2.667	1600	13.40	45
		2FP-H	44.533	2.617	2000	10.64	39
Duchemin et	B	GP-D	46.867	3.70	130	7.91	42
al. (2007)		GP-E	46.917	4.50	140	7.36	40
		GP-B	46.933	3.467	100	7.10	39
		GP-C	47.150	3.917	130	6.76	36
		GP-A	47.217	3.667	100	8.92	34
		GP-G	47.583	4.183	85*	5.40	30

Publication	Region	Station	Latitude (°N)	Longitude (°W)	Depth (m)	Fisher α index	Species number
Mojtahid et al. (2010)	B	FP13	43.70	1.983	320	13.20	35
		FP12	44.00	2.25	800	8.98	24
		FP11	44.45	2.65	1600	5.52	21
		FP1	46.33	5.00	2400	17.08	38
		FP2	45.50	6.50	4800	7.87	20
Schönfeld et al. (2010)	F	GeoB9220-2	51.445	11.751	893	4.9	8
		PO316-525	51.448	11.760	957	12.3	25
		GeoB9209-2	51.448	11.764	982	9.6	11
		GeoB9204-1	51.449	11.753	837		12
		GeoB9205-1	51.451	11.752	810	11.9	33
		GeoB9219-1	51.451	11.757	921	10.2	22
		M61/1-259	51.455	11.754	858	2.5	9
		GeoB9206-1	51.455	11.752	857	10.9	22
		GeoB9218-1	51.458	11.756	889	15.7	21

Appendix 2 (Chapter 2)

2.1 Taxonomic list of benthic foraminiferal species

Taxonomic references of Recent benthic foraminiferal species from the Celtic Sea reported in Dorst et al. (2014), as well as those of Sturrock and Murray (1981), Murray et al. (1982), and Schönfeld and Altenbach (2005).

A

Acervulina inhaerens Schultze, 1854

Adercotryma glomerata (Brady) = *Lituola glomerata* Brady, 1878

Adercotryma wrighti Brönnimann and Whittaker, 1987

Ammobaculites agglutinans (d'Orbigny) = *Spirolina agglutinans* d'Orbigny, 1846

Ammodiscus catinus Höglund, 1947

Ammodiscus planorbis Höglund, 1947

Ammodiscus sp.

Ammoglobigerina shannoni (Brönnimann and Whittaker) = *Globotrochamminopsis shannoni* Brönnimann and Whittaker, 1988

Ammolagena clavata (Jones and Parker) = *Trochammina irregularis* (d'Orbigny) var. *clavata* Jones and Parker, 1860

Ammomassilina alveoliniformis (Milett) = *Massilina alveoliniformis* Milett, 1898

Ammonia batavus (Hofker) = *Streblus batavus* Hofker, 1951 = T3S of Hayward et al. (2004)

Ammonia falsobeccarii (Rouvillois) = *Pseudoeponides falsobeccarii* Rouvillois, 1974 = T3 of Hayward et al. (2004)

Ammoscalaria pseudospiralis (Williamson) = *Proteonina pseudospiralis* Williamson, 1858

Ammoscalaria tenuimargo (Brady) = *Haplophragmium tenuimargo* Brady, 1884

Ammosphaeroidina sphaeroidiniformis (Brady) = *Haplophragmium sphaeroidiniforme* Brady, 1884

Amphicoryna scalaris (Batsch) = *Nautilus (Orthoceras) scalaris* Batsch, 1791

Anomalina ammonoides (Reuss) = *Rosalina ammonoides* Reuss, 1844

Astacolus crepidulus (Fichtel and Moll) = *Nautilus crepidula* Fichtel and Moll, 1798

Asterigerinata mamilla (Williamson) = *Rotalina mamilla* Williamson, 1858

Astrononion stelligerum (d'Orbigny) = *Nonionina stelligera* d'Orbigny, 1839

B

Bathysiphon capillare De Folin, 1886

Bigenerina nodosaria d'Orbigny, 1826

Biloculinella irregularis (d'Orbigny) = *Biloculina irregularis* d'Orbigny, 1839

Bolivina difformis (Williamson) = *Textularia variabilis* Williamson var. *difformis* Williamson, 1858

  Note: *Brizalina difformis* of Sturrock and Murray (1981) and Murray (2006)

Bolivina dilatata Reuss, 1850

Bolivina ordinaria Phleger and Parker, 1952

Bolivina pseudoplicata Heron-Allen and Earland, 1930

Bolivina pseudopunctata Höglund, 1947

Bolivina subaenariensis Cushman, 1922

Bolivina tongi Cushman, 1929

Bolivina variabilis (Williamson) = *Textularia variabilis* Williamson, 1858

Bolivina spp.
   Note: there are seven different species under these spp.-taxa, but with uncertain designation
Bulimina gibba Fornasini, 1902
Bulimina marginata d'Orbigny, 1826
Bulimina striata mexicana (Cushman) = *Bulimina striata* d'Orbigny var. *mexicana* Cushman, 1922
Bulimina striata striata d'Orbigny, 1826
Buliminella elegantissima (d'Orbigny) = *Bulimina elegantissima* d'Orbigny, 1839
Buliminella minutissima (Wright) = *Bulimina minutissima* Wright, 1902
   Note: *Bulimina minutissima* of Sturrock and Murray (1981) and Murray (2006)
Buzasina ringens (Brady) = *Trochammina ringens* Brady, 1879

C
Cancris auriculus (Fichtel and Moll) = *Nautilus auricula* Fichtel and Moll, 1798
Cassidulina crassa d'Orbigny, 1839
Cassidulina laevigata d'Orbigny, 1826
   Note: *Cassidulina carinata* (Silvestri, 1896) of Sturrock and Murray (1981), Murray et al. (1982) and Murray (2006)
Cassidulina minuta Cushman, 1933
Cassidulina neoteretis Seidenkrantz, 1995
Cassidulina obtusa Williamson, 1858
Cassidulina reniforme (Norvang) = *Cassidulina crassa* d'Orbigny var. *reniforme* Norvang, 1945
Cassidulina sp.
Cassidulinoides bradyi (Norman) = *Cassidulina bradyi* Norman, 1881
Cassidulinoides sp.
Chilostomella ovoidea Reuss, 1850
Cibicidella variabilis (d'Orbigny) = *Truncatulina variabilis* d'Orbigny, 1826
Cibicides lobatulus (Walker and Jacob) = *Nautilus lobatulus* Walker and Jacob, 1798
Cibicides refulgens Montfort, 1808
Cibicides spp.
   Note: there are two different species under these spp.-taxa, but with uncertain designation

Cibicidoides mollis (Phleger and Parker) = *Cibicides mollis* Phleger and Parker, 1951
Cibicidoides pachyderma (Rzehak) = *Truncatulina pachyderma* Rzehak, 1886
Cibicidoides sp.
Clavulina mexicana (Cushman) = *Clavulina humilis* Brady var. *mexicana* Cushman, 1922
Clavulina obscura Chaster, 1892
Cornuspira involvens (Reuss) = *Operculina involvens* Reuss, 1850
Cribrostomoides nitidus (Goes) = *Haplophragmium nitidum* Goes, 1896
Cristellaria acutauricularis (Fichtel and Moll) = *Nautilus acutauricularis* Fichtel and Moll, 1798
Crithionina albida (Schulze) = *Storthosphaera albida* Schulze, 1875
Crithionina goesi Höglund, 1947
Crithionina mamilla Goes, 1894
Crithionina sp.
Cuneata arctica (Brady) = *Reophax arctica* Brady, 1881
Cyclammina cancellata Brady, 1879

D
Dentalina communis (d'Orbigny) = *Nodosaria (Dentalina) communis* d'Orbigny, 1826
Dentalina sp.
Deuterammina (Deuterammina) balkwilli Brönnimann and Whittaker, 1983
Deuterammina (Deuterammina) rotaliformis (Heron-Allen and Earland) = *Trochammina rotaliformis* Heron-Allen and Earland, 1911
Deuterammina (Deuterammina) spp.
   Note: there are two different species under these spp.-taxa, but with uncertain designation
Deuterammina (Lepidodeuterammina) mourai Brönnimann and Zaninetti, 1984
Deuterammina (Lepidodeuterammina) ochracea (Williamson) = *Rotalina ochracea* Williamson, 1858
Deuterammina (Lepidodeuterammina) sinuosa (Brönnimann) = *Asterotrochammina sinuosa* Brönnimann, 1978
Deuterammina (Lepidodeuterammina) spp.
   Note: there are three different species under these spp.-taxa, but with uncertain designation

Discanomalina coronata (Parker and Jones) = *Anomalina coronata* Parker and Jones, 1857
Discanomalina semipunctata (Bailey) = *Rotalina semipunctata* Bailey, 1851
Discorbina polyrraphes (Reuss) = *Rotalina polyrraphes* Reuss, 1845
   Note: *Rosalina polyrraphes* of Sturrock and Murray (1981) and Murray (2006)
Discorbina sp. juv.
Discorbinella bertheloti (d'Orbigny) = *Rosalina bertheloti* d'Orbigny, 1839
Dorothia bradyana Cushman, 1936

E
Eggerella europea (Christiansen) = *Verneuilina europeum* Christiansen, 1958
Eggerelloides medius (Höglund) = *Verneuilina media* Höglund, 1947
Eggerelloides scaber (Williamson) = *Bulimina scabra* Williamson, 1858
Elphidium complanatum (d'Orbigny) = *Polystomella complanata* d'Orbigny, 1839
Elphidium crispum (Linné) = *Nautilus crispus* Linné, 1758
Elphidium discoidale (d'Orbigny) = *Polystomella discoidalis* d'Orbigny, 1839
Elphidium earlandi Cushman, 1936
Elphidium excavatum (Terquem) = *Polystomella excavata* Terquem, 1875
Elphidium incertum (Williamson) = *Polystomella umbilicatula* (Walker) var. *incerta* Williamson, 1858
Elphidium sp.
Epistominella exigua (Brady) = *Pulvinulina exigua* Brady, 1884
Epistominella rugosa (Phleger and Parker) = ?*Pseudoparella rugosa* Phleger and Parker, 1951
Epistominella vitrea Parker, 1953
Eponides repandus (Fichtel and Moll) = *Nautilus repandus* Fichtel and Moll, 1798
Eponides repandus var. *concameratus* (Montagu) = *Serpula concamerata* Montagu, 1808

F
Fissurina clathrata (Brady) = *Lagena clathrata* Brady, 1884
Fissurina laevigata Reuss, 1850
Fissurina lagenoides (Williamson) = *Lagena lagenoides* Williamson, 1848
Fissurina marginata (Montagu) = *Vermiculum marginatum* Montagu, 1803

Fissurina orbignyana Seguenza, 1862
Fissurina piriformis (Buchner) = *Lagena piriformis* Buchner, 1940
Fissurina quadrata (Williamson) = *Entosolenia marginata* (Montagu) var. *quadrata* Williamson, 1858
Fissurina sp.

G
Gaudryina rudis Wright, 1900
Gavelinopsis caledonia Murray and Whittaker, 2001
Gavelinopsis praegeri (Heron-Allen and Earland) = *Discorbina praegeri* Heron-Allen and Earland, 1913
Glabratella chasteri (Heron-Allen and Earland) = *Discorbina chasteri* Heron-Allen and Earland, 1913
Globobulimina affinis (d'Orbigny) = *Bulimina affinis* d'Orbigny, 1839
Globobulimina sp. 324 after Schiebel (1992), plate 2, fig. 7
Globocassidulina subglobosa (Brady) = *Cassidulina subglobosa* Brady, 1881
Guttulina problema (d'Orbigny) = *Polymorphina (Guttulina) problema* d'Orbigny, 1826
Gyroidina neosoldanii Brotzen, 1936
Gyroidina umbonata (Silvestri) = *Rotalia soldanii* d'Orbigny var. *umbonata* Silvestri, 1898
Gyroidina sp. juv.

H
Hanzawaia boueana (d'Orbigny) = *Truncatulina boueana* d'Orbigny, 1846
Hanzawaia concentrica (Cushman) = *Truncatulina concentrica* Cushman, 1918
Hanzawaia nitidula (Bandy) = *Cibicidina basiloba* (Cushman) var. *nitidula* Bandy, 1953
Hanzawaia sp.
Haplophragmoides bradyi (Robertson) = *Trochammina bradyi* Robertson, 1891
Haplophragmoides fragile Höglund, 1947
Hoeglundina elegans (d'Orbigny) = *Rotalia (Turbinulina) elegans* d'Orbigny, 1826
Hormosinella guttifera (Brady) = *Lituola (Reophax) guttifera* Brady, 1881
Hyalinea balthica (Schröter) = *Nautilus balthicus* Schröter, 1783
Hyperammina fragilis Höglund, 1947
Hyperammina friabilis Brady, 1844

Hyperammina laevigata (Wright) = *Hyperammina elongata* Brady var. *laevigata* Wright, 1891

J

Jaculella obtusa Brady, 1882

L

Labrospira jeffreysii (Williamson) = *Nonionina jeffreysii* Williamson, 1858
   Note: *Cribrostomoides jeffreysii* of Sturrock and Murray (1981), Murray et al. (1982) and Murray (2006)
Lagena hexagona (Williamson) = *Entosolenia squamosa* (Montagu) var. *hexagona* Williamson, 1848
   Note: *Oolina hexagona* of Sturrock and Murray (1981), Murray et al. (1982) and Murray (2006)
Lagena substriata Williamson, 1848
Lagena sulcata (Walker and Jacob) = *Serpula sulcata* Walker and Jacob, 1798
Lamarckina haliotidea (Heron-Allen and Earland) = *Pulvinulina haliotidea* Heron-Allen and Earland, 1911
Laryngosigma williamsoni (Terquem) = *Polymorphina williamsoni* Terquem, 1878
Lenticulina atlantica (Barker) = *Robulus atlanticus* Barker, 1960
Lenticulina gibba (d'Orbigny) = *Cristellaria gibba* d'Orbigny, 1839
Lenticulina rotulata (Lamarck) = *Lenticulites rotulata* Lamarck, 1804
Lenticulina spp.
   Note: there are two different juvenile species under these spp.-taxa, but with uncertain designation
Leptohalysis scottii (Chaster) = *Reophax scottii* Chaster, 1892
Liebusella cf. *goesi* (Höglund) = *Liebusella goesi* Höglund, 1947

M

Marsipella cylindrica Brady, 1882
Marsipella elongata Norman, 1878
Marsipella spiralis Heron-Allen and Earland, 1912
Massilina secans (d'Orbigny) var. *tenuistriata* Earland, 1905
Melonis barleeanum (Williamson) = *Nonionina barleeana* Williamson, 1858
Melonis sp.

Miliolinella elongata (Kruit) = *Miliolinella circularis* (Bornemann) var. *elongata* Kruit, 1955
   Note: *Miliolinella circularis* var. *elongata* of Sturrock and Murray (1981), Murray et al. (1982) and Murray (2006)
Miliolinella oblonga (Montagu) = *Vermiculum oblongum* Montagu, 1803
   Note: *Quinqueloculina oblonga* of Sturrock and Murray (1981) and Murray (2006)
Miliolinella subrotunda (Montagu) = *Vermiculum subrotundum* Montagu, 1803
Miliolinella valvularis (Reuss) = *Triloculina valvularis* Reuss, 1851
Miliolinella sp. juv.
Miniacina miniacea (Pallas) = *Millepora miniacea* Pallas, 1766
Mississippina concentrica (Parker and Jones) = *Pulvinulina concentrica* Parker and Jones, 1864

N

Neoconorbina millettii (Wright) = *Discorbina millettii* Wright, 1911
   Note: *Discorbinoides millettii* of Sturrock and Murray (1981), Murray et al. (1982) and Murray (2006)
Neoconorbina terquemi (Rzehak) = *Discorbina terquemi* Rzehak, 1888
Neoconorbina williamsoni (Chapman and Parr) = *Discorbis williamsoni* Chapman and Parr, 1932
   Note: *Rosalina williamsoni* of Sturrock and Murray (1981), Murray et al. (1982) and Murray (2006)
Neolenticulina peregrina (Schwager) = *Cristellaria peregrina* Schwager, 1866
Nonion pauperatus (Balkwill and Wright) = *Nonionina pauperata* Balkwill and Wright, 1885
Nonionella atlantica Cushman, 1947
Nonionella auricula Heron-Allen and Earland, 1930
Nonionella iridea Heron-Allen and Earland, 1932
Nonionella turgida (Williamson) = *Rotalina turgida* Williamson, 1858
Nonionella sp. juv.
Nonionellina labradorica (Dawson) = *Nonionina labradorica* Dawson, 1860
Nouria sp. after Mendes (2010), plate 1, fig. 2
Nuttallides pusillus (Parr) = *Eponides pusillus* Parr, 1950

O

Ophthalmidium balkwilli Macfadyen, 1939

Note: *Cornuloculina balkwilli* of Sturrock and Murray (1981), Murray et al. (1982) and Murray (2006)
Ophthalmidium sp.
Osangularia sp. juv.

P
Parafissurina lateralis (Cushman) = *Lagena lateralis* Cushman, 1913
Paratrochammina (Lepidoparatrochammina) haynesi (Atkinson) = *Trochammina haynesi* Atkinson, 1969
Paratrochammina (Paratrochammina) tricamerata (Earland) = *Trochammina tricamerata* Earland, 1934
Paratrochammina (Paratrochammina) wrighti Brönnimann and Whittaker, 1983
Patellina corrugata Williamson, 1858
Placopsilina confusa Cushman, 1920
Placopsilina sp.
Planispirinoides bucculentus (Brady) = *Miliolina bucculenta* Brady, 1884
Planorbulina distoma Terquem, 1876
Planorbulina mediterranensis d'Orbigny, 1826
Planulina ariminensis d'Orbigny, 1826
Pninaella nitidula (Chaster) = *Pulvinulina nitidula* Chaster, 1892
   Note: *Eoeponidella nitidula* of Sturrock and Murray (1981), Murray et al. (1982) and Murray (2006)
Polymorphina compressa d'Orbigny, 1846
Polymorphinindae spp.
   Note: the number of species under these spp.-taxa from Sturrock and Murray (1981) is unknown
Polystomammina nitida (Brady) = *Trochammina nitida* Brady, 1881
Polystomammina sp. juv.
Portatrochammina murrayi Brönnimann and Zaninetti, 1984
   Note: *Trochammina globigeriniformis* var. *pygmaea* of Sturrock and Murray (1981)
Portatrochammina pacifica (Cushman) = *Trochammina pacifica* Cushman, 1925
Procerolagena clavata (d'Orbigny) = *Oolina clavata* d'Orbigny, 1846
Psammosphaera fusca Schultze, 1875
Pyrgo depressa (d'Orbigny) = *Biloculina depressa* d'Orbigny, 1826

Pyrgo fornasinii Chapman and Parr, 1935
Pyrgo lucernula (Schwager) = *Biloculina lucernula* Schwager, 1866
Pyrgo oblonga (d'Orbigny) = *Biloculina oblonga* d'Orbigny, 1839
Pyrgo sp.

Q
Quinqueloculina angulata (Williamson) = *Miliolina bicornis* (Walker and Jacob) var. *angulata* Williamson, 1858
Quinqueloculina bicornis (Walker and Jacob) = *Serpula bicornis* Walker and Jacob, 1798
Quinqueloculina cliarensis (Heron-Allen and Earland) = *Miliolina cliarensis* Heron-Allen and Earland, 1930
Quinqueloculina dunkerquiana (Heron-Allen and Earland) = *Miliolina dunkerquiana* Heron-Allen and Earland, 1930
Quinqueloculina lamarckiana d'Orbigny, 1839
Quinqueloculina lata Terquem, 1876
Quinqueloculina pygmaea Reuss, 1850
Quinqueloculina seminulum (Linné) = *Serpula seminulum* Linné, 1758
Quinqueloculina spp.
   Note: there are three different species under these spp.-taxa, but with uncertain designation

R
Recurvoides trochamminiformis (Höglund) = *Recurvoides trochamminiforme* Höglund, 1947
Remaneica helgolandica Rhumbler, 1938
Reophax bilocularis Flint, 1899
Reophax calcareous (Cushman) = *Proteonina difflugiformis* (Brady) var. *calcarea* Cushman, 1947
Reophax curtus Cushman, 1920
Reophax difflugiformis Brady, 1879
Reophax micaceus Earland, 1934
Reophax moniliformis (Siddall) = *Reophax moniliforme* Siddall, 1886
Reophax scorpiurus Montfort, 1808
Reophax sp.
Reussoolina globosa (Montagu) = *Vermiculum globosum* Montagu, 1803
Rhabdammina abyssorum Sars, 1869

Rhizammina algaeformis Brady, 1879
Robertina arctica d'Orbigny, 1846
Robertina subcylindrica (Brady) = *Bulimina subcylindrica* Brady, 1881
Robertinoides bradyi (Cushman and Parker) = *Robertina bradyi* Chushman and Parker, 1936
Robertinoides normani (Goes) = *Bulimina normani* Goes, 1894
Robertinoides suecicum Höglund, 1947
Robertinoides spp.
   Note: there are two different juvenile species from our samples and an unknown number of species from a sample of Sturrock and Murray (1981) under these spp.-taxa, but with uncertain designation
Rosalina anglica (Cushman) = *Discorbis globularis* (d'Orbigny) var. *anglica* Cushman, 1931
Rosalina anomala Terquem, 1875
Rosalina bradyi (Cushman) = *Discorbis globularis* (d'Orbigny) var. *bradyi* Cushman, 1915
Rosalina globularis d'Orbigny, 1826
Rosalina neapolitana (Hofker) = *Neoconorbina neapolitana* Hofker, 1951
Rosalina obtusa d'Orbigny, 1846
Rosalina spp.
   Note: there are two different species under these spp.-taxa, but with uncertain designation
Rotaliammina concava (Seiglie) = *Tiphotrocha concava* Seiglie, 1964
Rotaliammina siphonata (Seiglie) = *Polysiphotrocha siphonata* Seiglie, 1964

S
Saccammina sphaerica Brady, 1871
Saccorhiza ramosa (Brady) = *Hyperammina ramosa* Brady, 1879
Seabrookia earlandi Wright, 1891
Sigmoilopsis schlumbergeri (Silvestri) = *Sigmoilina schlumbergeri* Silvestri, 1904
Siphonina bradyana Cushman, 1927
Siphotextularia bermudezi Mikhalevich, 1978
Siphotextularia caroliniana (Cushman) = *Textularia flintii* (Cushman) var. *caroliniana* Cushman, 1922
Siphotextularia cf. *occidentalis* (Cushman) = *Textularia foliacea* Heron-Allen and Earland var. *occidentalis* Cushman, 1922

Siphotextularia concava (Karrer) = *Plecanium concavum* Karrer, 1868
Siphotextularia curta (Cushman) = *Textularia flintii* Cushman var. *curta* Cushman, 1922
Siphotextularia flintii (Cushman) = *Textularia flintii* Cushman, 1911
Siphotextularia heterostoma (Fornasini) = *Textularia heterostoma* Fornasini, 1896
Siphotextularia sp.
Sphaeroidina bulloides d'Orbigny, 1826
Spirillina vivipara Ehrenberg, 1843
Spirillina wrightii Heron-Allen and Earland, 1930
Spiroloculina depressa d'Orbigny, 1826
Spiroloculina excavata d'Orbigny, 1846
Spiroplectinella sagittula (Defrance) = *Textularia sagittula* Defrance, 1824
   Note: *Textularia sagittula* and *Spiroplectammina wrightii* of Sturrock and Murray (1981), Murray et al. (1982) and Murray (2006)
Stainforthia concava (Höglund) = *Virgulina concava* Höglund, 1947
Stainforthia fusiformis (Williamson) = *Bulimina pupoides* d'Orbigny var. *fusiformis* Williamson, 1858

T
Textularia bigenerinoides Lacroix, 1932
Textularia earlandi Parker, 1952
Textularia pseudogramen Chapman and Parr, 1937
Textularia skagerakensis Höglund, 1947
Textularia sp.
Tholosina vesicularis (Brady) = *Placopsilina vesicularis* Brady, 1879
Tolypammina vagans (Brady) = *Hyperammina vagans* Brady, 1879
Tolypammina sp.
Trifarina angulosa (Williamson) = *Uvigerina angulosa* Williamson, 1858
Trifarina bradyi Cushman, 1923
Trifarina fornasinii (Selli) = *Angulogerina fornasinii* Selli, 1948
Trifarina pauperata (Heron-Allen and Earland) = *Uvigerina angulosa* (Williamson) var. *pauperata* Heron-Allen and Earland, 1932
Triloculina tricarinata d'Orbigny, 1826
Triloculina williamsoni Terquem, 1878
Triloculina sp.

Tritaxis conica (Parker and Jones) = *Valvulina triangularis* d'Orbigny var. *conica* Parker and Jones, 1865
Tritaxis fusca (Williamson) = *Rotalina fusca* Williamson, 1858
Trochammina advena Cushman, 1922
Trochammina astrifica (Rhumbler) = *Trochammina squamata* Heron-Allen and Earland var. *astrifica* Rhumbler, 1938
Trochammina squamata Jones and Parker, 1860
Trochammina spp.
   Note: there are six different species from our samples and four different species from samples of Sturrock and Murray (1981) and Murray et al. (1982) under these spp.-taxa, but with uncertain designation
Trochamminopsis pusilla (Höglund) = *Trochammina pusilla* Höglund, 1947
Tumidotubus albus Gooday and Haynes, 1983

U
Uvigerina auberiana d'Orbigny, 1839
Uvigerina cf. *bifurcata* (d'Orbigny) = *Uvigerina bifurcata* d'Orbigny, 1839
Uvigerina mediterranea Hofker, 1932

V
Vaginulina spp.
   Note: there are two different juvenile species under these spp.-taxa, but with uncertain designation
Valvulineria spp.
   Note: there are two different species under these spp.-taxa, but with uncertain designation
Vulvulina pennatula (Batsch) = *Nautilus (Orthoceras) pennatula* Batsch, 1791

2.2 Census data of benthic foraminifera

Foraminiferal census data reported in Dorst et al. (2014), as well as those of Sturrock and Murray (1981), Murray et al. (1982), and Schönfeld and Altenbach (2005). The following abbrevations applies to all three tables: mol = mode of life, f = free, a = attached, f/a = free and attached (opportunistic), ts = test structure, h = hyaline, a = agglutinated, p = porcelaneous, others = different species with uncertain designation.

Table 2.2.1 Foraminiferal census data of Dorst et al. (2014); grain size >63 μm (p. 128 – 142).

Table 2.2.2 Foraminiferal census data of Sturrock and Murray (1981) and Murray et al. (1982). Faunal data are from web file WA-118 of Murray (2006); grain size >63 and 76 μm; only living species.

Table 2.2.3 Foraminiferal census data of Schönfeld and Altenbach (2005). Partially published data (living *Uvigerina* species only); grain size >250 μm.

Station number			VH-97-32D		VH-97-33D		VH-97-34		VH-97-35		VH-97-36		VH-97-37		VH-97-49	
Latitude (°N)			49.001		48.739		48.451		48.154		47.866		47.549		47.554	
Longitude (°W)			5.943		6.206		6.447		6.688		6.951		7.250		7.241	
Depth in m			115		131		116		150		170		467		340	
Living/Dead			living	dead	living	dead	living	dead	living	dead	living	dead	living	dead	living	dead
Species	mol	ts														
Acervulina inhaerens	a	h		1.0		5.0		2.0		4.6		6.1				0.3
Adercotryma glomerata	f	a											1.3			
Adercotryma wrightii	f	a														
Ammobaculites agglutinans	f	a	0.7													
Ammodiscus planorbis	a	a	0.7			0.4										
Ammoglobigerina shannoni juv.	f	a														
Ammolagena clavata	a	a													3.3	1
Ammonia batavus (T3S)	f/a	h														0.6
Ammonia falsobeccarii (T3)	f	h				0.8										
Ammoscalaria tenuimargo	f	a			0.3				0.4							
Amphicoryna scalaris	f	h														
Anomalina ammonoides	f	h	0.7													
Astacolus crepidulus	f	h		0.2								0.3				
Asterigerinata mamilla	f/a	h	0.7	10.7	0.3	9.6		10.8		3.5						
Astrononion stelligerum	f	h			0.1											
Bigenerina nodosaria	f	a														
Biloculinella irregularis	f	p						0.4				0.3		0.6		
Bolivina difformis	f	h	2.0	2.2	3.8	5.4	9.1	2.0	24.9	1	13.4	2.3	3.9	2.9	1.3	0.9
Bolivina dilatata	f/a	h				1.2		0.1		0.2		0.3		0.3		
Bolivina ordinaria	f	h														
Bolivina pseudoplicata	f/a	h	0.7		0.2		0.4		0.4							
Bolivina pseudopunctata	f/a	h		0.2			0.3									
Bolivina subaenariensis	f	h														
Bolivina tongi	f	h														
Bolivina variabilis	f	h	1.3	0.7		0.4							6.5			
Bolivina spp.	f	h														
Bulimina gibba	f/a	h														
Bulimina marginata	f	h														
Bulimina striata mexicana	f	h						0.3		0.4			1.3	1.8	0.7	
Bulimina striata striata	f	h												0.3		0.3
Buliminella elegantissima	f	h	0.7													
Buzasina ringens	f	a														
Cancris auriculus	f/a	h		0.2												

Station number			VH-97-50		BG0812a-02		BG0812a-05		BG0812a-06		BG0812a-08		D78/95	
Latitude (°N)			47.574		47.799		48.201		47.899		48.496		48.516	
Longitude (°W)			7.218		6.908		7.598		7.898		8.503		5.964	
Depth in m			191		128		177		450		151		119	
Living/Dead			living	dead	living	dead	living	dead	living	dead	living	dead	living	dead
Species	**mol**	**ts**												
Acervulina inhaerens	a	h		0.003		2.6		1.8				0.4		8.1
Adercotryma glomerata	f	a												
Adercotryma wrightii	f	a							7.4		0.2			
Ammobaculites agglutinans	f	a												
Ammodiscus planorbis	a	a											0.2	
Ammoglobigerina shannoni juv.	f	a							1.2					
Ammolagena clavata	a	a												
Ammonia batavus (T3S)	f/a	h		0.4										
Ammonia falsobeccarii (T3)	f	h												
Ammoscalaria tenuimargo	f	a			0.6				0.5		0.4			
Amphicoryna scalaris	f	h							0.3	0.2				
Anomalina ammonoides	f	h												
Astacolus crepidulus	f	h												
Asterigerinata mamilla	f/a	h						0.3						4.6
Astrononion stelligerum	f	h							0.7	0.3				
Bigenerina nodosaria	f	a								0.1				
Biloculinella irregularis	f	p					0.3	0.6						
Bolivina difformis	f	h	4.2	10	18.5	2.8	23.5	8.1	2	22.5	7.2	9		0.6
Bolivina dilatata	f/a	h							0.5	0.8	0.1	1.7		
Bolivina ordinaria	f	h									0.5			
Bolivina pseudoplicata	f/a	h			0.6				0.3	0.3	0.4		0.2	
Bolivina pseudopunctata	f/a	h							1.5	0.3	0.4	0.3		
Bolivina subaenariensis	f	h								0.3		0.7		
Bolivina tongi	f	h							1.7					
Bolivina variabilis	f	h			1.3			0.2	0.5	0.2				
Bolivina spp.	f	h							0.6	0.3		0.3		0.2
Bulimina gibba	f/a	h								0.1				
Bulimina marginata	f	h							0.3		0.1	0.7		
Bulimina striata mexicana	f	h	1			0.3	0.2			0.1	0.1			
Bulimina striata striata	f	h		0.4						0.1	0.1	1.4		
Buliminella elegantissima	f	h												
Buzasina ringens	f	a							8.6					
Cancris auriculus	f/a	h												

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Station number			VH-97-32D		VH-97-33D		VH-97-34		VH-97-35		VH-97-36		VH-97-37		VH-97-49	
Latitude (°N)			49.001		48.739		48.451		48.154		47.866		47.549		47.554	
Longitude (°W)			5.943		6.206		6.447		6.688		6.951		7.250		7.241	
Depth in m			115		131		116		150		170		467		340	
Living/Dead			living	dead	living	dead	living	dead	living	dead	living	dead	living	dead	living	dead
Cassidulina crassa	f	h				0.3	0.7	0.7	4.6	0.8	13.8	0.288	2.6	1.5	2.6	0.3
Cassidulina laevigata	f/a	h						0.3		0.4		0.3		0.6		
Cassidulina minuta	f	h								0.2				2.9		
Cassidulina neoteretis	f	h														0.3
Cassidulina obtusa	f	h	0.7	3.6	1.2	1.2	1.3	3.9	3.8	1	8.8	3.4		3.5	0.7	2.8
Cassidulina reniforme	f	h														
Cassidulina sp.	f	h														
Cassidulinoides bradyi	f	h														
Cassidulinoides sp.	f	h													0.7	
Chilostomella ovoidea	f	h														
Cibicidella variabilis	a	h						0.4								
Cibicides lobatulus	a	h	1.3	13.3	2.0	23.9	1.6	31.9	0.8	38.5	0.9	10.7	2.6	17.4	0.7	12.6
Cibicides refulgens	a	h						0.1				3.4		8.5		22.6
Cibicides spp.	a	h														
Cibicidoides pachyderma	f/a	h		0.5		0.4		0.3		0.2		0.6		2.7		0.3
Cibicidoides sp.	f/a	h												4.1		8.4
Cornuspira involvens	f/a	p														
Cribrostomoides nitidus	f	a			1.1											
Cristellaria acutauricularis	f	h														
Crithionina goesi	a	a					0.004									
Crithionina mamilla	a	a												0.3		
Cuneata arctica	f	a														
Dentalina communis juv.	f	h														
Dentalina sp. juv.	f	h														
Deuterammina (Deut.) balkwilli	a	a										0.002				
Deuterammina (Deut.) rotaliformis	a	a	1.3		0.2		0.3		5.9		0.5					
Deuterammina (Deut.) spp.	a	a		0.2	0.2											
Deuterammina (Lepidodeut.) mourai	a	a														
Deuterammina (Lepidodeut.) ochracea	a	a			0.3		2.9		8		4.2		1.3		6.5	
Deuterammina (Lepidodeut.) sinuosa	a	a			0.8											
Deuterammina (Lepidodeut.) spp.	a	a									0.5					
Discanomalina coronata	a	h	0.7		0.2											4.3
Discanomalina semipunctata	a	h			0.5	0.2	0.7							0.3		0.02
Discorbina polyrraphes	a	h							2.5				2.6		0.7	

Station number			VH-97-50		BG0812a-02		BG0812a-05		BG0812a-06		BG0812a-08		D78/95	
Latitude (°N)			47.574		47.799		48.201		47.899		48.496		48.516	
Longitude (°W)			7.218		6.908		7.598		7.898		8.503		5.964	
Depth in m			191		128		177		450		151		119	
Living/Dead			living	dead	living	dead	living	dead	living	dead	living	dead	living	dead
Cassidulina crassa	f	h	7.3	2.4	3.8	0.9	8.1	0.6		1.6	0.2	1.4		
Cassidulina laevigata	f/a	h		0.4				0.9		3.5	1.1	8.6		0.2
Cassidulina minuta	f	h				0.6	0.5	0.001	0.5	2.6	1.9	1		
Cassidulina neoteretis	f	h		0.8				0.3	0.5	1		0.3		
Cassidulina obtusa	f	h	5.2	25.7	24.2	5.3	12.3	21.9	0.5	16.2	22.1	15.5	0.3	0.6
Cassidulina reniforme	f	h								1.8	0.1			
Cassidulina sp.	f	h								0.2				
Cassidulinoides bradyi	f	h							1.2					
Cassidulinoides sp.	f	h												
Chilostomella ovoidea	f	h								0.1				
Cibicidella variabilis	a	h				1.9		0.001						
Cibicides lobatulus	a	h	4.7	7.3	1.3	37.2	2.8	23.1		6.1	2.4	12.8	36	16.5
Cibicides refulgens	a	h	0.5	4		0.3	0.5	0.002					0.3	0.2
Cibicides spp.	a	h						0.3		0.1				
Cibicidoides pachyderma	f/a	h				0.6				1		0.7		0.2
Cibicidoides sp.	f/a	h			4.8									0.2
Cornuspira involvens	f/a	p											0.2	
Cribrostomoides nitidus	f	a												
Cristellaria acutauricularis	f	h							0.3					
Crithionina goesi	a	a												
Crithionina mamilla	a	a												
Cuneata arctica	f	a									1.3			
Dentalina communis juv.	f	h								0.2				
Dentalina sp. juv.	f	h	0.5											
Deuterammina (Deut.) balkwilli	a	a												
Deuterammina (Deut.) rotaliformis	a	a					2.4				0.7			
Deuterammina (Deut.) spp.	a	a											0.2	0.2
Deuterammina (Lepidodeut.) mourai	a	a					0.5							
Deuterammina (Lepidodeut.) ochracea	a	a	0.5		6.4		6.2				0.5		0.5	
Deuterammina (Lepidodeut.) sinuosa	a	a					0.2							
Deuterammina (Lepidodeut.) spp.	a	a											0.9	0.05
Discanomalina coronata	a	h		0.4										
Discanomalina semipunctata	a	h	2.6										1.9	0.2
Discorbina polyrraphes	a	h	1.6		1.3		1.7	0.3		0.2	2.7		0.7	

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Station number			VH-97-32D		VH-97-33D		VH-97-34		VH-97-35		VH-97-36		VH-97-37		VH-97-49	
Latitude (°N)			49.001		48.739		48.451		48.154		47.866		47.549		47.554	
Longitude (°W)			5.943		6.206		6.447		6.688		6.951		7.250		7.241	
Depth in m			115		131		116		150		170		467		340	
Living/Dead			living	dead	living	dead	living	dead	living	dead	living	dead	living	dead	living	dead
Discorbina sp. juv.	f/a	h			0.2											
Discorbinella bertheloti	a	h														
Dorothia bradyana	f/a	a			3.2					1.4		0.6				0.3
Eggerella europea	f	a			0.2											
Eggerelloides medius	f	a														
Eggerelloides scaber	f	a			0.2								1.3				
Elphidium complanatum	f	h														0.3
Elphidium crispum	f/a	h						0.5						2.9			2.8
Elphidium discoidale	f	h						0.4									
Elphidium earlandi	f	h														
Elphidium excavatum	f/a	h												0.6			0.3
Elphidium incertum	a	h														0.3
Elphidium sp.	f	h												0.6			
Epistominella exigua	f/a	h			0.2												
Epistominella rugosa	f/a	h								0.2			2.6				
Epistominella vitrea	f/a	h			0.2		0.2	0.4	0.4	0.001							
Eponides repandus	f/a	h			6.3		2.7		2.1	2		12.6					
Eponides repandus var. *concameratus*	f/a	h														2.2
Fissurina clathrata	f	h														
Fissurina laevigata	f	h			0.2												
Fissurina marginata	f/a	h												0.3			
Fissurina orbignyana	f	h						0.4		0.3				0.3			
Fissurina piriformis	f	h														
Fissurina quadrata	f	h			0.2												
Fissurina sp.	f	h														
Gaudryina rudis	a	a			1.0			0.1		1.2		2.9					1.6
Gavelinopsis caledonia	a	h			2.0	1.5	1.6	0.1	2.1					0.3			
Gavelinopsis praegeri	f/a	h	7.3	3.6	19.5	0.4	27.6	2.1	9.3	0.4	13.4	2	2.6	1.2	2	0.3
Glabratella chasteri juv.	f/a	h										0.3					
Globobulimina sp. 324	f	h														
Globocassidulina subglobosa	f/a	h		3.9	1.2	0.8	1.3	0.8	4.6	1.2	3.2	2.3	3.9	5.3		7.7
Guttulina problema	f	h								0.2						
Gyroidina umbonata	f	h														
Gyroidina umbonata juv.	f/a	h	4.0	1.2	7.4	2.3	2.0	0.5	5.1	0.2	1.4	0.3	6.5		3.3	0.3

Station number			VH-97-50		BG0812a-02		BG0812a-05		BG0812a-06		BG0812a-08		D78/95	
Latitude (°N)			47.574		47.799		48.201		47.899		48.496		48.516	
Longitude (°W)			7.218		6.908		7.598		7.898		8.503		5.964	
Depth in m			191		128		177		450		151		119	
Living/Dead			living	dead	living	dead	living	dead	living	dead	living	dead	living	dead
Discorbina sp. juv.	f/a	h											0.3	
Discorbinella bertheloti	a	h								0.1				0.01
Dorothia bradyana	f/a	a												
Eggerella europea	f	a	0.5								0.2			
Eggerelloides medius	f	a							0.3					
Eggerelloides scaber	f	a					0.2							
Elphidium complanatum	f	h										0.3		
Elphidium crispum	f/a	h		0.4										
Elphidium discoidale	f	h												
Elphidium earlandi	f	h								0.1				
Elphidium excavatum	f/a	h		0.003					0.3	1.7				
Elphidium incertum	a	h								0.2				
Elphidium sp.	f	h												
Epistominella exigua	f/a	h												
Epistominella rugosa	f/a	h	0.5						0.3	0.4				
Epistominella vitrea	f/a	h			0.6		1.4	0.6	2	0.7	22.7			
Eponides repandus	f/a	h				0.3						0.001		6.1
Eponides repandus var. *concameratus*	f/a	h		0.8										
Fissurina clathrata	f	h				0.3				0.1				
Fissurina laevigata	f	h												
Fissurina marginata	f/a	h	1							0.2		0.3		
Fissurina orbignyana	f	h												0.2
Fissurina piriformis	f	h						0.3						
Fissurina quadrata	f	h												
Fissurina sp.	f	h										0.3		
Gaudryina rudis	a	a		0.4		0.6								2.7
Gavelinopsis caledonia	a	h			1.3	0.3	0.2	0.9		0.1	1.5		0.3	
Gavelinopsis praegeri	f/a	h	9.9	2	8.3	1.3	5.5	5.4	0.5	4	12.1	6.2	7.9	0.5
Glabratella chasteri juv.	f/a	h								0.1				
Globobulimina sp. 324	f	h							0.5					
Globocassidulina subglobosa	f/a	h	1.6	18.9	1.3	0.6	1.7	9	1	20.5	4.8	4.5	1.5	
Guttulina problema	f	h												
Gyroidina umbonata	f	h							8.9					
Gyroidina umbonata juv.	f/a	h			5.7	0.9	3.3	1.2		2.8	1.2	0.3	0.3	

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Station number			VH-97-32D		VH-97-33D		VH-97-34		VH-97-35		VH-97-36		VH-97-37		VH-97-49	
Latitude (°N)			49.001		48.739		48.451		48.154		47.866		47.549		47.554	
Longitude (°W)			5.943		6.206		6.447		6.688		6.951		7.250		7.241	
Depth in m			115		131		116		150		170		467		340	
Living/Dead			living	dead	living	dead	living	dead	living	dead	living	dead	living	dead	living	dead
Gyroidina sp. juv.	f	h			0.2											
Hanzawaia boueana	a	h														
Hanzawaia concentrica	a	h														
Hanzawaia nitidula	a	h												0.3		
Hanzawaia sp.	a	h														
Haplophragmoides bradyi	f	a														
Hoeglundina elegans	f	h											2.6	0.6	3.3	0.9
Hyalinea balthica	f	h														
Jaculella obtusa	f	a														
Labrospira jeffreysii	f/a	a	6.0		3.6		1.3		0.4	0.2			2.6		0.7	
Lagena substriata	f/a	h	0.7													
Lagena sulcata	f	h												0.3		
Lamarckina haliotidea	f/a	h		0.5	0.2	0.4	0.7		0.4		1.4					
Laryngosigma williamsoni	f	h						0.4								
Lenticulina atlantica juv.	f	h														
Lenticulina gibba	f	h						0.1				0.3		0.6		
Lenticulina rotulata	f	h				0.2		0.1				0.3	2.6	3.5		4.3
Lenticulina spp.	f	h														
Leptohalysis scottii	f	a													0.7	
Liebusella cf. *goesi*	f	a			0.2						1.4					
Marsipella cylindrica	f	a														
Marsipella spiralis	f	a														
Massilina secans var. *tenuistriata*	f	p			0.2											
Melonis barleeanum	f	h														
Melonis sp.	f	h														
Miliolinella elongata	f/a	p														
Miliolinella subrotunda	f/a	p			0.2	0.5	0.4			0.3	0.4	0.3				0.3
Miliolinella valvularis	f/a	p										0.3				
Miliolinella sp. juv.	f/a	p														
Miniacina miniacea	a	h									1.005	2.9				
Mississippina concentrica	f/a	h										0.9				0.3
Neoconorbina millettii	a	h			0.2	0.3	1.0		0.4							
Neoconorbina terquemi	a	h				0.4										
Neoconorbina williamsoni	a	h	2.0		0.5	0.4	1.6	0.4	0.4		0.9					0.3

Station number			VH-97-50		BG0812a-02		BG0812a-05		BG0812a-06		BG0812a-08		D78/95	
Latitude (°N)			47.574		47.799		48.201		47.899		48.496		48.516	
Longitude (°W)			7.218		6.908		7.598		7.898		8.503		5.964	
Depth in m			191		128		177		450		151		119	
Living/Dead			living	dead	living	dead	living	dead	living	dead	living	dead	living	dead
Gyroidina sp. juv.	f	h												
Hanzawaia boueana	a	h									0.2	1.4		
Hanzawaia concentrica	a	h								0.1				
Hanzawaia nitidula	a	h								0.8	0.6			
Hanzawaia sp.	a	h						0.3						
Haplophragmoides bradyi	f	a							1					
Hoeglundina elegans	f	h												
Hyalinea balthica	f	h						0.6		0.1				
Jaculella obtusa	f	a		0.003			0.2		0.3					
Labrospira jeffreysii	f/a	a	6.3	0.4	1.3		4.7				0.6		1.5	
Lagena substriata	f/a	h						0.3						
Lagena sulcata	f	h												
Lamarckina haliotidea	f/a	h					0.2	0.3		0.1				
Laryngosigma williamsoni	f	h					0.2							
Lenticulina atlantica juv.	f	h			0.6									
Lenticulina gibba	f	h				0.4								0.2
Lenticulina rotulata	f	h	0.5							0.1				0.2
Lenticulina spp.	f	h					0.2	0.3						
Leptohalysis scottii	f	a												
Liebusella cf. *goesi*	f	a	0.5											
Marsipella cylindrica	f	a							4.7					
Marsipella spiralis	f	a							0.5					
Massilina secans var. *tenuistriata*	f	p												
Melonis barleeanum	f	h							12.1	0.1				
Melonis sp.	f	h							0.3					
Miliolinella elongata	f/a	p										0.3		
Miliolinella subrotunda	f/a	p						0.3		0.3	0.7	1		
Miliolinella valvularis	f/a	p				0.3	0.2				0.1	0.3		
Miliolinella sp. juv.	f/a	p				0.3								
Miniacina miniacea	a	h				0.7		0.003						0.02
Mississippina concentrica	f/a	h						0.6						
Neoconorbina millettii	a	h					0.2			0.1				
Neoconorbina terquemi	a	h												
Neoconorbina williamsoni	a	h			0.4	0.6	0.7	0.3		0.1				0.2

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Station number			VH-97-32D		VH-97-33D		VH-97-34		VH-97-35		VH-97-36		VH-97-37		VH-97-49	
Latitude (°N)			49.001		48.739		48.451		48.154		47.866		47.549		47.554	
Longitude (°W)			5.943		6.206		6.447		6.688		6.951		7.250		7.241	
Depth in m			115		131		116		150		170		467		340	
Living/Dead			living	dead	living	dead	living	dead	living	dead	living	dead	living	dead	living	dead
Neolenticulina peregrina juv.	f	h			0.2											
Nonion pauperatus	f/a	h	1.3	0.5	0.2	0.4		0.3	0.4							
Nonionella atlantica	f	h														
Nonionella auricula	f	h			0.2	0.5			0.8							
Nonionella iridea	f	h														
Nonionella turgida	f	h														
Nonionella sp. juv.	f	h														
Nonionellina labradorica	f	h														
Nouria sp.	f	a														
Nuttalides pusillus	f/a	h														
Ophthalmidium balkwilli	f/a	p		0.2	0.3		0.7									
Ophthalmidium sp.	f/a	p														
Osangularia sp. juv.	f	h														
Parafissurina lateralis	f	h			0.2											
Paratrochammina (Lepidopara.) haynesi	a	a	2.0													
Paratrochammina (Paratroch.) tricamerata	f/a	a			0.2											
Paratrochammina (Paratroch.) wrighti	f/a	a	0.7													
Patellina corrugata	a	h	2.0	0.2	0.9		0.7	0.1	2.1							
Placopsilina confusa	a	a								0.006		0.02		0.03	0.7	0.4
Placopsilina sp.	a	a													18.2	1.5
Planorbulina distoma	a	h									0.2					
Planorbulina mediterranensis	a	h									0.2	0.006				
Planulina ariminensis	a	h												1.2		
Pninaella nitidula	f	h			0.6		1.0		0.4							
Polymorphina compressa	f	h														
Polystomammina nitida	f/a	a			0.2		0.3		0.4		5.5		1.3		2	
Polystomammina sp. juv.	a	a														
Portatrochammina murrayi	f/a	a	14.6	0.5	4.5	0.4	3.2		5.9		5.1			0.3	2	
Portatrochammina pacifica juv.	f/a	a														
Procerolagena clavata	f	h														
Psammosphaera fusca	f/a	a														1.9
Pyrgo oblonga	f	p														0.3
Quinqueloculina angulata	f	p			0.2			0.1								
Quinqueloculina bicornis	f	p										0.3		0.3		

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Station number			VH-97-50		BG0812a-02		BG0812a-05		BG0812a-06		BG0812a-08		D78/95	
Latitude (°N)			47.574		47.799		48.201		47.899		48.496		48.516	
Longitude (°W)			7.218		6.908		7.598		7.898		8.503		5.964	
Depth in m			191		128		177		450		151		119	
Living/Dead			living	dead	living	dead	living	dead	living	dead	living	dead	living	dead
Neolenticulina peregrina juv.	f	h												
Nonion pauperatus	f/a	h			1.3		0.2	0.3	1.2	0.4		0.7		
Nonionella atlantica	f	h							1.7		0.1			
Nonionella auricula	f	h												
Nonionella iridea	f	h							2.7	0.1				
Nonionella turgida	f	h							0.5					
Nonionella sp. juv.	f	h								0.1				
Nonionellina labradorica	f	h								0.1				
Nouria sp.	f	a							0.5		0.1			
Nuttalides pusillus	f/a	h								0.9				
Ophthalmidium balkwilli	f/a	p					1.2				0.4			
Ophthalmidium sp.	f/a	p					0.5							
Osangularia sp. juv.	f	h								0.1				
Parafissurina lateralis	f	h												
Paratrochammina (Lepidopara.) haynesi	a	a			1.9	0.003								
Paratrochammina (Paratroch.) tricamerata	f/a	a					0.2				0.4			
Paratrochammina (Paratroch.) wrighti	f/a	a												
Patellina corrugata	a	h					0.5				0.1			
Placopsilina confusa	a	a	0.5	0.04	0.6	0.04		0.3				0.003	0.5	0.1
Placopsilina sp.	a	a	0.5	0.04				0.006				0.001		0.005
Planorbulina distoma	a	h												
Planorbulina mediterranensis	a	h				1		0.001				0.7	0.2	0.2
Planulina ariminensis	a	h	0.5											
Pninaella nitidula	f	h												
Polymorphina compressa	f	h				0.3								
Polystomammina nitida	f/a	a	2.1		5.1		0.2		3.5	0.1	0.5			
Polystomammina sp. juv.	a	a											0.2	
Portatrochammina murrayi	f/a	a	2.1		3.2		5.5				2.1		0.7	
Portatrochammina pacifica juv.	f/a	a			0.6		0.7				0.2			
Procerolagena clavata	f	h						0.3						
Psammosphaera fusca	f/a	a			0.02									
Pyrgo oblonga	f	p												
Quinqueloculina angulata	f	p												0.2
Quinqueloculina bicornis	f	p						0.3						0.2

Station number			VH-97-32D		VH-97-33D		VH-97-34		VH-97-35		VH-97-36		VH-97-37		VH-97-49	
Latitude (°N)			49.001		48.739		48.451		48.154		47.866		47.549		47.554	
Longitude (°W)			5.943		6.206		6.447		6.688		6.951		7.250		7.241	
Depth in m			115		131		116		150		170		467		340	
Living/Dead			living	dead	living	dead	living	dead	living	dead	living	dead	living	dead	living	dead
Quinqueloculina cliarensis	f	p												0.3		
Quinqueloculina dunkerquiana	f/a	p						0.3								
Quinqueloculina lamarckiana	f	p														
Quinqueloculina lata	f/a	p	1.5		1.5		0.4		0.2					1.5		1.6
Quinqueloculina pygmaea	f	p														
Quinqueloculina seminulum	f/a	p	4.6		2.7		1.3	1.7		1		0.9		2.4		0.9
Quinqueloculina spp.	f	p														
Recurvoides trochamminiformis	f	a														
Reophax curtus	f	a											24.7	1.2		
Reophax micaceus	f	a														
Reophax scorpiurus	f/a	a											1.3			
Reophax sp.	f	a														0.02
Reussoolina globosa	f	h														
Rhabdammina abyssorum	f/a	a			0.2											
Rhizammina algaeformis	f	a														
Robertina arctica	f	h					0.3									
Robertina subcylindrica	f	h							0.4	0.2	0.5					
Robertinoides normani	f	h														
Robertinoides suecicum	f	h												0.3		
Robertinoides spp.	f	h														
Rosalina anglica	a	h							0.7	0.4						
Rosalina anomala	f/a	h	2.4	0.5		5.0		3.7	1.3	2.8		0.6		0.3		
Rosalina bradyi	a	h					0.3	0.4		1.2		0.6	1.3	1.2		
Rosalina globularis	a	h				0.8		0.1		1.4				0.6		
Rosalina obtusa	a	h				0.4										
Rosalina spp.	a	h														
Rotaliammina concava	a	a							0.8		5.1		6.5		17.5	
Rotaliammina siphonata	a	a			0.3											
Saccorhiza ramosa	f/a	a														
Seabrookia earlandi	f	h														
Siphotextularia bermudezi	f/a	a														0.02
Siphotextularia caroliniana	f	a														0.3
Siphotextularia concava	f	a														
Siphotextularia curta	f	a														

Station number			VH-97-50		BG0812a-02		BG0812a-05		BG0812a-06		BG0812a-08		D78/95	
Latitude (°N)			47.574		47.799		48.201		47.899		48.496		48.516	
Longitude (°W)			7.218		6.908		7.598		7.898		8.503		5.964	
Depth in m			191		128		177		450		151		119	
Living/Dead			living	dead	living	dead	living	dead	living	dead	living	dead	living	dead
Quinqueloculina cliarensis	f	p												
Quinqueloculina dunkerquiana	f/a	p												
Quinqueloculina lamarckiana	f	p												0.2
Quinqueloculina lata	f/a	p		0.4										4.4
Quinqueloculina pygmaea	f	p								0.1				
Quinqueloculina seminulum	f/a	p				0.6		0.3		0.1		0.7		6
Quinqueloculina spp.	f	p		0.4		0.3				0.1	0.1			0.2
Recurvoides trochamminiformis	f	a									0.8			
Reophax curtus	f	a												
Reophax micaceus	f	a							0.3					
Reophax scorpiurus	f/a	a							0.3					
Reophax sp.	f	a												
Reussoolina globosa	f	h	0.5											
Rhabdammina abyssorum	f/a	a												
Rhizammina algaeformis	f	a							0.3					
Robertina arctica	f	h												
Robertina subcylindrica	f	h					0.2							
Robertinoides normani	f	h				0.3								
Robertinoides suecicum	f	h									0.2			
Robertinoides spp.	f	h						0.3		0.1				
Rosalina anglica	a	h												
Rosalina anomala	f/a	h				3.5		0.6				0.7		0.9
Rosalina bradyi	a	h		1.6		0.6	1	0.9	0.7	0.3	0.1	1	4.6	0.5
Rosalina globularis	a	h			1.3	0.3						0.7	0.7	0.3
Rosalina obtusa	a	h												
Rosalina spp.	a	h									0.1			0.2
Rotaliammina concava	a	a	3.7		1.3		1.4						4.2	
Rotaliammina siphonata	a	a												
Saccorhiza ramosa	f/a	a							1					
Seabrookia earlandi	f	h							0.5	0.1				
Siphotextularia bermudezi	f/a	a												0.2
Siphotextularia caroliniana	f	a							0.3					
Siphotextularia concava	f	a						0.6			0.1	0.001		
Siphotextularia curta	f	a								0.2				

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Station number			VH-97-32D		VH-97-33D		VH-97-34		VH-97-35		VH-97-36		VH-97-37		VH-97-49	
Latitude (°N)			49.001		48.739		48.451		48.154		47.866		47.549		47.554	
Longitude (°W)			5.943		6.206		6.447		6.688		6.951		7.250		7.241	
Depth in m			115		131		116		150		170		467		340	
Living/Dead			living	dead	living	dead	living	dead	living	dead	living	dead	living	dead	living	dead
Siphotextularia flintii	f	a											1.3	0.3	4.6	
Siphotextularia heterostoma	f	a			1.5		0.3			0.2						
Siphotextularia sp.	f	a														
Sphaeroidina bulloides	f/a	h														
Spirillina vivipara	a	h	1.3		0.3	0.4	0.7		1.3		3.2		1.3		4.6	0.08
Spirillina wrightii	a	h			1.2	0.4		0.3								
Spiroloculina depressa	f/a	p						0.1								
Spiroloculina excavata	f/a	p														
Spiroplectinella sagittula	a	a	6.0	13.6	0.9	15.8	2.0	21.3	1.3	23	3.2	28	1.3	9.7	2.6	5.9
Stainforthia concava	f	h														
Stainforthia fusiformis	f	h			0.2		0.3									
Textularia pseudogramen	f/a	a	20.5	12.1	18.3	6.2	8.8	4.2		5.9		3.4		1.2		1.9
Textularia skagerakensis	f	a													9.7	
Textularia sp.	f	a														0.3
Tholosina vesicularis	a	a								0.001						
Tolypammina vagans	a	a													1.3	0.8
Trifarina angulosa	f	h	15.9	1.5	21.0	1.5	26.0	3.4	7.6	1.6	12.4	0.6	2.6	12.7	5.2	3.7
Trifarina bradyi	f	h														
Trifarina fornasinii	f	h												0.3		0.9
Trifarina pauperata	f	h			0.5						0.5					
Triloculina williamsoni	f	p						0.1								
Triloculina sp.	f	p												0.3		
Tritaxis conica	a	a		6.8		5.4		2.5		3.3		12		0.3		0.9
Trochammina advena juv.	f	a														
Trochammina astrifica	f/a	a	0.7							0.001						
Trochammina squamata	f/a	a	4.0	0.2					1.3		0.9		5.2		3.3	
Trochammina spp.	f/a	a		0.5	0.2			0.1	0.8				1.3			
Trochamminopsis pusilla juv.	f/a	a											1.3			
Tumidotubus albus	a	a														0.06
Uvigerina auberiana	f	h											3.9	0.6	2	
Uvigerina mediterranea	f	h												0.6		
Vaginulina spp.	f	h			0.2											
Valvulineria spp.	f	h														
others					0.4							0.004				1.8

Station number			VH-97-50		BG0812a-02		BG0812a-05		BG0812a-06		BG0812a-08		D78/95	
Latitude (°N)			47.574		47.799		48.201		47.899		48.496		48.516	
Longitude (°W)			7.218		6.908		7.598		7.898		8.503		5.964	
Depth in m			191		128		177		450		151		119	
Living/Dead			living	dead	living	dead	living	dead	living	dead	living	dead	living	dead
Siphotextularia flintii	f	a	6.3	0.4										
Siphotextularia heterostoma	f	a					0.2			0.2	0.7	0.7		
Siphotextularia sp.	f	a		0.4						0.1				
Sphaeroidina bulloides	f/a	h					0.2							
Spirillina vivipara	a	h	3.1	0.02	1.3		1				0.2		9.3	0.8
Spirillina wrightii	a	h					0.2							1.1
Spiroloculina depressa	f/a	p												
Spiroloculina excavata	f/a	p												0.3
Spiroplectinella sagittula	a	a	6.3	12.9	0.6	27.7	1.4	11.4	0.3	1.5	0.6	8.3	2.9	22.4
Stainforthia concava	f	h							0.3					
Stainforthia fusiformis	f	h								0.1				
Textularia pseudogramen	f/a	a		0.4		2.5	0.5	3.6		0.1	0.2	4.5	10.6	8.6
Textularia skagerakensis	f	a	2.1											
Textularia sp.	f	a												
Tholosina vesicularis	a	a												
Tolypammina vagans	a	a		0.008										
Trifarina angulosa	f	h	20.8	2	2.6	1.6	5.5	2.1	0.5	1.1	3.5	9.7	10.6	0.2
Trifarina bradyi	f	h							7.9	0.2				
Trifarina fornasinii	f	h				0.3								
Trifarina pauperata	f	h								0.2				
Triloculina williamsoni	f	p										0.7		
Triloculina sp.	f	p												
Tritaxis conica	a	a				2.2		0.9				0.7		11.8
Trochammina advena juv.	f	a	0.5								0.6			
Trochammina astrifica	f/a	a												
Trochammina squamata	f/a	a			0.6	0.003	0.2		0.5		0.5	0.001	1	0.2
Trochammina spp.	f/a	a	0.5		0.6		0.7						0.3	
Trochamminopsis pusilla juv.	f/a	a											0.2	
Tumidotubus albus	a	a		0.003										
Uvigerina auberiana	f	h	1.6							1	0.1	0.3		
Uvigerina mediterranea	f	h							4.9					
Vaginulina spp.	f	h							0.3					
Valvulineria spp.	f	h							9.9					
others				0.84	0.6	0.006	0.2	0.3	1	1	0.7	0.6	0.8	

Station number	VH-97-32D		VH-97-33D		VH-97-34		VH-97-35		VH-97-36		VH-97-37		VH-97-49	
Latitude (°N)	49.001		48.739		48.451		48.154		47.866		47.549		47.554	
Longitude (°W)	5.943		6.206		6.447		6.688		6.951		7.250		7.241	
Depth in m	115		131		116		150		170		467		340	
Living/Dead	living	dead	living	dead	living	dead	living	dead	living	dead	living	dead	living	dead
number of individuals	151	412	661	260	308	763	237	510	217	350	77	340	154	323
population density (ind./10 cm3)	71	12379	303	30462	55	8751	25	13994	48	9803	12	1719	28	930
number of species	28	41	56	37	31	43	34	39	22	37	29	50	27	50
species number per 100 individuals	24	25	30	26	22	24	25	28	17	26	34	33	23	33
Fisher α index	10.12	11.32	14.61	11.79	8.60	9.86	10.87	9.83	6.12	10.45	16.92	16.17	9.48	16.55

Station number	VH-97-50		BG0812a-02		BG0812a-05		BG0812a-06		BG0812a-08		D78/95	
Latitude (°N)	47.574		47.799		48.201		47.899		48.496		48.516	
Longitude (°W)	7.218		6.908		7.598		7.898		8.503		5.964	
Depth in m	191		128		177		450		151		119	
Living/Dead	living	dead	living	dead	living	dead	living	dead	living	dead	living	dead
number of individuals	192	249	157	318	422	334	405	1161	846	290	592	638
population density (ind./10 cm3)	34	5641	84	37343	225	90962	95	139211	522	91654	140	4841
number of species	33	39	32	39	48	43	58	83	57	46	37	43
species number per 100 individuals	26	28	27	26	30	29	35	37	29	31	22	25
Fisher α index	11.48	12.98	12.15	11.67	13.94	13.13	18.54	20.46	13.79	15.4	8.75	10.41

Table 2.2.2 Foraminiferal census data of Sturrock and Murray (1981) and Murray et al. (1982).

Station number			12/97	3/13	18/166	17/152	1/1
Latitude (°N)			49.15	48.68	48.37	48.35	48.33
Longitude (°W)			5.75	6.93	6.15	6.98	7.53
Depth in m			122	145	145	176	170
Species	**mol**	**ts**					
Acervulina inhaerens	a	h			0.9	1.2	
Ammodiscus sp.	a	a	1.3				
Ammoscalaria pseudospiralis	f	a		1.6			
Bolivina difformis	f	h			3.5	3.6	2.0
Bolivina pseudoplicata	f/a	h		1.6	0.4		
Buliminella elegantissima	f	h			0.4		
Buliminella minutissima	f	h				0.6	
Cassidulina laevigata	f/a	h					4.0
Cassidulina obtusa	f	h		17.7	5.2	20.2	10.0
Cassidulina sp.	f	h		1.6	1.3	10.7	18.0
Cibicides lobatulus	a	h	2.6		12.1	1.2	
Clavulina obscura	f	a	9.2	1.6	7.4	1.2	
Dentalina sp.	f	h					2.0
Deuterammina (Deuterammina) rotaliformis	a	a				3.0	
Deuterammina (Lepidodeut.) ochracea	a	a			1.3	1.2	
Discorbina polyrraphes	a	h			0.9		2.0
Epistominella vitrea	f/a	h	1.3		1.7	0.6	
Fissurina lagenoides	f	h		1.6			
Fissurina orbignyana	f	h	2.6				
Gavelinopsis praegeri	f/a	h		1.6	7.8	4.8	2.0
Glabratella chasteri	f/a	h					2.0
Globocassidulinasubglobosa	f/a	h		3.2	3.0	10.7	4.0
Haplophragmoides fragile	f	a			0.4		
Labrospira jeffreysii	f/a	a	3.9	4.8	1.7	0.6	4.0
Lagena hexagona	f	h			0.4		
Lamarckina haliotidea	f/a	h					2.0
Miliolinella elongata	f/a	p	1.3				
Miliolinella oblonga	f/a	p		1.6			
Neoconorbina millettii	a	h	1.3				
Neoconorbina williamsoni	a	h			1.7	1.2	
Nonion pauperatus	f/a	h		1.6	0.9		
Ophthalmidium balkwilli	f/a	p	3.9	1.6	1.7		
Patellina corrugata	a	h		3.2	1.3	1.8	8.0
Planorbulina mediterranensis	a	h	1.3		0.4		
Pninaella nitidula	f	h	1.3				
Polymorphinidae spp.	f	h		1.6	0.4		
Polystomammina nitida	f/a	a		1.6		0.6	
Portatrochammina murrayi	f/a	a	7.9	8.1	5.6	0.6	
Quinqueloculina seminulum	f/a	p				0.6	
Remaneica helgolandica	a	a	1.3		0.4	4.8	4.0
Reophax moniliformis	f	a	3.9	1.6	0.4		
Reophax sp.	f	a	7.9	3.2	1.3	4.2	4.0
Robertinoides spp.	f	h					2.0
Rosalina anomala	f/a	h	1.3	1.6	1.7	0.6	
Rosalina bradyi	a	h				0.6	
Rosalina neapolitana	a	h			0.4		
Spirillina vivipara	a	h	13.2	11.3	6.5	3.6	12.0
Spiroplectinella sagittula	a	a	3.9		1.3	1.8	
Stainforthia fusiformis	f	h	1.3		0.9		

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Station number			12/97	3/13	18/166	17/152	1/1
Latitude (°N)			49.15	48.68	48.37	48.35	48.33
Longitude (°W)			5.75	6.93	6.15	6.98	7.53
Depth in m			122	145	145	176	170
Textularia bigenerinoides	f	a			0.4	0.6	
Textularia earlandi	f	a		1.6			
Trifarina angulosa	f	h	22.4	12.9	18.2	14.3	8.0
Tritaxis fusca	a	a	1.3				
Trochammina spp.	f/a	a	3.9	6.5	3.0	1.8	6.0
Valvulineria sp.	f	h	2.6	4.8	2.2	3.0	4.0
Unidentified flat Trochammina	a	a			1.3		
Unidentified Miliolina	f/a	p			0.4		
Unidentified Textulariina	f/a	a			0.9		
number of individuals			76	62	231	168	50
number of species			24	24	39	29	21
species number per 100 individuals			27	30	28	25	28
Fisher alpha			12.08	14.36	13.45	10.11	13.63

| Station number | | | 12/97 | 3/13 | 18/166 | 17/152 | 1/1 |

Table 2.2.3 Foraminiferal census data of Schönfeld and Altenbach (2005).

Station number			PO201/10-753		PO201/10-754		PO201/10-755	
Latitude (°N)			47.470		47.542		47.566	
Longitude (°W)			7.458		7.399		7.379	
Depth in m			684		398		207	
Living/Dead			living	dead	living	dead	living	dead
Species	**mol**	**ts**						
Acervulina inhaerens	a	h			1			0.4
Ammodiscus catinus	a	a			1.9	0.2	0.9	
Ammolagena clavata	a	a	0.9		1			
Ammomassilina alveoliniformis	a	a		0.7				
Ammosphaeroidina sphaeroidiniformis	f	a	0.9					
Amphicoryna scalaris	f	h	0.9	0.4		0.2		
Astacolus crepidulus	f	h			1	0.5	0.9	0.8
Bathysiphon capillare	a	a			1			
Bigenerina nodosaria	f	a	5.1	8.7				
Biloculinella irregularis	f	p					1.9	0.4
Bolivina dilatata	f/a	h				0.2		
Bolivina pseudopunctata	f/a	h	0.9					
Bolivina subaenariensis	f	h		2.6				
Bulimina striata striata	f	h			1	1.2		0.4
Cancris auriculus	f/a	h				0.2		
Cassidulina laevigata	f/a	h	2.5	0.7				0.4
Cibicides lobatulus	a	h	2.3	1.5	1	22.4	6.5	21.3
Cibicides refulgens	a	h	0.4	1.5	1	9.9	7.5	22.4
Cibicides sp.	a	h						0.4
Cibicidoides mollis	f/a	h		2.2				
Cibicidoides pachyderma	f/a	h		2.6				
Cibicidoides sp.	f/a	h				9.2		10.6
Clavulina mexicana	f	a		0.4				
Cristellaria acutauricularis	f	h			1			
Crithionina albida	a	a	0.9					
Crithionina sp.	a	a	2.1		2		2.8	
Cyclammina cancellata	f	a	0.9					
Deuterammina (Lepidodeut.) ochracea	a	a			1			
Discanomalina coronata	a	h		2.6				
Discanomalina semipunctata	a	h			1.1	4	1.4	3.5
Eggerelloides scaber	f	a	0.9					
Elphidium excavatum	f/a	h				0.5		
Epistominella rugosa	f/a	h	0.9	0.4				
Eponides repandus	f/a	h			1.9		0.9	
Eponides repandus var. *concameratus*	f/a	h				0.7		3.2
Gaudryina rudis	a	a			1.9	2.1	0.9	3.9
Gavelinopsis praegeri	f/a	h				0.2	1.9	
Globobulimina affinis	f	h				0.2		
Globobulimina sp. 324	f	h				0.2		
Globocassidulina subglobosa	f/a	h	0.9					
Gyroidina neosoldanii	f	h		0.4				
Hanzawaia concentrica	a	h	0.4					0.4
Hoeglundina elegans	f	h	2.5	0.7	2.9	0.2	0.9	0.4
Hormosinella guttifera	f	a	1.7					
Hyalinea balthica	f	h		11.6				
Hyperammina fragilis	f	a			2.9			
Hyperammina friabilis	f	a			0.4			
Hyperammina laevigata	f	a					0.9	
Jaculella obtusa	f	a	1.7		4.9	0.2	7.4	

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Station number			PO201/10-753		PO201/10-754		PO201/10-755	
Latitude (°N)			47.470		47.542		47.566	
Longitude (°W)			7.458		7.399		7.379	
Depth in m			684		398		207	
Living/Dead			living	dead	living	dead	living	dead
Labrospira jeffreysii	f/a	a			5.8		2.8	
Lagena sulcata	f	h					1.9	
Lenticulina atlantica	f	h		1.1	1.9		0.9	
Lenticulina gibba	f	h		0.4				
Lenticulina rotulata	f	h	0.9		1.9	4.7	1.9	4.7
Marsipella cylindrica	f	a	0.9					
Marsipella elongata	f	a			1.1			
Melonis barleeanum	f	h	1.7	1.8	1	0.2		
Miliolinella elongata	f/a	p				0.2		
Miliolinella subrotunda	f/a	p				0.2	0.9	
Mississippina concentrica	f/a	h			0.1	0.5	0.9	0.4
Nonionella auricula	f	h	0.9					
Placopsilina sp.	a	a	4		6.6		3.125	
Planispirinoides bucculentus	f/a	p			1			
Planorbulina mediterranensis	a	h				0.5		
Planulina ariminensis	a	h	3.2	6.9	0.1	1.4		
Polystomammina nitida	f/a	a			1		0.9	
Pyrgo depressa	f	p		0.4				
Pygro fornasinii	f	p				0.2	3.7	0.8
Pyrgo lucernula	f	p	0.9	0.7				
Pygro oblonga	f	p	0.9		1.9	0.2		
Pyrgo sp.	f	p					0.9	
Quinqueloculina lata	f/a	p				0.2		
Quinqueloculina seminulum	f/a	p		1.5	1	0.7	0.9	0.4
Reophax bilocularis	f	a	5.1					
Reophax calcareus	f	a			17.3	0.2	14.8	
Reophax difflugiformis	f	a			1		0.9	
Reophax scorpiurus	f/a	a	4.2	0.7	4.8			
Reophax sp.	f	a					0.9	
Rhabdammina abyssorum	f/a	a	3.4		1.9			
Robertinoides bradyi	f/a	h	0.9				1.5	
Robertinoides suecicum	f	h				0.7		
Rosalina anomala	f/a	h				3.8		
Rosalina globularis	a	h						1.6
Rotaliammina concava	a	a			1			
Saccammina sphaerica	f/a	a	0.2		2.9		1.9	
Saccorhiza ramosa	f/a	a			0.2			
Sigmoilopsis schlumbergeri	f	a		1.5				
Siphonina bradyana	f/a	h	0.9	0.7				
Siphotextularia bermudezi	f/a	a	0.9		1	0.2		
Siphotextularia caroliniana	f	a	0.9	0.7		4.7		3.2
Siphotextularia cf. *occidentalis*	f	a					2.8	1.6
Sphaeroidina bulloides	f/a	h	4.2	0.7				
Spirillina vivipara	a	h			0.4			
Spiroplectinella sagittula	a	a		0.7	1	8.2	4.6	4.3
Textularia pseudogramen	f/a	a			3.9	5.9	9.3	9.8
Tolypammina vagans	a	a			1			
Tolypammina sp.	a	a					1.9	
Trifarina angulosa	f	h			3.9	12.9	2.8	2.8
Trifarina bradyi	f	h	2.5	0.4	1.9	0.2		
Trifarina fornasinii	f	h				0.5	0.9	

Station number			PO201/10-753		PO201/10-754		PO201/10-755	
Latitude (°N)			47.470		47.542		47.566	
Longitude (°W)			7.458		7.399		7.379	
Depth in m			684		398		207	
Living/Dead			living	dead	living	dead	living	dead
Triloculina tricarinata	f/a	p		0.4				
Tritaxis conica	a	a	1.1		0.1			1.6
Tritaxis fusca	a	a	1.1		0.1			
Trochammina squamata	f/a	a	10.8		2.4			
Tumidotubus albus	a	a	4.9		1		0.9	
Uvigerina auberiana	f	h	0.9	0.4	1	0.7		
Uvigerina cf. *bifurcata*	f	h	7.6	4.4				
Uvigerina mediterranea	f	h	9.3	38.9				
Vulvulina pennatula	a	a		0.4				0.4
others			1.8	0.8	2	0.2	2.8	
number of individuals			118	275	104	425	108	254
population density (ind./10 cm^3)			11	1660	23	24044	23	6899
number of species			45	36	51	41	38	26
species number per 100 individuals			43	26	51	26	37	19
Fisher α index			26.56	11.07	39.58	11.19	20.88	7.26

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Plates

Plate 1

Scanning electron micrographs of abundant species from the Celtic Sea (chapter 2). All micrographs were taken with a CamScan 44/EDX scanning electron microscope.

Fig. 1 *Trifarina angulosa*

Fig. 2 *Gavelinopsis praegeri*, **a** dorsal view, **b** ventral view

Fig. 3 *Bolivina difformis*

Fig. 4 *Spiroplectinella sagittula*

Fig. 5 *Cassidulina obtusa*

Fig. 6 *Cibicides lobatulus*, **a** ventral view, **b** dorsal view

Fig. 7 *Trochammina squamata* juv., **a** ventral view, **b** dorsal view

Fig. 8 *Rotaliammina concave*, **a** ventral view, **b** dorsal view

Fig. 9 *Textularia pseudogramen*

Fig. 10 *Portatrochammina murrayi*, **a** ventral view, **b** dorsal view

Fig. 11 *Globocassidulina subglobose*, **a** dorsal view, **b** ventral view

Fig. 12 *Reophax curtus*

Plate 1
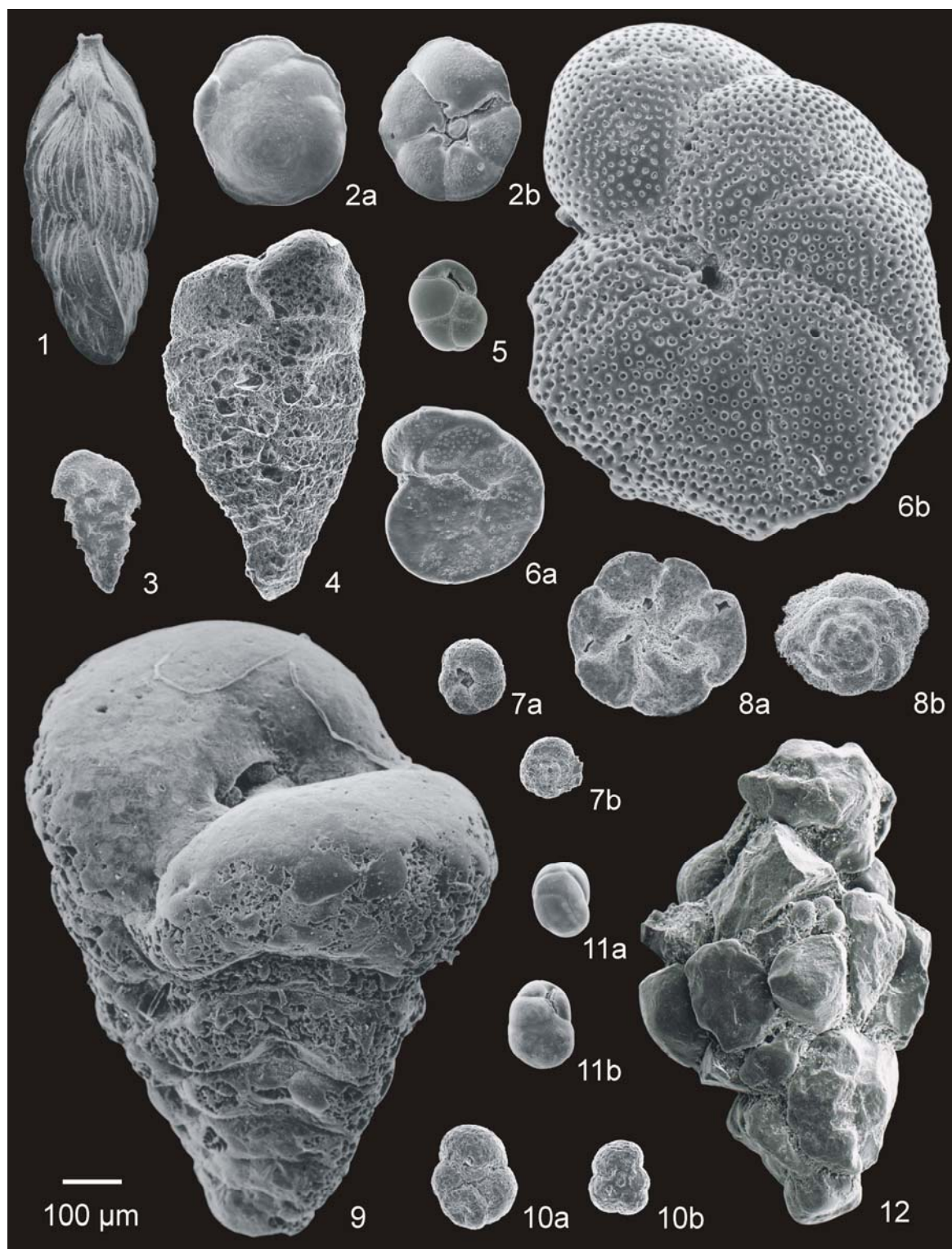
Plate 2

Optical microscope photographs of abundant species from the Celtic Sea (chapter 2). All photographs were taken with a Keyence VHX – 700 FD camera.

Fig. 1 *Reophax curtus*

Fig. 2 *Textularia pseudogramen*

Fig. 3 *Cassidulina obtusa*, **a** ventral view, **b** dorsal view

Fig. 4 *Rotaliammina concave*, **a** dorsal view, **b** ventral view

Fig. 5 *Trifarina angulosa*

Fig. 6 *Bolivina difformis*

Fig. 7 *Trochammina squamata*, **a** ventral view, **b** dorsal view

Fig. 8 *Cibicides lobatulus*, **a** dorsal view, **b** ventral view

Fig. 9 *Portatrochammina murrayi*, **a** dorsal view, **b** ventral view

Fig. 10 *Epistominella vitrea*, **a** dorsal view, **b** ventral view

Fig. 11 *Spiroplectinella sagittula*

Fig. 12 *Gavelinopsis praegeri*, **a** dorsal view, **b** ventral view

Plate 2
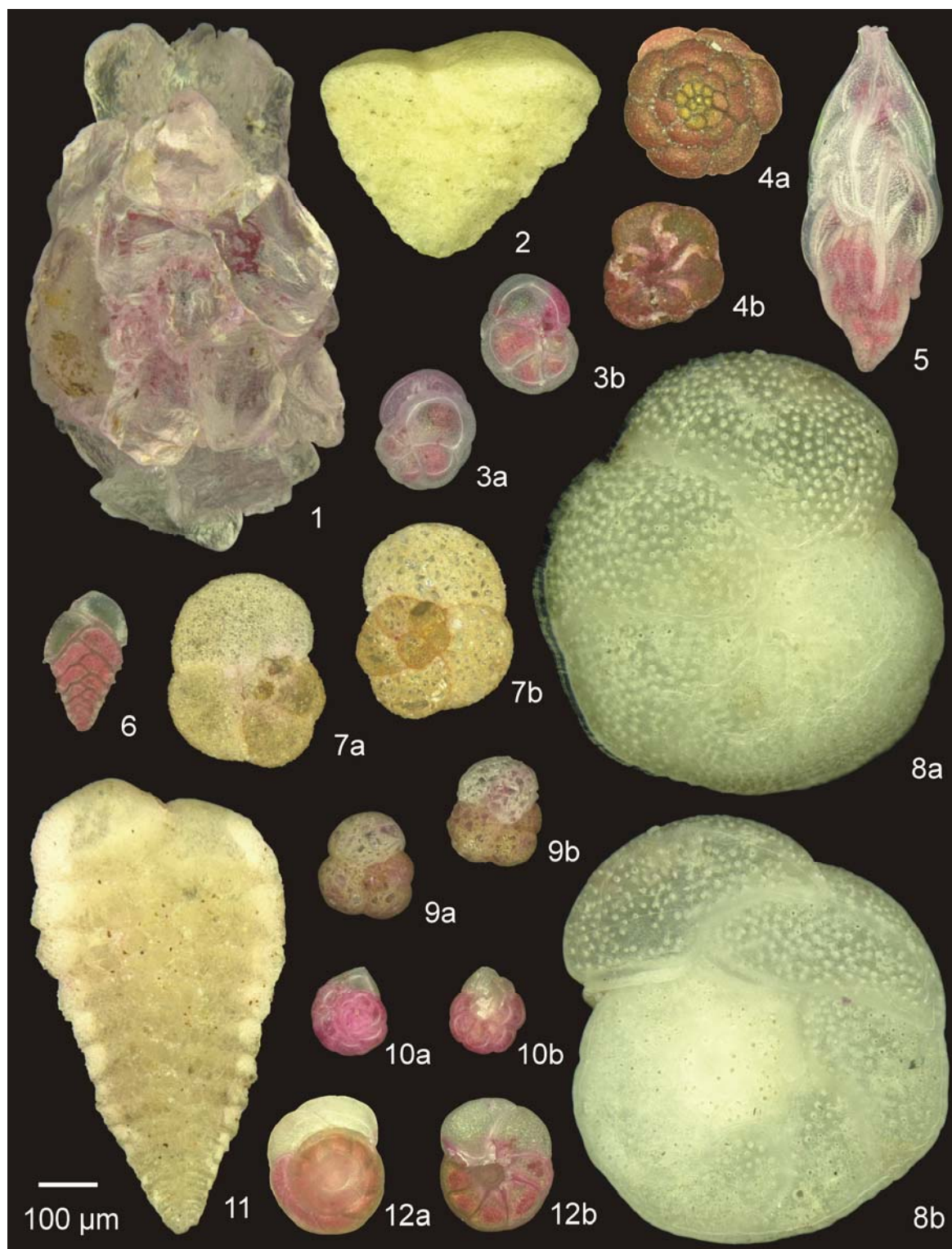
Plate 3

Optical microscope photographs of species of the family Trochamminidae from the Celtic Sea (chapter 3).

Fig. 1 *Paratrochammina (Paratrochammina) tricamerata*, **a** spiral view, **b** umbilical view

Fig. 2 *Trochammina advena*, **a** spiral view, **b** umbilical view

Fig. 3 *Portatrochammina pacifica*, **a** spiral view, **b** umbilical view

Fig. 4 *Deuterammina (Lepidodeuterammina) mourai*, **a** spiral view, **b** umbilical view

Fig. 5 *Rotaliammina siphonata*, **a** spiral view, **b** umbilical view

Plate 3
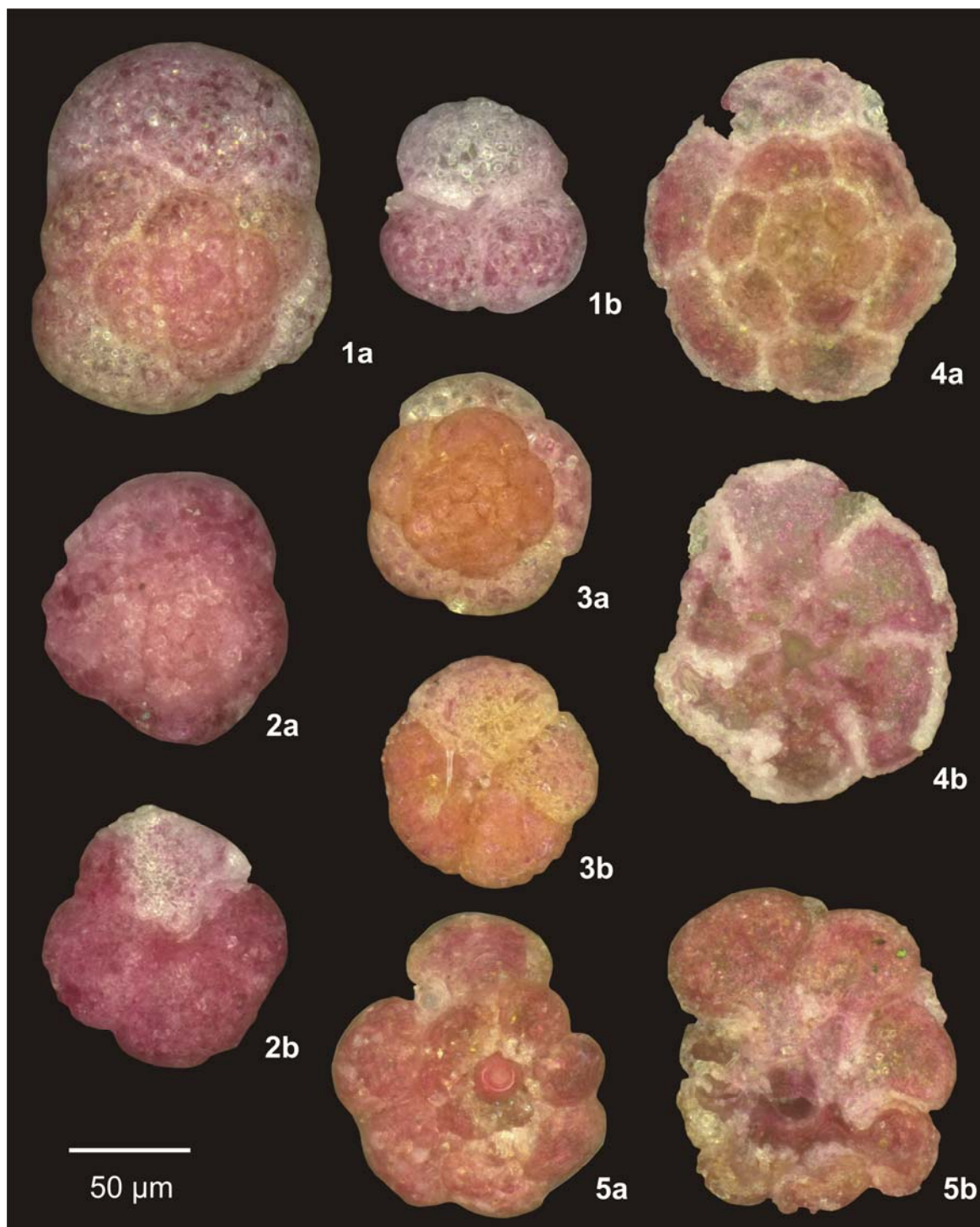
Plate 4

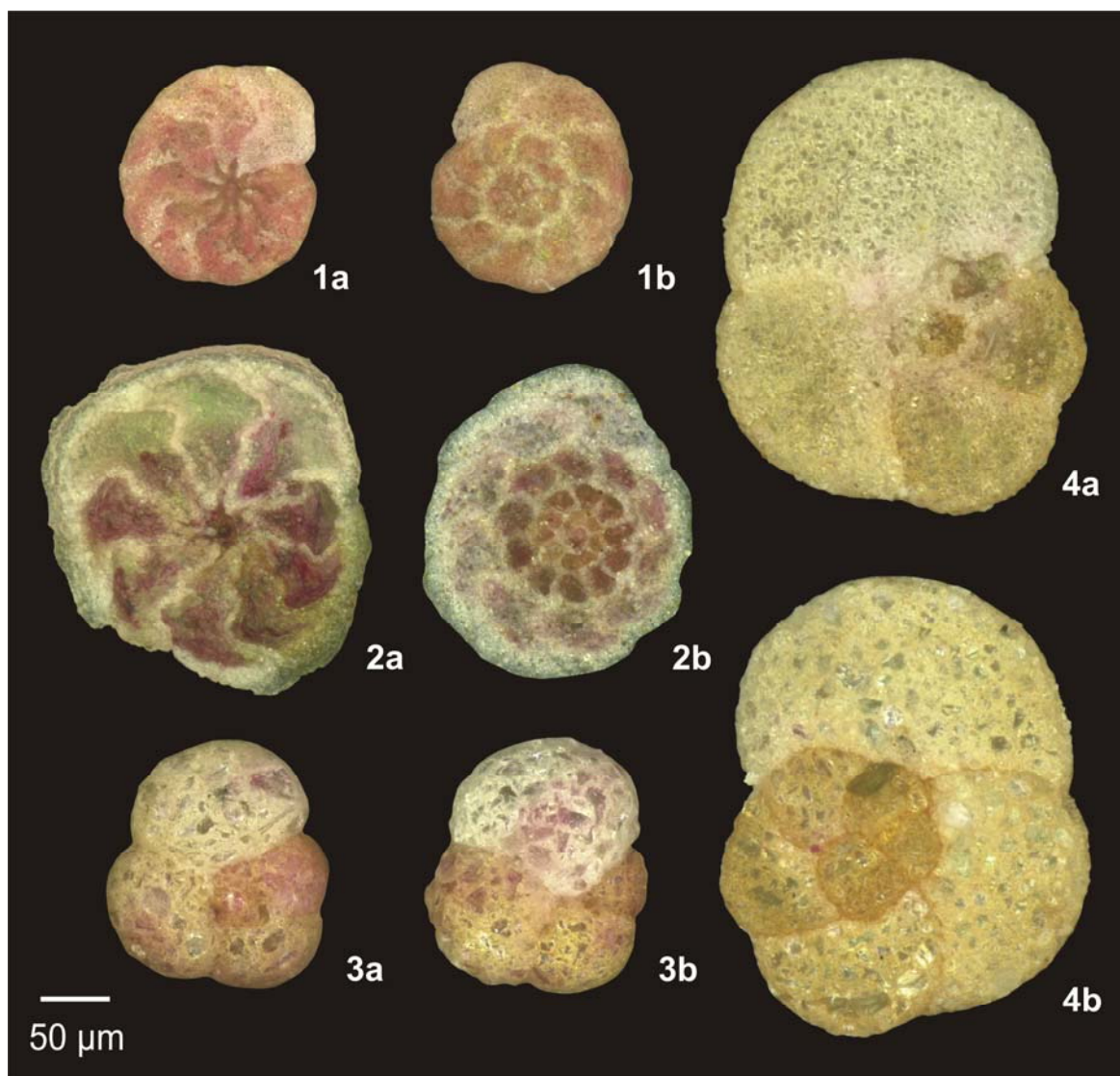Optical microscope photographs of species of the family Trochamminidae from the Celtic Sea (chapter 3).

Fig. 1 *Paratrochammina (Lepidoparatrochammina) haynesi*, **a** spiral view, **b** umbilical view

Fig. 2 *Trochammina astrifica*, **a** umbilical view, **b** spiral view

Fig. 3 *Deuterammina (Lepidodeuterammina)* sp., **a** spiral view, **b** umbilical view

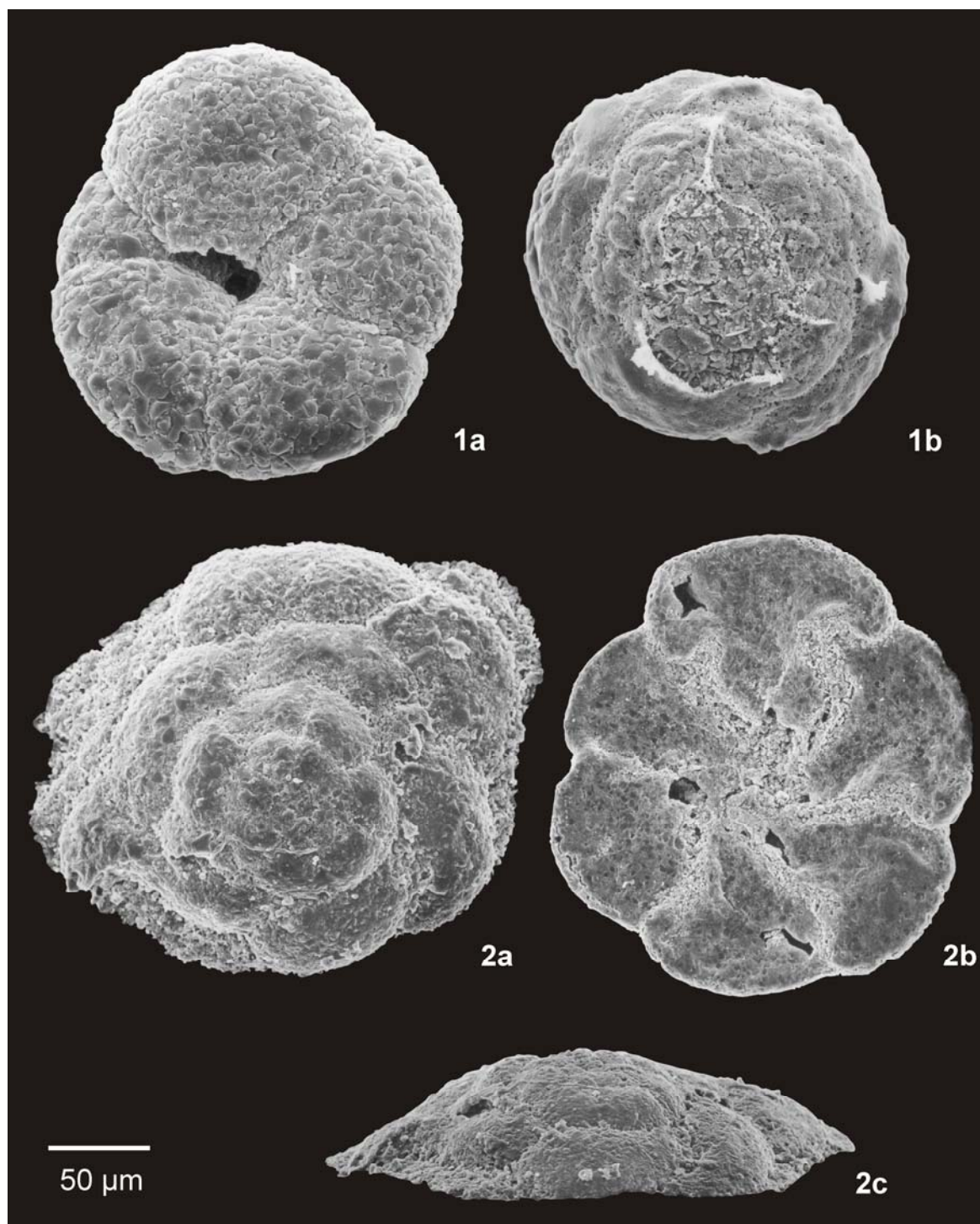**Fig. 4** *Deuterammina (Deuterammina) balkwilli*, **a** spiral view, **b** umbilical view

Plate 4
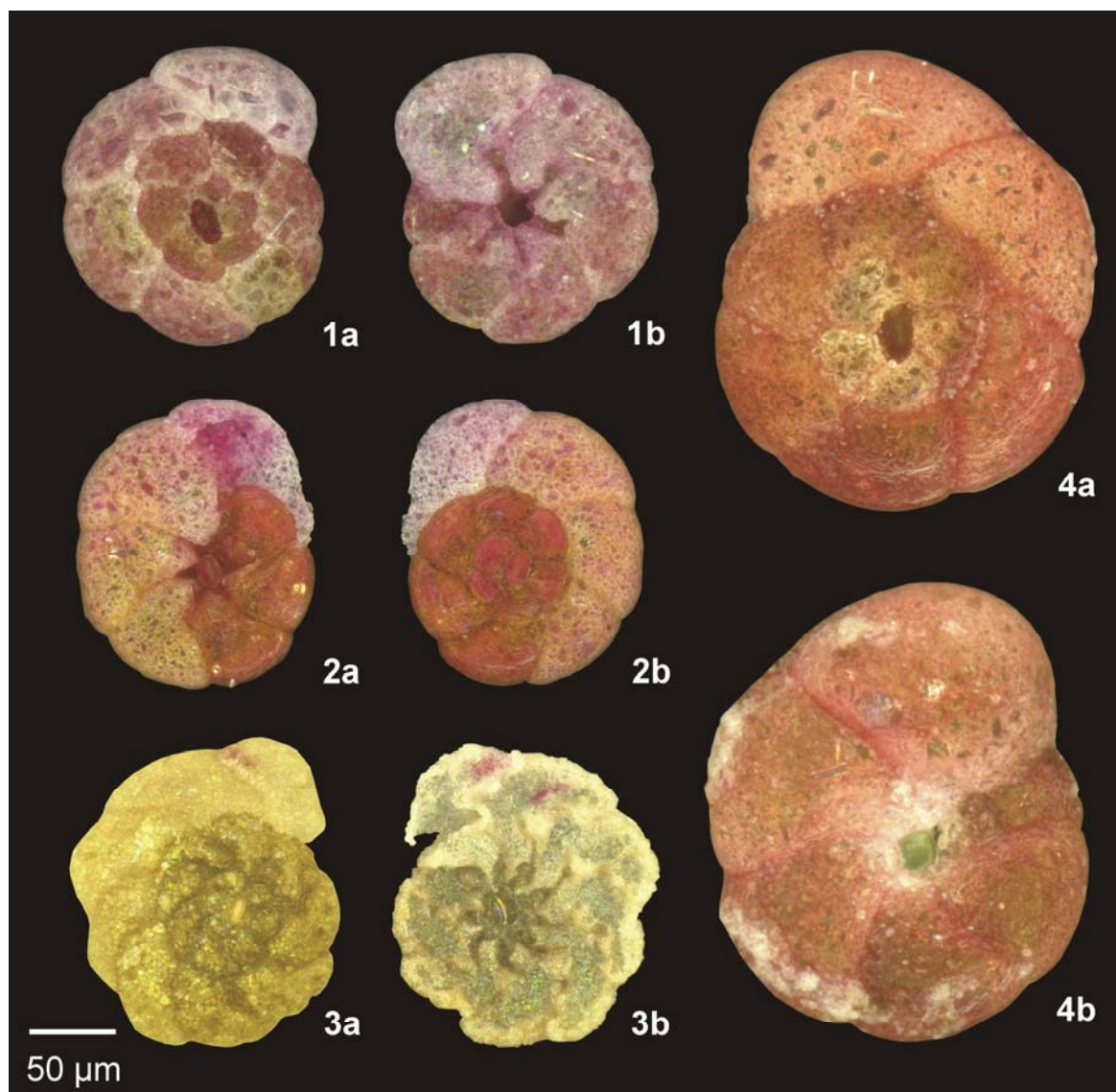
Plate 5

Scanning electron micrographs of species of the family Trochamminidae from the Celtic Sea (chapter 3).

Fig. 1 *Deuterammina (Lepidodeuterammina) sinuosa*, **a** umbilical view, **b** spiral view, **c** edge view

Fig. 2 *Deuterammina (Lepidodeuterammina) ochracea*, **a** umbilical view, **b** spiral view, **c** edge view

Fig. 3 *Portatrochammina murrayi*, **a** spiral view, **b** umbilical view

Fig. 4 *Trochammina squamata* juv., **a** umbilical view, **b** spiral view
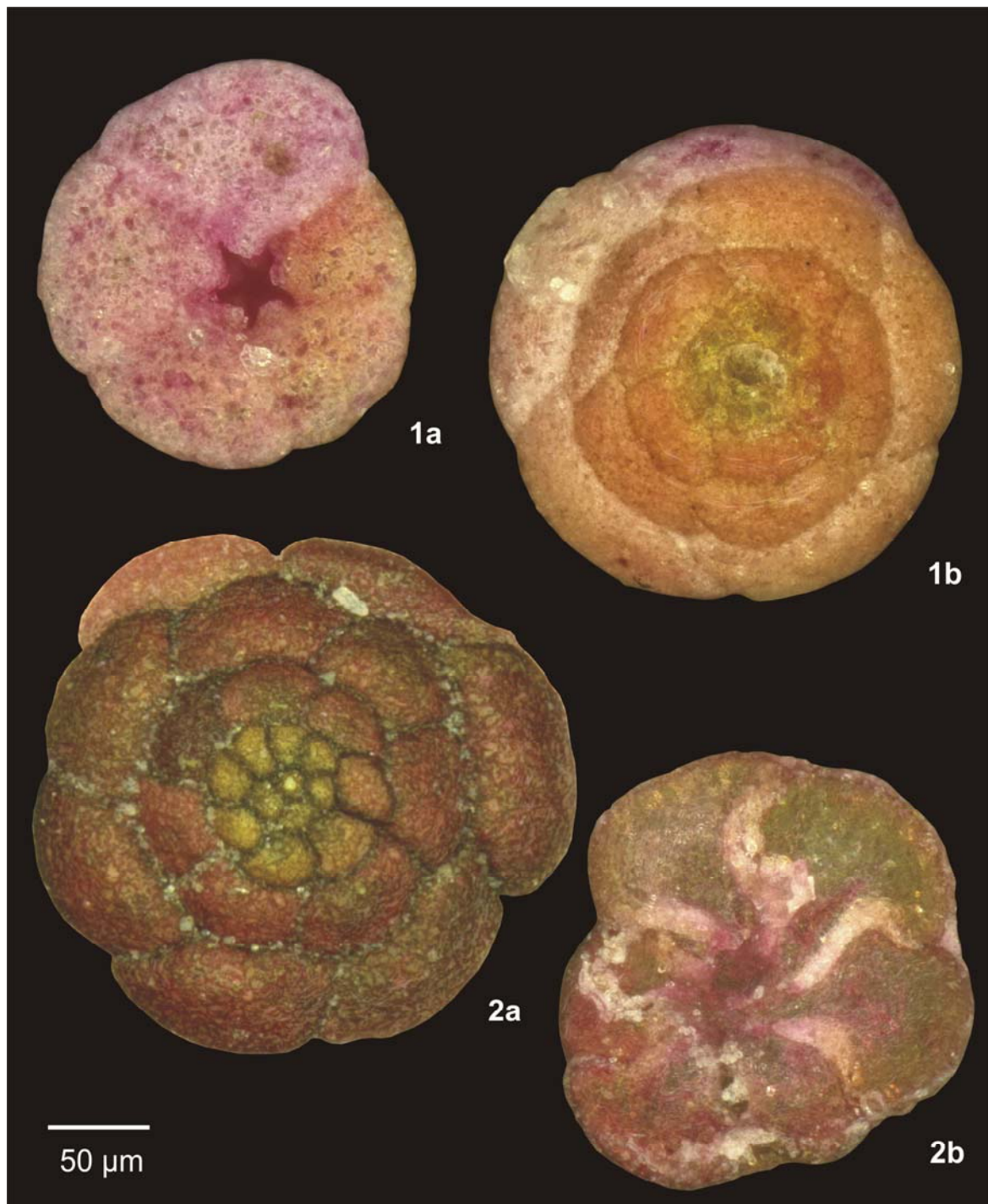
Plate 5
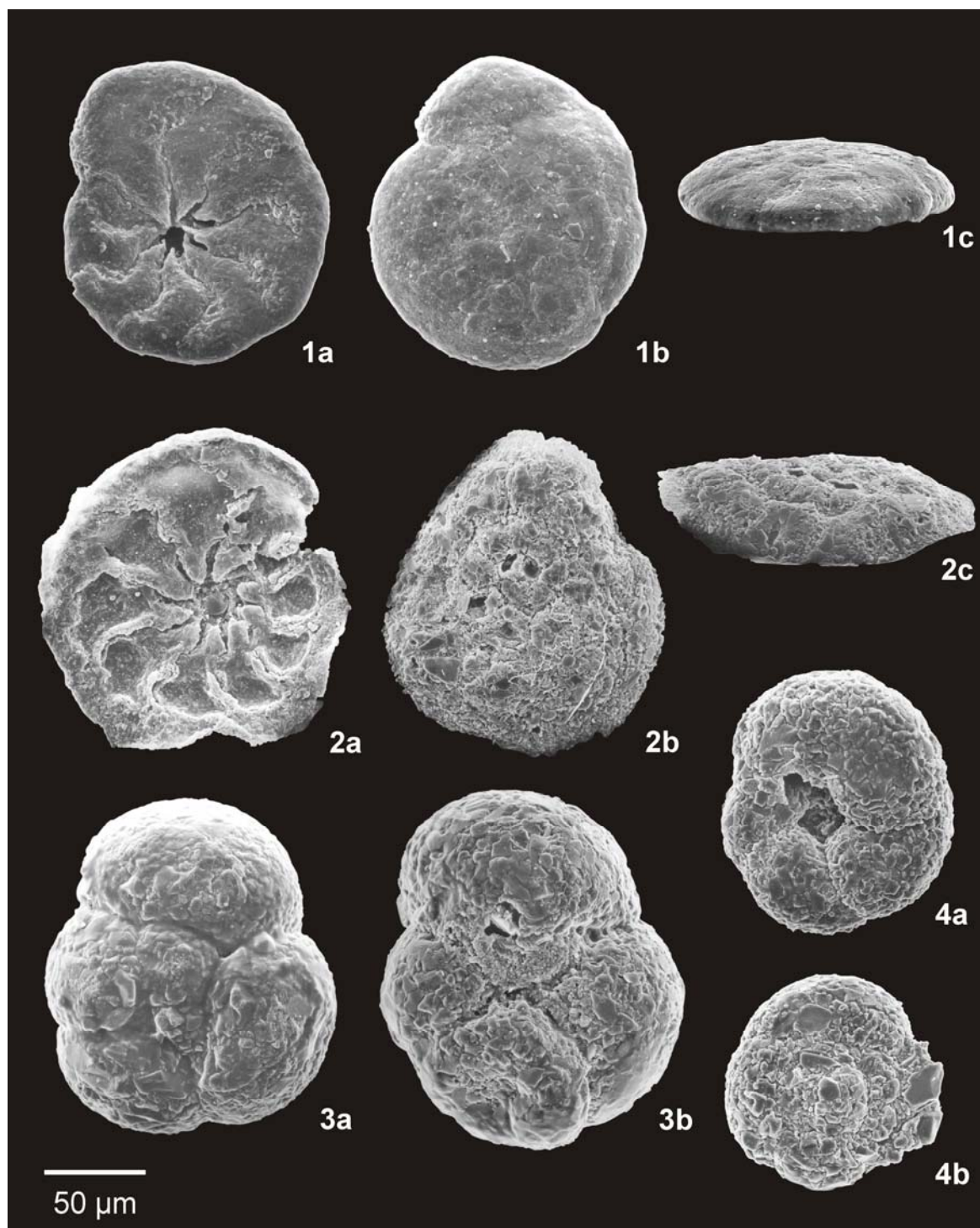
Plate 6

Optical microscope photographs of species of the family Trochamminidae from the Celtic Sea (chapter 3).

Fig. 1 *Deuterammina (Lepidodeuterammina) sinuosa*, **a** umbilical view, **b** spiral view

Fig. 2 *Deuterammina (Lepidodeuterammina) ochracea*, **a** umbilical view, **b** spiral view

Fig. 3 *Portatrochammina murrayi*, **a** spiral view, **b** umbilical view

Fig. 4 *Trochammina squamata*, **a** umbilical view, **b** spiral view

Plate 6

Plate 7

Scanning electron micrographs of species of the family Trochamminidae from the Celtic Sea (chapter 3).

Fig. 1 *Deuterammina (Deuterammina) rotaliformis*, **a** umbilical view, **b** spiral view
Fig. 2 *Rotaliammina concava*, **a** spiral view, **b** umbilical view, **c** edge view

Plate 7

Plate 8

Optical microscope photographs of species of the family Trochamminidae from the Celtic Sea (chapter 3).

Fig. 1 *Deuterammina (Deuterammina) rotaliformis*, **a** umbilical view, **b** spiral view

Fig. 2 *Rotaliammina concava*, **a** spiral view, **b** umbilical view

Plate 8

Plate 9

Optical microscope photographs of species of the family Trochamminidae from the Celtic Sea (chapter 3).

Fig. 1 *Polystomammina nitida*, **a** spiral view, **b** umbilical view

Fig. 2 *Ammoglobigerina shannoni*, **a** spiral view, **b** umbilical view

Fig. 3 *Tritaxis conica*, **a** umbilical view, **b** spiral view

Fig. 4 *Trochamminopsis pusilla*, **a** spiral view, **b** umbilical view

Plate 9
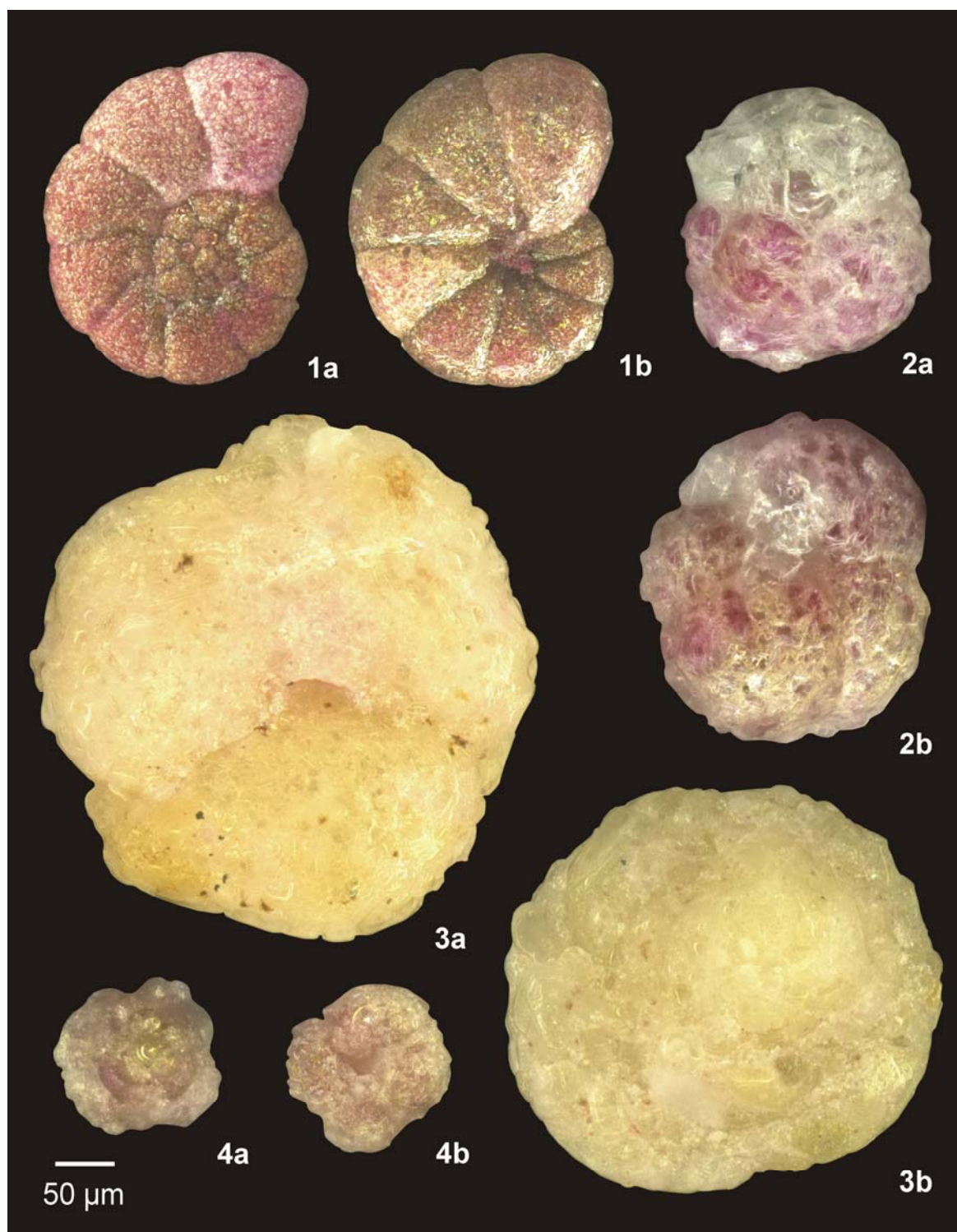
Plate 10

Optical microscope photographs of species of the family Trochamminidae from the Celtic Sea (chapter 3). All specimens are illustrated in edge view.

Fig. 1 *Tritaxis conica*

Fig. 2 *Polystomammina nitida*

Fig. 3 *Rotaliammina concava.*

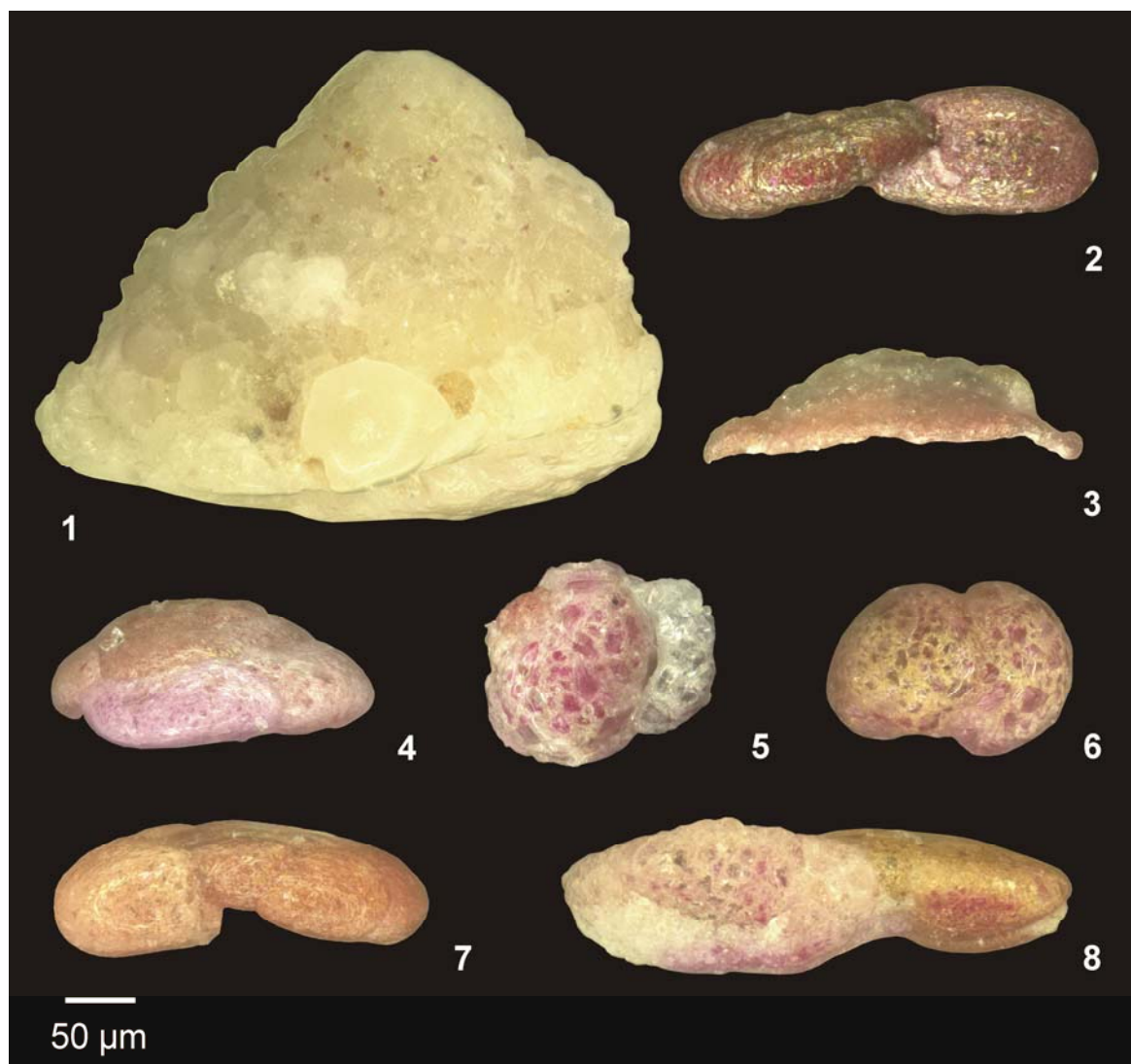**Fig. 4** *Deuterammina (Deuterammina) rotaliformis*

Fig. 5 *Ammoglobigerina shannoni*

Fig. 6 *Portatrochammina murrayi*

Fig. 7 *Deuterammina (Deuterammina) balkwilli*

Fig. 8 *Trochammina squamata*

Plate 10

Plate 11

Optical microscope photographs of species of the family Trochamminidae from the Celtic Sea (chapter 3). All specimens are illustrated in edge view.

Fig. 1 *Trochamminopsis pusilla*

Fig. 2 *Paratrochammina (Paratrochammina) tricamerata*

Fig. 3 *Deuterammina (Lepidodeuterammina) sinuosa*

Fig. 4 *Deuterammina (Lepidodeuterammina) ochracea*

Fig. 5 *Paratrochammina (Lepidoparatrochammina) haynesi*
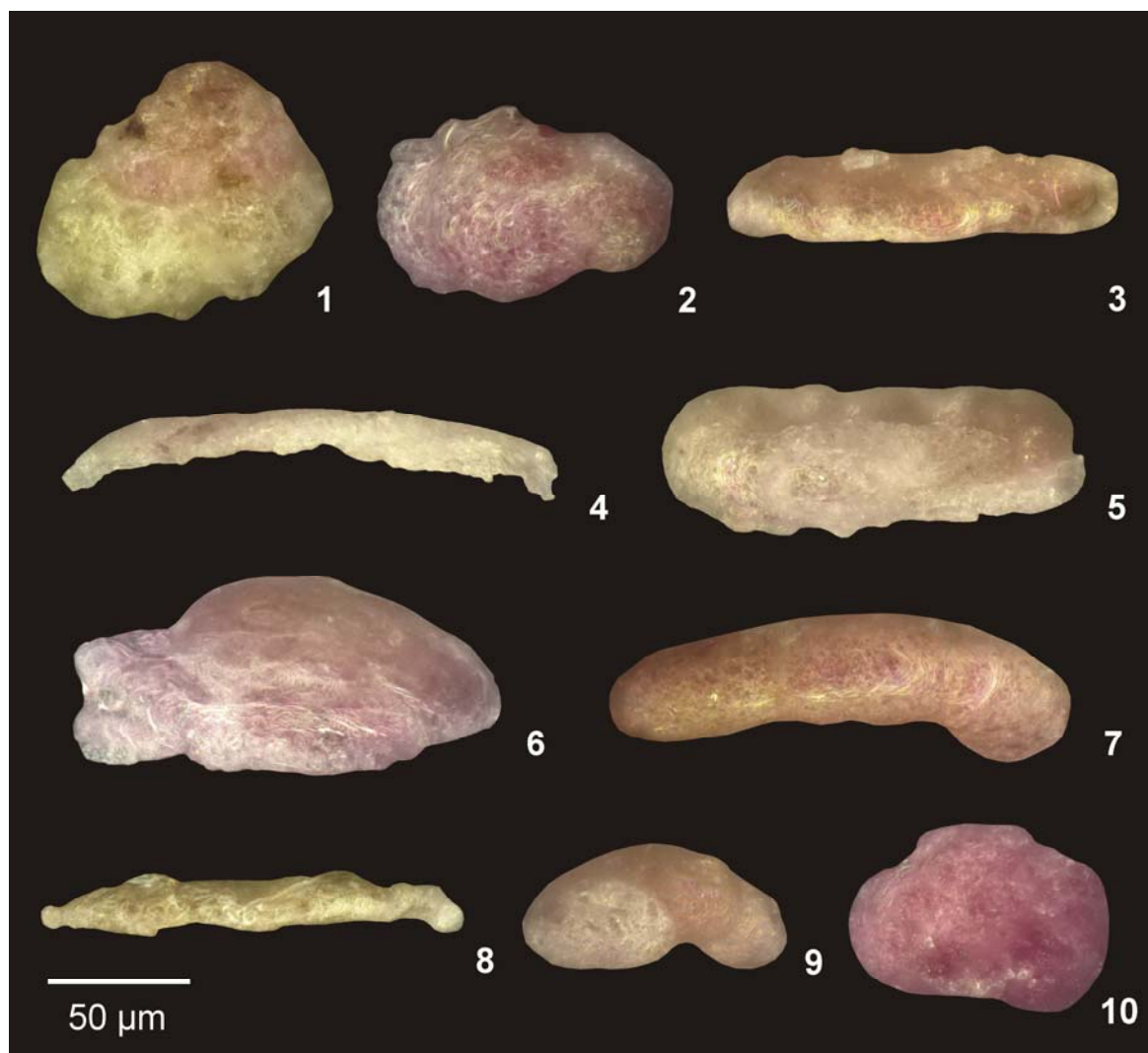
Fig. 6 *Deuterammina (Lepidodeuterammina) mourai*

Fig. 7 *Trochammina astrifica*

Fig. 8 *Deuterammina (Lepidodeuterammina)* sp.

Fig. 9 *Portatrochammina pacifica*

Fig. 10 *Trochammina advena*

Plate 11

Plate 12

Optical microscope photographs of species of the family Trochamminidae from the Celtic Sea (chapter 3) showing close-ups of axial depression and apertural features.

Fig. 1 *Trochammina advena*

Fig. 2 *Trochammina squamata*

Fig. 3 *Paratrochammina (Paratrochammina) tricamerata*

Fig. 4 *Paratrochammina (Lepidoparatrochammina) haynesi*

Fig. 5 *Portatrochammina murrayi*

Fig. 6 *Rotaliammina concava*

Fig. 7 *Rotaliammina siphonata*

Fig. 8 *Tritaxis conica*

Fig. 9 *Polystomammina nitida*

Fig. 10 *Deuterammina (Deuterammina) balkwilli*

Fig. 11 *Deuterammina (Deuterammina) rotaliformis*

Fig. 12 *Deuterammina (Lepidodeuterammina) mourai*

Fig. 13 *Deuterammina (Lepidodeuterammina) ochracea*

Fig. 14 *Deuterammina (Lepidodeuterammina) sinuosa*

Fig. 15 *Deuterammina (Lepidodeuterammina)* sp.

Plate 12