Benthic Foraminiferal Assemblage Formation: Theory and Observation for the European Arctic Margin

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Abstract:

We use theory and observation to determine how benthic foraminiferal populations living in a range of sedimentary microenvironments are translated into fossil assemblages along the continental margin of the European Arctic. We examine downcore stained (cell tracker green and rose Bengal) and total species shell abundances through the sediment mixing (bioturbation) zone. This, in combination with porewater geochemical measurements, allows us to establish zones of production and destruction for species' shells, and deduce how the fossil record is being generated by the living community. For many taxa, shell production is high in the upper, oxic, sedimentary layer, but destruction in this zone is also high. Hence, contribution to the fossil record is biased to more infaunal populations and species. Taxa producing near, or below, the anoxic boundary of the sediments are particularly important to the developing fossil record of the fjord environment. We find that taxon relative and absolute abundances change continuously through the biologically active sediment profile. This has implications for reconstructing paleoenvironments using benthic foraminiferal assemblages, and potentially for the geochemistry of individual fossil taxa.

Keywords: benthic foraminifera, Arctic European margin, foraminiferal assemblages, microfossil preservation, benthic biogeochemistry

1. Introduction

It has been long recognized that foraminiferal assemblages preserved in the marine record can differ markedly from taxon standing stocks in the same location (e.g. Murray, 1976; Boltovskoy and Wright, 1976; Scott and Medioli, 1980; Douglas et al., 1980; Mackensen and Douglas, 1989; Denne and Sen Gupta, 1989; Loubere and Gary, 1990; Murray, 1991; Mackensen et al., 1995; Duros et al., 2012). This difference has been ascribed to diagenesis and differential preservation of taxon shells (Smith, 1987; Loubere et al., 1993; Martin, 1999; Murray and Alve, 1999; for the northern North Atlantic: Steinsund and Hald, 1994; Hald and Steinsund, 1996; Alve and Murray, 1997; Alve et al., 2011). It will also be a product of differential rates of shell production among species (standing stock abundance counts do not reflect relative production rates among taxa; e.g. Scott and Medioli, 1980; Loubere, 1997).

For individual taxa, what enters the fossil record depends on an interplay of microhabitat location, geochemical gradients in the sediments and bioturbation mixing of shells through the reactive interval of the seabed. Foraminiferal production occurs in selected micro-environments in the BAZ (biologically active zone, Jorissen et al., 1995; Jorissen, 1999; Loubere, 1997). This production is filtered through different geochemical regimes which develop in the zone of active sediment mixing. Organic carbon oxidation in the sediment profile regulates pore water oxygen concentrations and the dissolution of carbonate (Emerson and Bender, 1981; Archer et al., 1989; Aller, 1982; Reaves, 1986; Jahnke et al., 1994; Sarmiento and Gruber, 2006). The former influences where different species of foraminiferal live (Loubere et al., 1993; Jorissen et al., 1995; Loubere, 1997), and the latter influences preservation of the shells those species generate (Loubere, 1989; Loubere et al., 2011).

Analysis of short lived radio-isotopes in the sediment profile has demonstrated that seabed bioturbation mixing is rapid (Sarmiento and Gruber, 2006). For instance, in most open ocean settings, with sedimentation rates generally between 1 and 50cm/kyr (0.01 to 0.5 millimeters per year), Pb-210 concentrations in the upper 5 to 10cm of the sediments are homogenized in spite of a half-life of only about 22 years. This would imply that empty foraminiferal shell abundances and distributions will also be rapidly homogenized in the mixing zone. Abundance trends in the bioturbated layer could only exist if created by dynamic processes with rates significantly higher than that of the mixing. Such processes include foraminiferal production of shells, and geochemical reactions within the sediments (summary in Sarmiento and Gruber, 2006). Both of these are fast enough to impose abundance/concentration gradients on a well mixed medium such as surficial marine sediments.

The dynamic interplay of shell production and geochemically driven destruction through the BAZ can be modeled in a theoretical sense (Fig. 1, Loubere, 1989).

Figure 1. Modeled (Loubere, 1989) shell abundances in a sediment profile in which there is a well developed bioturbation zone and foraminiferal taxa inhabiting three levels of microhabitat (a: epifaunal, b: shallow infaunal, c: deeper infaunal). Production is limited to those habitation zones, but shell destruction is assumed to occur at a constant rate through the bioturbation zone, and the bioturbation process is modeled as in Guinasso and Schink (1975) for typical marine sediments.

A simple model assumes that benthic foraminiferal species are broadly zoned into vertical microhabitats (epifaunal, shallow infaunal, deep infaunal) (e.g. Jorissen, 1999) in the BAZ, that sediments are uniformly bioturbated in that zone, that shells are destroyed at a constant rate through the BAZ, and that the fossil assemblage is stabilized at the base of BAZ (bottom of the bioturbation zone). Figure 1 shows that we may expect that foraminiferal taxa whose production is concentrated in surface sediments will show decreasing total shell abundance down to the base of the mixing zone, taxa which are shallow infaunal will show a subsurface peak in abundance, while deeper infaunal taxa will show increasing abundance towards the level of fossil assemblage stabilization.

The abundance profiles predicted by modeling are dynamic, with a steady state developed via a balance of shell production and destruction rates, and a sediment ‘diffusion’ rate via the vertical mixing caused by bioturbation.

The steepness of abundance gradients depends on having significant destructive processes in the sediments, as shown in Fig. 1. At high loss rates, the shell abundance profiles will converge on the standing stock (living specimen) abundance distribution in the sediments since shells will be lost as soon as their foraminiferal producers die or abandon them (nothing survives to fossilize).

It is important that in most open marine settings, shell abundance profiles within the sediment bioturbation zone will not be the result of recent (within the time span averaged in the mixing zone) changes in environmental conditions. This is because sedimentation rates in open ocean settings are low compared to the mixing rate of sediments in the BAZ (Sarmiento and Gruber, 2006). Consequently, mixing will tend to rapidly homogenize concentration gradients in the

sediments; and any gradients that are present must be actively maintained against the homogenization process.

The existence of foraminiferal shell abundance gradients within the mixing zone of sediments, should those be present, offers a means of analyzing where different taxa release shells into the sediment column, and the fate of those shells as they are processed prior to inclusion into the fossil record. It is clear that foraminiferal production is distributed among different microenvironments, that sediment mixing is rapid and efficient and that geochemical reactions driven by organic carbon oxidation occur at rates which will impact foraminiferal shell abundances in the sediment profile. So, we can expect that dynamically maintained taxon shell abundance gradients, similar to those shown in Fig. 1, are present in marine sediments, especially in settings with a limited supply of carbonate to buffer geochemically driven dissolution (e.g. sediments with higher terrigenous content).

2. Study Location and Environmental Conditions

We test for the presence of taxon abundance gradients within the mixed layer of marine sediments using a sample transect along the European Arctic continental margin. The northern North Atlantic is a region where benthic foraminiferal assemblages have been used routinely for paleoceanic/paleoclimate research (e.g. Mackensen et al., 1985; Wollenburg, 1995; Husum and Hald, 2002; Ślubowska-Woldengen et al., 2008; Jernas, 2012 and Jernas et al., 2013; Norgaard-Pedersen and Mikkelsen, 2009), and a better understanding of assemblage formation processes will allow refined analysis of the sediment foraminiferal record.

The European Arctic margin is a setting in which the primary environmental variable influencing foraminiferal microhabitats and shell preservation is changing labile organic carbon flux to the seabed (Table 1). This varying flux generates progressive change in the habitation

zone of the foraminifera and the geochemical profiles in the sediments which control shell destruction. Using a combination of living (stained) and total foraminiferal shell abundance profiles through the sediment mixing zone, along with geochemical analysis of pore waters, we are able to assess foraminiferal shell processing in the sediment column, and test our understanding of the way the fossil assemblage is formed.

Multi-core sediment profiles were collected in the Fram Strait and continental margin of Svalbard (Fig. 2) to provide data to test assemblage formation theory. Table 1 lists sites and conditions.

Table 1. Cores used in this study (see fig. 3). Bottom water (BW) temperature range from Conkright et al. (1994) and CTD at time of coring, bottom water oxygen range from micro-electrodes at contact with sediments. Oxygen flux estimated using the smoothest oxygen profile at each site and following standard methodology (e.g. Froelich et al., 1979; Goloway and Bender, 1982; Sarmiento and Gruber, 2006). Results provide a relative sense of benthic organic carbon oxidation rates across the depth transect.

Core	Date	Lat (N)	Long(E)	WD(m)	T(BW)	O ₂ (S-W ¹) (umol/l)	O ₂ flux(sed.) (umol/m ² sec)
NP08-16-40	8/21/08	78.9862	11.837	319	1.3-2	265-300	-0.6976
JM08WP349	8/13/08	75.989	13.644	1026	0 – 1	310-330	-0.0181
JM08WP348	8/12/08	75.9956	13.298	1264	0 – 1	310-330	-0.0155
JM08WP347	8/12/08	76.0023	12.8913	1500	0 – 1	310-330	-0.0101
JM08WP337	8/9/08	78.1355	8.507	1733	-1 – 1	300-340	-0.0184
JM08WP339	8/10/08	77.9955	5.9726	2343	-1 – 1	300-340	-0.0051
JM08WP344	8/12/08	75.982	8.323	2288	-1 – 1	310-330	-0.0038
JM08WP340	8/10/08	77.9953	5.3295	2633	-1 – 1	300-340	-0.0048
JM08WP341	8/11/08	77.9958	4.124	2952	-1 – 1	300-340	-0.0032
JM08WP342	8/11/08	75.9958	4.3265	3037	-1 – 1	300-340	-0.0073
JM08WP350	8/14/08	76.798	14.9801	245			

1 sediment-water interface

At each site multicores were collected and sediment pore water oxygen concentrations were measured using microelectrodes (Fig. 3; Loubere et al., 2011). Microelectrode profiles for each site permitted estimation of oxygen fluxes into the sediments (Table 1), which reflects rates of

oxygen uptake and organic carbon oxidation.

Thus the oxygen fluxes are a proxy for relative amounts of labile organic carbon reaching the seabed. Varying organic carbon flux to the seabed is a useful way of changing foraminiferal production and shell preservation in the BAZ as taxa respond to changing food supply and subsurface oxygen concentrations. Also, oxidation of organic matter in sediments drives geochemical gradients which cause carbonate dissolution in the subsurface (Emerson and Bender, 1981; Archer et al., 1989; summary: Sarmiento and Gruber, 2006). It is important that respiration of organic matter using oxygen releases acid which causes

carbonate dissolution; while organic carbon respiration with other oxidants (nitrate, sulfate, manganese and iron oxide) involves reactions which buffer the acid and favor carbonate preservation. So, the preservation of foraminifera within the sediments will depend on the depth of the anoxic boundary, and the position of this boundary with respect to the habitation zones of different foraminiferal taxa. For the transect used in this study, the sediments are entirely oxic at greatest water depth while anoxic conditions

Figure 2. The sampling transect area, extending between Greenland and Svalbard (inset, trapezoid shows location of study area in larger map). Core site locations from Table 1 are marked, those analyzed for total shell abundances are labeled in bold.

are encountered within a centimeter of the sediment-water interface in fjord locations (Table 1, and below).

In all the sampled locations the sediments are terrigenous muddy oozes (<63 μm fraction greater than 90% by weight, Kotwicki et al., 2004; Dijkstra, 2009; Elverhoi et al., 1983; Svendsen et al., 2002; Wlodarska-Kowalczyk and Pearson, 2004) and the temperatures for our sampling times ranged between 1 and 2°C in the fjords to 0 and -0.75°C on the continental slope.

Carbonate contents range from 20-30% on the Fram Strait abyssal plain to less than 5% in Svalbard fjords (Stein, 1996). This is a clastic environment receiving glacial sediment, with limited buffering capacity for acids evolved within the sediment profile. The water column is super-saturated for calcite at all water depths we sampled (Chung et al. (2003), so calcite dissolution will be primarily driven by sediment metabolic processes.

Available Pb-210 activity profiles from the Fram Strait and Kongsfjord indicate that bioturbation of the sediments is well developed in all environments we sampled to depths of at

Figure 3. Pore water oxygen profiles for transect regions and coring sites (Table 1). (A) Abyssal sites [340,341,342,344] (MZ = metabolic zone), (B) mid-slope sites [337,347], (C) upper slope sites [348,349], (D) Kongsfjord sites [Loubere et al., 2011].

least 5cm (Carignan et al., 2008; Zaborska et al., 2006). Even in the outer basin of Kongsfjord, near surface sediments were homogenous and there were abundant traces of polychaete burrowing (Zaborska et al., 2006; Loubere et al., 2011). This likely reflects the high bottom water oxygen concentrations at all locations which allow for extensive macrobenthic activity.

Sedimentation rates for our transect appear to range from about 1.5-0.5 millimeter per year in the outer reaches of Kongsfjord (Zaborska et al., 2006; Skirbekk et al., 2010; Jernas et al., 2013) to considerably less than that on the slope and abyssal plain (e.g. Rasmussen et al., 2007; Ślubowska-Woldengen et al., 2008).

It may seem paradoxical that bioturbation extends to 5 or more centimeters in locations, as in Kongsfjord, where anoxia is encountered just below the sediment-water interface as one might expect that sediment mixing would prevent steep oxygen gradients from developing; or that shallow anoxia would prevent deeper mixing. However, there is extensive evidence for biostructures extending well below the surface in sites with shallow anoxia (fjords of Svalbard, Loubere et al., 2011), and steep oxygen gradients can develop in spite of deeper sediment mixing because the diffusion rates for oxygen are much greater than the mixing rates of the sediments (Sarmiento and Gruber, 2006; sediment blending occurring over timescales of years to decades while oxygen diffusion rates provide responses in hours to days).

3. Methods

Sampling methods are detailed in Loubere et al. (2011). We collected sediments using a multicorer (model KC Denmark 72.021, six barrels: 110 x 800mm). We selected one core for pore-water oxygen profiling and sampling for foraminifera. At each site, the core surface was photographed for documentation of features and it was classified by the amount of surface that was occupied by obvious biostructures. Cores used in this study exhibited a sharp distinction in

surface properties. Most cores at shallow depths had abundant biostructures (tubes, burrows, pits), while deeper cores mostly had homogenous, nearly featureless, surfaces. Oxygen profiles for the homogenous cores followed a classic, exponential, profile; while those from cores with common biostructures were more complex.

We measured pore-water oxygen gradients using micro-electrodes and we subsampled the sediments to determine the distribution of living benthic foraminiferal species using two staining techniques (rose Bengal and cell tracker green (CTG)). It has been argued that CTG staining (Berhard et al., 2006) best identifies individuals alive at time of sampling since staining depends on active uptake across a cell membrane, while rose Bengal marks both living and recently dead individuals.

Water column properties were measured at most sites by CTD (911 Plus CTD with compact rosette; www.seabird.com). Pore-water oxygen concentrations were measured with Unisense micro-electrodes positioned using a custom made manipulator frame in conjunction with a temperature controlled seawater tank in which the top 15cm of multicores were placed so as to replicate seabed conditions. The tank was filled with local bottom water collected by CTD. The apparatus allowed controlled probing of the core top in the vicinity of sediment structures and had a positional accuracy of about 1mm in the horizontal and 100 um in the vertical.

Sediment for foraminiferal staining was taken from the multicore tubes used for oxygen measurements. Syringe cores (2.5cm diameter) were planted in the core and then extruded and sliced at 0.5cm intervals. Typically, 3 syringes were inserted in each multicore. For rose Bengal staining the sediment samples were placed in zip-loc bags containing a solution of rose Bengal in ethanol. For CTG staining the sediments were treated with a modification of the published protocol (Bernhard et al., 2006). Sediment was placed in mini-centrifuge tubes along with the

fluorescent probe and seawater at bottom water temperature. Tubes were sealed and then incubated at appropriate temperatures for at least 8 hours before fixing with ethanol. Samples were returned to the laboratory immediately after each cruise and stored in a refrigerator until preparation for counting. Samples were wet sieved with distilled water over a >63µm screen and placed in a wet picking tray for examination. The entire sample was scanned for stained foraminifera. Only specimens showing more than half the test chambers with distinct stain were counted.

Total (live + empty shells; unless these are specifically referred to) foraminiferal taxon abundance counts were conducted on samples taken for rose Bengal staining. For these data, samples were split using a tested, quantitative, micro-splitter, so as to have between 300 and 800 individuals present on the counting tray. Sample size was a uniform 2.45 cm³ and numbers reported here have been corrected for number of sample splits.

Taxonomy follows studies conducted in the Svalbard margin (e.g. Korsun and Hald, 2000; Wollenburg and Mackensen, 1998; Jernas et al., 2012), Loeblich and Tappan (1953) and Cedhagen (2006). **A full species list is in Appendix H.**

Results

4.1 Living (stained) and Total Foraminiferal Abundance Profiles

4.1.1 Fjord Sites: stained counts in Appendices A and B, total counts in Appendices C-1,2

Stainable (cell tracker green) foraminifera were common in the sediments of Kongsfjord over the multiple years we sampled (Loubere et al., 2011). Biostructures were also common, oxygen penetration was to 1cm or less in the sediments, there was visual evidence for sulfate reduction at depth and the foraminiferal habitation zone was to about 3cm for most taxa (Fig. 4).

Biostructures seem to provide localized oxygenated microenvironments to 5cm or more (Loubere et al., 2011).

Stained communities are dominated by *N. labradorica*, *N. auricula*, *Globobulimina*, *Fursenkoina* and *N. depressulus*. The dominant taxa in total assemblages are *N. labradorica*, *N. auricula*, *N. depressulus*, *Bolivina* sp., *I. helenae* and *Buliminella* sp.

Many taxa show living abundance peaks between 1 and 2 cm depth. A few, like *N. depressulus*, show abundance peaks at greater depth (Fig. 5). The latter include *Globobulimina* which is common in the stained community but rare in empty shell counts.

In core NP08-13-40 the stained abundances of common taxa, like *N. labradorica*, follow the pattern seen in previous studies (Loubere et al., 2011), and downcore total shell abundances show increases with depth (Fig. 6).

In general, the total abundance profiles of individual taxa for NP08-13-40 show two patterns: one in which taxon abundance peaks between 1 and 3cm downcore, and another in which abundance increases with depth (Fig. 6, 7).

Figure 4. Stained and total shell data from Kongsfjord. (A) Total stained shells (CTG) for a suite of core sites in Kongsfjord (Loubere et al., 2011, sites and data in Appendix A). (B) Total unstained calcareous shells in two subcores for core NP-16-40 (Table 1).

Figure 5. Stained (CTG) abundances of taxa from Kongsfjord and the adjacent continental shelf. (A) *N. labradorica* in a suite of cores from Kongsfjord (Loubere et al., 2011, data in Appendix B). (B) *N. depressulus* from shelf cores (Table 1).

Figure 6. Stained (rose Bengal) and empty shell abundances of *N. labradorica* in Kongsfjord core NP08-16-40 for two sub-cores (A,B).

Figure 7. Empty shell abundances downcore for NP08-16-40 showing two groups of taxon abundance profiles. (A) taxa, in addition to *N. labradorica*, with abundances increasing downcore; (B) common taxa with abundance profiles similar to the living community abundance profiles seen in Kongsfjord (Fig. 4A).

Figure 8. (A) stained (CTG) agglutinated taxa totals for a suite of cores in Kongsfjord (Loubere et al., 2011); (B) total agglutinated shells with depth for NP08-16-40.

The stained and total abundance profiles for agglutinated taxa in the fjord environment differ from those of the calcareous species (Fig. 8). The agglutinates inhabit surface to shallow subsurface microenvironments, and total shell abundances are highest at the surface while declining precipitously downcore.

4.1.2 Continental Slope Sites: total counts in Appendices D-1,2

Stained records from continental slope sites show most of the foraminiferal population within the upper 2 cm of the sediments (Fig. 9). There are scattered smaller, deeper populations to at least 4 or 5cm.

Total shell abundances follow a similar downcore trend to the stained populations (Fig. 10). Common individual taxa show three different abundance profiles: declining downcore, variable abundance downcore, and increasing abundance downcore (Figs. 11-14).

Both *I. helenae* and *Cibicidoides* species are very common in slope assemblages. On the slope they show stained populations mainly in the upper 2 cm of the sediments. In the fjord setting, stained populations of *I. helenae* were found to 4-5cm (Fig. 11), and slope records show subsidiary deeper populations as well.

Figure 9. Stained foraminifera in slope cores (Table 1). (A) two subcores of WP08-348, (B) cores WP08-337, 347 and 349, two subcores for each have been combined.

Figure 10. Total calcareous shells for slope core WP08-348.

Figure 11. Stained and total shell abundances for the common slope taxon *I. helenae*. (A) stained abundances for slope site WP08-348 (subcore B values divided by 2); (B) total shell abundance in fjord site NP08-16-40, and stained (CTG) abundance for fjord site NP09-13-14; (C) total shell abundances for slope site WP08-348.

Figure 12. *Cibicidoides* taxa in slope cores. (A) stained individuals of *C. wuellerstorfi* for sites WP08-337 and 347. (B) *C. wuellerstorfi* (W) and *C. pachyderma* (C) total shell abundances in two subcores for site WP08-348.

Figure 13. Abundance profiles for *C. reniforme* in slope cores. (A) stained individuals. (B) Total shells in two subcores of WP08-348

Total shell profiles for *Cibicidoides* species decline downcore (Fig. 12), while those of *I. helenae* are most abundant at the surface, decline rapidly in the upper centimeter and then appear to stabilize below that (Fig. 11).

Cassidulina reniforme is a common taxon at both slope and abyssal sites on the Svalbard margin. Its stained abundances are highly variable in cores we examined with populations scattered to at least 3cm depth (Fig. 13). Total shell abundance profiles are also highly variable for the slope site (Fig. 13), with

significant differences between sub-cores at the same location.

Melonis barleeaanum is present at upper-slope to shelf sites and shows a similar total abundance profile to *C. reniforme* (Fig. 14).

4.1.3 Abyssal Sites: total counts in Appendices E and F

At the abyssal sites we used (WP08-341 and 342), standing stocks of foraminifera were too low for reliable downcore stained abundance profiles at the small scale we used. Total abundance profiles of calcareous shells showed no significant downcore trends. However, abundance profiles for individual taxa did. Common taxa were *C. wuellerstorfi*, *C. reniforme*, *Cibicidoides pachyderma*, *Oridorsalis* sp., and *E. exigua*. Stained abundance profiles are available for several of these taxa from continental slope locations (*C. wuellerstorfi*, *C. reniforme*: Figs. 12, 13; *Oridorsalis*, *E. exigua*: Fig. 15).

Most of the taxa show stained abundance peaks in the upper 1.5cm of the sediments. An exception is *C. reniforme* which shows significant populations to at least 3cm.

Figure 14. Total abundance of *M. barleeaanum* at slope site WP08-348.

Figure 15. Stained abundances for the continental slope sites. (A) *Oridorsalis* sp. (B) *E. exigua* and *E. nipponica*. Site locations numbered as in Table 1.

Figure 16. Total shell abundances for abyssal sites WP08-341 and 342. (A) *C. wuellerstorfi*, (B) *C. pachyderma*, (C) *Oridorsalis* sp., (D) *E. exigua*, and (E) *C. reniforme*. Data from core 341 are divided by 2 as indicated.

Taxa have two patterns of total shell abundance at the abyssal sites we sampled: a surface peak with a minimum in the shallow subsurface and then an increase with depth and a subsurface peak with variable abundance downcore (Fig. 16). Note that absolute abundance of shells differs markedly between the sites we examined (difference in fine sediment fraction, and presumably clastic dilution) but general patterns are similar.

All of the common taxa except *C. reniforme* have abundance profiles with a maximum at the surface and a shallow subsurface minimum. They also show a modest increase in abundance downcore. This latter is not so consistent for *E. exigua*. In the case of *C. reniforme*, downcore abundances are more variable and there is a peak at greater depth with a minimum at the surface.

4.2 Abundance Profiles and Generation of the Fossil Assemblage:

A summary of microhabitat, seabed oxygen profiles, dissolution profile and foraminiferal taxon abundance profiles in relation to modeled profiles (Fig. 1) for the environments we sampled is given in Table 2.

4.2.1 Fjord Setting:

Although bottom water concentrations are high, oxygen penetrates to less than 1 cm into the sediments because of a high flux of organic carbon to the seabed (Table 1; Fig. 3). Foraminiferal habitation zones extend to at least 4cm depth even for taxa with demonstrated aversion to anoxia (Loubere et al., 2011). This indicates that the foraminifera take advantage of oxygenated biostructures, created by an abundant benthos, to inhabit otherwise hostile territory. The majority of the foraminiferal standing stock is in the upper 2 cm of the sediments. This is the interval in which most foraminiferal shell production must occur (Fig. 4). However, empty shell abundances are least near the surface and increase with depth. This type of abundance profile is that associated with input of shell material deeper in the mixing zone of the sediments (Fig. 1).

Table 2. Observed taxon abundance profiles compared to model expectations for environments sampled.

Setting	O ₂ gradient	Dissolution	Microhabitats	Abundance Profile Model type (fig. 1)	Taxa	Fig. ref.
Fjord	steep anoxic > 1cm	strong in upper centimeter	surficial, shallow	shallow	<i>Bolivina</i> sp.	7
			deeper infaunal	deep	<i>Fursenkoina</i> sp. <i>N. labradorica</i> <i>N. depressulus</i>	4-7
Slope	moderate anoxic >2.5-3cm	strong in upper 3cm.	surficial	surficial	<i>Cibicidoides</i> sp. <i>E. exigua</i>	9-12
			surficial – shallow mixed	shallow	<i>C. reniforme</i> <i>M. barleeaanum</i>	13 14
Abyssal Plain	limited to upper cm., oxic to depth	in upper 1/2cm	surficial, scattered infaunal populations signif. infaunal	surficial+infaunal mix shallow	<i>Cibicidoides</i> sp. <i>Oridorsalis</i> sp. <i>E. exigua</i> <i>C. reniforme</i>	15,16

These data indicate that while foraminiferal production may be higher in the upper sediments, shell destruction is higher there also. This is consistent with more intense shell degradation in the oxic to sub-oxic portion of the sediment column (Fig. 3, Table 2), and with improved preservation for anoxic conditions. In particular, lightly calcified taxa (Fig. 7, *Bolivina* sp., *Globobulimina* sp.) with most of the standing stock in the upper 2cm of the sediments, do not survive well and are attenuated in the developing fossil record. By contrast, those taxa which have more substantial shells, habitation zones extending into the anoxic zone (*N. labradorica*; Fig. 6) or with populations mainly at depth (*N. depressulus*; Fig. 7) preserve better and become more significant in the fossil record. Preservation bias is towards the portion of a species' production which occurs below the anoxic boundary in the sediments.

Production and preservation appear different for agglutinated foraminifera (Fig. 8). Standing stock is concentrated to the sediment surface, and total abundance profiles show strong reduction into the sediments. This indicates that microbial respiration of the organic matrix substrate of the agglutinates is active under both oxic and anoxic conditions, and shell survival potential is low in fjord settings of the type we sampled.

4.2.2 Assemblage Formation on the Continental Slope:

Organic carbon flux to the seabed is moderate in this setting, so oxygen penetrates to 2.5-3.5 cm depth (Fig. 3). The foraminiferal habitation zone is predominantly in the upper 2cm, with scattered populations at greater depth (Fig. 9). Total calcareous shell abundances (Fig. 10) decline with depth, with sharp decline in the upper 2 cm.

Most taxon total abundance profiles are similar to that for all shells (Figs. 11, 12), however there are taxa which show peaks at depth (*C. reniforme*, Fig. 13; *M. barleeaanum*, Fig. 14).

Moderately high labile organic carbon flux to the sediments creates an active oxic metabolic zone to between 2 and 3cm depth (Fig. 3). Below this there is anoxic metabolism. Benthic foraminifera inhabit mainly the oxic zone though some species are present to greater depth. This is probably in association with biostructures.

Shell abundance profiles (Table 2) indicate that destructive processes are active through the oxic zone of the sediments. The profiles are similar to that modeled for epi- to shallow infaunal taxa subjected to shell loss through the mixing zone (Fig. 1). The result is attenuation of foraminiferal shell abundances as they are mixed and processed through the bioturbation zone. More variable abundance profiles are present for species with significant downcore production (Table 2), especially at depths below 2-3cm (below the main oxic respiration zone). Less calcified species, such as *C. reniforme*, show fluctuating abundances downcore. This may be because they produce concentrations of shells in scattered locations (e.g. Loubere and Gary, 1990; biostructures, Loubere et al., 2011) within the sediments and these are preferentially degraded as they are mixed laterally, leading to irregular, patchy, sediment distribution.

4.2.3 Assemblage Generation on the Abyssal Plain

Organic carbon flux is low in this setting, so sediments are entirely oxic and respiration is concentrated in the upper centimeter (Fig. 3). Radio-isotope tracers indicate active bioturbation to at least 5cm depth. At time of sampling, foraminiferal standing stocks were sparse compared to the slope and fjord. The most common taxa in the sediment assemblage (empty shells) have surface to near-surface habitation zones, but there is evidence for infaunal foraminiferal production (e.g. *C. wuellerstorfi*, fig. 12). Nearly all the taxon total abundance profiles show peaks at the surface with a subsurface minimum, but then abundance increases modestly with

depth (fig. 16). This is seen at two sites with different locations and sedimentation characteristics. The abundance profile form indicates that maximum production occurs near the sediment surface, and that shell destruction occurs in the bioturbation zone, yielding downcore decreases in taxon abundance as in the modeled profile for epifaunal taxa (fig.1). However, the abundance profiles (fig. 16, Table 2) indicate that deeper in the sediments, where destructive processes are limited, addition of shells from deeper populations of most taxa make up for some of the lost material, resulting in increasing shell abundances downcore.

The abundance profiles show noticeable downcore variability. This may result from recent shell production (over the summer season, sampling towards the end of the Arctic productive season; Wassmann, 2001) in scattered subsurface locations and incomplete mixing, and dissolution, of recently produced shells away from the production centers.

5. What Gets Into The Fossil Record

Fossil assemblages are typically examined in terms of percentages of taxa rather than absolute sedimentary abundances. A simple way to assess the developing fossil assemblage is to compare taxon relative abundances through the sediment mixing zone (Figs. 17-19).

For the settings examined here, the foraminiferal assemblages are dominated by relatively few taxa. Overall, the same taxa remain dominant through the sediment column, but there are noticeable differences in relative abundances through the sediment mixing zone. Downcore changes can be ascribed to increasing representation by species with infaunal production, and reductions in abundances of thin-walled and more delicate taxa. So, for example, in the fjord setting *Bolivina* are common in surficial sediments, but are poorly represented several

centimeters deeper (Fig. 17). By contrast, *N. depressulus*, a taxon with evidence for infaunal production, is less abundant in surficial sediments and more so at depth.

Figure 17. Taxon percents in surface and bottom samples from Kongsfjord core NP08-16-40. 1 = *I. helenae*, 2 = *C. laevigata*, 3 = *Gyroidina* sp., 5 = *B. pseudopunctata*, 6 = *Bolivina arctica*, 7 = *Fursenkoina* sp., 8 = *Fursenkoina complanata*, 9 = *Globobulimina auriculata*, 10 = *G. turgida*, 12 = *B. tenerima*, 14 = *N. depressulus*, 15 = *N. labradorica*, 16 = *N. auricula*, 17 = *Nonionella scapha*, 18 = *C. neoteretis*, 21 = *C. reniforme*, 23 = *Epistominella* sp., 24 = *Stainforthia fusiformis*, 25 = *Cassidulina/Islandiella* sp. Complete taxon list in Appendix G.

Figure 18. Taxon percents in surface and deeper samples for slope site JM08-348. Subcore A: 1 = *C. wuellerstorfi*, 2 = *C. pachyderma*, 5 = *I. helenae*, 6 = *I. islandiella*, 7 = *C. reniforme*, 8 = *C. laevigata*, 18 = *Oridorsalis* sp., 19 = *P. bulloides*. Subcore B: 1 = *C. wuellerstorfi*, 2 = *C. pachyderma*, 5 = *I. helenae*, 7 = *C. reniforme*, 11 = *M. barleeianum*, 13 = *F. pseudopolymorphina*, 14 = *Fursenkoina* sp., 16 = *B. tenerima*, 17 = *P. bulloides*. Complete taxon list in Appendix G.

Figure 19. Taxon percents for abyssal sites.
 JM08-341: 1 = *C. wuellerstorfi*, 3 = *C. pachyderma*, 6 = *C. reniforme*, 12 = *Miliola* sp., 13 = *Oridorsalis* sp., 17 = *E. exigua*.
 JM08-342: 1 = *C. wuellerstorfi*, 3 = *C. pachyderma*, 5 = *Gyroidina* sp., 6 = *C. reniforme*, 11 = *Oridorsalis* sp., 16 = *E. exigua*. Complete taxon list in Appendix G.

Further insight to the developing benthic foraminiferal assemblage is provided by downcore assemblage correlation profiles (Fig. 20). A common feature of the correlation profiles is that greatest difference is found in the shallow subsurface between about 1 and 3cm depth. Below this, assemblages are more similar to that of the surface. This curious pattern is due to the input of shallow infaunal production from relatively thin shelled taxa like *C. reniforme*. This input is attenuated through mixing and taphonomic process so that it becomes less significant with time (vertical distance above and below the production zone in the sediments).

Figure 20. Correlation of downcore foraminiferal assemblages (taxon percents, total shell abundances) to the surface sediment assemblage. NP40 for Kongsfjord, 348A&B for the continental slope and 341&342 for the abyssal plain.

There is considerable variation in assemblage correlation profiles (Fig. 20) both downcore and between profiles from the same location (e.g. WP08-348). This likely reflects the concentration of production at particular loci in the sediments, the variable rate of production on the smaller scale, and the variable and discontinuous nature of sediment mixing. For example, in the continental slope profile pair (WP08-348; Fig. 18) *C. reniforme* is much more abundant in one than the other (Fig. 13). This likely reflects concentrated production of this species at a particular location in the subsurface, in the recent past, which has not been well mixed into surrounding sediments, and which has not yet undergone extensive loss due to taphonomic processes.

Overall, there are significant differences between the surface sediment assemblage and those towards the base of the mixing zone. The effect appears largest in the fjord setting where there is considerable loss of shallow subsurface shell production and substantial deeper production with enhanced preservation within anoxic sediments. It is interesting that the setting with the greatest shell loss, the continental slope, does not end up with the greatest downcore change in

assemblages. Apparently, the shell attenuation is roughly the same for the most common taxa present.

6. Conclusions

Foraminiferal taxon total shell abundances from all the environments we sampled showed often strong gradients within the bioturbation zone in near surface sediments. This is curious since the ratio of sediment mixing rate to sedimentation rate will be high for the settings we sampled. That means the sediments are mixing actively while material is accumulating on the sea floor relatively slowly (on the order of 1 to 50cm/kyr).

The abundance gradients we observed can be explained if the rates of shell production, and destruction, are even higher than that of the bioturbation. In that case, gradients can be imposed on the mixing zone. This is observed in pore water geochemical measurements which show strong concentration gradients in well mixed sediments because reaction rates far exceed the mixing rate. Foraminiferal shell dissolution is associated with geochemical reactions in the oxic portion of the sediment column, so taphonomic rates should exceed sediment mixing rates. As benthic foraminiferal standing stocks are observed to vary seasonally, production of shells is also rapid compared to mixing rate or sedimentation rate. So, shell production and destruction rates allow for a dynamic balance within the sediment mixing zone, and the existence of taxon abundance gradients.

The abundance gradients that develop depend on location of taxon microhabitats and the position of the anoxic boundary within the sediment mixing zone. In the settings we examined, high organic carbon flux to the seabed (fjord) resulted in a shallow subsurface anoxic boundary and significant foraminiferal production below this. Shell loss was strong for surficial

foraminiferal production, but less so for production at depth. Assemblage formation was biased to shell production deeper in the biologically active zone of the sediments.

On the continental slope, moderate organic carbon flux produced a well developed zone of oxic respiration in which taphonomic shell loss was significant, so shell abundance downcore was strongly attenuated. Fossil assemblage formation should be biased to the more robust taxa producing in near surface sediments, and those taxa which have productive populations in the lower part of the biologically active zone of the sediments. Low organic carbon flux to the seabed of the abyssal plain yielded foraminiferal production and taphonomy concentrated in the shallow subsurface. However, there was evidence for localized significant production by many taxa in the lower part of the sediment mixing zone.

It remains possible that some taxon abundance variability in the sediment mixing zone could result from responses to recent changes in environmental conditions in the northern North Atlantic. Spielhagen et al. (2011) document such changes in the northern Fram Strait and show a strong shallow sediment decrease in planktonic foraminiferal abundances in a deep sea core. Interestingly, the large abundance gradient does not directly correlate to independent, geochemical and instrumental, tracers of environmental change. Based on our work, it is reasonable to propose that a significant part of the foraminiferal abundance gradient is due to sediment mixing and diagenesis; factors not considered in the published work.

Nevertheless, it is clear that environmental change has occurred in the North Atlantic in the past several centuries, and, since mixing and diagenesis are variable processes, some of that change is reflected in the benthic foraminiferal abundance profiles we examined. It is unlikely that the environmental change is the dominant cause of our abundance profiles since an abundance of research has demonstrated the nature of sediment mixing and carbonate diagenetic

processes in marine sediments. Further, the gradients we observe fit well with expectations for the mixing process combined with our knowledge of taxon microhabitats and diagenetic reactions in the sediments based on measured pore water oxygen concentration profiles. Finally, we examined cores which undoubtedly have quite different sedimentation rates, but we find abundance changes occurring at similar depths in all of them (e.g. Fig. 20). If the abundance gradients were driven by regional environmental change then we would expect to see gradients developing at different depths in different cores, depending on rates of sediment accumulation at different sites.

The results imply that, across the range of environments sampled, the interplay of shell production and destruction through the sediment mixing zone produces fossil assemblages which can be significantly different from both the standing stock and the assemblage at the sediment surface. Generally, there is a bias towards the preservation of shells which are produced deeper in the sediment profile, or the portion of the taxon's production which occurred deeper in the sediments. Only further research will show the extent to which the processes we have attempted to examine affect assemblage formation broadly across the open ocean realm.

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