Reproduction

5

Continuity of the species in the vastness of the deep ocean is ensured by adaptive mechanisms characteristic of pelagic organisms to promote sufficient reproductive success. Whereas wide dispersal poses no problem for monoecious (offspring produced from a single parent) organisms, gametes of sexually reproducing dioecious organisms with different parents need to fuse for successful reproduction. Therefore, dioecious organisms with a wide dispersal as assumed for planktic foraminifers need a strategy to ensure successful reproduction (cf. Hemleben et al. 1989).

The standing stock of planktic foraminifers is rather heterogeneous at an average of 10–100 individuals per m^3, i.e., one specimen per 10–100 L of seawater, or a distance of about 25–60 cm between individuals. Given an average size of a planktic foraminifer test of 250 µm, the distance between the individuals would be ~1000–4000 times their size. Assuming random (plankton-like) movement of the individuals, the distance would possibly be too long for successful reproduction in a limited time-interval of a couple of days, even at unlimited fertility. In addition, the distribution of planktic foraminifer species is patchy including temporal scales from sub-seasonal to interannual time-intervals, and spatial scales from local (kilometer scale) to meso-scale of some tens to hundred kilometres, as well as different depth habitats spanning the surface to mesobathyal depths in the water column (e.g., Schiebel and Hemleben 2000; Siccha et al. 2012).

Since the odds against gametes of the same species coming into contact in the open ocean are extremely large given the average distance between individuals, planktic foraminifers have developed adaptive strategies that help to maximize the probability of gamete fusion. These include (1) release of large numbers of gametes, (2) production of motile gametes that contain sufficient food reserves for prolonged locomotion, (3) synchronization of gamete release at distinct frequencies, and (4) establishment of a depth preference for reproduction to limit the vertical range and enhance the chance of mating. All of the four strategies have been reported for different planktic foraminifer species both from laboratory observation and field data (Spindler et al. 1978, 1979; Almogi-Labin 1984; Hemleben et al. 1989; Bijma et al. 1990, 1994; Erez et al. 1991; Bijma and Hemleben 1994; Marchant 1995; Schiebel et al. 1997).

Direct observations of the reproduction of planktic foraminifers in the laboratory, and data from natural assemblages provide statistical evidence on their reproductive behavior. Processes in reproduction also provide information on the biology of planktic foraminifers necessary to understand calcification and chemistry of their tests including stable isotope signals and chemical element ratios, and hence are relevant for the use of planktic foraminifers as proxy in paleoceanographic research.

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5.1 Gametogenesis

Release of gametes in planktic foraminifers was reported as early as 1911 by Rhumbler. Le Calvez (1936) described gamete release in *Globigerinella siphonifera* and *Orbulina universa*. Details of gametogenesis and reproduction were described later from laboratory experiments and by applying electron microscopy (SEM and TEM) (e.g., Bé and Anderson 1976). Planktic foraminifers reproduce by release of flagellated cells, i.e. gametes, as observed in the spinose species *Hastigerina pelagica*, *O. universa*, *Globigerinoides conglobatus*, *Globigerinoides ruber*, *Globigerinoides sacculifer*, *Globigerina bulloides*, *Turborotalita humilis*, and *G. siphonifera*, and non-spinose *Globigerinita glutinata*, *Neogloboquadrina pachyderma*, *Neogloboquadrina dutertrei*, *Globorotalia inflata*, *Globorotalia truncatulinoides*, *Globorotalia hirsuta*, and *Globorotalia menardii* (Hemleben et al. 1989, and references therein). The vast numbers of the flagellated cells released by a single parent cell (typically 300,000–400,000) and their small size (ca. 3–5 µm) suggests that these flagellated swarmers are indeed gametes. Definitive evidence of syngamy (fusion of the swarmers) or definitive evidence for the haploid nature of the gametes still needs to be confirmed.

5.1.1 Succession of Events in Gametogenesis

As a first sign of impending gametogenesis in laboratory experiments, the normally floating spinose individuals sink to the bottom of the culture dish (Hemleben et al. 1989). Shortly after sinking, the spinose species shorten their spines by resorption from top to base (Fig. 5.1, Table 5.1) (Bé et al. 1983). Spine-fragments are discarded by rhizopodial streaming (Plate 5.1-1). In *G. sacculifer*, the formation of a final sac-like chamber is the earliest visual indication of impending gametogenesis (Fig. 5.1). Symbiont-bearing species consume or expel their symbionts, which appear as moribund masses of yellow-brown pigmented particles around the test. The cytoplasm becomes granular and milky white, or orange to reddish due to masses of fat in many species, and withdraws to the inside of the test. Some feeble rhizopodia with granular cytoplasm may remain outside of the test and exhibit cytoplasmic streaming. Subsequently, a mass of granular cytoplasm appears in the aperture, and gradually enlarges to form a substantial bulge (Plate 5.1-2). The bulge eventually ruptures, sometimes explosively, and hundreds of thousands of flagellated gametes are released, which swim away from the parent cell with a slight undulating motion (Spindler et al. 1978). Partially expelled gametes may form string-like masses issuing from the aperture of the parental test in early stages of gamete release, then gradually spread distally, and separate into individuals or clumps of flagellated cells (Plate 5.1-6), which disperse into ambient water (Plate 5.1-3 to -5). When gamete-release is completed, only the empty parental test remains. The gross morphological and cytoplasmic events during gametogenesis of *G. sacculifer* are similar in *G. ruber*, *G. conglobatus*, *G. siphonifera*, and *O. universa*. In *G. sacculifer*, *O. universa*, *G. truncatulinoides*, *G. hirsuta*, and *H. pelagica*, remnants of fine rhizopodia may occasionally be attached to the parental test after gamete release, and exhibit rhizopodial streaming for up to 8 h before dissipating.

Due to architectural (spinose vs. non-spinose species) and autecological (symbiont-bearing *vs.* symbiont-barren species) differences, the overall pattern of reproduction varies among species. Abnormal gametogenesis is occasionally observed in individuals maintained in laboratory culture, resulting in abortive release of gametes. In some cases, the bulge forms, but the gametes are not expelled, or some gametes may be released, but the majority of the cytoplasm remains sequestered in the test and is moribund (cf. Hemleben et al. 1989).

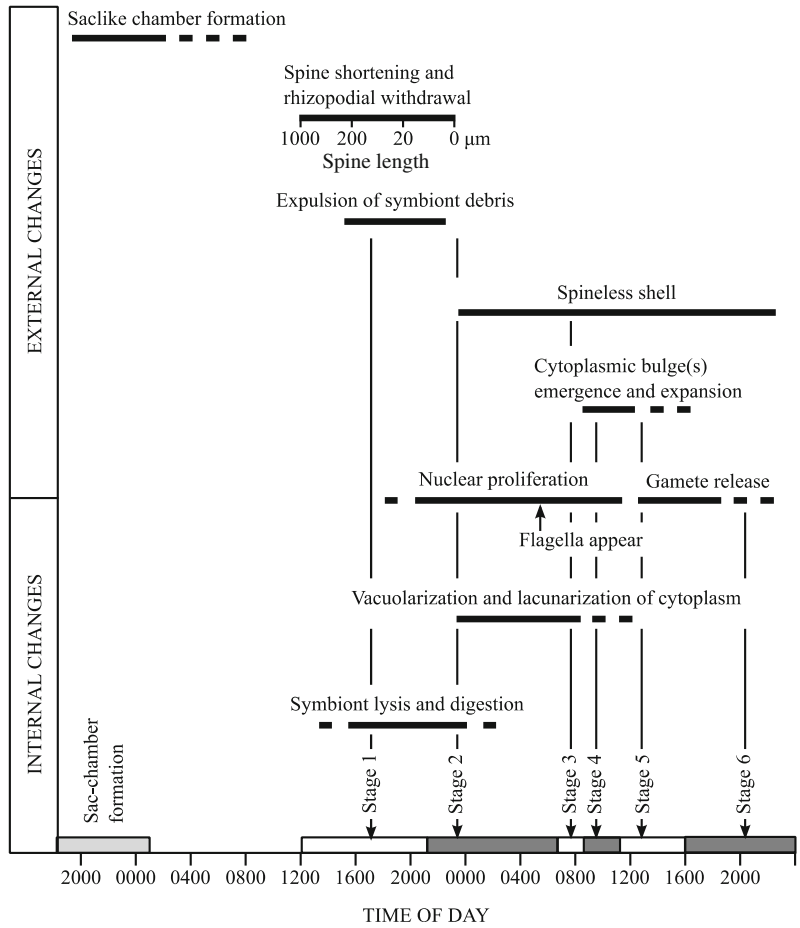

Fig. 5.1 Timetable of external and internal cellular changes associated with gametogenesis in *G. sacculifer*. Duration of the six stages of gametogenesis given by white and dark gray horizontal bars is based on numerous (i.e. hundreds of cases) observations. Arrows indicate the average time of day of each stage. Occasionally, formation of a final sac-like chamber, the earliest visual indication of impending gametogenesis, occurs in some individuals. Gradual shortening of the spines at midday and complete shedding of the spines at midnight on the day preceding gamete release clearly signal the onset of gametogenesis. Fine structural analyses indicate the onset of nuclear division, and development of large vacuoles within the cytoplasm occurs during the period from midnight until noon of the day when gametes are released. Flagella appear on the multinucleid cytoplasmic masses early in the morning, and gamete formation and release occurs in the afternoon and the early evening. Redrawn after Bé et al. (1983)

5.1.2 Fine Structural Processes During Gametogenesis

Early during gametogenesis, as exemplified by *H. pelagica*, the foraminifer descends in the water column. While sinking, prior to shedding of the bubble capsule, the cytoplasm changes from orange to bright red color. The color change commences as a small patch near the center of the cell and gradually disperses to encompass the entire cytoplasm in *H. pelagica* (Spindler et al. 1978). Upon descent of the reproducing individual (in the culture dish, and possibly also in the natural environment) early in gametogenesis, the fibrillar bodies, which are assumed to aid flotation, are reduced in abundance (cf. Chap. 3). In some specimens, fibrillar bodies persist into the late stages of gamete release, and appear as dense tubules (in TEM imagery) within an expanded vacuolar membrane (Hemleben et al. 1989). The vacuolar bodies are occasionally surrounded by a thin layer of cytoplasm.

Plate 5.1 (*1*) Spines are discarded before gamete release (GR) in *G. sacculifer* (Kage Microphotography©, with permission). When gametogenesis starts (*2*) the cytoplasmic bulge expands, and (*3*) gametes are released. Gametes are released and (*4*) are still in close vicinity to the parental tests (*N. dutertrei*). (*5*) Released gametes around parental test (*H. pelagica*). (*6*) TEM image of stained gamete of *H. pelagica* with flagella of different lengths and whip-like ends (from Spindler et al. 1978). Bars (*1*,*3*,*4*) 200 μm, (*2*) 50 μm, (*5*) 500 μm, (*6*) 2 μm ▶

Table 5.1 Generalized schedule of gamete release in reproduction of planktic foraminifers. Gametes are released predominantly during the early afternoon. Compiled from Spindler et al. (1978), Hemleben et al. (1979), and Spindler and Hemleben (1982). After Hemleben et al. (1989)

Event	Time before gamete release	
Formation of ultimate chamber	5–1	Days
Spine shortening and shedding (in spinose species)	24–10	hours
Nuclear division	20–4	hours
Vacuolization of cytoplasm	14–6	hours
Development of flagella	9–7	hours
Cytoplasmic bulge emerges and expands	6–2	hours
Gamete release	0	hours

The lipids disperse within the cytoplasm, and droplets reduce in size upon descent of the reproducing individual (Spindler et al. 1978). The lipids will eventually be passed over to gametes as energy reserves. In symbiont-bearing species, there is increasing evidence of symbiont lysis within the perialgal vacuoles, which appear to be converted to digestive vacuoles. Excess moribund symbionts are expelled by exocytosis into the surrounding environment, and the digestive vacuoles entirely disintegrate until the late stages of gametogenesis (cf. Hemleben et al. 1989).

The nucleus commences repeated divisions producing hundreds of thousands of small daughter nuclei (Spindler et al. 1978). Each of the small nuclei are enclosed within a double membranous envelope sourced from annulate lamellae produced in quantity in the cytoplasm of *H. pelagica*, and also in other spinose species during early stages of gametogenesis prior to nuclear proliferation (Spindler and Hemleben 1982). The endoplasmic reticulum in the vicinity of the Golgi complex is transformed into flat vesicles piled up in successive layers to form the annulate lamellae, which proliferate and disperse throughout the cytoplasm. At a later stage (12–16 h before gamete release) most annulate lamellae are assembled in whorls (Plate 5.2-1). Eventually, the lamellae are arranged next to the cytoplasmic side of the membranous envelope surrounding dividing nuclei (Plate 5.2-1), and contribute to the expanding nuclear membrane during mitosis and production of daughter nuclei (Spindler and Hemleben 1982). Similarities in pore configuration within the membranes of the lamellae and those of the nuclear envelope, and the close association of lamellae with expanding and dividing nuclei of reproducing *H. pelagica* further support the conclusion that the lamellae are the origin of the massive increase in nuclear membrane during production of daughter nuclei. Similar annulate lamellae have been observed in early reproductive stages of *G. sacculifer* during spine shedding, and prior to production of the daughter nuclei (Spindler and Hemleben 1982; Bé et al. 1983).

After the nuclei are fully dispersed throughout the cytoplasm (Plate 5.2-3 and -4), the cytoplasm is separated into interconnected, multinucleated masses possessing lipid droplets, mitochondria, endoplasmic reticulum, and a full array of typical organelles found in the cytoplasm of the parent cell. Flagella begin to project from the plasma membrane surrounding the masses of multinucleated cytoplasm (cf. Hemleben et al. 1989). The interconnected network of flagellated cytoplasm becomes increasingly dispersed into individual flagellated gametes, which, upon release from the parent test, are biflagellated with flagellae of unequal length (Plate 5.1-6), similar to those found in the benthic foraminifer *Myxotheca* (Angell 1971). Each planktic foraminifer gamete consists of a dense nucleus (in TEM imagery) surrounded by an irregular zone of mitochondria,

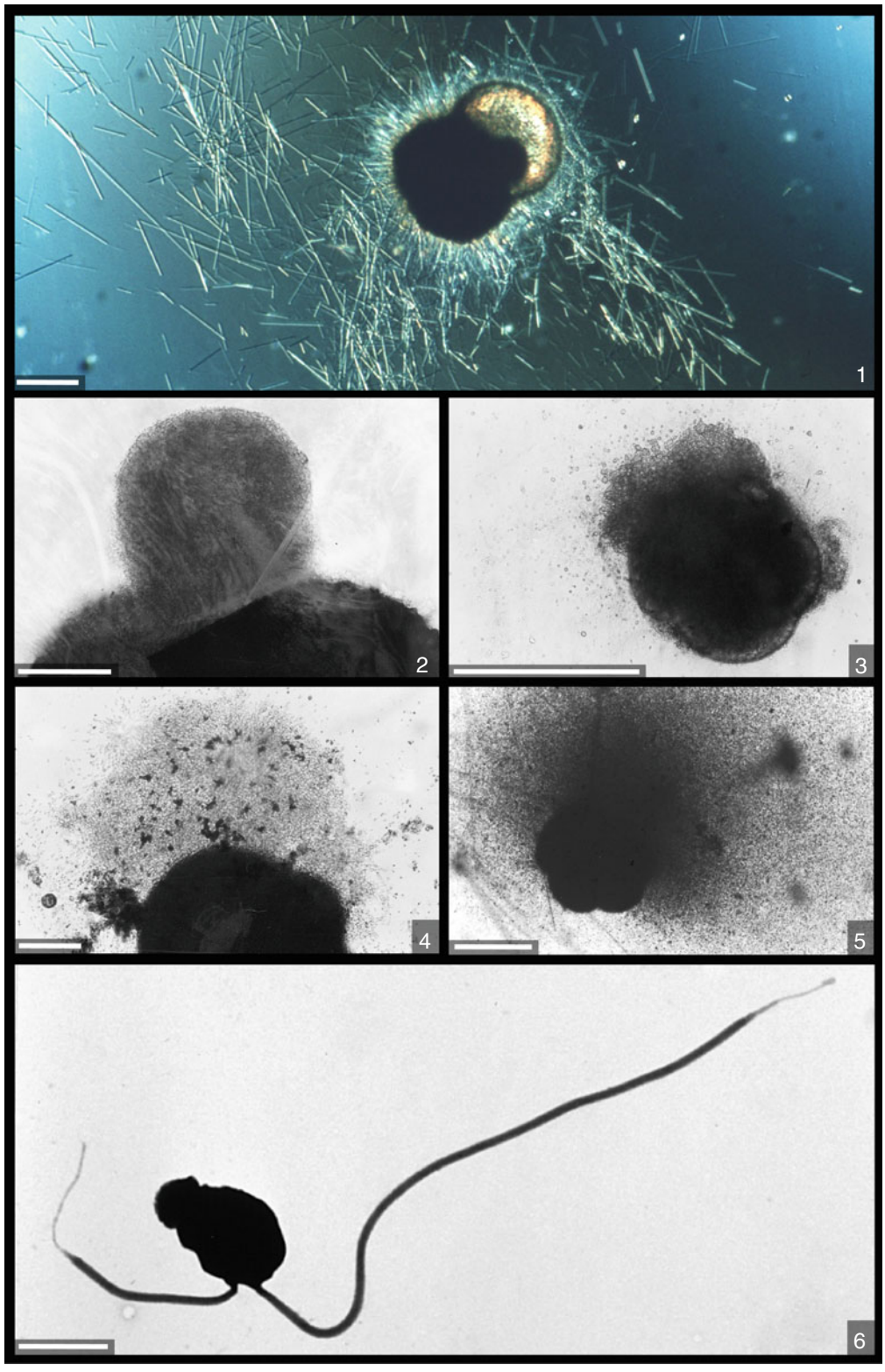
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Plate 5.2 (*1*) Annulate lamellae in *H. pelagica* forming concentric aggregates when transported toward the nucleus ▶ 12–16 h before gamete release (Spindler and Hemleben 1982). (*2*) Gamete nucleus (N) of *G. ruber* with separating chromosomes (*white arrow*), and flagella in cross-section (*red arrows*). (*3*,*4*) Vacuolated cytoplasm with gamete nuclei (N) and flagella in longitudinal (*black arrows*) and cross-section (*red arrows*) of (*3*) *G. ruber* and (*4*) *G. sacculifer*. (*5*) Spherical bodies close to the empty shell of *H. pelagica* after gamete release, with (*6*) large central vacuole (V) including debris, and some nuclei in the surrounding cytoplasm (from Spindler et al.1978). (*7*a) Offspring of *G. truncatulinoides* with protoconch (dark) and deuteroconch (light). (*7*b) Offspring of *G. glutinata* with protoconch (*dark red*), deuteroconch (*light red*), and 3rd chamber (uncolored). (*8*) Offspring of *G. glutinata* with pustules and deuteroconch with pores (*7*b and *8* from K. Kimoto, with permission). Bars (*1–4*,*6*) 1 µm, (*5*,*7*) 100 µm, (*8*) 10 µm

endoplasmic reticulum, and at the periphery typical basal bodies and their flagella (Hemleben et al. 1989).

The gametes of planktic foraminifers contain a single nucleus with finely dispersed chromatin. Lipid droplets form conspicuous inclusions in the cytoplasm. Gametes are distinguished from possible motile stages of the symbionts by their nucleus with a 'foraminifer-type' fine structure (as in the parent cell cytoplasm), which is not mesokaryotic (containing persistently condensed chromatin) as in the dinoflagellate symbionts of some spinose planktic foraminifers. In addition, chloroplasts and other inclusions characteristic of symbionts are absent in the gametes, and no algal symbionts are associated with the gametes. Symbionts are present in the intratest cytoplasm of *G. sacculifer* and *G. ruber*, but not before the three-chambered ontogenetic stage of the test, and it is not known how symbiont-bearing species acquire their symbionts (see Chap. 4).

Species-specific variations in cytoplasmic fine structural processes during gametogenesis include differences in the size and shape of reproductive nuclei. Large spheroidal cytoplasmic residual bodies (spherical bodies) of some tens of micrometers in diameter are produced by *H. pelagica* during reproduction (Plate 5.2-5 and -6). They consist of a thin layer of cytoplasm with several nuclei bearing flagella at the periphery, surrounding a massive vacuole containing waste materials (Spindler et al. 1978). Similar vacuolar bodies often of smaller size have also been observed in the final mass of cytoplasm released during gametogenesis in other spinose species. Those bodies are expelled during gametogenesis, and appear to be residual digestive vacuoles. They are situated within the protective sheath of cytoplasm, which prevents the gametes from potentially destructive effects of lytic enzymes that are isolated within the digestive vacuoles. The process of gametic nuclei proliferation is not yet entirely understood, and additional observations of the earliest stages of nuclear division would be needed to fully document the proliferation.

The small gametogenic nuclei are almost isodiametric. Additional daughter nuclei are formed by binary fission (Plate 5.2-3). During karyokinesis (nuclear fission), the nuclear envelope remains intact. Microtubular centers outside of the nuclear envelope with attached microtubules pass through it into the nucleoplasm. When the chromosomes separate (Plate 5.2-2), the nuclear envelope expands, and finally when it is in telophase two daughter nuclei are produced. The initial production of daughter nuclei from the non-reproductive nucleus appears to occur very rapidly, either by repeated budding off of smaller nuclei from the larger nucleus, or by simultaneous fragmentation of the large nucleus into many smaller nuclei (Hemleben et al. 1989). Successful reproduction results in large numbers of offspring. The earliest calcified stages of juveniles include a protoconch and a deuteroconch (Plate 5.2-7 and -8, see Chap. 6).

5.1.3 Morphological Changes of Tests During Gametogenesis

The tests remaining after gamete release bear distinct signs of gametogenesis. Resorption and shedding of spines during early stages of

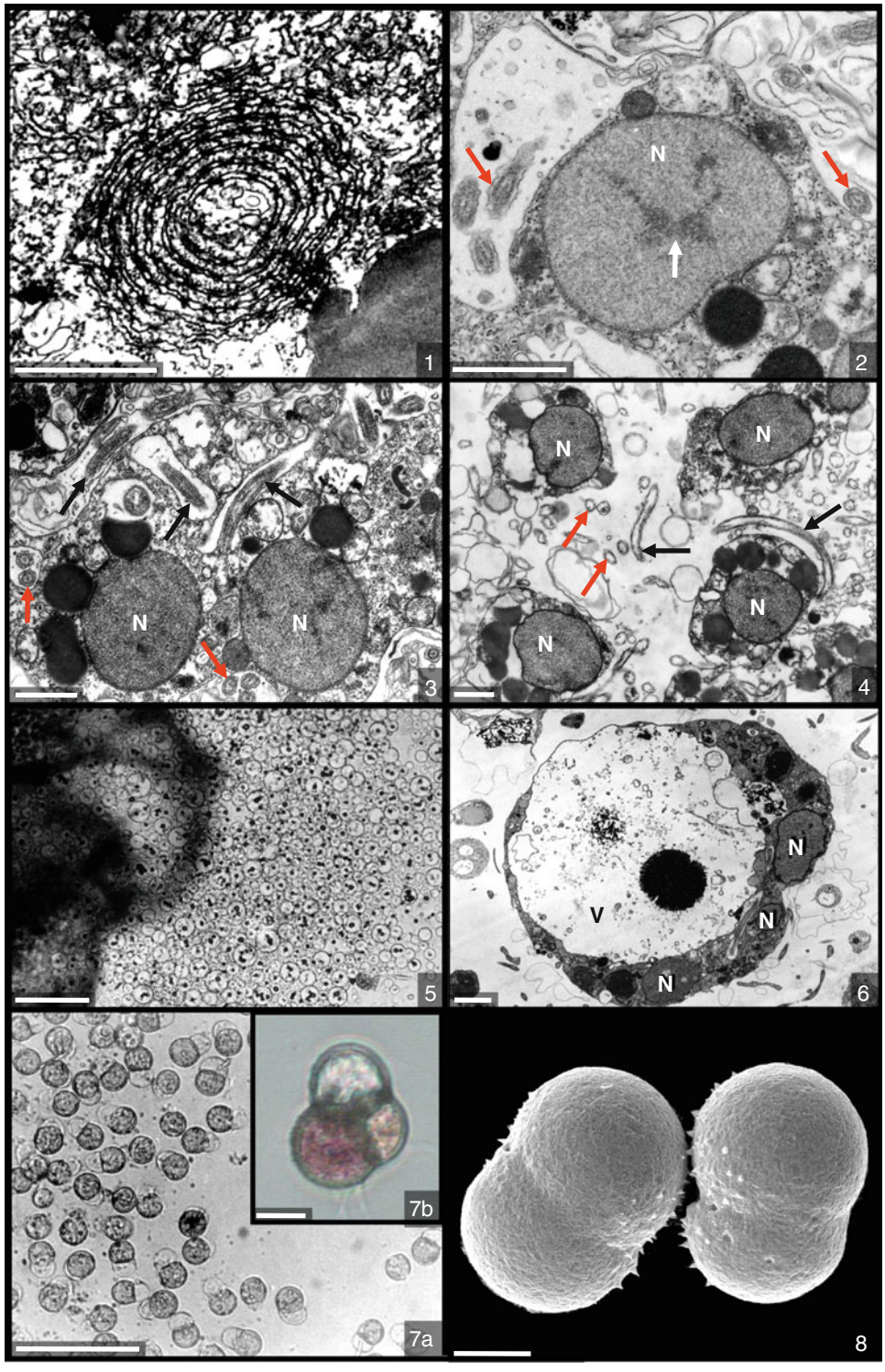
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Plate 5.3 (*1–3*) Increasing GAM calcification in *G. sacculifer*. (*1*) Spine holes and remains of spines (*red arrows*) are visible, (*2*) some spines holes covered, and (*3*) all spine holes are covered by GAM calcite (*blue arrows*). (*4*) Some remains of spines (*red arrows*) are visible in *G. bulloides*. (*5,6*) Empty tests of *H. pelagica* after gametogenesis in the laboratory, with spines and septae resorbed (from Hemleben et al. 1979, 1989). (*7*) Thin-walled broken kummerform chambers in *G. sacculifer*. (*8*) *N. dutertrei* with enlarged final chamber. (*9,10*) 'Biorbulina' types of *O. universa* may indicate reproduction and/or excess food availability, e.g., when overfed in laboratory culture. (*10*) Incomplete second sphere surrounding previous sphere. Bars (*1–4*) 10 µm, (*5–10*) 200 µm ▶

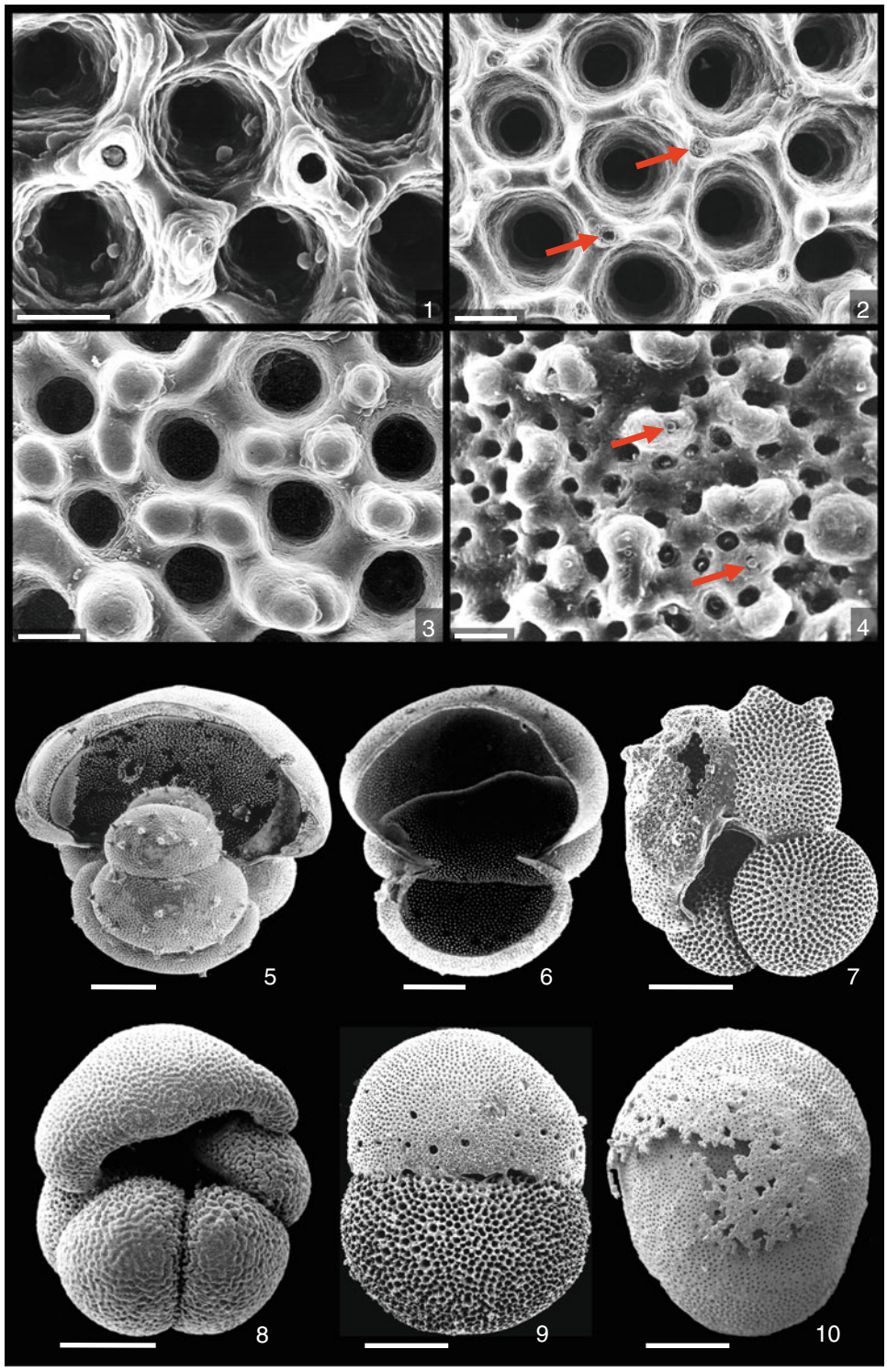
gametogenesis leave characteristic spine remnants, as exemplified in *H. pelagica* (Hemleben et al. 1979). Holes remain where spines were shed, and distinguish all modern and fossil spinose (subsequent to the C/T boundary) from non-spinose tests (Plate 5.3-1 to -4). These spine-holes may be entirely or partially covered by additional deposition of calcite during gametogenic (GAM) calcification (Plate 5.3-2 and -3) (Bé 1980; Hemleben and Spindler 1983). Resorption of internal septae, and dissolution of the test wall as in *H. pelagica* (Plate 5.3-5 and -6) is assumed to aid gamete release (Hemleben et al. 1979).

Variations in final test morphology may indicate gametogenesis in existing and fossil specimens (Hemleben and Spindler 1983). One or more (up to four) chambers may be smaller (kummerform) than the last pre-gametogenic chamber (Berger 1970). In spinose species, the kummerform chambers often lack spines, and may be either incompletely calcified or rather thick-walled, with scarce and scattered pores. In fossil specimens, kummerform chambers are often broken (Plate 5.3-7) because of their insufficiently calcified walls, and might only leave a rim where the wall was attached to the earlier chambers. In *G. sacculifer*, one polymorphous sac-like chamber, including the 'fistulose' type may be produced (Plate 5.3-7; see also Chap. 2, Plate 2.9-6 and -9). In other cases, the final chamber may be significantly larger than the previous chambers (Plate 5.3-8). In mature specimens of *O. universa*, the formation of a second sphere joined to the first one (Plate 5.3-9) or surrounding it (Plate 5.3-10) produces so-called 'Biorbulina' morphotypes (see also Chap. 4.1.5). In most cases, the final chamber may well be of normal shape and size following the logarithmic growth phase even if reproduction had occurred.

Kummerform chamber: The term kummerform (German for kümmerlich, klein, i.e. measly, small) was defined by Berger (Berger 1969, 1970), who favored the interpretation that stress, i.e. non-optimum growth conditions cause formation of kummerform chambers (see also Hecht and Savin 1972, stable isotope data of kummerform chambers). Olsson (1973) concluded that kummerform phenotypes represent mature individuals, which have achieved full adult size, and suggested that comparisons between kummerform and normal-form individuals are insignificant, and the use of the term kummerform is confusing (for summaries see Kennett 1976; Hemleben et al. 1989). Kummerform chambers are formed last in ontogeny prior to reproduction, and may be smaller or equal in size compared to the previous chamber. To speculate, the size of kummerform chambers depends on the internal calcium pool of the individual.

5.1.4 Gametogenic Calcification

An additional more or less patchy calcite layer covering the whole test after shedding of spines may be formed up to 16 h before gamete release (e.g., Bé 1980). Consequently, the test surface is thickened by additional deposition of calcite, i.e. gametogenic calcification (GAM). Spine holes are closed to varying degrees by additional calcification as observed by SEM visualization.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Gametogenic calcite deposited on top of the test surface (Plate 5.3-2 to -4) is an unequivocal indicator of reproduction, as found also in fossil specimens (Bé 1980). However, not all gametogenic specimens produce a substantial gametogenic calcite layer. The amount of thickening of the test wall appears to be related to the amount of excess calcium stored in the cytoplasm at the time of gametogenesis (cf. Chap. 6). It is assumed that test wall thickening in gametogenesis serves as physiological disposal of excess calcium prior to cellular changes of nuclear proliferation and gamete production (Hemleben et al. 1989).

The amount of $CaCO_3$ deposited prior to gametogenesis is specimen-specific, and may be absent or present to a varying degree in both symbiont-barren and symbiont-bearing species (cf. Bé 1980; Hemleben and Spindler 1983). Close to 100 % of adult *G. bulloides* (>150 µm in test diameter) produce a more or less complete layer of gametogenic calcite. GAM calcification in *G. bulloides* starts at structures, which are elevated above the surface of the outer shell (Plate 5.3-4), and may finally merge to form a thin veneer of calcite over most of the outer shell (Schiebel et al. 1997).

The chemical composition of the planktic foraminifer test represents a mixed signal related to the dwelling depth of the foraminifer, and is formed at the average dwelling-depth plus water depth of reproduction (Berger et al. 1978). The gametogenic calcite layer covering the test surface of *G. bulloides*, and other species, such as *Globorotalia truncatulinoides* and *Globorotalia tumida*, may be depleted in Mg relative to the pre-gametogenic test calcite, while being enriched in Mg in *G. sacculifer*, or varying in the Mg/Ca ratio as in *N. pachyderma* (Eggins et al. 2003). These differences are assumed to result from the relative position of reproduction in the water column, which is shallower in *G. truncatulinoides* and *G. tumida*, and deeper in *G. bulloides* (e.g., Hemleben et al. 1985; Schiebel et al. 2002; Schiebel and Hemleben 2005). These differences may be attributed to various factors including the presence (e.g., *G. ruber*) and absence of symbionts (e.g., *G. bulloides*), as well as regional hydrographic conditions.

GAM calcification may add about 4–20 % additional calcite to the shell that was formed during earlier ontogeny of 'thin-walled' morphotypes (and genotypes, de Vargas et al. 1999) of the symbiont-bearing species *O. universa* (Hamilton et al. 2008). In addition to differences in calcite precipitation between different species, and within the same (morpho-) species (e.g., the genotypes of *G. bulloides*, Darling and Wade 2008) GAM calcite may produce tests of differential size-normalised weight (Spero and Lea 1996). The same is true for *G. sacculifer* cultured under varying light intensity (Bé et al. 1982; Spero and Lea 1993). However, in contrast to *G. bulloides*, *G. sacculifer* has only one genotype including various morphotypes (André et al. 2013). Differences in presence, amount, and composition of gametogenic calcite within and between genotypes, plus resulting changes in dissolution susceptibility, add complexity to the interpretation of chemical data of tests from sediments (Eggins et al. 2003).

5.2 Reproduction Inferred from Population Dynamics

Shallow-dwelling species have been shown to reproduce once per month (*G. bulloides*), or twice each month (*G. ruber*), triggered by the synodic lunar cycle (Berger and Soutar 1967; Spindler et al. 1979; Reiss and Hottinger 1984; Schiebel et al. 1997). Lunar periodicity has also been inferred from population dynamics of *Globigerinella calida*, *Globigerinella siphonifera*, *Globigerinita glutinata*, *Globigerinoides sacculifer*, *Globorotalia menardii*, *Neogloboquadrina dutertrei*, *Orbulina universa*, and *Pulleniatina obliquiloculata* (e.g., Jonkers et al. 2015). However, not all specimens may reach the reproductive ontogenetic stage during one reproductive cycle and may reproduce during one of the following cycles (Spindler 1990). Intermediate to deep-dwelling species are assumed to reproduce less often than shallow-dwelling species (Hemleben et al. 1989; Schiebel and Hemleben 2005). The deep-dwelling species *G. truncatulinoides* is believed to reproduce only once per year

(Hemleben et al. 1989). For reproduction, *G. truncatulinoides* ascends from depths to the sea surface during early spring, possibly at the margins of the subtropical gyres (cf. Hemleben et al. 1985: Sargasso Sea; Schiebel et al. 2002: Azores Current). In contrast, shallow-dwelling species are assumed to descend for reproduction in the upper water column to water depths around the Deep Chlorophyll Maximum (DCM) (see also Chap. 7, Ecology, Fig. 7.7). The reproductive descent possibly marks the greatest water depth that shallow-dwelling planktic foraminifers attain during their ontogenetic cycle (Schiebel and Hemleben 2005).

Although lunar reproductive cyclicity is well known especially in the reproduction of metazoans (Richmond and Jokiel 1984), among other organisms, triggering mechanisms are still under debate, i.e., for example whether it is the affects of light and/or gravitation. The concept of lunar cyclicity (i.e. a synodic cycle) in the life cycle of some spinose planktic species is largely coherent (Schiebel and Hemleben 2005). However, as spinose species differ significantly in their biological behavior and habitat, reproductive modes may differ between species (Bijma et al. 1990; Schiebel et al. 1997). The spatial and temporal components of the population dynamics of *G. sacculifer*, *G. ruber*, and *G. siphonifera* from the Red Sea, and *G. bulloides* from the eastern North Atlantic, indicate differential lunar reproduction cyclicity from the population dynamics compared to those that are analyzed from net tow samples of the surface waters. Whereas the cohorts of the *G. sacculifer* and *G. bulloides* assemblages show quite clear synodic lunar cyclicity (Figs. 5.2 and 5.3), the distributions of *G. ruber* and *G. siphonifera* are rather less well defined and within the semi-lunar domain (Bijma et al. 1990; Jonkers et al. 2015). In *G. ruber* (white), biweekly reproduction was already suspected by Berger and Soutar (1967) and Almogi-Labin (1984). In turn, *G. siphonifera* has been assumed to reproduce on a synodic lunar frequency by Schiebel and Hemleben (2005, data from the Arabian Sea).

The ontogenetic development of species provides information on the timing of reproduction as reconstructed from large individuals (>100 μm). The diameter of the proloculus of *G. bulloides* is 20 μm on average (see Chap. 6). Juvenile specimens grow rapidly, and a test size of >100 μm can be reached in less than 10 days after reproduction (Hemleben et al. 1989; Spero and Lea 1996). Growth rates are affected by various factors, such as temperature, and quality and abundance of food. Accordingly, resulting pulses of young adult tests >125 μm were recorded between the second half of the waxing moon and the new moon of the following lunar cycle (Fig. 5.3). Those small specimens possibly resulted from the reproduction of adult (i.e. large) *G. bulloides*, mainly during the first half of the waxing moon. During the second half of the waxing moon, and during the waning moon, these individuals reach maturity, and during the first week of the following waxing moon large numbers of terminal test stages (GAM individuals) generate a new start of the ontogenetic life cycle (Fig. 5.3). All other surface dwelling species have been found (from plankton net data >100 μm) to reproduce once per fortnight or once per month (Schiebel and Hemleben 2005; Jonkers et al. 2015).

A rather blurry distribution of cohorts of *G. siphonifera* and *G. ruber*, and differences in assemblage data from different ocean basins might result from the somehow lower standing stocks than in *G. bulloides*, and hence larger standard deviations. In addition, different 'types' (morphotypes and genotypes?) of *G. ruber* and *G. siphonifera* (Huber et al. 1997; Bijma et al. 1998; Wang 2000; Darling and Wade 2008; Aurahs et al. 2011) may reproduce at different schedules, and display varying distribution patterns resulting from biological and ecological prerequisites. The analyzed samples originate from different geographic locations, from different seasons and years, and different ecologic conditions as indicated by regional differences of temperature and salinity of the surface water. However, taking into account that reproduction in *G. bulloides*, or in any other shallow-dwelling planktic foraminifer species is triggered by the synodic lunar cycle, temporal changes in the specific population structure (e.g., size

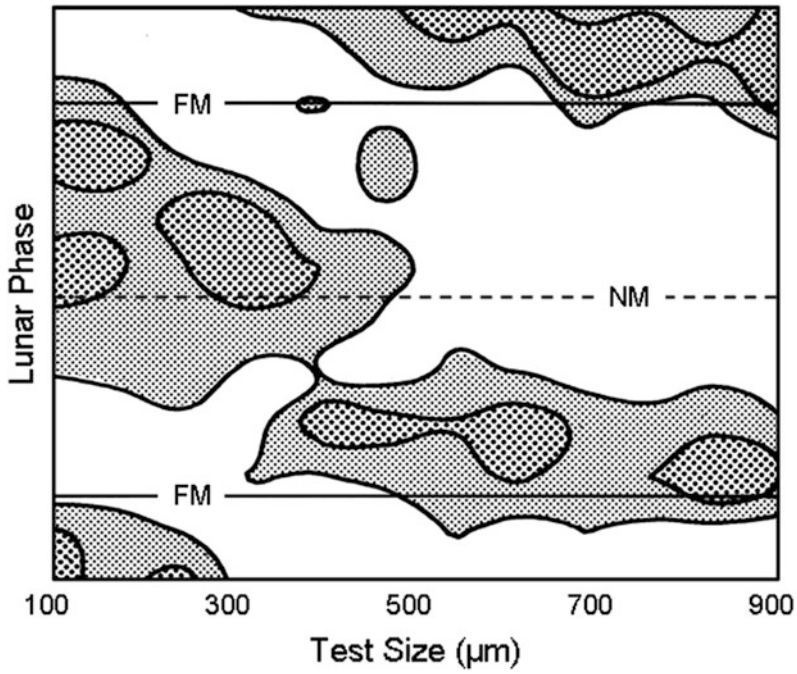

Fig. 5.2 Test-size distribution of *G. sacculifer* over an entire synodic lunar cycle from October 1 through November 17, 1984, from the Gulf of Aqaba. FM full moon, NM new moon. Surface samples were obtained every 4th day, and specimens were measured individually. Contour lines show residuals of test-size classes. Distribution of tests of any size, either under-represented, over-represented, or at maximum abundance, is given in white, fine stippled, and coarse stippled areas, respectively. Specimens grow larger over the synodic lunar cycle starting from around the first FM (*upper line*) to the following FM. The cycle is repeated as indicated by the contour lines before the 1st and after the 2nd FM. From Hemleben et al. (1989), and Bijma et al. (1990)

distribution) should be similar at equivalent longitudes, although local biotic and abiotic parameters may mask the signal. Consequently, each sample represents a transitional state of the standing stock of any species, and appears to be affected by the time of collection including season, geographic location, and day within the synodic lunar cycle.

According to data from vertical plankton tows, reproduction of shallow-dwelling planktic foraminifers at best takes place close to or within the Deep Chlorophyll Maximum (DCM), at the base of the mixed layer (i.e. thermocline, pycnocline). The DCM is thought to be the depth level where trophic conditions best support alimentation of juvenile planktic foraminifers (Hemleben et al. 1989; Schiebel and Hemleben 2005). Reproduction depth may thus be not only biologically fixed, but also affected by variations in hydrology and ecology, i.e. food sources. After reproduction close to the base of the productive layer in the water column, the empty adult tests sink toward the seafloor. The export layer hence contains mostly post-gametogenic specimens, i.e. empty tests or tests filled with various amounts of cytoplasm remnants.

Synchronized reproduction at a narrow depth range located near the seasonal thermocline and DCM enhances the chance of successful fertilization (gamete fusion), and favors survival of the offspring by providing prey in abundance, perhaps in the form of more or less degraded

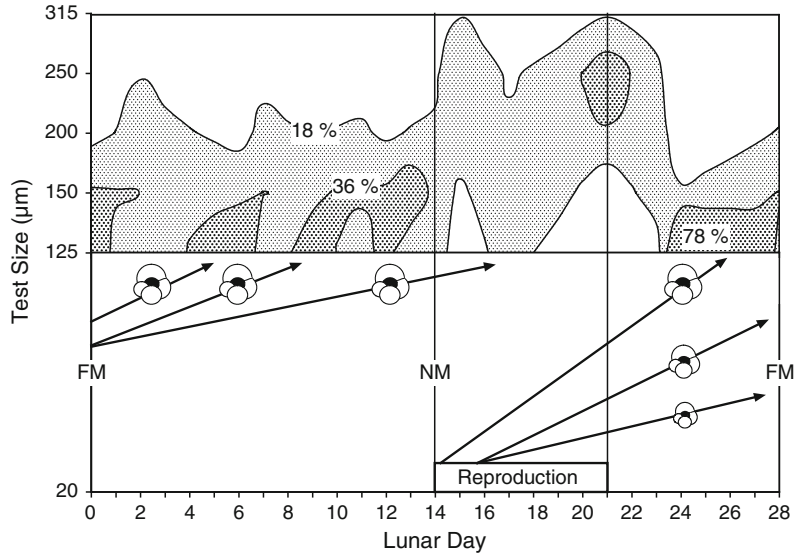

Fig. 5.3 Average test-size distribution of *G. bulloides* over a synodic lunar cycle, with FM full moon (Day 0), NM new moon (Day 14). Data in the upper panel show the relative distribution of tests >125 µm from plankton tows of the surface 60 m of the water column (linear time-scale, and 4-point interpolation). Largest individuals are assumed to reproduce mostly between Day 14 and 21. The offspring grows larger and reaches the >125-µm test-size fraction from Day 23. The lower panel shows assumed schematic growth curves of small (<125 µm) individuals starting from 20 µm (see Chap. 6), i.e. a hypothetic proloculus of *G. bulloides.* Redrawn from Schiebel et al. (1997)

organic tissues (e.g., Bijma et al. 1990; Erez et al. 1991). *Hastigerina pelagica* releases up to 500,000 gametes (Spindler et al. 1979), and other species release thousands to some tens of thousands gametes (Bé and Anderson 1976). Reproduction in *H. pelagica* occurs during the same time of day, i.e., the early hours of the afternoon (Spindler et al. 1979), which further enhances the chance of successful contact between the gametes of different parents.

Size-variations of prolocuili of the same planktic foraminifer species are statistically insignificant (Parker 1962; Sverdlove and Bé 1985; Brummer et al. 1987). Therefore, alternation of different generations (i.e. sexual and asexual) is likely limited, and it is assumed reproduction is predominantly sexual. However, asexual reproduction has been reported from individually cultured *Neogloboquadrina incompta* (Kimoto and Tsuchiya 2006, and written communication K. Kimoto 2014).

In contrast to the results discussed above, *G. bulloides* is assumed to reproduce twice per month (Marchant 1995), according to data from sediment trap samples from 2173 and 3520 m water depth off the coast of Chile. From the same samples, *N. pachyderma*, *N. dutertrei*, and *G. calida* are discussed as probably reproducing once per month (Marchant 1995; cf. also Jonkers et al. 2015 for sediment trap data from the Gulf of Mexico). From an ecologically similar sampling setup off Namibia, Lončarić et al. (2005) conclude that the only species bearing a synodic lunar reproduction strategy is *H. pelagica*, and all other 27 analyzed species bear no such lunar periodicity. Any other frequency of reproduction is reported in the 16–90 days domain, with *G. trilobus* (i.e. the trilobus type of *G. sacculifer*, Plate 2.9.1 to -3) assumed to reproduce on a 42-day cycle (Lončarić et al. 2005). However, reproduction cycles inferred from specimens from sediment trap samples are possibly affected by differential settling velocities of different species and test sizes, as well as transport of tests by currents. Those affects are increasingly difficult to account for with increasing sampling depths (cf. Berelson 2002; Von Gyldenfeldt et al. 2000; Jonkers et al. 2015). Best proof of timing

and periodicity of reproduction may be derived from observations using laboratory cultures as done for *H. pelagica*. In turn, planktic foraminifers are sensitive to exogenous changes including sensitivity to ecologic conditions. Therefore, laboratory cultured planktic foraminifers might not accurately display the natural reproductive behavior of any planktic foraminifer species reproducing in the natural environment (Spindler 1990).

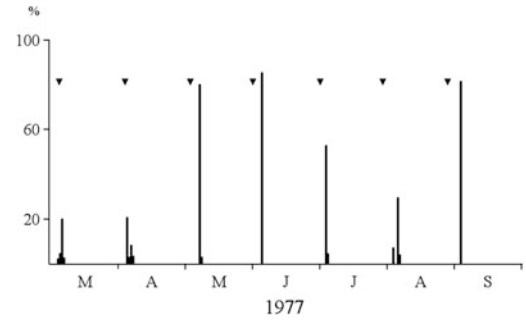

Fig. 5.4 Percentage of field-collected *H. pelagica*, which reproduced in the laboratory on the days indicated over a 7-month time-period from March through September 1977. The full moon is indicated by triangles. From Spindler et al. (1979)

5.3 Deviations from the Synodic Lunar Cycle in *H. pelagica* According to Laboratory Experiments

Deviations from the synodic lunar cycle provide information to better understand the reproduction cycle, and the effect of the moon (i.e. gravitation and tides, and light) on planktic foraminifer reproduction in general. Out of a total of 848 cases of gametogenesis of *H. pelagica* observed in the laboratory, 80.7 % (97.8 %) of the specimens released their gametes between Day 3 and 7 (Day 1–9, respectively) after the full moon (Figs. 5.4 and 5.5) similar to the gametogenesis observed in the natural habitat. Only 2.2 % of all specimens reproduced earlier (up to 7 days before the full moon) or later (up to 15 days after the full moon) possibly depending on the availability of food and light (i.e., light-and-dark cycles). The closer in time before the full moon that *H. pelagica* was sampled from surface waters and transferred to the laboratory, the higher was the chance of successful reproduction (Spindler 1990).

To examine the effect of light on reproduction, specimens of *H. pelagica* were sampled one or two days before the full moon, and exposed to varying light-and-dark cycles under laboratory conditions (Spindler 1990). Depending on the number of days of prolonged light or dark periods of several days, all specimens reproduced later than the control group of specimens. Reproduction was retarded according to the number of days of both prolonged continuous (A) light or (B) dark periods (Fig. 5.6). *Hastigerina pelagica* seemed to have registered (perhaps by a physiological clock) the number of dark and light periods to synchronize reproduction, which would argue against an affect of gravitation/tides on the synodic lunar reproduction cycle. It still remains unclear, how *H. pelagica* senses the light, and in which way light affects the timing of reproduction. Experiments on sub-circadian light-and-dark cycles would add information on the trigger and synchronization of the reproduction of *H. pelagica*.

The synchonized release of gametes during the same time of day (i.e., early afternoon) would possibly indicate *H. pelagica* as being heterogamous (Spindler et al. 1979). However, the cyclic reproduction of *H. pelagica* might be an exception within the planktic foraminifers, since the genus *Hastigerina* is different from other planktic foraminifers, especially such characteristics as the mono-lamellar shell, triradial spines, and the cytoplasmic bubble capsule (Spindler et al. 1979). Cyclic reproduction triggered by the synodic lunar cycle in all other planktic foraminifer taxa (Schiebel and Hemleben 2005) has so far been inferred from statistical models on population dynamics, and hence likely affected by any one or more of the following factors: Physical (e.g., expatriation by currents), ecological (e.g., availability of food), and biological (e.g., mortality), which may occur on much shorter or longer time-scales (cf. Lončarić et al. 2005).

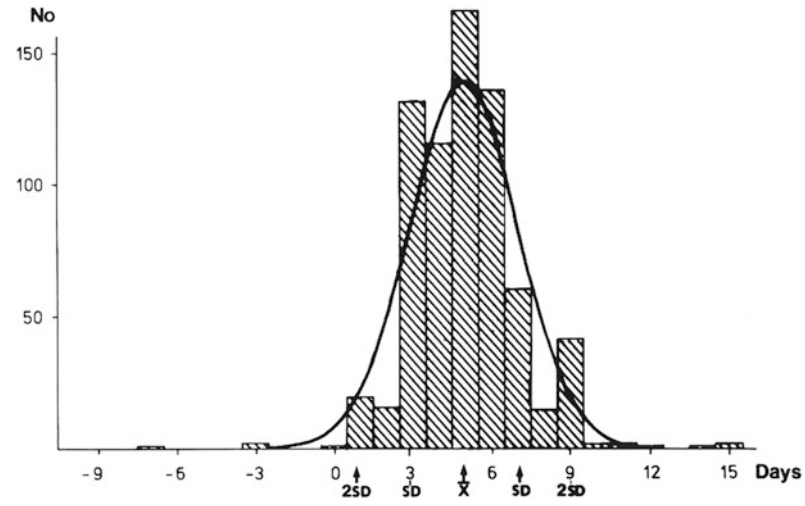

Fig. 5.5 Numbers (No) of specimens of *H. pelagica* reproducing relative to the day of the full moon (0 days). Observations started nine days before the full moon (−9), and were terminated 15 days after the full moon (15). Mean value ($\overline{X}$), standard deviation (SD). From Spindler et al. (1979)

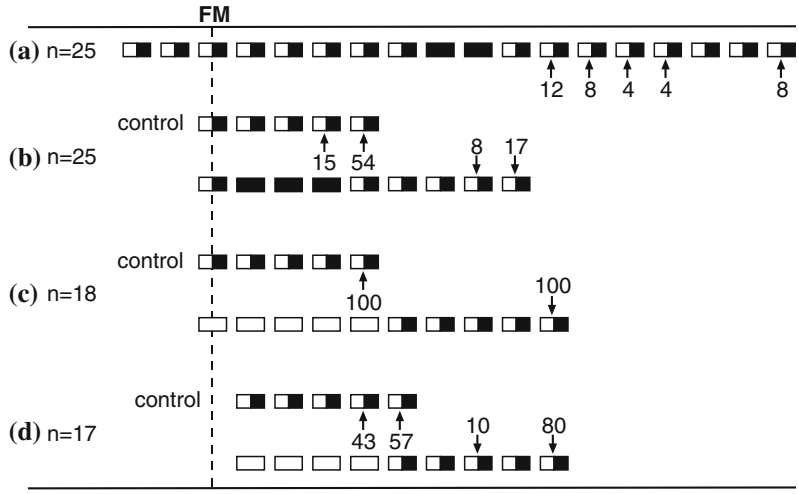

Fig. 5.6 Laboratory experiments of the effect of light-and-dark cycles on the timing of gametogenesis in *H. pelagica*. Experiments include circadian changes of 12-h light and 12-h dark (*white-black symbols*), 24 h darkness (*black symbols*), and 24 h light (*white symbols*). Day of reproduction and percentage of specimens which reproduced indicated by arrows with numbers. Full moon is given by FM and a dashed line. **a** 25 specimens, collected 2 days before the full moon were kept under a 12-h light/12-h dark cycle for 6 days after the full moon, then for 2 days in darkness, and from the morning of day 8 exposed to a 12-h/12-h light/dark cycle again. Consequently, reproduction was retarded and occurred between 9 and 15 days after the full moon. Experiment (**a**) was carried out without a control group. **b** After having been collected on the day of the full moon, part of the specimens were kept in darkness for 3 days, and reproduction occurred 3 and 4 days after the time when the specimens of the control group reproduced, which were continuously kept under 12-h/12-h light/dark cycles. **c** and **d** Same experiments as in (**b**) but part of the specimens were exposed to continuous light for several days. After Spindler (1990)

5.4 Summary and Concluding Remarks

Morphological changes, including spine shedding, and gametogenic calcification characterize specimens that undergo gametogenesis. Asexual reproduction (i.e. a haploid generation) in planktic foraminifers is assumed much less likely to be the case than sexual reproduction (cf. Hemleben et al. 1989, and references therein). Morphological alternation of microspheric (diploid generation) and macrospheric (haploid generation) generations as in benthic foraminifers has not yet been reported among planktic foraminifers. Size-variations of proloculi of the same planktic foraminifer species are statistically insignificant, supporting the assumption of predominantly sexual reproduction in planktic foraminifers. In turn, asexual reproduction has been reported from individually cultured *Neogloboquadrina incompta*.

Strong evidence shows that the reproductive cycle in spinose species living in the photic zone is linked to a synodic lunar or semi-lunar cycle, particularly well established for *H. pelagica*, *G. sacculifer*, *G. siphonifera*, *G. ruber*, and *G. bulloides*. Subsurface dwelling species such as *G. truncatulinoides* and *G. hirsuta* appear to have an annual or semi-annual reproduction frequency. Despite detailed knowledge of timing and cytoplasmic events during reproduction of planktic foraminifers, the complete life cycle is still not sufficiently known. More complete information from laboratory cultures and natural populations is needed to understand the events of reproduction early ontogeny of planktic foraminifers.

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