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# The young microspheric (diploid) life cycle stage of benthic softbottom foraminiferans is adapted for planktonic dispersal

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ABSTRACT: This study examines the dispersal ability of megalospheric (haploid) and microspheric (diploid) foraminiferan generations in their natural soft bottom habitat. Foraminiferans typically exhibit an alternation between microspheric and megalospheric generations. Both generations display similar shapes, sizes, habitat preferences, and lifestyles. However, subtle morphological differences exist, particularly in their test (= shell) details, allowing for their differentiation. Colonization experiments were conducted along the Swedish west coast where a container with soft-bottom sediment was suspended 2.5 m above the sea bottom at 40 m water depth. They demonstrated that sublittoral benthic foraminiferans possess the capability to disperse planktonically. Reproduction and settling activities were observed year-round, peaking in the late autumn and showing a smaller second peak in April—May, coinciding with the seasonal sedimentation of algal plankton blooms. The lowest settling numbers were recorded during winter (January—March). Notably, various species reproduced at different times throughout the year, with the microspheric stage (the growing zygote) identified as the primary dispersal stage, following a pattern observed in many organisms where dispersal follows sexual reproduction. Post-dispersal, the microspheric stage undergoes growth and asexual reproduction through schizogony (meiosis and fission). In contrast, haploid offspring (megalospheric schizozoites) generally exhibit limited dispersal (cm to dm), remaining within established habitats to exploit available resources. This research sheds new light on foraminiferan dispersal patterns. It highlights that attached littoral foraminiferans in turbulent environments commonly engage in gamontogamy (aggregation between haploid gamonts) to ensure fertilization, while soft-bottom species often release flagellated gametes into the sediment or near-bottom water.

KEY WORDS: Planktonic dispersal · Diploid juvenile · Benthic foraminiferans

## 1. INTRODUCTION

The present study addresses whether a particular stage in the biphasic (haploid—diploid) life cycle of foraminiferans is specialized for dispersal, through experiments conducted entirely in natural settings. Foraminiferans provide a convenient subject for studying dispersal in relation to the life stage due to their 'classical' life cycle, which alternates between a diploid and a haploid generation (Goldstein 1999). Unlike other organisms with alternating generations, the shapes and behaviours of the 2 generations generally have many similarities. However, many species have distinct differences in the early test (= shell) morphology. The initial test chamber, known as the proloculus, forms as a cast around the zygote or haploid offspring soon after it becomes active. Among haploids (gamonts), the proloculus is typically relatively large (megalospheric), while among diploids (schizonts), it tends to be relatively small (micro-

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spheric). This size difference arises because the proloculus in the diploid test originates from the zygote, which is generally small because the gametes are small. The haploid generation (schizozoites or 'juvenile gamonts') is produced through meiosis followed by asexual division (schizogony) of the adult diploid (schizont). The offspring (schizozoite) inherits a larger proportion of cell contents from the parent. The diameter of the microspheric proloculus typically ranges from 11 to 14 µm, compared to 23 to 56 µm for the megalospheric proloculus. Consequently, the haploid generation generally has a larger proloculus, as depicted in Fig. 1. These stages of the life cycle are applicable to most investigated species (Loeblich & Tappan 1964, Boltovskoy & Wright 1976, Margulis et al. 1989, Goetz et al. 2022). However, deviations from this pattern exist in many larger benthic foraminiferans. For variations within foraminiferan life cycles, see the reviews by Lee et al. (1991) and Goldstein (1999), and the discussion about life cycle variations in Section 4 below. A specific complication of the 'classical' life cycle is trimorphism where the diploid schizont can undergo multiple fission and produce a new diploid generation. This asexually produced diploid generation can either undergo repeated multiple fission or produce haploid gamonts. All of these asexually produced propagules (haploid or diploid) are megalospheric. The megalospheric diploid schizonts remain in close proximity to the parent individual, and no signs of planktonic dispersal have been reported among them (Krüger et al. 1997, Dettmering et al. 1998).

One of the primary hypotheses regarding the benefits of sexual reproduction centers on the idea that genetic variation confers advantages to offspring dispersing in unpredictable environments. In such scenarios, sexual recombination is believed to generate some offspring that exhibit higher fitness in novel environmental conditions (Williams 1975, Maynard Smith 1978). Numerous examples illustrate how environmental variability can trigger sexual reproduction, as observed in Cladocera Rotatoria and ciliates (Hebert 1987, Margulis et al. 1989, Brusca et al. 2016).

Various incidental observations regarding foraminiferal dispersal have been documented. Benthic foraminiferans have been found in plankton samples (Murray 1965, 1982, 1987, Loose 1970), while Richter (1965) and DePatra & Levin (1989) reported on drifting and resuspension of shallow-water foraminiferans. Gerlach (1977) noted that *Elphidium* has the capacity to 'float'. Passive dispersal of foraminiferans, particularly as epifauna on floating plant material, has been reported by Bock (1970) and Gerlach (1977), as well as on mobile fauna (Zann et al. 1975, Farmer 1977, Mullineaux & DeLaca 1984, Moore 1985, Cedhagen 1988, Cedhagen & Middelfart 1998). Guy-Haim et al. (2017) showed that foraminiferans can survive the passage through fish digestive tracts and consequently be dispersed. Rieth (1957) found living marine foraminiferans in inland saline swamps during salt mining operations and proposed that they had dispersed from the sea, likely attached to bird feet. Efficient dispersal is also indicated by the rapid colonization of opportunistic foraminiferans in diverse environments (Wefer & Richter 1976, Widbom 1983, Choi 1984, Gooday 1988, Van Dover et al. 1988, Buzas et al. 1989). Finally, the wide, sometimes cosmopolitan, distribution of many deep-sea foraminiferal species (Gooday & Jorissen 2012, Hayward & Holzmann 2023) also suggests that they can disperse easily.

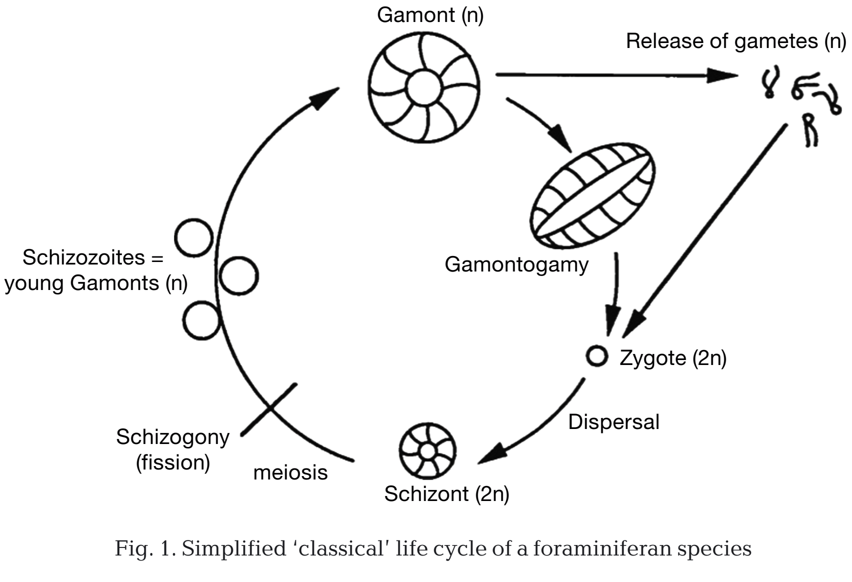

Fig. 1. Simplified 'classical' life cycle of a foraminiferan species

Alve & Goldstein (2003, 2010) conducted laboratory incubations with natural deep-water sediment, providing compelling evidence that young propagules of shallow-water foraminiferans must have undergone dispersal across remarkably extensive distances, and even to depths of several hundreds of meters. Their incubations showed convincingly that the young microspheric stage undergoes dispersal, and they concluded that the juvenile microspheric generation is the primary vector for dispersal. However, they also concluded that the megalospheric generation to some degree had the same capability (but see Section 4 below). No other experimental studies about the dispersal of certain life cycle stages in benthic foraminiferans have ever been conducted in nature, but the ability of dispersal based on indirect evidence or occasional older publications is extensively discussed in several recent publications (Alve & Goldstein 2002, 2014, Nomura et al. 2010, Goldstein & Alve 2011, Gooday & Jorissen 2012, Winston 2012, Takata et al. 2019, Goetz et al. 2022, Morard et al. 2022).

Dispersal ability can be studied by colonization experiments, offering insight into the relationship between the foraminiferans' life cycle and their distribution patterns — the real result of natural dispersal. The present study addresses this aspect and illustrates the contrasting dispersal abilities of the megalospheric (haploid) and microspheric (diploid) generations of these organisms based on observations of colonization after pelagic dispersal, conducted entirely in the natural environment. Another aim is to relate the results to existing knowledge about dispersal and life cycle stages existing in the literature to the benthic sublittoral foraminiferans. The results are also relevant to the evolution of planktonic foraminifera.

## 2. MATERIALS AND METHODS

### 2.1. Colonization experiment

Colonization experiments were carried out in Kosterfjorden, southeast of Lilleskär (58° 59′ 12″ N, 11° 06′ 53″ E) on the northern Swedish west coast, at about 40 m depth, below the halocline. A colonization container with soft bottom substrate was positioned approximately 2.5 m above the seafloor (Fig. 2). This setup was designed to avoid contamination resulting from resuspension caused by bioturbating bottom fauna. Selecting a depth below the halocline was deliberate, as it provides a significantly greater diversity of benthic species compared to shallower brackish waters, owing to the stenohaline nature of most organisms in this region. The clay bottom was selected because it consists of a fairly wide uniform area without much bottom topography. It is also located at least 20 m shallower and 0.5 km away from trawled bottoms.

The colonization container employed was a cylindrical plastic tube, 50 cm long and 15 cm wide. This aspect ratio was chosen to prevent any resuspension of foraminifera, and also of clay, from occurring within the container. Its bottom was closed while most of its sides were replaced with plankton netting (mesh size 100 µm) to prevent stagnation and oxygen depletion. A float was used to maintain the container in an upright position, well above the bottom. Various ropes, weights up to ca. 50 kg, and other components were arranged to minimize disturbances caused by currents, boat traffic, tides (less than 30 cm), wind and wave action (Fig. 2). The moraine sediment used as substrate was sampled from above the highest Pleistocene coastal line to avoid any subfossil foraminiferans. It was stored indoors until thoroughly dry and subsequently sifted in filtered seawater from 36 m depth at the colonization site (Grade 3 filter paper). The <0.1 mm fraction with a sediment thickness of 1–2 cm was used in the experiments because it resembled the surrounding largely clay bottoms. The first period of the colonization experiment commenced on 4 January 1984 and concluded on 7 January 1985. The second series commenced on 5 October 1984 and ended on 23 May 1985. The experiment terminated prematurely due to equipment loss. In the first series, the substrate was collected and replaced at intervals of 1–2 mo to precisely determine the timing of dispersal and colonization, prevent substantial growth, and subsequent reproduction of settled specimens. The second series featured a longer

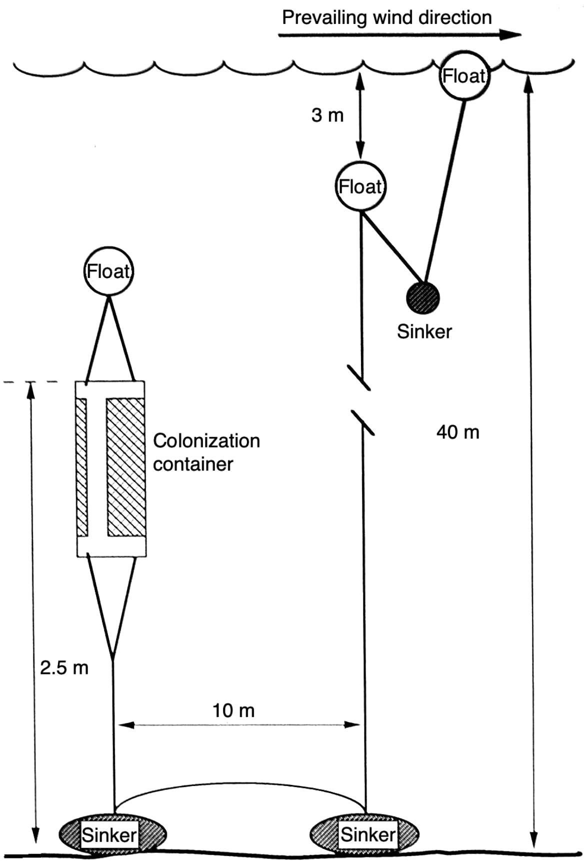

Fig. 2. Principal features of the colonization device. Thick lines linking the container, floats, and sinkers indicate ropes

time interval to allow settled specimens to grow and reproduce and to determine whether the second generation tended to remain in close proximity to the parent specimen or if it dispersed.

The sampled substrate was fixed in 4–10% formalin buffered with borax (disodium tetraborate). Subsequently, it was sieved through a series of sieves, 500, 300, 200, 100 µm mesh (where only the finest fraction contained settled foraminiferans), stained with Rose Bengal and sorted under a stereomicroscope (Wild M5). The specimens were transferred from water to 80% ethanol for preservation. To increase test transparency, specimens were then transferred from alcohol to xylol and proloculus diameters measured using a calibrated ocular micrometer scale. Höglund (1947) described 24 multilocular, sublittoral, soft-bottom species, for which both generations are known, from Skagerrak, including Kosterfjorden. The average diameter of the respective pairs of the micro- and megalospheric generations are plotted in a graph (Fig. 3). From this it can be seen that the selection of a diameter of ⩽20 µm is representative for the microspheric generation in this region.

### 2.2. Additional studies on *Ammonia* cf. *aomoriensis*

Littoral sediment was collected from Kalø Bådhavn (Egå Strandvej) north of Aarhus, Denmark (56° 14′ 42.58″ N, 10° 20′ 18.60″ E), by taking the top centimeter of sediment at a water depth of 0.2 m (low tide). The sediment was sieved in the field and the 200–300 and 300–500 µm fractions were brought to the laboratory together with saltwater from the same site. Foraminiferans, *Ammonia* cf. *aomoriensis* (Asano, 1951), were picked under a stereomicroscope by the use of a pair of entomology forceps. It was easy to identify the living individuals, even when they were disturbed by handling and consequently retracted the pseudopodia, because they contain yellow cytoplasm. Samples from the same locality were used for a previous study (Cedhagen et al. 2021) but were also used for other purposes. When used for teaching, individuals collected 14 May 2001 were kept at room temperature and photographed in the laboratory the following day using an inverted microscope (Zeiss Axiovert 135M). Additional such samples were collected 24 April 2024. Ninety foraminiferans were picked and kept in a petri dish at room temperature, where the behaviour of large individuals was observed.

## 3. RESULTS

### 3.1. Colonization experiments

The results of the sediment colonization experiments are presented in Tables 1 & 2. While a wide variety of species was obtained, each was typically represented by a relatively small number of specimens, in some cases only 1 individual. However, these results show that benthic soft-bottom foraminiferans have planktonic dispersal. They also show that almost all settled individuals (573) were very small (all passed through a 200 µm and were retained on a 100 µm mesh sieve). Consequently, they dispersed soon after reproduction.

In the case of 21 species, totaling 242 specimens, it was impossible to differentiate between generations based on their test morphology. These species were either agglutinated monothalamids or possessed test walls that were too thick to become transparent through xylol treatment, making it impossible to determine whether the specimens were megalospheric (haploid) or microspheric (diploid). The remaining 25 species were represented by 328 specimens, almost all (>99%) of them microspheric juveniles, with a proloculus inner diameter of ⩽20 µm, confirm-

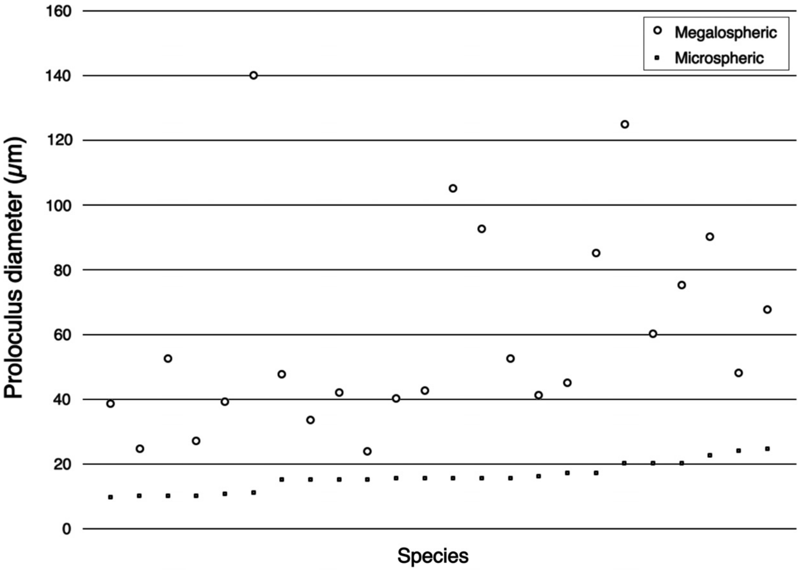

Fig. 3. Proloculus diameter in soft-bottom foraminiferan species from Skagerrak where both micro- and megalospheric individuals are known to occur. Data from Höglund (1947)

Table 1. Results of the colonization experiments with young foraminiferans that have settled in the soft sediment substrate. It shows the numbers of foraminiferans belonging to different species that were found in the collection device at the end of each 1–2 mo sampling interval

| Species | First series | | | | | | | | Second series | | Sum |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 4 Jan– 6 Mar 1984 | 6 Mar– 18 Apr 1984 | 18 Apr– 29 May 1984 | 29 May– 25 Jul 1984 | 25 Jul– 31 Aug 1984 | 31 Aug– 5 Oct 1984 | 5 Oct– 13 Nov 1984 | 13 Nov 1984– 7 Jan–1985 | 5 Oct 1984– 7 Jan 1985 | 7 Jan– 23 May 1985 | |
| **Microspheric (diploid)** | | | | | | | | | | | |
| *Ammoscalaria pseudospiralis* (Williamson, 1858) | | | | | | | | | 2 | | 2 |
| *Labrospira kosterensis* Höglund, 1947 | | | 1 | | | | | | 1 | | 2 |
| *Reophax scorpiurus* Montfort, 1808 | | 1 | | | | | | | | | 1 |
| *Reophax scottii* Chaster, 1892 | 1 | | | | 1 | | | | 2 | | 4 |
| *Textularia bocki* Höglund, 1947 | | | | | | | | | 1 | | 1 |
| *Textularia kattegatensis* Höglund, 1947 | | | | | | | | | 1 | | 1 |
| *Rotaliammina adaperta* (Rhumbler, 1938) | | | 3 | | | | | | | | 3 |
| *Cornuspira foliacea* (Philippi, 1844) | | | | | 3 | 2 | 2 | | 4 | | 11 |
| *Pateoris hauerinoides* (Rhumbler, 1936) | | | | 1 | 6 | | | | | | 7 |
| *Silicosigmoilina groenlandica* (Cushman, 1933) | | | | 2 | | | | | | | 2 |
| *Ammonia batavus* (Hofker, 1951) | | 3 | 1 | | | | | | 12 | | 16 |
| *Anomalina balthica* (Schröter, 1783) | | | | | | | | | 3 | | 3 |
| *Bolivina spathulata* (Williamson, 1858) | | | | | | 1 | | | 3 | | 4 |
| *Stainforthia fusiformis* (Williamson, 1848) | | | | | | | | | 2 | | 2 |
| *Bulimina marginata* d'Orbigny, 1826 | | 15 | | | | | 2 | | 12 | | 29 |
| *Lobatula lobatula* (Walker & Jacob, 1798) | | 1 | 24 | 6 | | | 3 | 27 | 27 | 15 | 103 |
| *Neoconorbina williamsoni* (Chapman & Parr, 1932) | | | 1 | 1 | | | | | | | 2 |
| *Discorbis* sp. | | | | | | | 1 | | | | 1 |
| *Cribroelphidium incertum* (Williamson, 1858) | | | | | | | | | 1 | | 1 |
| *Elphidium* sp. | | 1 | | | | | | | | | 1 |
| *Elphidium umbilicatulum* (Walker & Jacob, 1798) | | | | 1 | | | | | | 1 | 2 |
| *Globobulimina turgida* (Bailey, 1851) | 1 | | | | | | | | | | 1 |
| *Nonionellina labradorica* (Dawson, 1860) | | | | | 1 | | | | 1 | | 2 |
| *Nonionina turgida* (Williamson, 1858) | | | | | | | | | 1 | | 1 |
| *Rosalina globularis* d'Orbigny, 1826 | | | 33 | 14 | 14 | 1 | | 60 | 3 | 1 | 126 |
| **Megalospheric (haploid)** | | | | | | | | | | | |
| *Rosalina globularis* d'Orbigny, *1826* | | | | | 2 | 1 | | | | | 3 |

Table continued on next page

Table 1 (continued)

| Species | First series | | | | | | | | Second series | | Sum |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 4 Jan– 6 Mar 1984 | 6 Mar– 18 Apr 1984 | 18 Apr– 29 May 1984 | 29 May– 25 Jul 1984 | 25 Jul– 31 Aug 1984 | 31 Aug– 5 Oct 1984 | 5 Oct– 13 Nov 1984 | 13 Nov 1984– 7 Jan–1985 | 5 Oct 1984– 7 Jan 1985 | 7 Jan– 23 May 1985 | |
| **Life cycle stage unknown** | | | | | | | | | | | |
| *Psammophaga crystallifera* (Dahlgren, 1962) | | | | | | | 1 | 5 | 2 | 1 | 9 |
| Allogromiidae spp., indet. | | | | | | | 2 | 7 | 3 | | 12 |
| *Nemogullmia longevariabilis* Nyholm, 1953 | | | | | | | 1 | 2 | | | 3 |
| *Nemogullmia* sp. | | | | | | 1 | 8 | | 3 | | 12 |
| *Adercotryma glomeratum* (Brady, 1878) | | | | 1 | | | | | | | 1 |
| *Bathysiphon argenteus* Heron-Allen & Earland, 1913 | | | 1 | | 3 | | 5 | 8 | 27 | | 44 |
| *Bathysiphon* cf. *rufus* De Folin, 1886 | | | | | | | | | 4 | | 4 |
| *Eggerella scabra* (Williamson, 1858) | | 2 | | | | | | | | | 2 |
| *Gromia oviformis* Dujardin, 1835 | 1 | | 1 | | | 8 | 10 | 38 | | 10 | 69 |
| *Hemisphaerammina* sp. | 1 | | | | | | | | | 1 | 2 |
| *Bathysiphon cf. flexibilis* (Wiesner, 1931) | | | | 1 | | | | | | | 1 |
| *Hyperammina* sp. | | | | | | | | | 1 | | 1 |
| *Proteonina fusiformis* (Williamson, 1858) | | 1 | | | | | | | 8 | | 9 |
| *Psammosphaera fusca* Schultze, 1875 | | | | | 5 | | | | | | 5 |
| *Spiroplectammina biformis* (Parker & Jones, 1865) | | | | | | | | | 2 | | 2 |
| *Technitella legumen* Norman, 1878 | | | | 1 | | | | | | | 1 |
| *Tholosina bulla* (Brady, 1881) | | | | 1 | | | | | | | 1 |
| *Thurammina papillata* Brady, 1879 | | | | | | | | 17 | | | 17 |
| *Eggerelloides medius* (Höglund, 1947) | | 27 | | | | | | 3 | 5 | | 35 |
| *Acervulina inhaerens* Schultze, 1854 | | | | | | | | 3 | 1 | | 4 |
| *Cassidulina laevigata* d'Orbigny, 1826 | | | | | 1 | | | | 8 | | 9 |
| *Melonis pompilioides* (Fichtel & Moll, 1798) | | | | | | | | | | | 0 |
| **Sum** | 4 | 51 | 65 | 29 | 36 | 14 | 35 | 170 | 140 | 29 | 573 |

ing that they were diploid. Notably, no juvenile megalospheric (haploid) specimens were encountered. However, 3 adult megalospheric *Rosalina globularis* d'Orbigny individuals were found, firmly attached to drifting substrate fragments composed of algae and a hydroid. The results also show that a successful settling of a microspheric individual is a rare event. On each sampling occasion, the colonization container (177 $cm^2$ cross section) yielded only 4–170 individuals (0.023–0.96 ind. $cm^{-2}$), compared to the 6974–8443 individuals (353–431 ind. $cm^{-2}$) reported by Höglund (1947, Table 5 therein) in core samples (19.6 $cm^2$ surface area) from a similar sediment substrate in the same region.

Settling was observed throughout the year, reaching a peak in the late autumn. A secondary smaller peak occurred in April–May, aligning with the sedimentation of seasonal algal plankton blooms. The lowest settlings were recorded during the winter months (January–March). Nevertheless, it is worth noting that several foraminiferan species exhibited settling at various times throughout the year (e.g. *Reophax scottii*, *Cornuspira foliacea*, *Ammonia batavus*, *Lobatula lobatula*, *Rosalina globularis*, *Bathysiphon argenteus*, *Gromia oviformis*, *Egerelloides medius*).

The samples collected during January and February contained traces of hard bottom materials, including byssus threads from *Mytilus edulis* and fragments of algae and hydroids. Additionally, some dead tests of adult foraminifera, belonging to species typically living in soft bottom habitats, were obtained.

### 3.2. Additional studies on *Ammonia* cf. *aomoriensis*

Foraminiferans, collected 14 May 2011 and photographed in the laboratory the following day, released large numbers of isogametes in the

Table 2. Summary of the results from the colonization experiments shown in Table 1

| Foraminiferans settled in the colonization container | No. of ind. |
|---|---|
| No. of microspheric specimens (diploid juveniles) | 328 |
| No. of megalospheric specimens (haploid adults) attached to drifting algal fragments | 3 |
| Specimens impossible to identify to life cycle stage (juveniles) | 242 |
| Total no. of settling foraminiferans | 573 |

water (Fig. 4). Ninety foraminiferans were collected 24 April 2024 and kept at room temperature. After 4 d of incubation in the petri dish with a water depth of 5 mm, 12 individuals out of 90 had moved to the water surface from which they were observed hanging (Fig. 5).

## 4. DISCUSSION

### 4.1. Dispersal

Dispersal is a multifaceted phenomenon that confers many benefits, including the avoidance of competition and inbreeding (Horn 1978, Maynard Smith 1978, Vermeij 1978, Krebs 2009). Nevertheless, dispersal is not without its risks; the majority of dispersing organisms do not survive, and only a minority achieve success. Consequently, for an organism capable to survive within a particular environment, growing and reproducing is more advantageous than dispersing. As a result, dispersal is best undertaken subsequent to sexual reproduction (Williams 1975).

### 4.2. Passive and active dispersal work differently

Both passive and active dispersal mechanisms are observed among foraminiferans, but their functions differ significantly. Passive dispersal impacts both juveniles and adults. Generally, an adult specimen should avoid dispersal due to the associated risk of ending up in an unsuitable environment. Passive dispersal by resuspension is probably less hazardous for epizoic or epiphytic organisms than for sediment-dwelling species, as motile or drifting substrates are often deposited in an environment similar to that from which they originated. Resuspension could avoid abrasion caused by sand-grinding during storms. Passive dispersal through resuspension likely operates at a local scale (Hicks 1988), while drifting on floating objects or ships may be crucial for attached shallow-water species. Indeed, many attached littoral species have

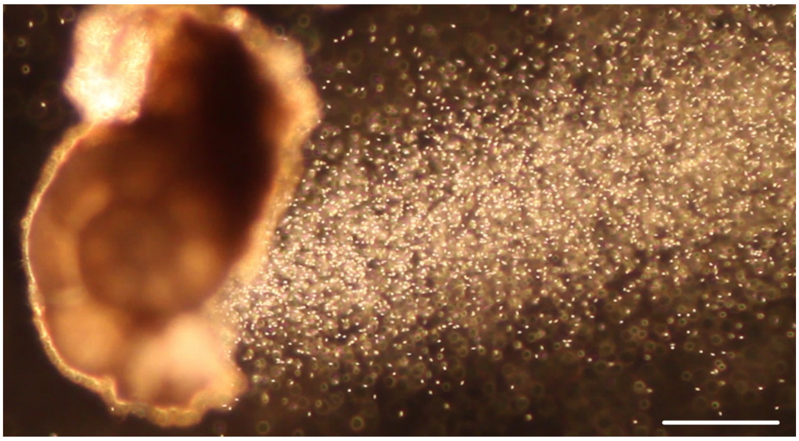

Fig. 4. Release of isogametes from an individual of *Ammonia* cf. *aomoriensis* collected from a clay bottom north of Aarhus, Denmark (56° 14′ 42.58″ N, 10° 20′ 18.60″ E), 0.2 m water depth (low tide), 14 May 2011 and photographed in the laboratory the following day. Scale bar = ca. 100 µm

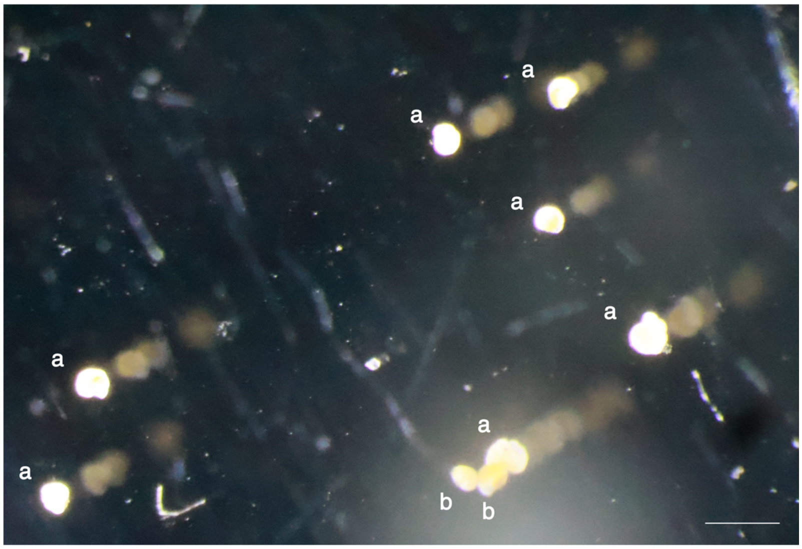

Fig. 5. *Ammonia* cf. *aomoriensis* individuals floating on the water surface (5 mm depth) in a petri dish. Those individuals appear white (a), producing reflections on each side of the petri dish and in the stereomicroscope glass plate below. Two individuals appearing yellow (b) lay on the bottom and, consequently, produce no such reflections. Scale bar = ca. 1 mm

cosmopolitan distribution. Other forms of passive long-distance dispersal that may have influenced the geographic distribution include human-mediated transport of ballast water, sand, or stones (Emery 1955, 1968, Radziejewska et al. 2006).

Active dispersal can be accomplished through 2 methods: locomotion on the sediment surface or an active movement of the stage subsequent to reproduction from the bottom to the water mass, probably by buoyancy regulation, and further passively transported by currents. The former is likely of local significance, but the latter has substantial potential for long-distance dispersal.

### 4.3. Reproduction and dispersal in foraminiferans

The presence of juvenile microspheric individuals (dispersing) only and the absence of megalospheric individuals (non-dispersing) in the colonization containers is consistent with the scarcity of microspheric forms and the dominance of megalospheric forms in both recent and fossil habitats (e.g. Ross 1972, Boltovskoy & Wright 1976, Goldstein 1988). The survival chances for the foraminiferan propagules after reproduction and planktonic dispersal is likely low, as in small planktonic invertebrate larvae (Young & Eckelbarger 1994, Young et al. 2006). Yet, the few individuals that do survive manage to thrive in an environment that is also conducive to the survival, growth, and reproduction of the ensuing megalospheric generation. All species obtained are common or frequent in the Skagerrak area and in bottoms surrounding the colonization containers (e.g. Höglund 1947). No exotic species were found. Another factor explaining the low number of settled individuals could be that only individuals larger than the 100 µm mesh size were investigated. The reason for this is that specimens are increasingly difficult to identify to species, or even as foraminiferans, the smaller they are. Longer experiments would probably have resulted in the collection of more juveniles that would have grown into larger adults.

Alve & Goldstein (2003) concluded that the juvenile microspheric generation is the primary vector for long-distance dispersal, but they also concluded that the megalospheric generation (found later in the season) to some degree had the same capability. It is difficult to base conclusions on negative results, but if the juvenile megalospheric individuals were as well adapted to planktonic dispersal as the microspheric ones then numerous, or at least some, megalospheric juveniles would be expected in the colonization containers. In natural sediments, the ratio between micro- and megalospheric individuals is often greatly dominated by the megalospheric form (e.g. Myers 1942, Boltovskoy & Wright 1976), for the calculation here, say 1:100. Based on the number of settled microspheric individuals (328), a corresponding natural sediment established a long time ago would contain around 32 800 megalospheric individuals. Settling of such numbers of young megalospheric individuals did not happen in my containers.

Four microspheric individuals of *Ammonia* and 2 individuals of *Eggerella* (life cycle stage unknown) settled in the colonization container in March–April, but none of them in the autumn. Reproduction in *A.* cf. *aomoriensis* collected and incubated in Denmark during April–May was also observed (Fig. 5). These observations support the existence of seasonality for the sexual reproduction as proposed by Alve & Goldstein (2003).

The results of the present study suggest that planktonic dispersal occurs and is undertaken by the zygote, or microspheric juvenile. In a new and potentially suboptimal environment, the probability of survival is usually higher for these diploid than for haploid individuals. This advantage is due to the presence of various heterozygous genes, which can encode a broader array of enzymes, thereby enhancing tolerance to diverse environmental conditions. The only observation of this in foraminiferans comes from Hofker (1930), who observed that only microspheric (diploid) individuals of *A. flevensis* (reported as *Rotalia beccarii flevensis*) in the Zuyderzee were capable of surviving harsh winter conditions or hot summer conditions exceeding 20°C, contrary to the megalospheric (haploid) ones. The offspring of the diploid specimen is haploid, resulting in a variable haploid population due to recombination and segregation during meiosis. Thus, selection has a range of variation to act upon, albeit confined to the genome within the diploid parent. Similar arguments have been presented by Hallock (1985) and Alve & Goldstein (2002, 2003, 2010).

While gametes could potentially serve as a dispersing stage (Fig. 4), the likelihood of syngamy (fusion of gametes) diminishes as the concentration of gametes quickly becomes diluted in the turbulent free water mass. Due to turbulent diffusion and the relatively short life span of gametes, the fertilization rate decreases as dispersal distance increases (Denny 1988). In contrast, the zygote possesses the capacity to perform all the life functions of an adult specimen, as explained below, and has the potential to feed and grow even before starting to build the proloculus.

The schizozoite, which represents the young haploid stage, is often observed migrating only a short distance from the diploid schizont (cm or dm) in numerous species (Schaudinn 1894, Le Calvez 1935, Myers 1935, 1936, 1943, Føyn 1936, Grell 1954, 1957, 1958a,b, 1959/60, 1988, Sliter 1965, Weber 1965, Berthold 1971, Röttger 1972, 1974, 1978, 1981, Salami 1976, Goldstein 1988, Pawlowski & Lee 1992, Cedhagen 1994, Kitazato & Matsushita 1996, Preobrazhenskaya & Tarasova 2004, Kitazato & Bernhard 2014). The short migration from the parent specimen is also reported for the asexually produced megalospheric agamont in trimorphic species (Krüger et al. 1997). This phenomenon is also commonly found in opportunistic species and parasites, where massive asexual reproduction without dispersal serves as an effective strategy for a local resource exploitation. The absence of megalospheric juveniles is indirect evidence of the same phenomenon. Unfortunately, the loss of colonization containers in the present study prevented the development of a second generation of foraminiferans during the extended incubation periods.

### 4.4. Relationships between foraminifera and the sediment

Resuspension of live benthic foraminiferans does occur in shallow areas (e.g. Loose 1970) but is likely of limited significance on deeper bottoms. Different water masses mix with difficulty (Dietrich et al. 1963). Resuspension of benthic foraminiferans due to storm events etc. is probably most important in the uppermost mixohaline water, typically 10–15 m deep, but of less importance in the deeper euhaline water mass. In a few of the colonization samples collected during winter in the present study, resuspended material (byssus) and a few megalospheric foraminiferans attached to floating substrata were encountered. In the English Channel, most of the benthic foraminiferans collected using plankton nets after winter storms were found as dead tests (Murray 1965, 1982, 1987), which illustrates that flume studies may be pertinent in marine geology studies.

Kontrowitz et al. (1978, 1979) conducted flume studies to determine the velocity at which empty foraminiferal tests could be resuspended. It is important to note that such studies lack relevance for living foraminiferans on natural sediment bottoms. Aquarium and flume investigations from the present study have shown that foraminiferans on clay bottoms are securely anchored by their pseudopodia and are rarely resuspended by water current or bioturbation. Resuspension only occurred at current velocities exceeding 10 cm $s^{-1}$ (T. Cedhagen unpubl., data not shown), as natural sediment tends to be stabilized by interwoven pseudopodia and (bacterial) mucus (Madsen et al. 1993).

### 4.5. Relative dispersal capabilities of gametes and zygotes

Zygotes can be formed through 3 distinct processes. (1) Gametogamy occurs when gametes are released into the water (Fig. 4) and fuse. (2) Gamontogamy involves the aggregation of 2 or more gamonts, leading to the transformation of their nuclei and cytoplasmic contents into gametes, ultimately resulting in the formation and release of zygotes. (3) Autogamy takes place when gametes within a single gamont fuse, giving rise to zygotes that subsequently escape. Reproduction has been investigated in only a limited number of foraminiferans (see Goldstein 1997 for a review). Most benthic foraminiferans used in culture for life cycle studies are littoral epibenthic species that are attached to hard substrates. This bias can likely be attributed to the ease of direct observation of epibenthic species compared to infaunal foraminiferans. Additionally, littoral species tend to be more resilient and better suited for survival in laboratory cultures. Nevertheless, it is still possible to infer some general patterns from these studies.

Foraminiferans inhabiting soft-bottom environments, such as clay substrates, release their gametes either within the sediment or at the sediment surface, as described in Process 1 above (Goldstein 1997). Some foraminiferans reproduce below the sediment surface (Frankel 1972), resulting in high localized concentration of gametes. Such soft bottom habitats are typically found in areas where near-bottom currents are relatively slow, allowing the development of a viscous sublayer (laminary boundary layer). This viscous sublayer effectively prevents turbulence from reaching the sediment surface, thereby maintaining a relatively high concentration of buoyant particles over an extended period (Wimbush & Munk 1970, Cedhagen 1993, Vogel 1994). Gametes in soft-bottom foraminiferans are approximatively spherical and possess a density closely resembling that of water. Their typical size falls within the range of 2–10 µm, a measurement derived from direct observations or inferred from the small size of the nuclei within the multinucleate, microspheric generation responsible for gamete formation (Boltovskoy & Wright 1976). This places them well below the critical size limit making them subject to Brownian motion, approximately 50 µm in accordance with Stokes' Law, which contributes to keeping them afloat (e.g. Daniels & Alberty 1966). The diffusion of gametes within the sediment interstices or the viscous sublayer is also facilitated by the beating motion of the flagellated gametes (Goldstein 1997). These processes help to maintain the mixing of gametes and sustains their concentration at a relatively high level for an extended duration, ultimately increasing the probability of successful fertilization. Furthermore, the viscous sublayer acts as a barrier to dispersal by turbulence, reducing the risk of predation in the more turbulent boundary layer, where suspension feeding macrofauna are more active (Mattson & Cedhagen 1989, Cedhagen 1993, Vogel 1994, Riisgård & Larsen 2010, Hamann & Blanke 2022).

Unlike gametes, the zygote possesses the capacity to perform all the life functions of an adult specimen. Following fertilization, various processes, including bioturbation, water ventilation by infaunal macrofauna, or active movement, help the zygotes to exit the viscous sublayer. Zygotes, being smaller than other life cycle stages (excluding gametes), may exhibit increased buoyancy in the water (Vogel 1994), especially prior to development of their tests. Furthermore, zygotes must navigate their way into the turbulent boundary layer and adjust their buoyancy to enable dispersion. While the specific mechanisms of buoyancy regulation in foraminiferans have yet to be studied comprehensively, it is essential to note that all planktonic foraminifera with calcareous tests must be able to modulate their buoyancy effectively to prevent sinking or floating to the surface. For a comprehensive overview of buoyancy mechanisms, see Schmidt-Nielsen (1997). This principle also applies to the calcareous benthic species in the genus *Tretomphalus*, which have a calcareous planktic stage adapted to dispersion (Le Calvez 1936, Myers 1943), and was also observed in the present study when *A.* cf. *aomoriensis* in a petri dish moved to the water surface (Fig. 5).

The gamete size was found to be 2 µm in *A. tepida* and 2 other species (Goldstein 1997). The volume of a sphere with this diameter is 4.19 $\mu m^3$. The combined volume of 2 spheres with this diameter is 8.38 $\mu m^3$. A sphere with this volume has a diameter of 2.52 µm. Alve & Goldstein (2003) reported the microspheric proloculus diameter of *A. beccarii* to be 15–30 µm (mean 22.5 µm). This mean value corresponds to a volume of 5955 $\mu m^3$. When these values are used, the latter volume corresponds to the combined volume of 1421 gametes. My conclusion is therefore that the zygote is free-living and growing for some time before it starts to secrete its test, the proloculus.

The results of colonization experiments in the present study are consistent with previous observations. Small juvenile microspheric (diploid) individuals of sediment-dwelling species dominated the foraminifera found in the colonization containers, although the numbers obtained were low in individual experiments. This observation shows that the dispersal stage primarily is the zygote or a stage that immediately follows it. It also indicates either that their transportation occurs sporadically, or that their concentration in the pelagial is generally low. The presence of small gametes and zygotes allows for a larger population of dispersing offspring, potentially enhancing their chances for survival following pelagic dispersal. Notably, the absence of juvenile stages of megalospheric (haploid) individuals in the colonization substrate of the present study indicates that this particular stage in the life cycle is not adapted for planktonic dispersion. Previous studies (see Section 4.3 above) show that young megalospheric individuals typically exhibit limited mobility, allowing them to stay in close proximity to the microspheric parent specimen, where favorable conditions for survival prevail. Consequently, they play a significant role in establishing a natural population structure, where the megalospheric generation constitutes the predominant portion, often at a ratio of approximately 100:1. This overarching pattern has been observed in a multitude of both recent and fossil species, as mentioned in Section 4.3.

Foraminiferans living attached to hard bottoms and algae typically do not release gametes directly into the free water, but they employ gamontogamy (Schaudinn 1895, Heron-Allen 1915, Myers 1935, 1940, Grell 1954, 1958a,b, 1959/60, Weber 1965, Lipps & Erskian 1969, Berthold 1971, Cedhagen 1994, Preobrazhenskaya & Tarasova 2004, Kitazato & Bernhard 2014) or release their gametes within reproductive cysts. Such species tend to inhabit environment characterized by wave action, strong water currents, which generate much turbulence. Releasing gametes directly into this environment would likely result in rapid dilution, substantially diminishing the probability of successful fertilization (Denny 1988). Consequently, aggregation through gamontogamy plays a vital role in facilitating the reproductive success of species residing in turbulent waters.

### 4.6. Origin of planktonic foraminifera

The invasion of the pelagic realm was probably mediated by microspheric generations of benthic foraminifera dispersing into the water column. The results of the present study are consistent with such theories. It occurred repeatedly in the Early Mesozoic (Boudagher-Fadel 2015, Gradstein et al. 2021). Until recently, only sexual reproduction and no dimorphism was thought to occur in planktonic foraminifera in nature (Schiebel & Hemleben 2017). This is a strong argument for their initial evolution from microspherical generations of benthic foraminifera. Although megalospheric individuals have recently been discovered in some planktonic species (Meilland et al. 2023), it remains the case that microspheric individuals strongly predominate (Schiebel & Hemleben 2017). Some recent benthic foraminiferans migrate to the sea surface where they release their gametes. Certain species even develop flotation chambers, e.g. in *Tretomphalus bulloides*, *Neoconorbina concinna* and *Cymbaloporetta* spp. (Le Calvez 1936, Myers 1943, Banner et al. 1985), while other publications report observations of benthic species that are able to float (Gerlach 1977 and Fig. 5). Another aspect is related to the water surface itself. Closest to the water surface, there is a phase boundary where the equivalent of a laminar boundary layer can develop under certain conditions. A calm water surface is influenced by surface tension, and just below this there is an increased influence of capillary forces (adhesive forces). However, the influence of capillary forces decreases with increasing turbulence (de Gennes et al. 2004). Gametes released into a large turbulent 3-dimensional body of water soon become diluted so that the likelihood of fertilization becomes very low (Denny 1988). Foraminifera such as the genus *Tretomphalus* and similar species avoid this effect of dilution by migrating to the water surface. The release of gametes there means that they are confined to a much smaller volume (which is thus more 2-dimensional), so that the local concentration of gametes and thus the probability of fertilization increases. The influence of capillary forces also reduces internal water movements in this near-surface boundary layer (de Gennes et al. 2004), which further reduces gamete dilution. Thus, the use of the top layer of water is a mechanism for increasing the probability of fertilization.

## 5. CONCLUSIONS

(1) Young microspheric (diploid) sublittoral soft-bottom foraminiferans were present in the colonization container, demonstrating their planktonic dispersal ability. This aligns with the evolutionary theory that dispersal typically occurs following sexual reproduction.

(2) Young megalospheric (haploid) sublittoral soft-bottom foraminiferans were not found in the colonization container, indicating their lack of planktonic dispersal. This supports the evolutionary theory that asexual reproduction is an effective strategy for exploiting resources without dispersal.

(3) Soft-bottom foraminiferans release gametes into or on the sediment surface. The viscous sublayer (laminar boundary layer) hinders immediate dilution, maintaining relatively high gamete concentrations. Brownian motion and the movement of self-propelled flagellated gametes aids gamete mixing prior to dispersal.

(4) Foraminiferans in high-energy, turbulent environments (like wave-swept areas) typically avoid releasing gametes directly into the water to prevent rapid dilution. Instead, they enhance fertilization chances through gamontogamy (gamont aggregation, by gamete-producing individuals), forming the zygote prior to release.

(5) Mortality is likely high among dispersing microspheric (diploid) juveniles. However, the few that survive do so in conditions favorable for their survival, growth, and reproduction also of the subsequent megalospheric (haploid) generation. This helps explain why microspheric individuals typically are rare, while megalospheric ones are common in both recent and fossil habitats.

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