

Chapter 2

The Natural Laboratory of Algal Symbiont-Bearing Benthic Foraminifera: Studying Individual Growth and Population Dynamics in the Sublittoral

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Abstract Reproduction period, longevity and the chamber-building rate of symbiont-bearing benthic foraminifera, which are important for population dynamic studies can be estimated from field data. Laboratory investigations changing the grade of ecological variables cannot substitute for the complexity of natural conditions. Therefore, methods are developed, especially for the deeper sublittoral species, to estimate reproduction, lifespan and the individual growth rate under natural conditions for demonstrating the influence of environmental parameters.

Keywords Longevity • Natural growth • Reproduction • Standardization • Sublittoral sampling

2.1 Introduction

Investigations on the biology of algal symbiont-bearing benthic foraminifera (in the following shortened as SBBF) living in the eulittoral and upper sublittoral were predominantly based on laboratory studies. Soon after starting in the early fifties of the twentieth century, laboratory experiments on SBBF culminated in the works of Rudolf Röttger and co-workers, where reproduction and growth were studied in *Heterostegina depresssa*, the flagship of laboratory investigations on SBBF (e.g. Röttger 1972, 1976; Röttger and Spindler 1976; Röttger et al 1980),

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followed by *Cycloclypeus carpenteri* (Krüger 1994; Lietz 1996), *Nummulites venosus* (Krüger 1994), *Calcarina gaudichaudii* (Röttger et al. 1990) and *Amphistegina lessonii* (Dettmering 1997). Further important studies on laboratory cultures of SBBF were performed by John J Lee (e.g. Lee et al. 1980; Lee et al. 1991), Pamela Hallock and co-workers (e.g. Toler and Hallock 1998; Toler et al. 2001), while Kazuhiko Fujita and Sven Uthike, both with co-workers, recently conducted laboratory experiments under different environmental conditions (e.g. Fujita and Fujimura 2008; Hosono et al. 2012; Uthicke and Fabricius 2012; Uthicke et al. 2012).

Field observations on the biology of SBBF concentrate on eulittoral species living on the reef crest (Sakai and Nishihira 1981; Hohenegger 2006) or in regions of the shallowest sublittoral (e.g. Zohary et al. 1980; Fujita and Hallock 1999; Fujita et al. 2000; Fujita 2004; Osawa et al. 2010; Uthicke and Altenrath 2010; Reymond et al. 2011; Ziegler and Uthicke 2011). Observation on SBBF in the deeper sublittoral is more difficult due to intense hydrodynamics that hinder secure fixing of technical equipment for studies in the natural environment.

For the investigation of reproductive timing, growth and longevity of generations (agamonts, gamonts and schizonts) in SBBF, the chamber-building rate is of primary importance. The chamber-building rate represents the independent character for measuring the influence of time-dependent environmental factors like spring tides or seasonality in reproduction and growth. These environmental factors cause changes in temperature, solar irradiation, water transparency, input of inorganic and organic nutrition etc.

Growth experiments in laboratory cultures cannot represent natural conditions, although the objective is to simulate them; thus they cannot give reliable information about reproduction time, growth, longevity and life cycles. Two examples may show these difficulties. In September 1992 *Peneroplis antillarum* was sampled from intertidal pools of the reef crest NW of Sesoko Island (Hohenegger 1994) and put into Petri-dishes. Only water was changed weekly using sea water from the upper sublittoral in front of the Sesoko Marine Laboratory. Except water movement, other factors influencing growth were kept as natural as possible because the Petri-dishes were exposed to natural sun light. After three months, the laboratory sample was compared with a sample taken from the same pool where the lab sample originated. The differences were striking; while the sample from the pool showed individuals with undisturbed growth that can be modelled by a logarithmic spiral, individuals kept in the laboratory showed restricted growth and several growth disturbances leading to deviations from the logarithmic spiral (Fig. 2.1).

Similar results have been observed comparing *Heterostegina depressa* tests from individuals collected from the natural environment with individuals kept under laboratory conditions. A comprehensive way to study and illustrate test morphology en toto in space is the use of computed tomography. More details on this technique, its uses and applications in foraminiferal biology and palaeontology are reported in two other papers contained in this book.

Two specimens have been scanned with a micro computer tomograph (microCT) at the Department of Palaeontology, University of Vienna. The very high scanning resolution (<4 μm) allowed the visualization and the quantification of almost any morphological parameter. In Fig. 2.2, a specimen (specimen's name: A1) of

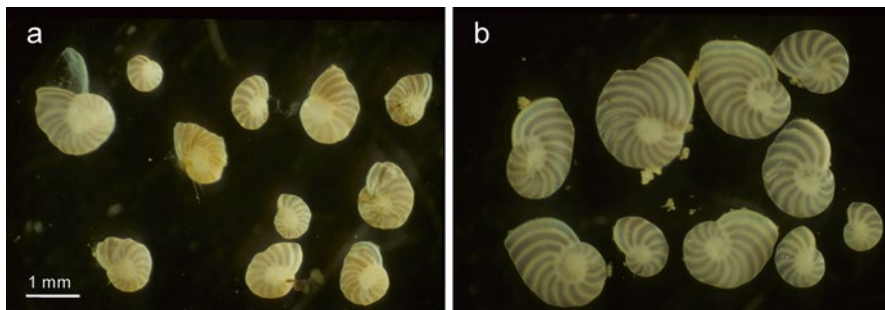


Fig. 2.1 Light microscope micrographs of *Peneroplis antillarum* (a) sampled in September 28, 1992 and kept living in the laboratory until December 5, 1992; (b) sampled in December 5, 1992 from the same sampling location

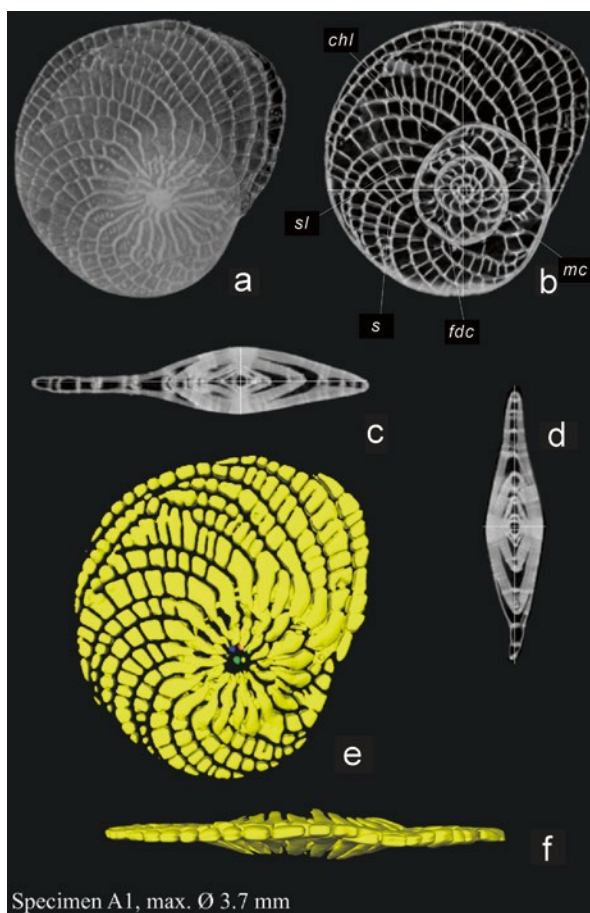


Fig. 2.2 MicroCT scans of *Heterostegina depressa* specimen A1, (a) external view of the 3D model, (b) equatorial section of the specimen, (c, d) axial section of the specimen along the axes visible in b, (e) equatorial view of all segmented chambers, operculinid chambers are visible in the central part and are not yellow colored, (f) axial view of the segmented chambers. *fdc* first divided chamber, *mc* marginal chord (see marginal canal within), *s* setpum, *sl* septulum, *chl* chamberlet

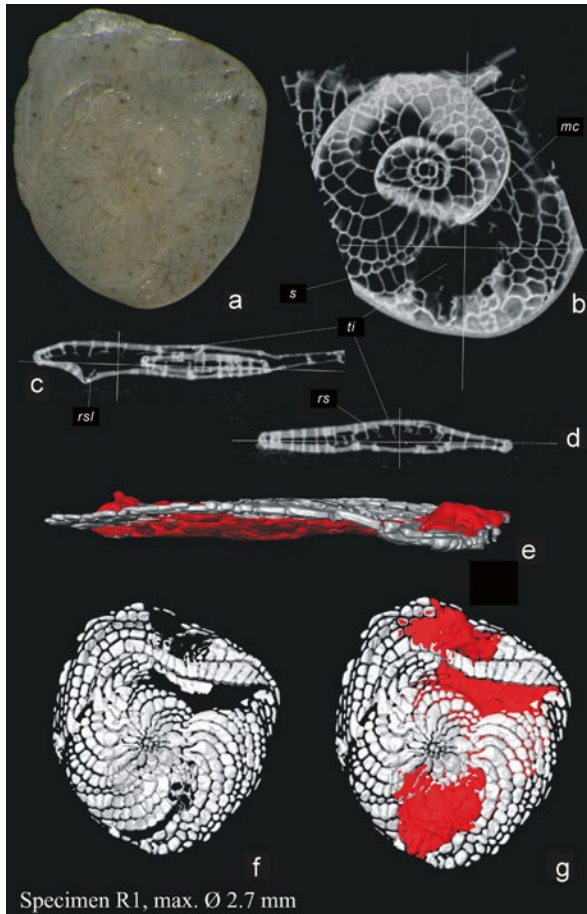


Fig. 2.3 *Heterostegina depressa* specimen R1, (a) external view of the specimen under microscope, (b) equatorial section of the specimen (note the large hole created at chamber 45), (c, d) axial section of the specimen along the axes visible in b (note the incomplete septula), (e) axial view of the segmented chambers (in red, the large hole which is extending through the test), (f, g) equatorial view of the segmented chambers (in f without the large hole, in g with the view of the large hole in red). *mc* marginal chord, *ti* test inflation, *s* septum, *rs* reduced septum, *rsl* reduced septulum

Heterostegina depressa was collected alive at 20 m depth in front of Sesoko Island (Hohenegger et al. 1999) and immediately dried. In Fig. 2.3, a specimen of the same species (specimen's name: R1) is displayed; it was cultivated under laboratory condition at the University of Kiel, Germany (Röttger 1972; Röttger and Spindler 1976; Krüger 1994). For each specimen, microCT slices, 3D model reconstructions and specimen segmentation are reported.

The shell morphology of specimen A1 represents the general and common shape of specimens belonging to this species: a slightly evolute spiral coiled test (Fig. 2.2a) with several undivided initial chambers, then followed by chambers divided into

chamberlets formed by complete septula (Fig. 2.2b–d) and a centrally thickened shell becoming much flatter at the periphery by increasing the distance between the septa (Fig. 2.2e, f).

On the contrary, specimen R1 (Fig. 2.3), which seems to have a normal shape by observing it under the microscope, as surely Röttger did in his lab, shows several strong shell variations: the inconstant curvature of the septa (Fig. 2.3b), the sudden inflation of the test (Fig. 2.3b–d) and (connected to this morphology) the vertical reduction of septa and septula (Fig. 2.3e, f).

The thick marginal chord and the septa in Fig. 2.2b, where both marginal and septal canal systems are visible, are completely lost in specimen R1 (Fig. 2.3b), where the septa appear to be made of compounded bulging singular septula. This pattern starts to emerge after approximately the 10th chamber in R1. Furthermore, on the axial slices of specimen R1 (Fig. 2.3c, d), taken along the axes visible on the equatorial section (Fig. 2.3b), a big cavity or an inflation of the test walls instead of a normal chambered internal structure is visible (Fig. 2.3e–g, in red). This hollow space starts around the 45–47th chamber, but early chambers also show a trend of septal reduction resulting in complex chamberlet geometries. Coincidental to the forming of this cavity, specimen R1 shows a vertical reduction of the septula, which extend neither to the following septum nor laterally to the test wall (Fig. 2.3c, d).

Possible explanations for such abnormal growth must be connected to particular culturing conditions, which according to the published material was very advanced for the late 1970s, but still not representative of natural conditions.

Therefore, it is necessary to study individual and population growth under natural conditions. Because the installation of technical equipment is difficult in regions with extreme hydrodynamics like the upper sublittoral and often equipment can be destroyed by tropical storms, investigation by sampling in more or less constant intervals over a time period of at least one year is a possible solution. In the following, sampling, data collection and evaluation will be demonstrated.

2.2 Sampling

The best sampling method in the upper sublittoral from 5 to 60 m depth is by SCUBA diving. The sampling procedure is described in detail below.

- a. The determination of *location*, *water depth* and *sedimentary conditions* must be based on former investigations about the regional distribution and abundance maximum of the species if interest. For example, investigations by Hohenegger (2004) NW of Sesoko Island, Okinawa, Japan, demonstrated optimum conditions for *Palaeonummulites venosus* at 50 m depth on sandy bottom in the northern transect, while *Heterostegina depressa* has its optimum at 20 m depth on firm substrates, which are structured coral rock and boulders.
- b. A *sampling interval* must be selected, but actual sampling events will typically depend on weather conditions, which may hinder consistent intervals. Irregular sampling intervals may range from weeks to months, where the latter represents

the upper limit, because larger intervals could obliterate the data set. To investigate the influence of tides, weekly sampling close to spring and neap tides is necessary.

- c. To make measures on environmental conditions—especially irradiation—comparable over seasons, noon should be the *time of day* for *sampling*.
- d. *Sampling methods* depend on the substrate. For *soft substrates* with grain sizes of pebble to clay according to the Udden-Wenworth grain size classification (Boggs 2006), a prismatic plastic box with a secure lid should be used. At the sampling point, the sediment has to be dredged into the box, where only the upper 2 to 3 cm of the sediment should be taken as the maximum dredging depth. Afterwards, the box must be closed by securing the lid.

For investigating species living on *firm substrates*, boulders and cobbles must be gathered and put into closable plastic carrier bags.

Additional *water samples* should be taken for investigating the chemical composition of seawater in the laboratory.

- e. The *number of sampling points* at the location must be ≥ 4 , randomly distributed and in considerable distance from each other (approximately 5 m) for smoothing the effects of patchy distributions.
- f. During sampling, on-site measurements of physical factors like *temperature* and *light intensity* (= irradiance) should be measured at the sampling location. Irradiance must also be measured at the surface, because *relative irradiance*, which is independent of weather conditions, relates irradiance at the sampling depth to sea surface irradiance by

$$irrad_{rel} = \frac{\ln(irrad_{sample})}{\ln(irrad_{sea\ surface})} \quad (2.1)$$

where the unit of irradiance corresponds to

$$6 \cdot 10^{17} \text{ photons m}^{-2} \text{ sec}^{-1} = 1 \text{ microEinstein} (\mu E) \text{ m}^{-2} \text{ sec}^{-1}$$

Logarithms must be used, because irradiation follows an exponential decrease (Hohenegger et al. 1999). Using relative irradiation, changes in light intensities over seasons due to inorganic or organic input can be calculated independent of weather conditions on the sampling date.

For studying individual and population growth in species with their distribution optimum deeper than 60 m, sampling by SCUBA diving is difficult or impossible. Sampling in the deeper sublittoral can be performed by *crab-sampling*, *coring* or *dredging*. While individual growth over the year can be measured using all sampling methods, population growth that needs a standardized substrate surface can be estimated using crab sampling or coring, where the bottom surface area is either determined by the core diameter or can be approximated by measuring the opening of the crab sampler. Area determination of a dredged bottom surface is difficult to impossible using dredgers with unfixed penetration depth.

2.3 Concentrating Living Individuals

Picking living foraminifera out of the samples depends on substrate conditions. This should be done in the laboratory using vessels filled with sea water. Vessel size should not be too deep making investigation with a binocular microscope impossible.

- a. *Boulders* and *cobbles* must be intensively cleaned over the investigation vessel using a dental brush. Afterwards, specimens that could not be removed by brushing must be picked under the binocular and put into the investigation vessel. Cleaned boulders and cobbles should be washed with freshwater, dried and stored for further investigations, or returned to seawater and returned to the collection site, if required by local regulations.

Soft sediment is directly placed into the investigation vessel filled with sea water. Because the thickness of the sediment layer in the vessel should not exceed 2 mm, only parts of the sampled sediment can be put into the vessel. The proportion depends on vessel area that must be equally covered by the sediment. To extract fine organic and fluffy material that could be abundant in fine-grained sediment, repeat decantation using sea water is necessary. Decantation of fine silt to mud from sandy sediments is also necessary. This fine fraction should be put in separate vessels for grain size analysis.

Depending on vessel area and sample size, soft sediments require several investigation vessels simultaneously.

- b. Investigation vessels should *rest for one day* at least, because living foraminifera, retract their colored protoplasm due to disturbance by sampling and preparation, but will refill the final chambers during this calm resting period.
- c. Living foraminifera can now be *picked* out using fine and flexible forceps and put into separate cups filled with sea water. The *identification of living SBBF* is easy compared to non symbiont-bearing foraminifera, because SBBF are colored by their symbiotic microalgae. Living peneroplids can be identified by their purple color (*Porphyridium* belonging to rhodophyta), archaiasinids and *Parasorites* by green colour (*Chlamydomonas* belonging to chlorophyta), soritids by olive to ochre colors (*Symbiodinium* belonging to dynophyta), while alveolinids and all hyaline SBBF are characterized by light ochre color caused through symbiotic bacillariophyta (diverse genera and species of diatoms).

Difficulties for identifying living individuals may arise in hyaline SBBF, especially nummulitids, because they can be colored by bacteria or other non-symbiotic microalgae after leaving the test by reproduction or death. In contrast to living individuals, which are evenly colored by light ochre, coloring of empty tests is more intense, spotty or dark-stained.

- d. After picking all living individuals, the remaining sediments must be washed in freshwater, dried and stored for further investigations.
- e. The picked living individuals are now ready for further investigations, either becoming the base for laboratory experiments or for investigating individual and population growth. For studying the chamber building rate, individuals of the species of interest should be washed in freshwater, dried and stored.

2.4 Determination of Environmental Parameters

On-site measurements at the sampling station over the sampling period provide information about changes in *temperature* and relative *irradiance*.

The crossing of *storms* must be recorded, because they can intensively disturb the bottom surface down to 100 m water depth, especially entraining and transporting foraminifera living on soft substrate. Disturbances by storms can be expressed either in the composition of the foraminiferal fauna or in distinct changes of grain size. Disturbance in the faunal composition was noted in a sample collected in 1992 from 50-m water depth that was taken after the first seasonal crossing of a typhoon. In contrast to samples from 50 m taken before the typhoon season, abundant living *Peneroplis pertusus*, *P. antillarum*, *Dendritina ambigua* and *D. zhengae*, which are typically restricted to the shallowest sublittoral (<30 m), were found at this depth, obviously having been transported to deeper sites. Therefore, *grain size analysis* is necessary for each sampling location and event.

Water taken from the sampling station should be investigated in the laboratory just after sampling. Chemical parameters characterizing the environment of the sampling station like pCO_2 , pH, nitrate concentration, O_2 and the organic carbon content should be measured.

2.5 Investigating Individual Growth and Population Dynamics

2.5.1 Measurements

For SBBF, only three simple measurements are necessary for the determination of chamber-building rate and population dynamics. These are the number of individuals n , number of chambers m_i and the largest diameter d_i of individual i .

The determination of a standardized in situ surface area of the sample, which is necessary for population dynamic investigations, depends on the sampling method. Using cores, sample surface a^2 is given by the inner core diameter d_{core}

$$a_{observed}^2 = (d_{core} / 2)^2 \pi. \quad (2.2)$$

This area can be approximated in crab sampling by the opening size of the sampler. Cores can be taken by SCUBA.

The area of firm substrates like cobbles and rubble exposed to the water column can be measured using *image analysis*.

For soft sediments, the volume v of the dried sediment can be obtained using a *graduated measurement vessel*. Presuming a mean dredging depth l of the box used by the diver, sampling surface a^2 can be calculated by

$$a_{observed}^2 = v / l \quad (2.3)$$

Now, the standardized individual number n^* for sample j is given by

$$n_j^* = \frac{a_{\text{theoretical}}^2}{a_{\text{observed}}^2} n_j \quad (2.4)$$

Standardization is always necessary for comparing samples of different sizes.

2.5.2 Statistical Investigation

Chamber number m_{ij} and size d_{ij} of n_j individuals of the sample j can be used to determine reproduction period, longevity and chamber-building rate of the species of interest.

Peneroplis antillarum sampled from tidal pools on the reef crest NW of Sesoko Island between September 1992 and August 1993 will be used as an example (Hohenegger 2006). Sampling was performed in different intervals depending on weather condition and spring tides trying to approximate monthly sampling. Because the first samples from September and October 1992 were not treated in the requested manner, data processing started with the beginning of December 1992 (Fig. 2.4).

To demonstrate how reproduction, growth and longevity can be estimated, the largest diameter of *P. antillarum* shells was used.

- a. First, a *frequency graph* must be constructed for every sample. In case of size measurements, the *histogram* is particularly useful for graphical representation of the frequency distribution. The lower and upper limit of the measurement scale must be identical for all histograms and interval width must be the same for all sample histograms, whereby the number of intervals should not exceed the square root of the largest sample. For comparison of frequencies, the abundance scale must be equal for all samples (Fig. 2.4).

Contrary to size, which is a continuous variable, a *bar diagram* is the correct graph to show frequencies of the meristic (= natural numbers including 0) character chamber number (Fig. 2.5),

- b. When in situ sampling surface areas are different, class abundance in the histogram or in the bar diagram must be *standardized* according to Eq. (2.4).
- c. Using size in species with shells that can be modelled by a logarithmic spiral (like *Operculina*, *Planoperculina*, *Planostegina*, *Palaeonummulites* and *Heterostegina* in sublittoral SBBF), the histograms are always left-side skewed (like in the eulittoral *P. antillarum*; Fig. 2.4). To get normal-distributed histograms the transformation of original measurements into logarithms is necessary

$$d_{ij}^* = \ln d_{ij} \quad (2.5)$$

- d. The *upper limit of minimum* size and/or chamber number characterizing the *offspring* has to be determined by investigating the size of offspring obtained in laboratory investigations or measuring the size of the embryonal apparatus (in *P. antillarum* all individuals smaller than 0.3 mm). Thereafter, *offspring frequencies* can be obtained for all samples using the cumulative frequency distributions up to this limit (Fig. 2.4).

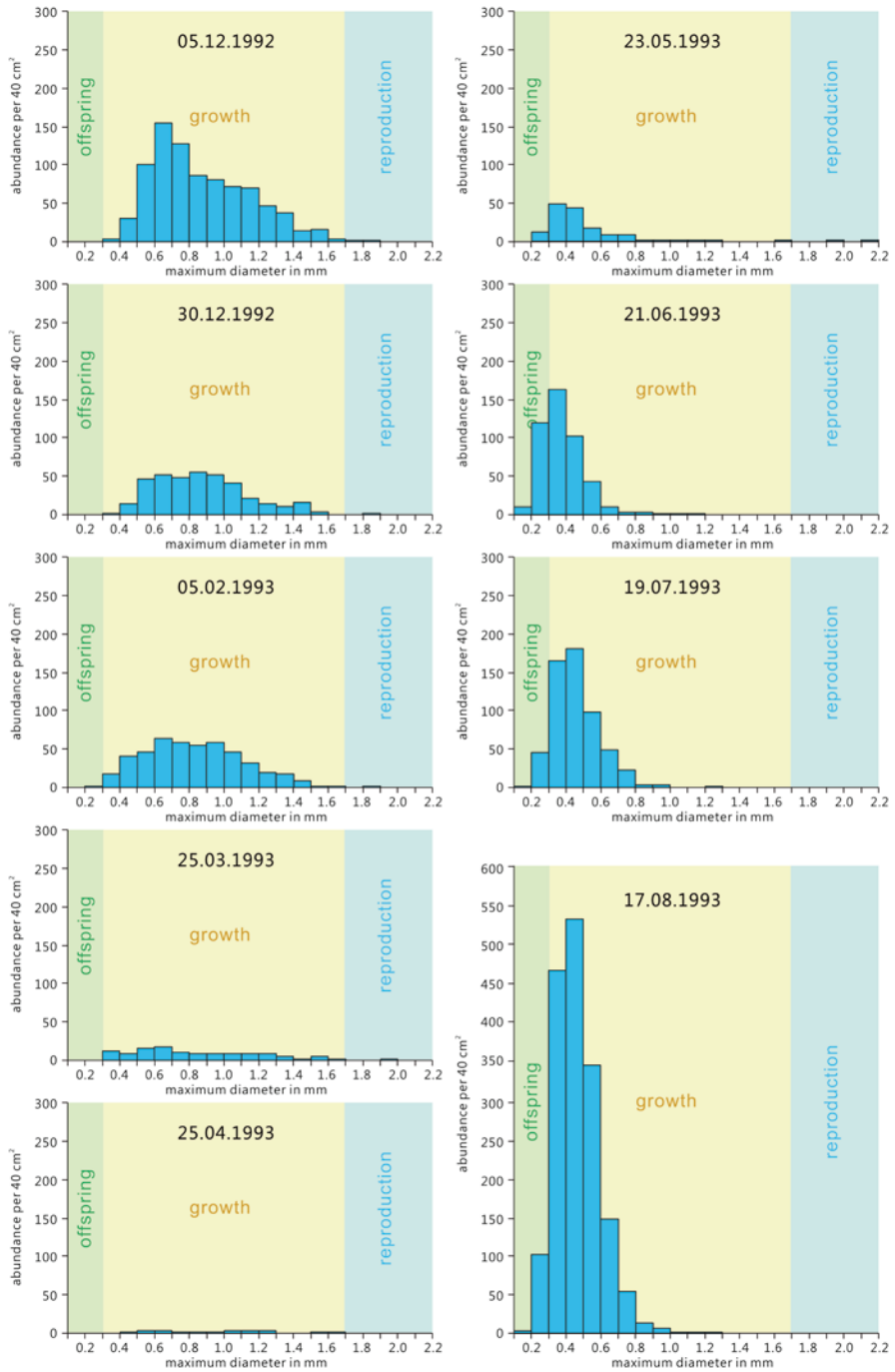


Fig. 2.4 *Penereolis antillarum*: Histograms of test size measured as the largest diameter; test size <0.3 mm characterizing offspring and test size >1.6 mm characterizing individuals ready for reproduction are marked

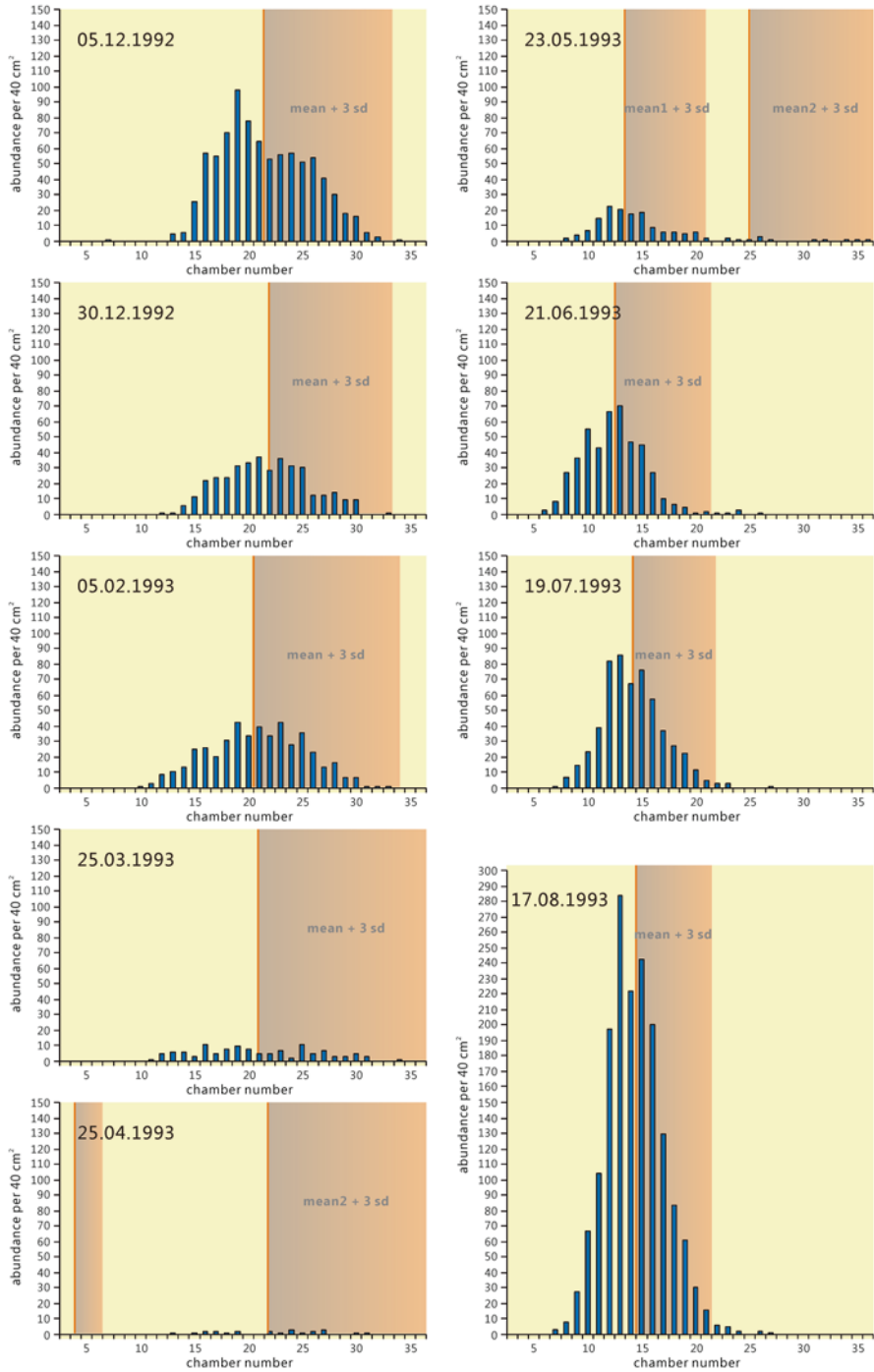


Fig. 2.5 *Peneroplis antillarum*: Bar diagrams of chamber numbers; the maximum chamber number defined as the arithmetic mean plus 3 times the standard deviation (Eq. (2.10))

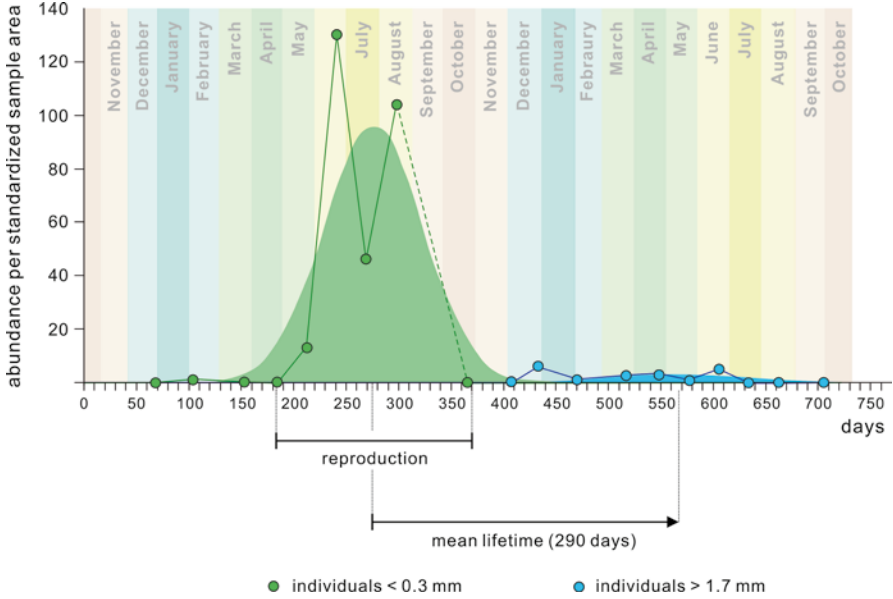


Fig. 2.6 Determination of reproduction period and lifetime in *Peneroplis antillarum*

- e. Afterwards, an artificial *lower limit* of *maximum size* and/or chamber number characterizing specimens ready for *reproduction* has to be determined using different statistical parameters like three-fourths of the total size range (in *P. antillarum* all individuals larger than 2.6 mm) or the 3rd Quartile of the sum of all distributions. The abundance of largest individuals must be counted for all samples as cumulative frequency distributions starting from this lower limit (Fig. 2.4).
- f. Offspring and reproduction abundance of all samples should be put into a frequency diagram with the *time scale* as the independent variable (Fig. 2.6). Since frequencies depend on seasons, thus being periodic functions, the time scale should start before the first offspring (February 5, 1993 in our example) and continues after the end of the investigation period with data from the beginning (December 5, 1992 in our example; Fig. 2.4).
- g. The parameters *mean* \bar{x} and *standard deviation* s must be calculated for both distributions (individuals just after reproduction and largest individuals ready to reproduce). Because of incomplete data and variable intervals, both parameters can be estimated by numerical (iterative) regression methods (PASW Statistic 19, 2010).
- h. *Reproduction period* $t_{\text{reproduction}}$ can be calculated by

$$t_{\text{reproduction}} = \left(\bar{x}_{\text{offspring}} + 2s_{\text{offspring}} \right) - \left(\bar{x}_{\text{offspring}} - 2s_{\text{offspring}} \right) \quad (2.6)$$

because 96 % of observations are positioned within this interval (Fig. 2.6).

In our example, the reproduction period is from the end of April until the end of October, peaking in July (Fig. 2.6).

Table 2.1 Statistical parameters of chamber numbers for calculating the chamber building rate

Datum	Days	Mean chamber number	Standard deviation	Coefficient of variation	Maximum chamber number
4/25/1993	1	4.0	0.81		6.4
5/23/1993	28	13.5	2.49	5.41	21.0
6/21/1993	57	12.4	3.01	4.13	21.5
7/19/1993	85	14.2	2.89	4.92	22.8
8/17/1993	114	14.4	2.70	5.32	22.5
10/24/1992	182	22.3	3.36	6.63	32.3
12/5/1992	224	21.5	4.13	5.21	33.9
12/30/1992	249	21.6	3.97	5.44	33.5
2/5/1993	286	20.9	4.42	4.71	34.1
3/25/1993	334	20.8	5.46	3.81	37.2
4/25/1993	366	22.1	4.93	4.48	36.9
5/23/1993	394	24.8	5.46	4.55	41.2

i. An averaged *lifetime* t_{life} can be calculated by

$$t_{life} = \bar{x}_{reproduction} - \bar{x}_{offspring} \tag{2.7}$$

In our example the averaged lifetime is 290 days (Fig. 2.6). Measuring lifetime using the interval between the first offspring (February 5) and the first individuals indicating reproduction (December 5) last for 302 days, similar to the estimation by the distance of means. Therefore, the lifetime of *P. antillarum* can be estimated as approximately one year.

Calculation of the *chamber building rate* is more complex depending on the reproduction period and longevity. The following steps are proposed:

- j. Find sample j , where the first offspring during the investigation period appears ($j=1$; May 23 in our example, Fig. 2.4). Start the investigation period $t=1$ (in days) with the datum of the sample just before the first offspring sample (April 25 in our example, Fig. 2.4).
- k. Calculate the *mean* \bar{x}_j and *standard deviation* s_j of chamber number for all samples j (Table 2.1).

l. Calculate the **coefficient of variation**

$$CV_j = \bar{x}_j / s_j \tag{2.8}$$

for all samples and check their constancy by linear regression analysis. In case of significant constancy calculate the averaged coefficient of variation, otherwise calculate the regression coefficients (Table 2.1).

- m. Set the time of initial sampling period ($j=0$; April 25 in our example), which corresponds to the sample just before $j=1$, as $t_0=1$. The chamber number m_0 is based on the chamber number $m_{offspring}$ of the offspring grown in the laboratory. In *Peneroplis antillarum*, this chamber number is 3. Since most foraminifera build the following chamber within one day (Röttger 1972; Krüger 1994; Lietz 1996), the chamber number of the first day after offspring becomes

$$m_0 = m_{offspring} + 1 \tag{2.9}$$

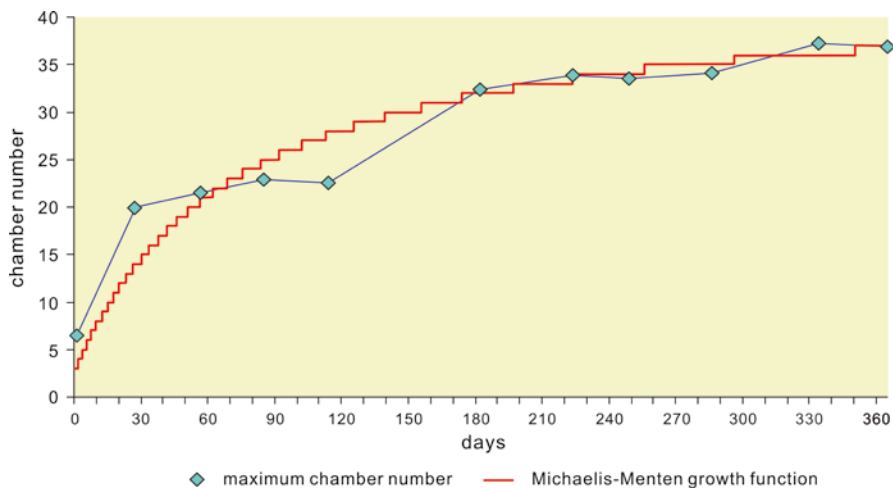


Fig. 2.7 Determination of the chamber building rate using the Michaelis–Menten growth function based on the maximum chamber numbers (Fig. 5)

which is 4 in *Peneroplis antillarum*.

- n. Calculate the upper distribution limit for all samples by

$$m_{j\max} = \bar{x}_j + 3s_j \quad (2.10)$$

To get the upper limit for the initial sample $j=0$, the necessary standard deviation can be calculated by

$$s_0 = m_0 / CV_{mean} \quad (2.11)$$

- o. Based on the relation between time t in days and the maximum chamber number m_{\max} , the chamber building rate can be calculated using the Michaelis–Menten function

$$t = am_{\max} / (b + m_{\max}) \quad (2.12)$$

with the reverse function

$$m_{\max} = bt / (a - t) \quad (2.13)$$

To standardize this function by the chamber number of the offspring at $t = 0$, the value of function 2.12 at $m_{\text{offspring}}$ must be subtracted from the function values t of Eq. (2.12):

$$t_j^* = am_{j\max} / (b + m_{j\max}) - am_{\text{offspring}} / (b + m_{\text{offspring}}) \quad (2.14)$$

The subtrahend in *Peneroplis antillarum* is 4.9, leading to the function

$$t = -67.619m / (-44.073 + m) - 4.9$$

- p. The results of chamber building rate can now be represented as a function graph (Fig. 2.7).

These statistical methods can be used to determine chamber building rate, reproduction period and lifetime of algal SBBF in all environments by taking standardized samples in more or less regular intervals over at least one year.

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