



Dispersal, survival and delayed growth of benthic foraminiferal propagules

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ABSTRACT

New data support our previously published propagule dispersal hypothesis and show that propagules of some benthic foraminiferal species can survive for two years before growth commences. Following exposure to simulated shallow-water conditions, shallow-water species of benthic foraminifera appeared and grew in large numbers (commonly >100 ind/12 ml sediment) in the <32 µm-size sediment fraction collected from 320 m water depth in the Skagerrak basin (North Sea). None of the shallow-water species that grew abundantly (*Planorbulina mediterraneensis*, *Morulaepecta bulbosa*, *Bolivina pseudoplicata*, *Cuneata arctica*, *Eggerelloides scaber*, *Gavelinopsis praegeri*) seem to grow or reproduce at or in the vicinity of the sampling site. Consequently, they must have been transported there as <32 µm-sized individuals. Their sudden appearance when exposed to shallow-water conditions suggests that they had been transported to the sampling site as propagules and that they could survive in the sediments until conditions became suitable for growth and, for some, reproduction. The lack of agglutination on the proloculi of the agglutinated taxa that appeared in the growth-chambers may enhance their passive transport via currents and, thereby, dispersal. Of all the indigenous foraminiferal species that occur at the sampling site, only *Textularia earlandi* and *Bolivina pseudopunctata* continued to grow and reproduce when transferred from bathyal (320 m) to simulated shallow-water (0 m) conditions. The former is considered a highly opportunistic species. According to the literature, most of the morphospecies which grew in the experiments are cosmopolitan. Our results indicate substantial inter-specific differences in dispersal potential and support previous suggestions that among free-living species, some serial forms have the potential for long-distance dispersal. Still, oceanographic, physical and ecological boundaries and barriers constrain the distribution of most species. In addition to benthic foraminifera, *Gromia* spp. (rhizarian protists related to the foraminifera) grew in >60% of the experimental growth-chambers.

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1. Introduction

Understanding dispersal mechanisms is important for understanding the historical development of biogeography and biodiversity patterns. What processes drive and limit protist dispersal and colonization? Are protistan biogeographic patterns characterized fundamentally by cosmopolitan distributions as outlined in the “ubiquity model” (e.g., Fenchel, 2005; Finlay et al., 2006), or rather does the “moderate endemicity model” prevail (Foissner, 2006; Weisse, 2008)? Although a range of different organisms from terrestrial to marine habitats have been considered, benthic foraminifera, which comprise one of the most common, diverse and widespread marine microfossil groups throughout the Phanerozoic, have received relatively little attention.

Based on a survey of all reported occurrences of living (stained) benthic foraminifera from the world's oceans today, Murray (2007)

concluded that most of the ~2140 known hard-shelled morphospecies are rare and endemic; very few (5% or less) are cosmopolitan. If indeed most are endemic, how can we explain the broad biogeographic, bathymetric and environmental ranges that are recorded for some species (e.g., Belasky 1996; Gooday et al., 2004, 2007; Pawlowski et al., 2007; Brandt et al., 2007; Hayward et al., 2007b; Pawlowski and Holzmann, 2008)? Are broad distributions a result of long geological ranges (e.g., Pawlowski et al., 2007), or, alternatively, do these broad patterns stem from differential life history dynamics, propagule survival, and dispersal potential among different foraminiferal species? As for many other groups of organisms, taxonomic problems, including misidentifications and synonymies, hamper the delineation of biogeographic patterns. Indeed, Murray (2007) suspects that 10–25% of all live species names are synonyms. Further, if most species are rare, it is likely that many have not been reported as living (i.e., under-sampling). In addition, the extent of cryptic species occurrences in benthic foraminifera has yet to be systematically assessed.

Traditionally, biogeographic studies on benthic foraminifera have focused on where different species are recorded, whereas the

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mechanisms concerning how they got there, are seldom discussed. Plankton studies have shown that permanently benthic foraminifera (i.e., those lacking a meroplanktonic life stage), up to several hundred microns in size, may be present in the water masses (discussion in Alve, 1999). However, because dispersal is passive, the smaller the size of an individual, the greater the potential for long-distance dispersal, which in turn depends on survival time.

Experiments (Alve and Goldstein, 2002, 2003) have suggested passive transport of propagules (tiny juveniles) as an efficient means of dispersal in some shallow-water species. Our data showed that both sexually- and asexually-produced propagules of inter- to shallow subtidal species can rest and survive in a cryptic state for months. Following passive transport, they constitute a substantial bank of individuals in environments beyond the natural distribution of conspecific adults, and may grow in sediments from these environments when exposed to favourable conditions.

Here we address new questions regarding foraminiferal dispersal by propagules: Do shelf basin sediments contain propagules of “exotic” species which do not grow and reproduce *in situ*? If so, can they survive for extended periods (here up to two years) before growth and reproduction commence? To focus on the dispersal potential of the smallest possible ontogenetic stages of benthic foraminifera (i.e., the lightest ones with the highest potential for transport), we only used the <32 μm -sized fraction of sediments. Unless otherwise stated, our discussion on the biogeography of particular taxa concerns morphospecies.

2. Material and methods

To address these questions, sediment was collected via boxcoreing from a 320 m deep site in the Skagerrak basin (North Sea), midway between Norway, Sweden and Denmark (58° 07.90'N; 9° 54.00'E). This site is ~50 km from the nearest shore (Fig. 1). After collection (see below), the sediment was divided in half. One half (Experiment 1) was used to experimentally assess whether “exotic” benthic foraminiferal taxa would grow from the fine sediment fraction. The other half (Experiment 2) was used to determine whether any of the propagules present, indigenous or exotic, would remain viable for an

extended period of time (2 years) following storage under cold (ambient), dark conditions.

2.1. Collection

Sediments used in this study were collected on the 12th of August, 2002, with an Olausson box corer. Just after arrival on deck of the RV “Arne Tisselius”, 9L of the ambient sea water immediately above the sediment–water interface was transferred to a plastic container, and 29 cm \times 26 cm of the surface sediment (top 2 cm) was randomly transferred to 6 transparent plastic containers (sediment height 1–1.5 cm in each) and sealed. Both water and sediment were kept in dark cold-rooms at ambient temperatures, first on the ship (5 °C) and later at Oslo University (7 °C), until the onset of the experiments (Fig. 2). The bottom water temperature and salinity at the sampling site are fairly stable at about 5.0–6.4 °C (SD 0.6) and 35.1 (SD 0.8), respectively, as shown by mean values from March and August during the period 1952–1994 (Danielssen et al., 1996).

2.2. Experiment 1

On 21st August 2002, sediment from three of the six containers of raw sediment was mixed and sieved with ambient sea water on 32, 63, 125 and 1000 μm sieves. The remaining three containers were stored for two years (see Experiment 2 below). The <32 μm fraction was left to settle in the cold-room overnight, after which the water was removed by siphoning and retained for later use. The fine-grained sediment was gently homogenised, and 12-ml aliquots were transferred to each of 76 transparent plastic 40-ml growth-chambers (Joni DK, no. 41610001). Most chambers were topped with ambient sea water whereas 27 were topped with sea water collected some months earlier at 60 m water depth in the middle part of the Oslofjord. The results showed no notable difference between chambers which had either ambient or 60-m deep sea water added to them; they are therefore not differentiated in the results. The growth-chambers were sealed with a lid and transparent Nesco film and maintained on a window ledge for 0.5–24 months to simulate shallow-water conditions (air temperature 7.8–39.9 °C). All growth-chambers remained sealed throughout the experimental period. The

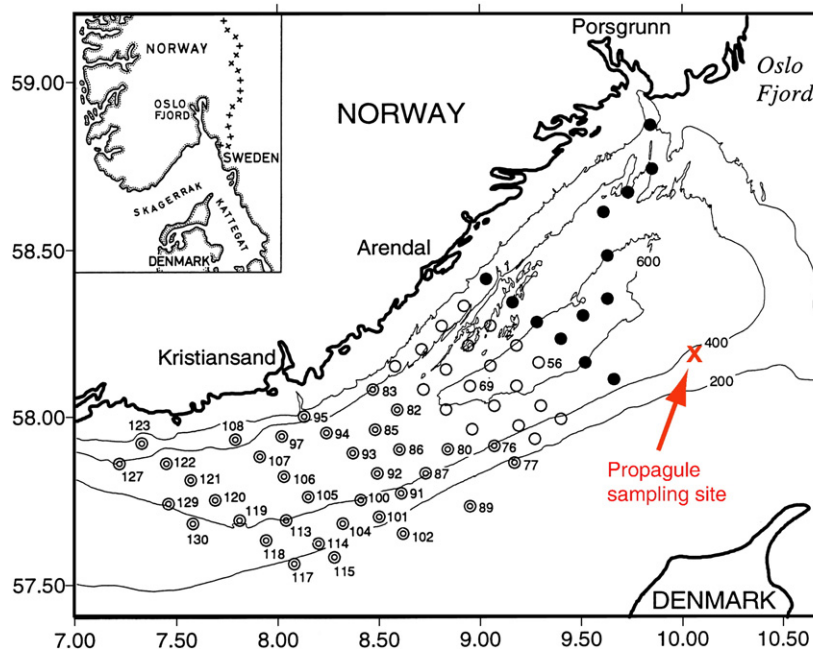


Fig. 1. X = Location of the sampling site midway between Norway, Sweden and Denmark. Circles = Sites investigated for live (stained) foraminifera in neighbouring areas (Alve and Murray, 1995, 1997).

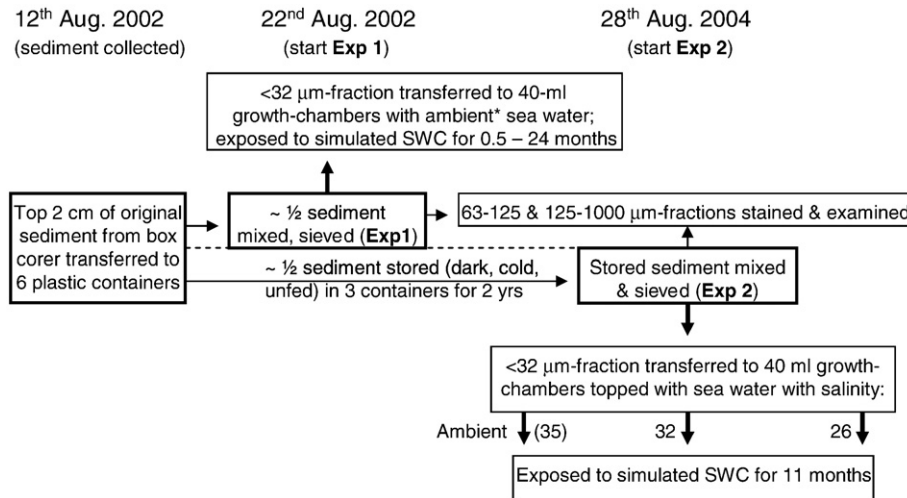


Fig. 2. General outline of experimental approach. Fat arrows point to growth-chambers exposed to simulated shallow-water conditions. * = Some chambers were topped with filtered sea water from 60 m depth rather than ambient water, see Section 2.2. SWC = Shallow-water conditions.

surface sediment of arbitrarily chosen growth-chambers was examined under the microscope and harvested at irregular intervals between 8th September, 2002, and 25th August, 2004. The growth-chambers were harvested by washing the sediment through a 63- μm sieve. The >63- μm fraction was preserved in 70% rose Bengal stained ethanol (1 g/L) and examined for foraminiferal content.

2.3. Experiment 2

The other half of the sediment collected at 320 m water depth in August 2002 was stored (sediment height 1–1.5 cm in each) in three sealed, transparent plastic 1000 ml containers (Joni DK, no. 50300001) in the dark cold-room for two years. The original, ambient sea water was stored the same way. On the 27th August, 2004, the sediment had a light gray colour (i.e., no sign of sulphides) and two containers had polychaete tubes protruding upward into the overlying water. During the two years storage, bioturbation within the thin sediment-layer (see also Hemleben and Kitazato, 1995) and oxygen penetration through the container walls probably prevented the sediments from turning anoxic. The stored sediment was carefully mixed, treated as described for Experiment 1, and 12-ml aliquots of the <math><32\ \mu\text{m}</math>-sized sediment were transferred to 67 growth-chambers. Based on the results from Experiment 1, two treatments with reduced salinity were added to Experiment 2 to determine whether hyposaline, shallow-water species could grow from the propagule bank under these conditions. Therefore, 22, 30, and 15 of the growth-chambers were topped with ambient (35 psu), 32-psu, and 26-psu sea water, respectively (Fig. 2). The 26- and 32-psu sea waters were collected in the Oslofjord on 26th August, 2004, at 0 and 30 m water depth respectively and filtered (8 μm) prior to use. All growth-chambers were sealed and maintained at room temperature on a window ledge (i.e., exposed to direct sunlight) for 11 months, as described for Experiment 1.

Sediments finer than 32 μm , rather than bulk sediments, were used in both experiments to determine if growth commenced from small juveniles (propagules). To characterize the indigenous foraminiferal taxa that grew and reproduced at the sampling site, both live (stained) and dead (unstained) foraminifera from the pre-experiment sediments ($t=0$) were examined for both Experiments 1 and 2. The 63–125 μm - and >125 μm -sediment fractions from the fresh 2002-collection used in Experiment 1, and the same size fractions from the sediments used in Experiment 2 (i.e., those which had been standing untouched for 2 years), were fixed in 4% buffered formalin in sea water, later re-sieved,

and preserved in 70% ethanol with rose Bengal (1 g/L) before examination for foraminiferal content.

3. Results

The sediment in most growth-chambers prior to harvesting was covered by a dense mat of algae (and associated microbiota; taxa not identified). Differences in colour, both within and between growth-chambers, were clearly seen as patchy distributions of different shades of green, yellow and brown. There was no obvious connection between these differences and the abundance or faunal composition of benthic foraminifera in the chambers.

3.1. Experiment 1

After two months (22nd October 2002) algae were observed on the sediment surface of some chambers and by the end of November, algae were recorded in most chambers. Of 12 chambers harvested between 2 weeks and 4.5 months after the onset of the experiment, ten were barren and two contained a total of five >63 μm -sized foraminifera (Fig. 3), including four juvenile *Planorbulina mediterraneis* (after

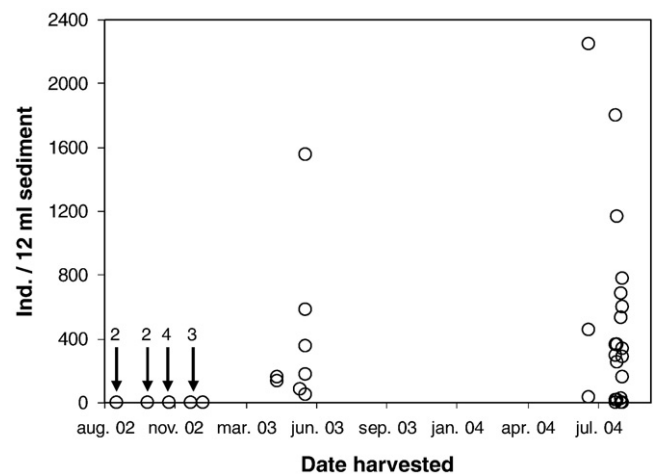


Fig. 3. Experiment 1. Number of foraminifera (>63 μm) per experimental growth-chamber (individuals/12 ml <math><32\ \mu\text{m}</math>-sized sediment) at the date they were harvested. Experimental period 22nd August 2002 to 25th August 2004. The first four circles represent 2–4 growth-chambers each.

3 months), 2 of which were found in agglutinated “cysts”, and one deformed (see below) *Textularia earlandi*. Between April 2003 and August 2004, an additional 46 growth-chambers were harvested. Of these, 4 were barren of foraminifera, 4 contained >63 µm-sized individuals of indigenous species, and 38 (83%) contained exotic shallow-water species in addition to the indigenous ones. All foraminifera were counted in 27 growth-chambers (table 1 in Appendix A), whereas only the presence–absence was recorded in the remaining 19. The maximum number of individuals/12 ml sediment was 2247 (Fig. 3).

Of the three most commonly occurring species (i.e., present in >80% of the counted chambers), *T. earlandi* was most abundant (max 1986 individuals/12 ml sediment), whereas *Morulaeplecta bulbosa* rarely had >50 individuals/12 ml sediment and *Cuneata arctica* (with one exception of 778) commonly had <10 (Fig. 4, Table 1). *P. mediterraneensis* occurred in 78% of the growth-chambers, generally with 100–250 individuals/12 ml sediment, whereas *Bolivina pseudoplicata*, which occurred in 63% of the growth-chambers, generally showed abundances of <15 individuals per chamber. Except for one chamber which contained 237 individuals of *Bolivina pseudopunctata*, this species and *Gavelinopsis praegeri* only occurred with 1–2 individuals in 19% of the growth-chambers. Triserial agglutinated individuals with a loop-shaped, *Bulimina*-like aperture occurred in 41% of the growth-chambers (max abundance 143 individuals/12 ml sediment). The test characteristics closely fit those described for megalospheric *Eggerelloides scaber* by Höglund (1947; as *Eggerella scabra*) and Haynes

(1973; as *Eggerelloides scabrum*) but some individuals are probably microspheric *Liebusella goësi* (see discussion, Appendix A; Plates I and II).

In *M. bulbosa*, *P. mediterraneensis*, *G. praegeri*, and *E. scaber*, the proloculus was hidden by later chambers and difficult to measure. However, in some individuals of *P. mediterraneensis* carbonate dissolution allowed measurements of the inner organic lining. Of 48 individuals from August 2004, the prolocular diameter measured 30–40 µm in 47 individuals, and 50 µm in one. The *Cibicides*-like young individuals of *P. mediterraneensis* reached a maximum diameter of about 230 µm before the planorbilinid growth pattern commenced. Adult individuals could reach 800 µm in diameter. In *P. mediterraneensis*, most individuals were polygonal to strongly irregular in outline; only occasional individuals showed the characteristic quadrate shape (Plates I and III). Irregular individuals often showed a >30° change in coiling plane after the first few whirls (i.e., at a young stage). Some *T. earlandi*, *M. bulbosa*, and *E. scaber* showed strongly deformed tests. The deformities were typically seen as a bend (sometimes >90°) in the otherwise rectilinear growth direction, accompanied by a sudden increase in chamber size (Plate II). In 14 growth-chambers, each with >30 *T. earlandi*, 0–35% (average 9%) were deformed and in 11 growth-chambers each with >30 *M. bulbosa*, 0–17% (average 8%) were deformed (Fig. 5).

P. mediterraneensis was commonly found on the walls of the growth-chambers, on the sediment surface (some had fallen from the growth-chamber wall), and underneath the chamber lids. Their

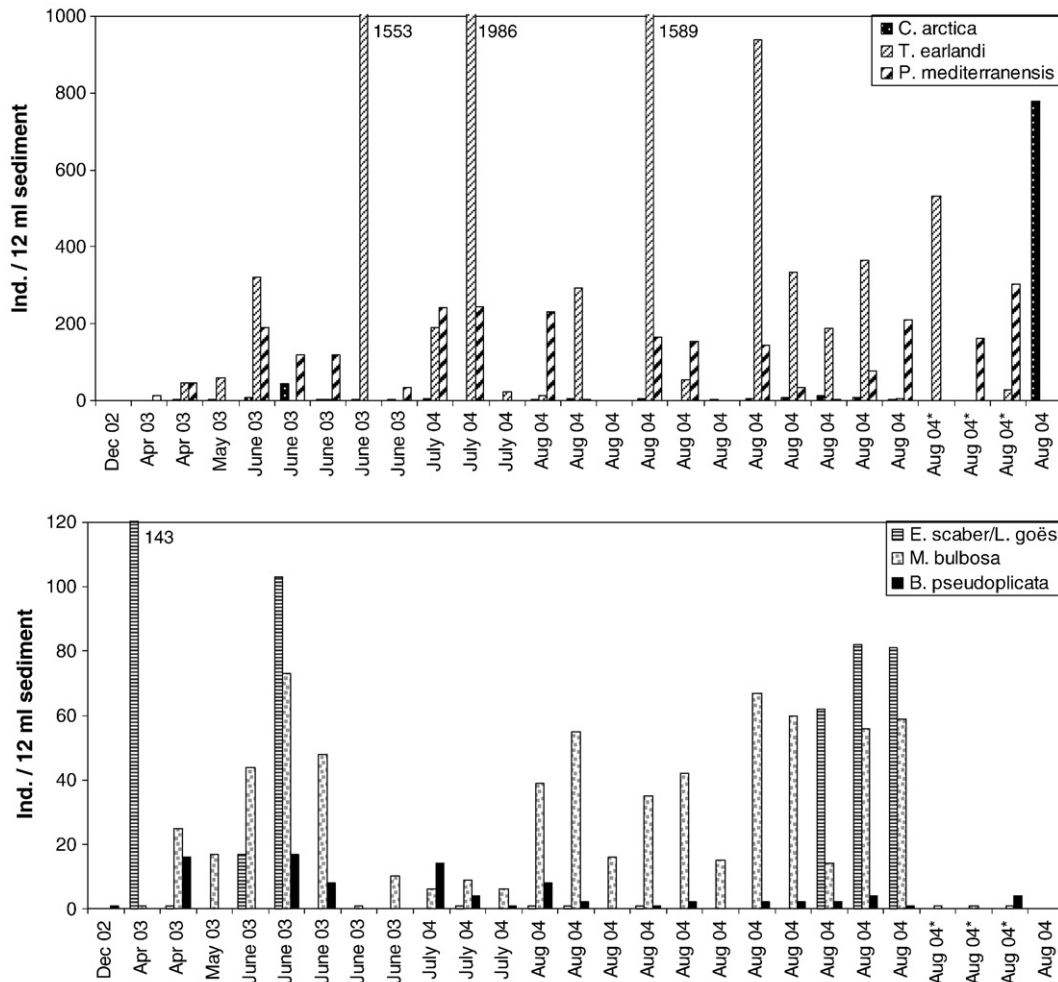


Fig. 4. Experiment 1. Absolute abundance (ind./12 ml sediment) of the most common species emerging from the <32 µm-fraction of sediments collected at 320 m water depth after exposure to simulated shallow-water conditions. * = Individuals retained on a 125- rather than a 63-µm sieve.

Table 1
Observations of species which grew in <32- μ m sediment collected at 320 m water depth (in the Skagerrak, midway between Norway, Denmark and Sweden) following exposure to simulated shallow-water conditions.

Species and occurrence ^a in growth-chambers	Max abundance (ind./12 ml sed)	Observations
<i>T. earlandi</i> Exp 1 = 89% Exp 2 = 80%	Exp 1 = 1986 Exp 2 = 397	Commonly 200–400 μ m long. Deformed individuals larger; max 850 μ m: last pairs of chambers swollen and grown in an angle (some >90°) relative to growth direction of preceding chambers. Infaunal, may stand aperture down in algae on sediment surface.
<i>C. arctica</i> Exp 1 = 81% Exp 2 = 10%	Exp 1 = 778 Exp 2 = 1	Proloculus, organic wall without agglutination giving a golden appearance 12–20 μ m; max no. of chambers 14; length commonly 150–200 μ m, max 450 μ m. Infaunal but also recorded on sediment surface. Not present in salinity 32 and 26 treatments.
<i>P. mediterraneensis</i> Exp 1 = 78% Exp 2 = 57%	Exp 1 = 303 Exp 2 = 259	Proloculus 30–50 μ m; <i>Cibicides</i> -like young <230 μ m; adult, max 800 μ m. Present as growth-stages in the sediment or up on growth-chamber wall in organic “cysts” with or without detrital grains. Cytoplasm brightly orange or yellow-greenish with orange-red inner part. Movements recorded. Generally, juvenile individuals dominate.
<i>B. pseudopunctata</i> Exp 1 = 19% Exp 2 = 10%	Exp 1 = 237 Exp 2 = 1	Proloculus ~20 μ m. Not present in salinity 26 treatment.
<i>E. scaber</i> Exp 1 = 41% Exp 2 = 23%	Exp 1 = 143 Exp 2 = 21	Most 400–600 μ m long (max 710 μ m), megalospheric individuals, proloculus 60–80 μ m. Not present in salinity 26 treatment. Some records include microspheric <i>Liebusella goësi</i> .
<i>G. praegeri</i> Exp 1 = 19% Exp 2 = 17%	Exp 1 = 30 Exp 2 = 121	Most 150–250 μ m diameter. Some in “cysts”. Yellowish-orange cytoplasm. Not present in salinity 26 treatment.
<i>M. bulbosa</i> Exp 1 = 93% Exp 2 = 53%	Exp 1 = 73 Exp 2 = 35	Length commonly 200–350 μ m. Infaunal but also recorded on sediment surface. Only 3 individuals in the salinity 26 treatment.
<i>B. pseudoplicata</i> Exp 1 = 63% Exp 2 = 33%	Exp 1 = 17 Exp 2 = 556	Length commonly 130–240 μ m, max 720 μ m. Proloculus 10–15 μ m. Orange-red cytoplasm. Only 1 individual in salinity 26 treatment.

^a Occurrence expressed as percent of growth-chambers where the species occurs, relative to total number of chambers counted in each experiment. Exp 1 based on freshly collected sediment; Exp 2 based on sediment stored for two years.

distribution on the chamber walls did not show any clustering or patchy pattern. One August 2004 growth-chamber had >100 *C. arctica* on the green algae-covered sediment surface. *T. earlandi* was recorded standing aperture down in algae covering the sediment surface. *Gromia* spp. (organic-walled rhizarian protists) appeared at the same time as the foraminifera. They occurred in 85% of the counted chambers with up to 15 elongate to nearly spherical individuals that measured 200–630 μ m in length.

Of the 1851 live (stained) and 7587 dead foraminifera isolated from the original, pre-experimental sediments, no *P. mediterraneensis*, *B. pseudoplicata* or *E. scaber* occurred, whereas 1 dead *M. bulbosa*, 5 dead *C. arctica*, and 1 dead *G. praegeri* were recorded. Live and dead *T. earlandi* and *B. pseudopunctata* were common in the 63–125 μ m-fraction but not recorded in the >125 μ m-fraction. However, *L. goësi* (Plate 1, 9 and 11) was abundant in the coarser fraction, but absent from the finer fraction.

3.2. Experiment 2

Adult *T. earlandi* and various juvenile stages of *P. mediterraneensis* were recorded on the sediment surface six months after the onset of the experiment. At the end of the experiment (11 months), eleven arbitrarily chosen growth-chambers from each of the three salinity treatments were examined. The most abundant species was *T. earlandi* which occurred in 70% of the 33 chambers. Except for maximum records of 556 *Bolivina pseudoplicata* and 121 *G. praegeri* (ambient salinity), the number of individuals of all species was low compared to Experiment 1 and there were clearly more species in the higher salinity treatments compared to the 26-psu salinity treatment (Figs. 6 and 7; table 2 in Appendix A).

Most chambers had some adult individuals of *P. mediterraneensis*, but juveniles (<250 μ m) dominated. Larger individuals had an irregular growth pattern. One 32-psu growth-chamber had two enlarged, deformed individuals of *T. earlandi* each with three juvenile *P. mediterraneensis* attached to their test. For one growth-chamber with ambient salinity, the position of 47 *P. mediterraneensis* was marked in March 2005. Four months later they had all moved. In one 26-psu chamber, at least 64 *P. mediterraneensis* were found attached to the

moist under-side of the lid (i.e., above the sediment–water interface). One ambient sea water-treatment had many small (80–90 μ m), one-chambered, coarsely agglutinated individuals. In addition, *Gromia* spp. occurred in 63% of the growth-chambers, with ≤ 7 individuals per chamber, irrespective of the salinity treatment.

Among 909 live (stained) and 9659 dead individuals of the pre-Experiment 2 fauna (after cold storage for 2 years), no *B. pseudoplicata* or *E. scaber*, whereas 3 dead *G. praegeri*, and 1 dead of each of *M. bulbosa*, *C. arctica*, and a juvenile *P. mediterraneensis* were recorded. *T. earlandi*, *B. pseudopunctata*, and *L. goësi* were common.

4. Discussion

4.1. Biogeography and local distribution of surviving species

The sediment in the experimental growth-chambers consisted solely of material from the middle part of the Skagerrak (320 m water depth, Fig. 1) which had passed through a 32- μ m sieve. Still, after three months or more of exposure to simulated shallow-water conditions, most growth-chambers contained abundant benthic foraminifera, >63 μ m in size. The species which survived and subsequently grew following this drastic environmental change represent two groups: those which grow and reproduce in the Skagerrak at or close to the sampling site, Group 1, and those which do not, Group 2. To gain perspective on the dispersal and survival potential of these taxa, the known biogeographic distribution and environmental requirements of the most common species are summarized. However, taxonomic uncertainties remain a result of incomplete growth stages for some taxa and incomplete knowledge of intra-specific morphological variability for others. This in turn confounds the assessment of cosmopolitan versus provincial distribution patterns of these morphospecies (e.g., Mitchell and Meisterfeld, 2005).

4.1.1. Group 1: Species native to the sampling site

Of the 86 hard-shelled living (stained) morphospecies recorded in 56 samples (>63 μ m fraction) from the open Skagerrak (Alve and Murray, 1995, 1997; Fig. 1), 52 (i.e., 60%) were found at the propagule sampling site. Of these 52, *T. earlandi*, *B. pseudopunctata*, and *L. goësi*



Plate I. Micrographs of species emerging from <math><32\ \mu\text{m}</math>-sized sediments collected at 320 m water depth after exposure to simulated shallow-water conditions: 1–3. *Planorbulina mediterraneensis* d'Orbigny. 1 and 3; D = about 500 μm . 2; D = 270 μm . 4. Megalospheric *Eggerelloides scaber* (Williamson). L = 400 μm . 5. Rose Bengal stained, juvenile, microspheric *Liebusella goësi* Höglund. L = 450 μm . 6. *Textularia earlandi* Parker, with three juvenile, rose Bengal stained *P. mediterraneensis*. L = 500 μm . 7–8. *Cuneata arctica* (Brady). 7; L = 390 μm . 8; transmitted light, L = 170–290 μm . Individuals reflect transitions between blunt and more pointed last chamber. The proloculi are not agglutinated. 9. Growth stages of pre-experiment, megalospheric *L. goësi*. As opposed to individuals growing during the experiment, these include the uniserial part. L = 1030–2380 μm . 10. *Morulaepecta bulbosa* Höglund. L = 340–510 μm . 11. Growth stages of pre-experiment, microspheric *L. goësi*. As opposed to individuals growing during the experiment, these include the uniserial part. L = 1270–2250 μm . 12. *Bolivina pseudoplicata* Heron-Allen and Earland. L = 130–240 μm .

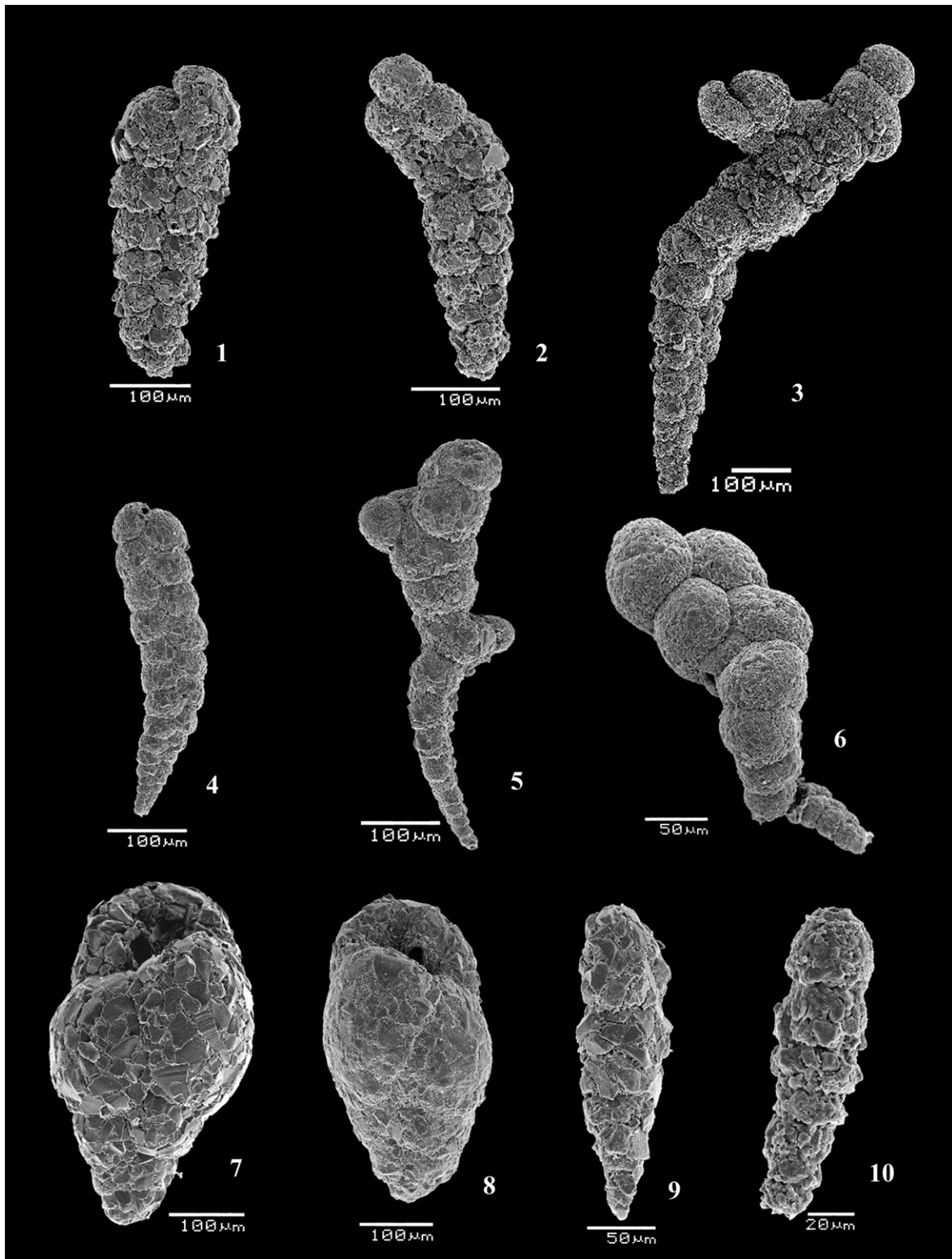


Plate II. Scanning electron micrographs of species emerging from <math><32\ \mu\text{m}</math>-sized sediments collected at 320 m water depth after exposure to simulated shallow-water conditions: 1–3. *Morulaepecta bulbosa* Höglund. 2–3. Deformed tests. 4–6. *Textularia earlandi* Parker. 5–6. Deformed tests. 7. Megalospheric *Eggerelloides scaber* (Williamson). 8. Juvenile, microspheric *Liebusella goësi* Höglund. 9–10. *Cuneata arctica* (Brady). 10. Small individual with proloculus broken off.

plus rare individuals of other species grew in the present experiments when exposed to simulated shallow-water conditions. The former two were by far the most common in the growth-chambers.

Textularia earlandi is a cosmopolitan species described based on material from the Mediterranean, South Georgia, the Falkland Islands and the Antarctic (discussion in Höglund, 1947, as *T. tenuissima*) and

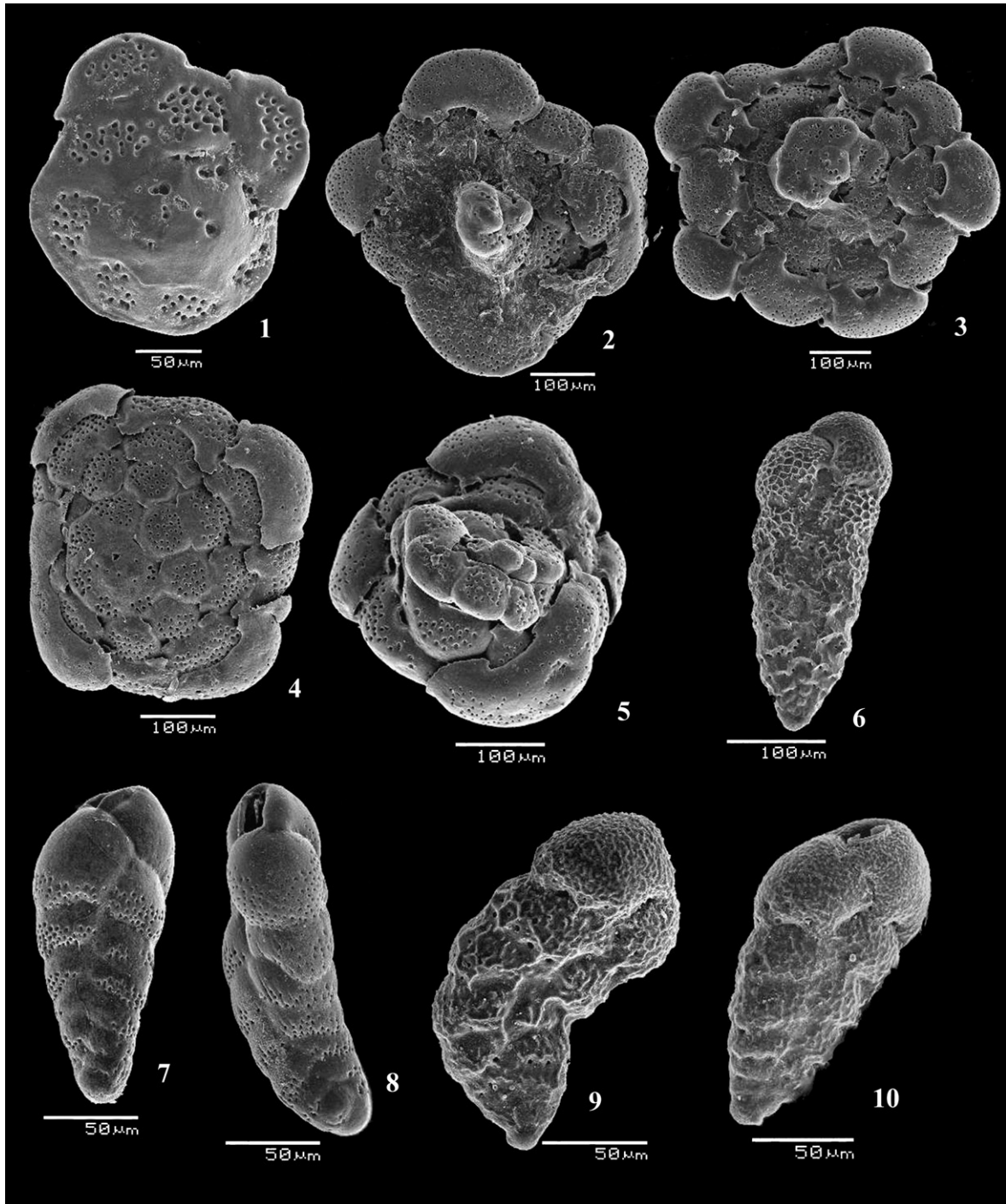


Plate III. Scanning electron micrographs of species emerging from <math><32\ \mu\text{m}</math>-sized sediments collected at 320 m water depth after exposure to simulated shallow-water conditions: 1–5. *Planorbulina mediterraneensis* d'Orbigny. 2, 3, 5. Irregular tests. 6, 9, 10. *Bolivina pseudopunctata* Heron-Allen and Earland. 9. Deformed test. 7–8. *Bolivinelina pseudopunctata* (Höglund).

later reported from shelf to intertidal environments worldwide (Murray, 2006). It is one of the most abundant benthic foraminifera in muddy Skagerrak- and adjacent fjord-sediments (Höglund, 1947; Alve and Murray, 1995, 1997) and is well-adapted to dysoxia (Bernhard et al., 1997, as *Spiroplectammina earlandi*).

Bolivinelina pseudopunctata is reported living in European waters from the Mediterranean to the Norwegian Sea (Murray, 2006). It is common in oxygen-depleted, *Stainforthia fusiformis*-dominated, Swedish and Norwegian silled fjords (Gustafsson and Nordberg, 2001; Alve, unpublished

data). Canadian Pacific, oxygen-deficient silled fjords have similar assemblages dominated by *Stainforthia feylingi*, with subsidiary *Bolivina pacifica* (probably = the Scandinavian *B. pseudopunctata*) (Patterson et al., 2000). Given the vast geographic distance between these oxygen-depleted fjord systems, the similarity in faunal composition is striking.

Liebusella göesi is reported as living (stained) only in European waters: at 168–652 m water depth in the open Skagerrak (Alve and Murray, 1995, 1997), shallower in adjacent fjords (e.g. Alve and Nagy, 1986), at 170–218 m in the Muck Deep on the continental shelf west

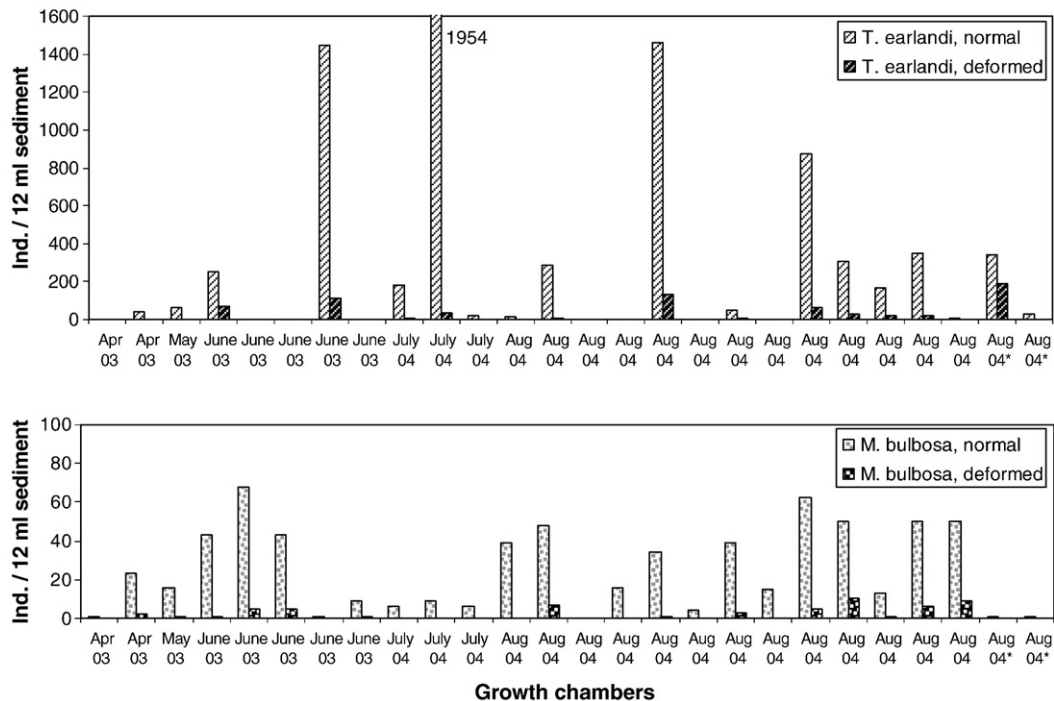


Fig. 5. Experiment 1. Absolute abundance (ind./12 ml sediment) of normal and deformed *Textularia earlandi*- (upper) and *Morulaepecta bulbosa*- (lower) populations growing in <32 μm -sized sediments (collected at 320 m water depth) after exposure to simulated shallow-water conditions.

of Scotland (Murray, 2003), at 80–140 m in the Bay of Biscay (Duchemin et al., 2008), and possibly in the Adriatic Sea (as *Martiniottiella* sp., deStigter et al., 1998). However, recent studies indicate that it may occur as juveniles in deep-water around New Zealand (Bruce W. Hayward, pers. com. June 2009).

4.1.2. Group 2: “exotic” species

These include *P. mediterraneis*, *M. bulbosa*, *Bolivina pseudoplicata*, *E. scaber*, *C. arctica* and *G. praegeri*. All, possibly except *G. praegeri*, are inner-neritic species commonly living at <100 m water depth.

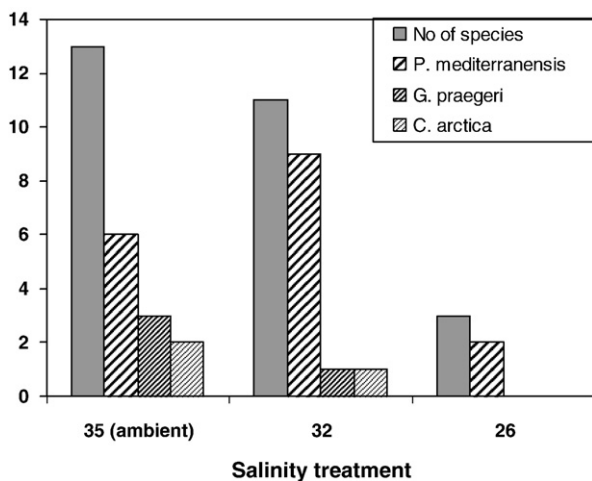


Fig. 6. Experiment 2. Total number of species in each treatment and number of growth-chambers where >63 μm -sized *Planorbulina mediterraneis*, *Gavelinopsis praegeri*, and *Cuneata arctica* appeared in <32 μm -sediments which had been collected at 320 m water depth, stored for two years and exposed to simulated shallow-water conditions for 11 months. Salinity of growth-chambers: 35 (ambient), 32, and 26. Number of growth-chambers for each treatment = 11.

Planorbulina mediterraneis is an attached, cosmopolitan species that lives primarily within the photic zone, generally shallower than 30 m (Murray, 2006). However, it has also been reported living (stained) down to 201 m water depth (Altenbach et al., 2003). It commonly lives epiphytically on seagrasses with large, flat or arch-shaped leaves. It has a life-span of >10 months and its depth distribution (15–30 m) corresponds to that of the plant (Langer, 1993). In a colonization experiment on carbonate- and PVC-substrates in Kosterfjord, Sweden, *P. mediterraneis* showed a clear abundance maximum (nearly 5000 individuals/m²) at 7 m water depth after 2 years, and abundance decreased with increasing water depth (Wisshak and Rüggeberg, 2006). Consequently, it is not expected to live in muddy sediments at 320 m water depth in the Skagerrak, and, accordingly, it was not (except one dead juvenile) present among the thousands of live or dead individuals examined from our sampling site. Yet, due to its abundance following exposure to shallow-water conditions (Figs. 4 and 6), it must have been present as <32 μm propagules in the original basin sediments. The prolocular diameter of microspheric individuals is 11–14 μm and that of megalospheric ones is 23–56 μm (Loeblich and Tappan, 1987). Consequently, the individuals transported to the sampling site must have included microspheric forms which reproduced asexually during the experiment to produce megalospheric offspring (diameter 30–50 μm , Table 1; see also Section 4.2). The growth and subsequent reproduction of this species was probably triggered in part by the establishment of filamentous algae in the growth-chambers, a view supported by the individuals’ yellow-greenish coloured cytoplasm. During the experiment, individuals of this species attached to virtually all available substrates within the growth-chambers (e.g., chamber walls, lids, other foraminifera).

Morulaepecta bulbosa is, to the authors’ knowledge, only reported from European shallow-waters but bears a striking resemblance to the illustration of *T. earlandi* from New Zealand in Hayward et al. (1999, Plate 2, Figs. 22–23). It is a common living species at 32 m water depth in the northern Adriatic Sea (e.g., Barmawidjaja et al., 1992; Ernst et al., 2002).

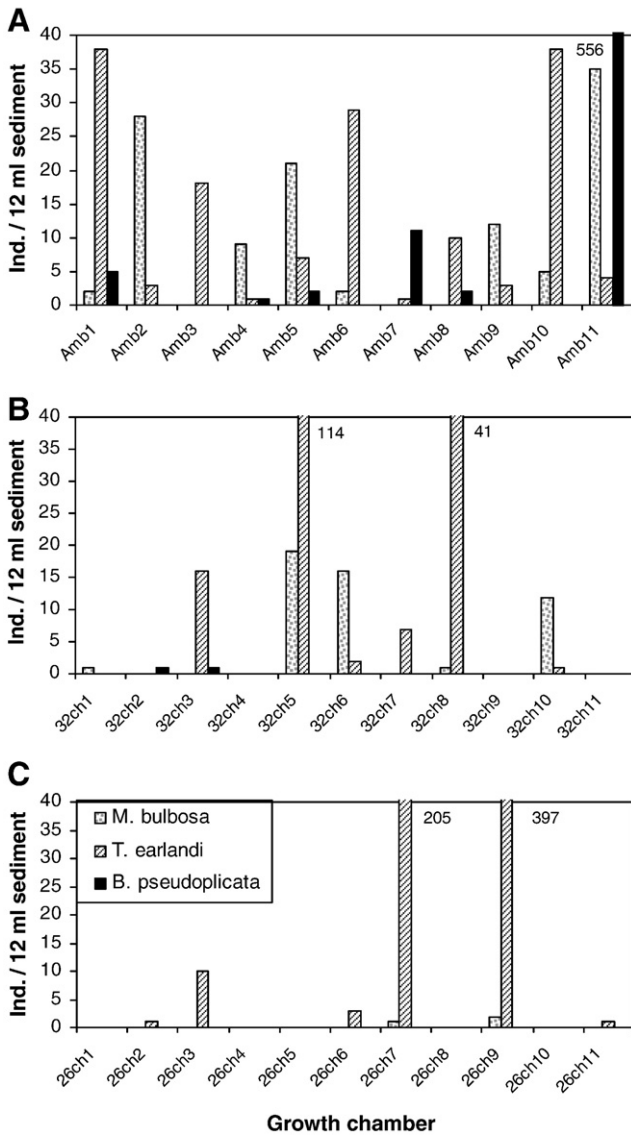


Fig. 7. Experiment 2. Absolute abundance (ind./12 ml sediment) of the most common species (>63 μm) growing in <32 μm sediment collected at 320 m water depth, stored dark and cold for two years and exposed to simulated shallow-water conditions for 11 months. Salinity of growth-chambers A) 35 = ambient; B) 32; and C) 26.

Bolivina pseudoplicata is an inner-neritic, cosmopolitan species (Sliter, 1970), reported living (stained) in shallow (<50 m) estuaries and lagoons from Japan and both sides of the Atlantic Ocean (Murray, 2006).

eggerelloides scaber is a common inner shelf species in NW Europe, also recorded from Brazil, the Mediterranean, West Africa (Murray, 2006), and recently from the subantarctic southwest Pacific (Hayward et al., 2007a). Höglund (1947) characterised it as a shallow-water form in the Gullmarfjord, Sweden, occurring with thousands of specimens in each core sample at 15–20 m depth. He rarely recorded it deeper than 60 m. However, in the Skagerrak, he found unstained individuals down to 204 m. In the Kattegat, the *E. scaber* assemblage typically occurs at 14–35 m water depth (Conradsen et al., 1994). On the inner shelf of the southern North Sea, *E. scaber* dominates parts of the year at 52 m water depth and can make up 1–10% of the live assemblage at 63 m (Murray, 1992), and Murray (2003) reported it living at 170 m in the Muck Deep, just off Scotland (see Appendix A). *E. scaber* lives epiphytically on seagrass (Debenay,

2000) and its occurrence has been suggested to be related to the presence of *Zostera* (Mendes et al., 2004). Herbivory also fits with our observations including individuals with green cytoplasm. On the other hand, in the western Baltic Sea (23.5 m) organic detritus, which triggered reproduction in *Elphidium excavatum*, did not seem to have the same effect on *E. scaber* (Schönfeld and Numberger, 2007). Also, an unfed disturbance experiment showed that it survived 3 weeks of burial without moving up or down in the sediment, suggesting that the required food was evenly distributed (Duijnsteet et al., 2003). In concert, this points to an omnivorous feeding strategy.

Cuneata arctica is recorded (probably dead) down to 100 and occasionally 200 m in all oceans, mainly in the northern part of the northern hemisphere (Loeblich and Tappan, 1987), but also off Argentina (references in Haynes, 1973), in coastal lagoons on the southeastern coast of Australia (Yassini and Jones, 1995), and around New Zealand (Hayward et al., 1999). On the Danish side of the Skagerrak, Höglund (1947) recorded unstained *Reophax nana* at 66–400 m. Live (stained) individuals are reported from 17 m in the Oslofjord (Alve and Nagy, 1986), from 32 m in the northern Adriatic Sea (as *Acostata mariae*, Ernst et al., 2002; Duijnsteet et al., 2003), and with a few individuals (as *Clavulina obscura*) generally at <80 m (occasionally down to 150 m) in the southern North Sea and the English Channel (Murray, 2006, web tables WA 114, 117, 118). Live *R. nana* are abundant in salt marshes on the Atlantic side of North America (Goldstein and Watkins, 1998) and down to 40 m off Baja California on the Pacific side (references in Murray, 2006).

Gavelinopsis praeegeri is a cosmopolitan, clinging/attached species (Murray, 2006) which occasionally moves around with a speed of ~1.24 $\mu\text{m}/\text{min}$ (Gross, 2000). Although commonly considered a shelf species (Murray, 2006), including estuaries (e.g., Debenay et al., 2006), it has been reported living (stained) down to 3736 m water depth in the Gulf of Guinea (Altenbach et al., 2003). In the Skagerrak basin, living individuals of *G. praeegeri* are extremely rare. In a total of 56 samples examined from 117 to 652 m water depth (Fig. 1), only 2 individuals were recorded at the shallowest station on the Danish side (Alve and Murray, 1995, 1997). Because it is epifaunal in high energy environments, its test may readily be transported. Indeed, a few dead tests of *G. praeegeri* (and other species transported from shallow-water) were recorded on the southern slope of the Skagerrak basin, NW of Denmark (Bergsten et al., 1996; Alve and Murray, 1997) probably reflecting a shallower, southern source. Considering that 1) live (stained) individuals of the species were not recorded at the present sampling site, 2) that only two live (stained) individuals (at 117 m water depth) were recorded in the extensive data set reported by Alve and Murray (1995, 1997), and 3) that it only occurred with 4 dead examples among the nearly 20,000 tests examined from the sampling site, it is inferred that it does not grow and reproduce in soft sediment at 320 m in the Skagerrak.

4.2. Survival and dispersal potential

How could shallow-water species which do not grow and reproduce at the sampling site appear in the fine-fraction of sediments collected there following exposure to simulated shallow-water conditions (Exp. 1)? How could the same happen in sediments that had been kept isolated in the dark at ambient temperature for two years (during which time none of the shallow-water species grew) before exposure to shallow-water conditions (Exp. 2)? Our experiments show that the six Group 2-species were transported to the sampling site as <32 μm -sized propagules (juveniles), and that they must be particularly resilient, have a good survival potential, and be able to remain dormant for two years. Survival for years in culture without reproduction has been reported for adult populations (e.g., deep-sea species in Hemleben and Kitazato, 1995) and a high survival potential has been indicated for some of the present species (e.g., Ernst et al., 2002; Duijnsteet et al., 2003). The present results extend this resilience and survival potential to include juveniles. Formation of “cysts” is a common feature in many

foraminiferal species serving numerous functions such as feeding, reproduction, growth and protection (e.g., Myers, 1936; Heinz et al., 2005, and references therein). For *P. mediterraneensis* and *G. praegeri*, residing in “cysts” on the walls of the growth-chambers is in accordance with Gross' (2000) observations, and it probably aided survival under otherwise stressful conditions.

Of all the indigenous foraminiferal species recorded at the sampling site, only *T. earlandi* and *B. pseudopunctata* grew and continued to flourish when transferred from bathyal (320 m) to simulated shallow-water (0 m) conditions. The explosive reproduction of the widely occurring *T. earlandi* probably reflects a particularly opportunistic life strategy. The fact that it was recorded standing aperture down in algae indicates herbivory. Why didn't other shelf species grow in the present experiments? First, the environmental conditions (e.g., sun light and UV radiation, temperature, lack of appropriate food and biochemical exchange with surrounding environment) in the growth-chambers were dramatically different from those at 320 m in the Skagerrak. Second, the experimental design using <32 µm sediments only, excluded species with larger proloculi, including the megalospheric generation in some species (e.g., *E. scaber* and *L. goësi*; for proloculi sizes, see Appendix A). Third, the high abundance of *T. earlandi* may have suppressed growth of other infaunal species. Fourth, life history dynamics or limited survival capabilities of propagules of other shallow-water species may have precluded their occurrence in basinal sediments of the Skagerrak.

Overall, the environmental conditions in the growth-chambers must have been hostile to many species, implying that the ones which did grow are hardy species with a substantial survival potential, and all these morphospecies seem to be cosmopolitan. Their broad distribution is probably in part due to a high survival and dispersal potential in their propagules. For the agglutinated forms, the lack of agglutination of the proloculi in *M. bulbosa*, *T. earlandi*, *C. arctica* (as *R. nana*), and microspheric *E. scaber* (Höglund, 1947) may increase buoyancy, thus aiding dispersal of the juvenile stage compared to the subsequent heavier agglutinated growth stages.

Kuhnt et al. (2005, p. 105) suggested that bolivinids and serial agglutinated species are “highly capable of survival, rapid dispersal, and rapid to explosive population increase”. Indeed, except for the temporarily attached *P. mediterraneensis* and *G. praegeri*, the foraminifera growing in our experiments are exactly bolivinids and serial agglutinated species. Examples of resilient serial agglutinated species include survival and colonization of *Textularia cushmani* in the Red Sea during early Holocene (Almogi-Labin et al., 1996) and the sudden appearance of *T. earlandi* in an oil-treated mesocosm experiment (Ernst et al., 2006). The fact that bolivinids are among the most commonly reported live benthic foraminifera in plankton tows (references in Alve, 1999), that a bolivinid appeared and flourished in a sealed culture of isolated individuals of the protist *Gromia oviformis* (Alve and Goldstein, 2002), and the indication that lower Miocene, planktic, biserial *Streptochilus* spp. evolved from benthic ancestors (Smart and Thomas, 2007) point in the same direction.

Although attached forms may be transported, and thereby dispersed, together with their substrate (e.g., on floating algae, Spindler, 1980), species of some, for instance *Cibicides*, are suggested to disperse as “larvae” (Svavarsson and Davidsdottir, 1995) or propagules (Beaulieu, 2001). Dispersal through propagule transport is probably essential for large-sized and attached foraminifera (Alve and Goldstein, 2003). The appearance of *P. mediterraneensis* and *G. praegeri* in the present experiments supports this view.

Essential biological characteristics, such as modes of reproduction vary among benthic foraminifera, and their life cycle is more varied than in virtually any other group of protists (Goldstein, 1999). Furthermore, lack of significant genetic differences between specimens collected at depths ranging from 1000 to 6300 m suggests that

Bathyallogromia weddellensis is adapted to conditions that span a broader bathymetric range than for most species (Gooday et al., 2004). Consequently, it is not unreasonable that other biological properties, such as resilience, dispersal mechanisms and potentials, also vary within the group. On the contrary, field experiments have shown that the rate of settlement and colonization of larger foraminifera onto new hard substrates vary between species (Fujita, 2004), and the present experiments indicate substantial inter-specific differences in dispersal potential.

To our knowledge, a distinction between micro- and megalospheric populations of the exotic species growing in the experiments is only known for *P. mediterraneensis* (Loeblich and Tappan, 1987) and *E. scaber* (Höglund, 1947). In both species, the prolocular size of the megalospheric generation is larger than the sediment grain size used in the experiments. This is interesting because whereas microspheric forms of *E. scaber* commonly constitute only about 5% of the natural Skagerrak coastal-populations (Höglund, 1947) they were transported to our sampling site and initially grew and reproduced asexually in the present experiments. Consequently, for *P. mediterraneensis* and *E. scaber*, the dispersed propagules belonged to the diploid, sexually-produced microspheric generation. This implies higher genetic variability in the populations (Hallock, 1985) and thereby enhances the possibility of speciation in recently colonized areas.

Transport of growth stages is well-known in benthic foraminifera (examples in Alve, 1999), but, as long as their survival potential is good, small propagules are likely to travel further than larger individuals. Our evidence for propagule dispersal supports Myers' (1936, p. 134) suggestion that “...juvenile Foraminifera are capable of increasing their flotation or surface resistance by extending numerous filose pseudopodia. This would also tend to lower the specific gravity of the organism, since the extension of pseudopodia is accompanied by the absorption of water.” Murray (2007, p. 172) posed the question: “If propagules aid dispersal of benthic foraminifera (.....) why are so many species endemic?” As pointed out, biological characteristics vary between species and there is no reason why survival- and dispersal-properties should be different. However, due to under-sampling and rarity, endemism may be less than so far appreciated (Finlay et al., 2004). An example is that six agglutinated species not previously recorded from the Scottish shelf were found there for the first time by dissolving away all the calcareous taxa leaving behind (i.e., concentrating) the (originally rare) agglutinated forms only (Murray, 2003).

Furthermore, survival and dispersal potential are not the only factors that influence a species' successful dispersal. For example, neritic benthic macrofaunal biogeographic provincial boundaries are commonly associated with oceanographic boundaries and agree with those of benthic foraminifera (e.g., Culver and Buzas, 1999). This indicates that even though benthic foraminifera, as opposed to benthic macrofauna, lack a pelagic larval stage, similar factors limit their distribution/dispersal. Such boundaries probably dictate the distribution of many species despite a high dispersal potential. Due to physical and ecological barriers not even planktic foraminifera, which are capable of long-distance dispersal, are ubiquitously dispersed throughout the domains to which they are adapted (Darling and Wade, 2008). Still, 53 of 878 benthic species are currently occurring ubiquitously around North and Central America. Further, these must have evolved recently and dispersed rapidly as they have no fossil record (Buzas and Culver, 1991). Additionally, genetically verified species such as the shallow-water *Ammonia* type 1 and *Psammophaga* sp. are widely distributed (Pawlowski and Holzmann, 2008) and the genetic diversity in some typically abyssal foraminiferal species is minimal on a global scale (Pawlowski et al., 2007). In concert, it seems that the biogeographic distribution of benthic foraminifera depends on an interplay between dispersal potential of different species and the position of environmental boundaries. According to Vanormelingen et al. (2008, p. 393) “...the

Table A1Experiment 1. Number of foraminifera (>63 µm) and *Gromia* per growth-chamber (ind./12 ml <32 µm-sized sediment) after exposure to simulated shallow-water conditions. Barren growth-chambers not included.

Growth-chamber harvested	Nov 02	Dec 02	Apr 03	Apr 03	May 03	June 03	June 03	June 03	June 03	June 03	July 04	July 04	July 04	Aug 04	Aug 04	Aug 04	Aug 04	Aug 04	Aug 04	Aug 04	Aug 04	Aug 04	Aug 04	Aug 04	Aug 04	Aug 04	Aug 04	Aug 04	Aug 04	Aug 04
Name of growth-chamber	60 m	Amb	Amb	Amb D	Amb #II	Amb	Amb	Amb	Amb	Amb D	Amb	Amb	Amb	Amb	Amb	Amb	Amb	Amb	Amb	Amb	Amb	Amb	Amb	Amb	Amb	60 m	60 m	60 m	60 m	60 m
	21.11	23.12	24.04	24.04	27.05	03c	03e	03f	03 g	03 h	04a	04b	04c	1	2	4	5	7	8	9	12	18	19	1	2*	6*	7*	11		
<i>Cuneata arctica</i>				3	2	8	44	3	3	2	5	1	1	3	4		6	1	2	6	8	14	8	2			1		778	
<i>Eggerella europeum</i>						1									2		2		1		3									
<i>Eggerelloides scaber/</i>			143	1		17	103							1	1		1													1
<i>Liebusella goësi</i>																														
<i>Leptohalysis catella</i>																					1									
<i>Leptohalysis catenata</i>																				1										
<i>Leptohalysis scottii</i>									1										1											
<i>Morulaplecta bulbosa</i>			1	25	17	44	73	48	1	10	6	9	6	39	55	16	35	42	15	67	60	14	56	59	1	1	1			
<i>Reophax fusiformis</i>										1										2										
<i>Textularia earlandi</i>		1		45	60	322		2	1553		189	1986	24	14	294	1	1589	53	1	939	333	187	366	6	531	1	29	1		
<i>Textularia skagerrakensis</i>																				1										
<i>Trochamminopsis quadriloba</i>																				1										
Trochamminid					2																				1		1			
Trochamminid					6																									
<i>Bolivina pseudoplicata</i>		1		16			17	8			14	4	1	8	2		1	2		2	2	2	4	1			4			
<i>Bolivinellina pseudopunctata</i>													1		2						237	3	1							
<i>Brizalina skagerrakensis</i>																					1									
<i>Brizalina spathulata</i>							1																							
<i>Buliminella elegantissima</i>				1		1														1			1							
<i>Cassidulina laevigata</i>									1												1									
<i>Gavelinopsis praegeri</i>						1					1														1			1	1	
<i>Globobulimina auriculata</i>																				1										
<i>Planorbulina mediterraneanensis</i>	2	1	13	46		191	119	118	1	33	242	244		232	3		165	153		143	34	3	78	210		>162	303			
<i>Pullenia osloensis</i>																				3	1									
<i>Stainforthia fusiformis</i>						1				4			2				1	2		2	3				1					
Sum	2	3	157	138	87	585	358	179	1559	51	456	2247	35	299	361	17	1800	256	19	1169	681	289	596	361	533	>165	339	780		
No. of foraminiferal species	1	3	3	7	5	8	7	5	5	6	5	8	6	7	7	2	8	9	4	13	11	9	8	8	3	4	6	3		
No. of <i>Gromia</i>	0	3	1	0	2	13	1	2	4	7	0	1	0	5	15	1	13	1	8	12	5	4	1	0	5	3	8	3		

* = >125- rather than >63-µm fraction examined.

Table A2

Experiment 2. Number of foraminifera (>63 µm) and *Gromia* per growth-chamber (ind./12 ml <32 µm-sized sediment). Harvested in July 2005 after 11 months exposure to simulated shallow-water conditions.

Growth-chamber	Amb1	Amb2	Amb3	Amb4	Amb5	Amb6	Amb7	Amb8	Amb9	Amb10	Amb11	32ch1	32ch2	32ch3	32ch4	32ch5
<i>Ammobaculites</i> sp.													1		1	
<i>Bathysiphon</i> sp.															1	
<i>Cuneata arctica</i>		1					1									
<i>Eggerella europeum</i>		1				2				1	1					
<i>Eggerelloides scaber</i> / <i>Liebusella goësi</i>		1	1		1	1			1							
<i>Leptohalysis catella</i>																
<i>Leptohalysis gracilis</i>						1				1						
<i>Morulaplecta bulbosa</i>	2	28		9	21	2			12	5	35	1				19
<i>Reophax fusiformis</i>																
<i>Textularia earlandi</i>	38	3	18	1	7	29	1	10	3	38	4			16		114
Trochamminid						1										
<i>Bolivina pseudoplicata</i>	5			1	2		11	2				556	1	1		
<i>Bolivinelina pseudopunctata</i>		1								1						
<i>Brizalina difformis</i>	1							1								
<i>Brizalina</i> sp.														1		
<i>Gavelinopsis praegeri</i>				121		1	1						1			
<i>P. mediterraneensis</i>	176	42	97					23		80	222	259	37	150	171	74
<i>Stainforthia fusiformis</i>											1					
Sum	222	77	116	132	31	37	14	36	16	126	819	260	40	170	171	207
No. of foraminiferal species	5	7	3	4	4	7	4	4	3	6	6	2	4	6	1	3
No. of <i>Gromia</i>	3	1	2	0	0	1	2	0	3	3	0	0	2	2	5	6

geographic distribution of diatoms ranges from global to narrow endemic" and the cosmopolitan distribution in many microbial species has probably been attained slowly and incrementally (Telford et al., 2006). It is reasonable to assume that the same applies to benthic foraminifera.

At the moment, we can only point to possible mechanisms and processes concerning benthic foraminiferal dispersal. In order to obtain more concrete knowledge we should follow the advice of Mitchell and Meisterfeld (2005), by striving to agree on a definition for what a species is and improve the taxonomy by combining morphological and molecular characters.

4.3. Propagule source

No live (stained) and only a few dead individuals of Group 2-species were recorded among the thousands of live and dead individuals examined from the original (>63 µm) pre-experiment ($t=0$) sediments. Neither are they reported live from other >300 m water depth-stations in the Skagerrak basin (Corliss and van Weering, 1993; Alve and Murray, 1995, 1997). Consequently, the Group 2-species, *C. arctica*, *P. mediterraneensis*, *G. praegeri*, *E. scaber*, *M. bulbosa*, and *Bolivina pseudoplicata*, are exotic forms which do not grow and reproduce at 320 m water depth in the Skagerrak. *P. mediterraneensis* is not reported living in the North Sea or the open Skagerrak (Murray, 2006). Adult populations of two or more of them commonly occur together in shallow subtidal habitats along the European coastline from the Mediterranean to the North Sea (e.g., Donnici and Serandrei Barbero, 2002; Scott et al., 2003; Mendes et al., 2004; de Nooijer et al., 2008). Also, the presence of a few dead Group 2-tests reflects that the sampling area occasionally receives sediment transported out from shallower areas, probably from the Danish side of the Skagerrak. Transport of dead *Ammonia* spp. (as *A. beccarii*), *E. scaber*, and *P. mediterraneensis* from the south to the upper part of the Danish slope of the Skagerrak basin was shown by Alve and Murray (1997). Consequently, based on the above and considering the dominant NE direction of the Jutland Current flowing along the western

coast of Denmark, the propagule-source areas probably lie south and southwest of our sampling site.

Why didn't more marginal-marine species, like *Ammonia* spp. and *Haynesina germanica*, grow in the present experiments as they did in previous experiments (Alve and Goldstein, 2002, 2003)? One likely explanation is that by far most water flowing over the sampling site is sourced from outer rather than inner coastal areas. If this is correct, the propagule content of the sediments actually traces the dominant circulation pattern of the passing water masses.

4.4. Test irregularities and deformation

Development of abnormal or deformed tests occurs in both agglutinated and calcareous benthic foraminifera and may be triggered by chemical (including food shortage) or mechanical (i.e., physical damage followed by regeneration) environmental stress either natural or human induced (discussion in Alve, 1995, in press; Geslin et al., 2002). The reasons why, and how, it happens are far from understood but for some calcareous forms, it seems to be related to calcification processes (Geslin et al., 1998) and increase in sea-water temperature can cause retarded growth (Nigam et al., 2008). In the present experiment, the coiling plane in *P. mediterraneensis* commonly changed >30° after only a few whirls of growth (Plate III). Some *P. mediterraneensis* were attached to the walls of the growth-chambers but for those juveniles that were attached to other foraminifera (Plate I) the coiling plane may have been forced to change as the individual grew larger than its attachment surface. This is consistent with the observations that the morphology of *P. mediterraneensis* mirrors the topography of the attachment surface (Langer, 1993). Not even salinities down to 26 caused higher abundance of irregularly shaped individuals. Rather, the results showed that *P. mediterraneensis* could grow in large numbers in one of the 26 salinity treatments but its higher growth-frequency in the 32 and 35 salinity chambers (Fig. 6) suggests that it thrives better with salinities >30. This agrees with Wisshak and Rüggeberg (2006) who characterise *P. mediterraneensis* as being euryhaline and eurytherm. They

32ch6	32ch7	32ch8	32ch9	32ch10	32ch11	26ch1	26ch2	26ch3	26ch4	26ch5	26ch6	26ch7	26ch8	26ch9	26ch10	26ch11
		1														
					1											
		1														
16		1		12								1		2		
2	7	41		1			1	10			3	205		397		1
		1														
3	95		2		47						1		181			
21	103	44	2	13	48	0	1	10	0	0	4	206	181	399	0	1
3	3	4	1	2	2	0	1	1	0	0	2	2	1	2	0	1
3	5	5	1	7	0	0	0	0	4	0	2	1	5	0	0	0

did not report any test irregularities even at the 7 m-station where salinity frequently dropped below 25 coupled with temperatures of ~1–18°C.

The deformation in the agglutinated species *T. earlandi* and *M. bulbosa* included a sudden increase in chamber size which caused a change in growth direction (Plate II). Salinity can be ruled out as a cause since deformations developed in ambient salinity sea water. Neither can physical disturbance nor addition of any chemical substances be the cause as the growth-chambers stood still and were sealed (i.e., nothing added) throughout the experimental period. A probable cause is rapid daily variation in temperature, particularly on sunny days, when direct sunlight leads to temperatures higher than sea-water.

5. Conclusions

The Skagerrak basin sediments contain abundant “pools” of exotic propagules (<32 µm in size) from benthic foraminiferal species transported from subtidal areas probably S-SW of the sampling site which was located at 320 m water depth. These transported propagules were able to survive (without growth) for two years before exposure to simulated shallow-water conditions, after which they grew and reproduced. Exotic taxa appear to have been transported to the study site as tiny propagules belonging to the sexually-produced, diploid, microspheric generation. Some species developed a high proportion (up to 35%) of strongly deformed individuals, probably in response to stress (e.g., strong daily variation in temperature). The present experiments show that propagules of certain species are sufficiently resilient to survive transport, remain “dormant” for two years, and then start growing and reproducing once conditions permitted. Hence, our sampling site has a cryptic diversity which is larger than that revealed through traditional faunal analyses. *T. earlandi* seems to be an exceptionally robust species with an opportunistic life strategy, high resilience, and good survival potential. The experiments indicate that the resilience and survival capacity differ between benthic foraminifera.

This, together with oceanographic, physical and ecological boundaries/barriers causes some species to be widely distributed and others endemic.

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We thank Bruce Corliss for his kind agreement to deviate from the original schedule and stop the “RV Arne Tisselius” in the middle of the Skagerrak. Without this gesture, the present paper would never have been written. We are grateful to John E. Whittaker for taxonomic advice and to the reviewers Ellen Thomas and Bruce W. Hayward for interesting and useful comments which helped in improving the manuscript.

Appendix A. Faunal reference list

Generic classification follows Loeblich and Tappan (1987). The original descriptions can be found in the Ellis and Messina world catalogue of foraminiferal species on www.micropress.org. The taxa are listed alphabetically.

Bolivina pseudoplicata Heron-Allen and Earland, 1930. Proloculus diameter 16–22 µm (Sliter, 1970). Strongly resembles *Bolivina subexcavata* Cushman and Wickenden, 1929.

Bolivinellina pseudopunctata (Höglund) = *Bolivina pseudopunctata* Höglund, 1947.

Cuneata arctica (Brady) = *Reophax arctica* Brady, 1881. Proloculus diameter ~20 µm (Haynes, 1973). There is a range of similar forms which are difficult to separate on morphological grounds, including *Clavulina obscura* Chester (1892), *Reophax nana* Rhumbler (1913), and *R. mariae* Acosta (1940). Based on morphological similarity, it is reasonable to assume that our individuals belong to the same species as the one Höglund (1947) called *R. nana* Rhumbler, 1913. Höglund synonymised his form with ?*Reophax communis* Lacroix, 1930, but even though his form approached *R. arctica* Brady 1881, he concluded that they were not the same

because, according to Lacroix, *R. arctica* and *R. communis*, cannot be confused. However, it is likely that Rhumbler, when describing *R. nana*, was not aware of Brady's 1881-description of *R. arctica*, as he made no reference to Brady's work from the rather unknown Austro-Hungarian North-Polar Expedition (J.E. Whittaker, pers. com., 2008). Furthermore, there is a strong resemblance between our form and *Reophax mariae* Acosta, 1940. Brönnimann et al. (1992) described a new genus, *Acostata*, with *R. mariae* as type species and stated that the main difference between *Acostata* and *Cuneata* is that the latter is compressed in transverse section, while the former is not. This feature is probably not a good criterion because Höglund's individuals of *R. nana* are "...usually round in transverse section, but it is not uncommon to find more or less compressed specimens, as Rhumbler also observed in his material" (Höglund, 1947, p. 92–93). Except for the more or less compressed nature, it is not clear from Brönnimann et al.'s (1992) rather detailed descriptions how *Acostata mariae* differs from *C. arctica*. The same authors consider the species which Lutze (1974, pl. 1, fig. 16) called *R. nana* Rhumbler to be *A. mariae* but they do not discuss *R. nana*. The published, morphologically-based criteria used to distinguish between the above-mentioned forms are too vague to draw firm conclusions as to whether or not they are different morphospecies. Consequently, the oldest name is used here.

Eggerelloides scaber (Williamson) = *Bulimina scabra* Williamson, 1858. Proloculum of microspheric forms (diameter 8–13 µm) are not agglutinated, whereas that of the megalospheric form (diameter 35–70 µm) is agglutinated (Höglund, 1947). The triserial individuals in the present experiment showed a plastic morphology ranging from typical *E. scaber* to what looked like juvenile megalospheric *Liebusella goësi*. However, of the hundreds of individuals examined, none had developed the uniserial stage typical of *L. goësi*. Juvenile micro- and megalospheric individuals of *L. goësi* from the original, pre-experiment assemblage ($t=0$) have a loop shaped *Bulimina*-like aperture, bordered by a lip, extending from the basal suture of the last chamber up the slightly excavated apertural face, just as in *Eggerelloides* (Haynes, 1973). Due to their morphological resemblance, it is likely that deep shelf records of *E. scaber* are in fact microspheric juveniles of *L. goësi*.

Epistominella vitrea Parker, 1953.

Gavelinopsis praegeri (Heron-Allen and Earland) = *Discorbina praegeri* Heron-Allen and Earland, 1913.

Leptohalysis scottii (Chaster) = *Reophax scottii* Chaster, 1892.

Liebusella goësi Höglund, 1947. Proloculum of microspheric forms (diameter 9–13 µm) are not agglutinated, whereas that of the megalospheric form (diameter 90–190 µm) is agglutinated (Höglund, 1947). Due to strong morphological similarity, it is likely that microspheric juveniles of this species (i.e., individuals which have not yet developed the uniserial part) have been mistaken as *E. scaber* by some authors.

Morulaeplecta bulbosa Höglund, 1947. Proloculus diameter 17–33 µm (Höglund, 1947). Considered by Duijnsteet et al. (2003) to be the same as *Caronia silvestrii* Brönnimann, Whittaker and Valleri, 1992. Barmawidjaja et al. (1992, pl. 1, Figs. 5–7) report *M. bulbosa* living in the same general shallow-water area (N Adriatic) as where Brönnimann et al. (1992) collected their *C. silvestrii*. As Brönnimann et al. (1992) did not mention *M. bulbosa* and it is beyond the scope of the present paper to go into a taxonomic discussion, we use the older name, *M. bulbosa*, for our present form.

Planorbulina mediterraneensis d'Orbigny, 1826. Proloculus diameter 11–14 (microspheric) and 23–56 µm (megalospheric) (Loeblich and Tappan, 1987).

Stainforthia fusiformis (Williamson) = *Bulimina pupoides* d'Orbigny var. *fusiformis* Williamson, 1858.

Textularia earlandi Parker, 1952 = *Textularia tenuissima* Earland, 1933. The species is named *Spiroplectammina earlandi* (Parker) by some

authors (e.g., Haynes, 1973) due to the very small planospire consisting of 3 or 4 chambers closely coiled around the proloculus (for details, see Höglund, 1947). Duchemin et al.'s (2008, pl. 1, Fig. 9) illustration of *Textularia porrecta* (Brady), which dominates the foraminiferal assemblage at 80 m water depth in the Bay of Biscay, bears close resemblance with our species.

Trochamminopsis quadriloba (Höglund) = *Trochammina pusilus* Höglund, 1947.

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