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Population dynamics of *Amphisorus hemprichii* (Foraminifera) in the Gulf of Elat (Aqaba), Red Sea

By TAMAR ZOHARY[1]), ZEEV REISS[2]) and LUKAS HOTTINGER[3])

ZUSAMMENFASSUNG

Die Populationsdynamik von *Amphisorus hemprichii* EHRENBERG aus 4 m tiefen *Halophila*-Rasen wurde untersucht mit Hilfe von Proben der Population, welche zweimal monatlich zwischen November 1978 und November 1979 aufgesammelt worden waren. Grössenverteilung und Populationsdichte im Jahresgang zeigen, dass sich diese Foraminiferenart in einem jährlichen Zyklus einmal asexuell fortpflanzt während einer kurzen Reproduktionsperiode im Frühjahr, wenn die Wassertemperaturen ansteigen. Während der übrigen Zeit des Jahres wachsen die Individuen synchron. Mittlere Wachstumsraten des Schalendurchmessers erreichen 100 µm in der Woche in Herbst und Winter; vor der Reproduktionsperiode nehmen sie ab. In den aufeinanderfolgenden Generationen waren der Durchmesser der megalosphärischen Embryonen, die Wachstumsrate der Schalen, die Populationsdichte und das Auftreten der microsphärischen Formen verschieden.

Aus den Daten Schalendurchmesser/Trockengewicht, Populationsdichte und Lebenslänge wird die jährliche Karbonatproduktion von *A. hemprichii* auf *Halophila*-Rasen in seichtem Wasser des Golfs von Elat auf 160 g Ca CO_3/m^2 geschätzt.

ABSTRACT

The population dynamics of *Amphisorus hemprichii* EHRENBERG, from 4 m deep *Halophila* meadows in the Gulf of Elat was analyzed by means of population samples collected biweekly, between November 1978 and November 1979. Size frequency distribution and standing crop indicate an annual life cycle of this species, with one, short reproductive period in spring, and synchronous growth of the populations during most of the year. The average growth rates calculated from the field data reached 100 µm (diameter)/week during fall and winter, but slowed down towards the reproduction period. Samples from two consecutive generations differed in average growth rate, standing crop, occurrence of microspheric specimens, as well as in biometrical characters of the embryonal apparatus.

From data on a) diameter:dry weight relationship, b) standing crop, and c) life span - the annual carbonate production by *A. hemprichii* was estimated to be 160 g $CaCO_3$ per m^2 per year.

Introduction

Amphisorus hemprichii EHRENBERG 1839 is a large, tropical, benthic Soritid species (LEHMANN 1961), bearing symbionts (DOYLE & DOYLE 1940; LEUTENEGGER 1977*a, b, d;* LEE et al. 1979). Distributional studies of larger foraminifera in the Gulf of Elat (Aqaba), Red Sea (SAID 1950; REISS et al. 1961; HOTTINGER 1972, 1977),

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have shown that *A. hemprichii* is widely distributed in shallow bottoms (0–40 m) and is highly abundant.

Although the life cycle and growth rates of several larger, tropical benthic foraminifera were studied in the laboratory (ROSS 1972; RÖTTGER 1974; RÖTTGER & SPINDLER 1976), little is known about their population dynamics from field observations (MULLER 1974, 1977). No data were available hitherto on *Amphisorus.*

The present study concerns a quantitative analysis of *A. hemprichii* populations, in their characteristic habitat - *Halophila* meadow. The study is based on biweekly sampling, over a one-year period. This analysis, coupled with biometric studies, provided information on the standing crop, growth rates, seasonality, turnover rate and life cycle of this species, in the Gulf of Elat - a warm, hypersaline and oligotrophic body of water (KLINKER et al. 1976, 1978; LEVANON et al. 1979; SOURNIA 1977).

Because of its high abundance and relatively large calcareous test, it was suggested that *Amphisorus* could be an important carbonate producer in the Gulf. The present study made it possible to estimate the annual carbonate production of this foraminifer, and to compare the estimate with carbonate production values calculated previously for larger benthic foraminifera from more productive seas (MULLER 1974, 1977).

Methods

A typical *Halophila* meadow, located 2 km south of the H. Steinitz Marine Biological Laboratory, Elat, was selected as a sampling site (Fig. 1). The meadow is covering a flat, sandy bottom, at 4 m depth. At this site *Amphisorus* is accompanied by several other species of foraminifera, adhering to the *Halophila,* of which the most common are *Sorites orbiculus* EHRENBERG, *Amphistegina lobifera* LARSEN, *A. lessonii* D'ORBIGNY and *Peneroplis planatus* FICHTEL & MOLL. However, *A. hemprichii* is the dominant species throughout the year.

Two 1.75×1.75 m plastic frames, each comprising a grid of 25 randomly numbered squares, were anchored to the bottom. An area of 225 cm^2 from each square was sampled by SCUBA diving. All *Halophila* plants with the foraminifera, which are usually strongly adhering (see Fig. 2), were hand-picked. The samples contained about 300 living individuals each, a sufficient number for statistical evaluation. A <1 cm thick layer of top sediment was collected by means of a plastic shovel (Fig. 3).

The *Halophila* leaves and the sediment were washed with water over a 125 μm mesh sieve (in order to eliminate particles smaller than *Amphisorus* juveniles) and subsequently air-dried. Foraminifera still adhering to the dry plants were retrieved by rewashing over a sieve and by gentle finger scraping of each leaf. The clean *Halophila* leaves were then dried again and weighted. The dried sediment samples were also weighted, and all living and dead *Amphisorus* were picked from among the sand grains, under the stereoscopic microscope.

Sampling was carried out approximately every two weeks, between November 1978 and November 1979. A few additional observations were made during 1980.

Amphisorus individuals, when alive, have a characteristic brownish color, due to pigmentation of their symbiotic algae. In individuals collected alive, this colour

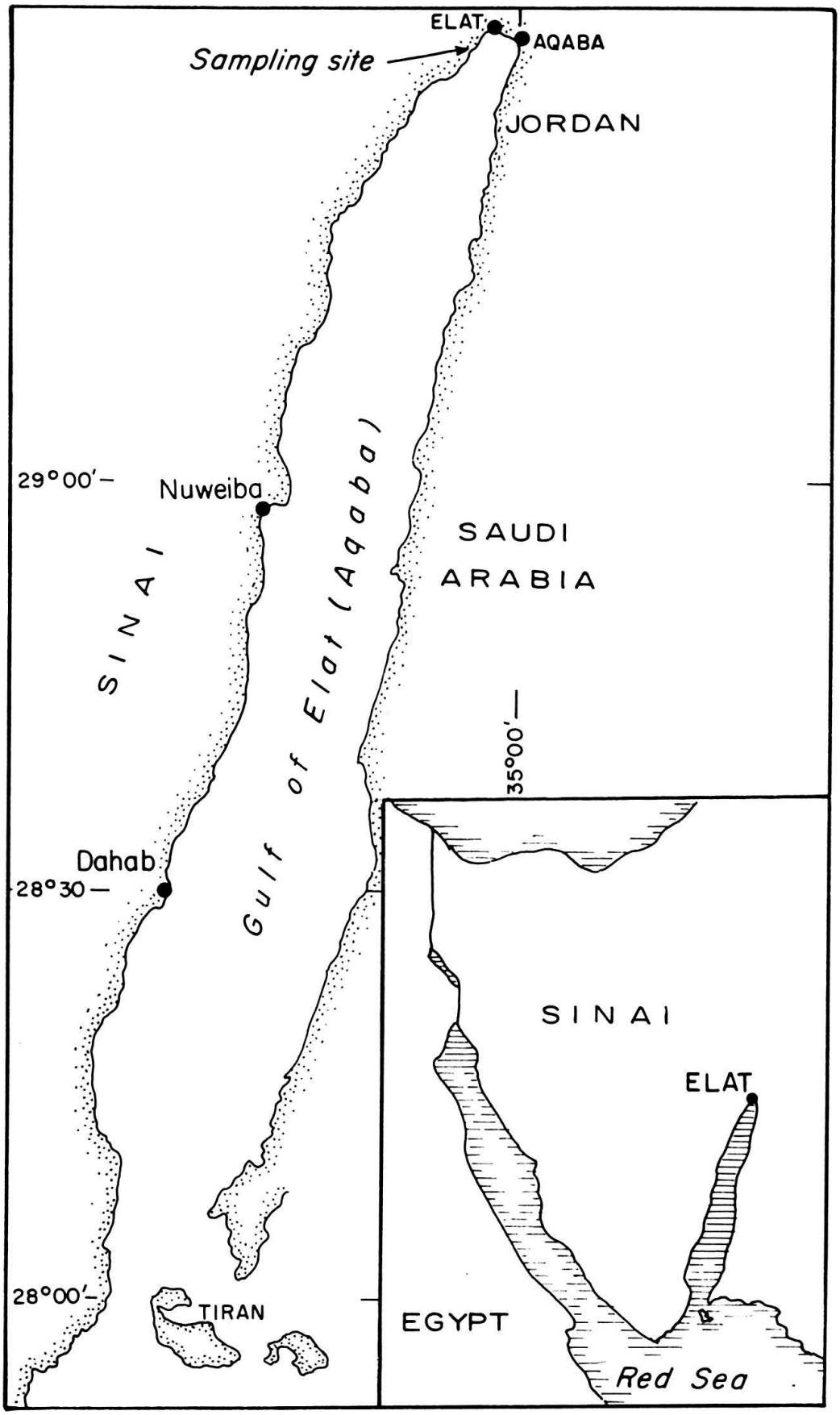

Fig. 1. Location map.

persists for a long time, even after drying. In contrast, individuals which are dead when collected, lack this pigmentation and appear whitish, being thus easily distinguished from the living ones. Thus, hereafter, specimens with the characteristic brownish color are referred to as "living", while whitish ones are considered "dead". The "Rose-Bengal" staining method for detecting living foraminifera has not been applied, as it was proved unreliable (LE CALVEZ & CESANA 1972).

The living and dead specimens of *Amphisorus* from plant and sediment samples were counted, dry-weighted and mounted on multiple cells. Their diameter was measured by means of an ocular micrometer. Microspheric specimens were counted and measured separately from the megalospheric ones.

A total of 18,609 specimens from 23 samples were measured.

Equatorial and axial sections of randomly chosen specimens were prepared for biometric analysis of the embryonal apparatus and for diameter:volume ratio measurements.

Results

Standing crop

The results of living and dead *Amphisorus* counts during a one-year period, coupled with weather data, are presented in Figure 4 (data in appendix 1, 2).

Standing crop from different *Halophila* leaves samples had to be determined on the basis of leaf surface area, rather than of sampled square area, since the *Halophila* plant density varied from one sampled square to another. Assuming that available leaf area limits the foraminiferal population density, *Halophila* leaves surface area was calculated from their dry weight, according to the method described by LARSEN (1976). For each sample a "standard standing crop" was calculated, referring to 225 cm^2 of leaf surface area. This value was plotted in Figure 4.

Standing crops from sediment samples were readily comparable: living specimens always place themselves on top of the sand grains (HOTTINGER 1977). Therefore, regardless of the thickness of the sampled sediment layer (or the weight of the total sediment sample), standing crops in different samples relate to equal surface areas.

Standing crop between November 1978 and until the reproduction period five months later were more or less stable (Fig. 4): 100–200 living individuals regularly occupied 225 cm^2 of leaf surface area, while 10–50 living individuals occurred in the top sediment. As a result of reproduction in April–May 1979 the standing crop of *Amphisorus* on *Halophila* increased by an order of magnitude to estimated value of several thousand specimens. Juveniles were found on the leaves, arranged in clusters comprising several tens to more than a hundred individuals each (compare the "Kindergarten" of *Amphistegina* described by LARSEN 1976). Living juveniles were not found in the sediment samples, and for this reason the estimated standing crop from sediment samples did not change during the reproduction period.

Juvenile *Amphisorus* specimens smaller than 500 μm in diameter could not be distinguished from juvenile *Sorites* without sectioning of each individual. For this reason data for small specimens are incomplete.

After reproduction, the new generation, the new generation's standing crop stabilized with time. Between September 1979 and November 1979 the standardized

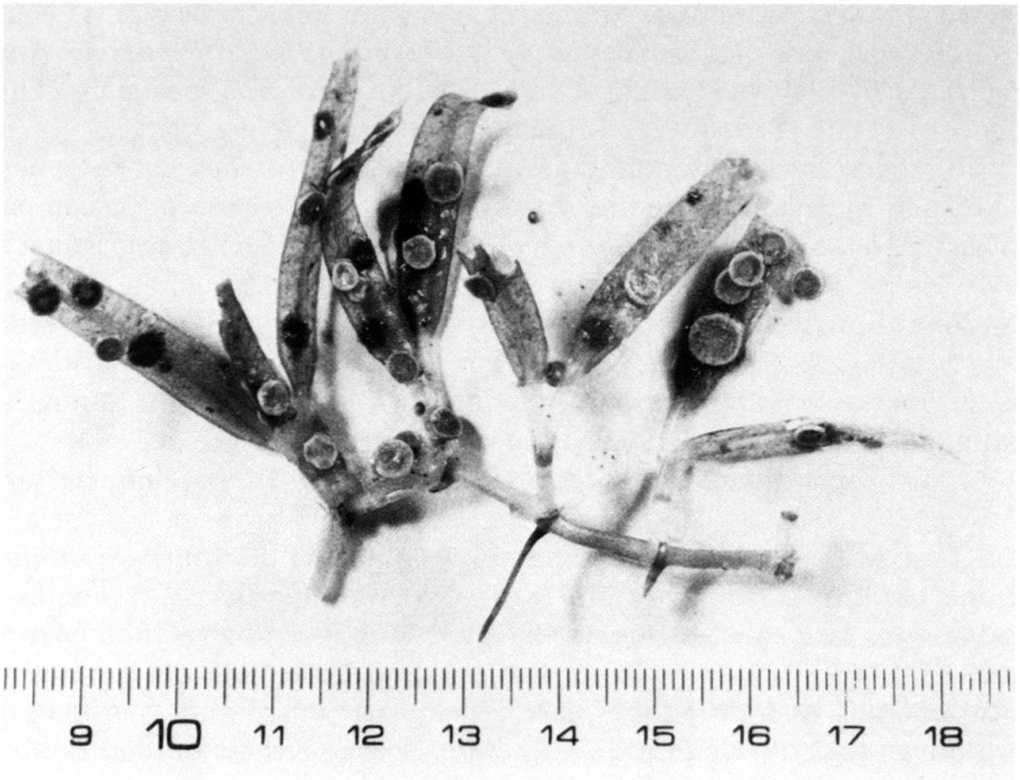

Fig. 2. Living *Amphisorus hemprichii* adhering to *Halophila* leaves. Gulf of Elat (Aqaba), Red Sea.

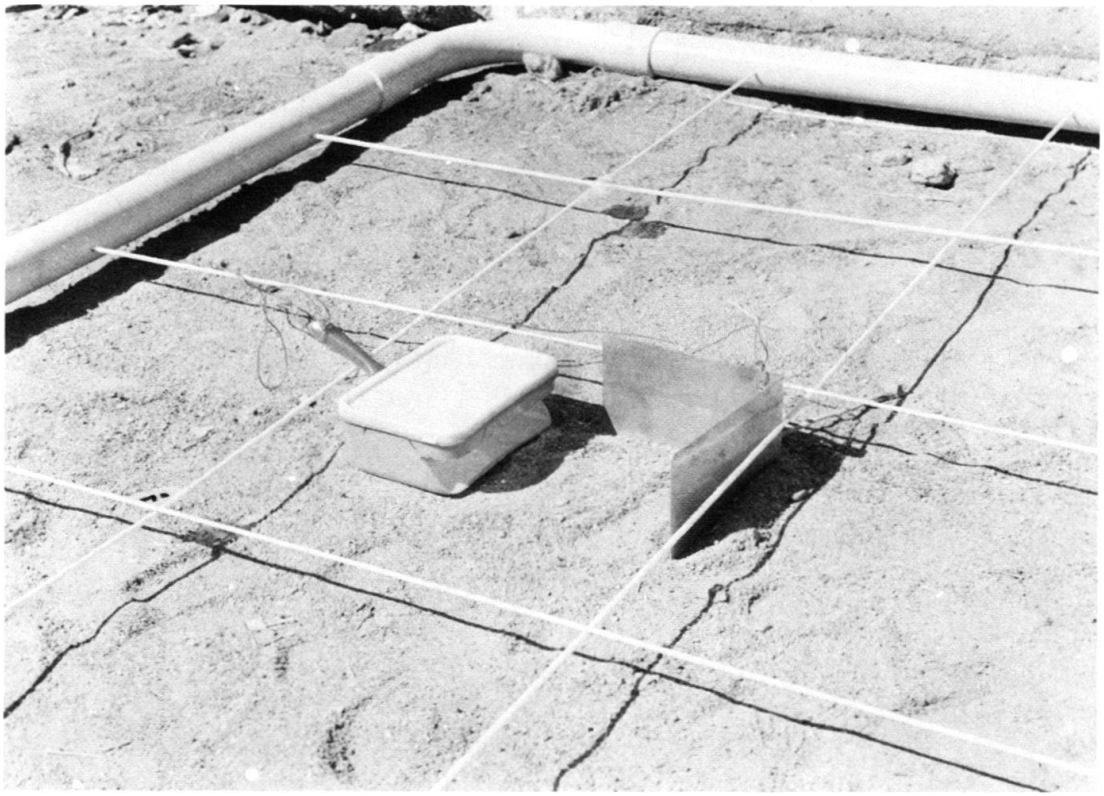

Fig. 3. Gridded frames and plastic shovel used for sampling.

standing crop ranged from 300 to 750 specimens per 225 cm^2 leaves, as compared with 100–200 specimens for November 1978 to April 1979 (appendix 1). A sample collected in April 1980 yielded the standardized value of 320 specimens. Thus, the standing crop during 1979/80 was distinctly higher than during 1978/9.

The differences in average standing crop between two consecutive generations may be related to changes in the relative frequency of *Amphisorus* as compared to the associated discoïdal soritid *Sorites orbiculus*. Both species, coexisting on the *Halophila* leaves, are similar in many ways: their general morphology is roughly the same and they apparently harbor the same dinophycean symbionts (LEUTENEGGER 1977*a*, *b*; see also MÜLLER-MERZ & LEE 1976), suggesting further similarities in their metabolic processes. Both were observed in this study to have an annual growth cycle, with only one main period of asexual reproduction per year.

Altogether it seems most likely that *Amphisorus* and *Sorites* compete for living space on the *Halophila* at the sampling site, and slight changes in ecological conditions determine which species will dominate. It appeared that *Sorites* outnumbered *Amphisorus* in samples from winter 1978/9, started to reproduce 2–3 months earlier than *Amphisorus*, and subsequently reached comparatively high standing crop (4000 specimens/225 cm^2). For unknown reason, most of the new *Sorites* generation died within two months, and during the year 1979/80, when the standing crop of *Amphisorus* was much higher than in the year before, *Sorites* occurred rather rarely in the samples. To a certain degree a sharing of the habitat was observed: *Sorites* was often found on the stalks of plants, adjusting its shell curvature to the rounded shape of the stalk; *Amphisorus*, whose test is more rigid, adheres only to flat leaf surfaces. In places where *Amphisorus* is missing (the mangroves, at <0.5 m depth, for example) *Sorites* is found on the leaves rather than on the stalks.

Size distribution of living populations

The size distribution of the sampled populations from *Halophila* leaves (megalo- and microspheric individuals) and their changes with time, are presented in Figure 5. Specimens were grouped into consecutive 0.2 mm size groups, by diameter, and the percentage frequency in each size group was plotted. A gradual shift of the mode from small to large diameter, in each size distribution curve, can be observed, starting with November 1978 and continuing until after reproduction (May–June 1979). This shift reflects an overall enlargement with time of the average individual size, in the populations.

Starting in April 1979, with the rise of temperature in the Gulf (Fig. 4) and with the renewed flourishing of the *Halophila* plants, a new generation of *Amphisorus* appeared, as indicated by high frequencies of the smallest size groups. By May–June 1979 the previous generation died out. The growth of the second generation is again indicated in the curves (Fig. 5) by a small-to-large diameter shift with time.

Additional observations on the development of the second generation took place after the termination of the one-year study period. It happened that the following winter (of 1979/80) was unusually cold and long (in comparison to the "normal" 1978/9 winter), and typical winter temperatures (21–22 °C) persisted for about two months longer than usual. In this year *Amphisorus* juveniles were encountered on

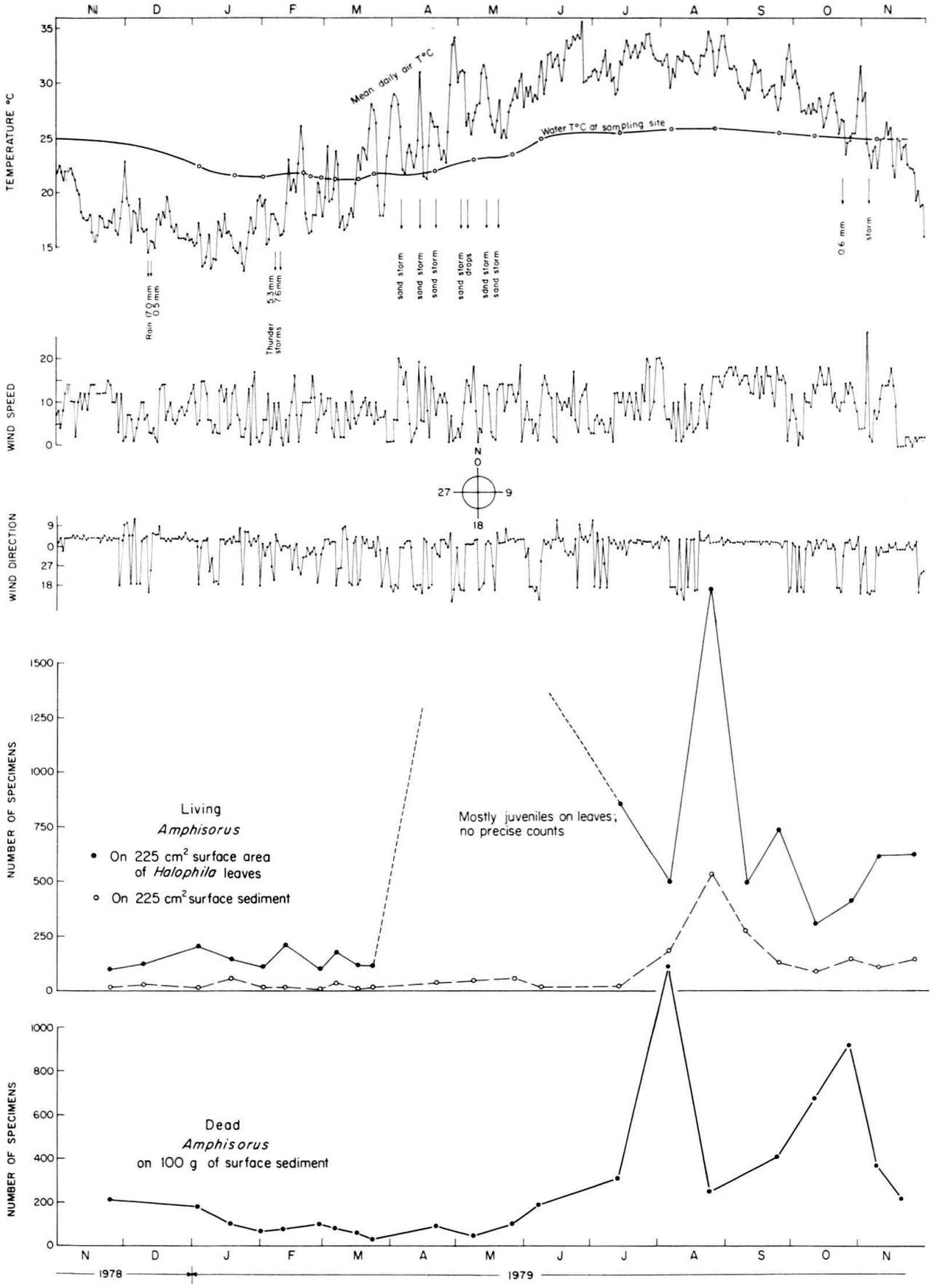

Fig. 4. Seasonal variations in standing crop and dead assemblages of *A. hemprichii* from the Gulf of Elat. Water temperature measured in situ during sampling, daily air temperature, wind speed and wind direction (in 36 major directions) during the year of study. (Data from the Meteorological station, Elat.)

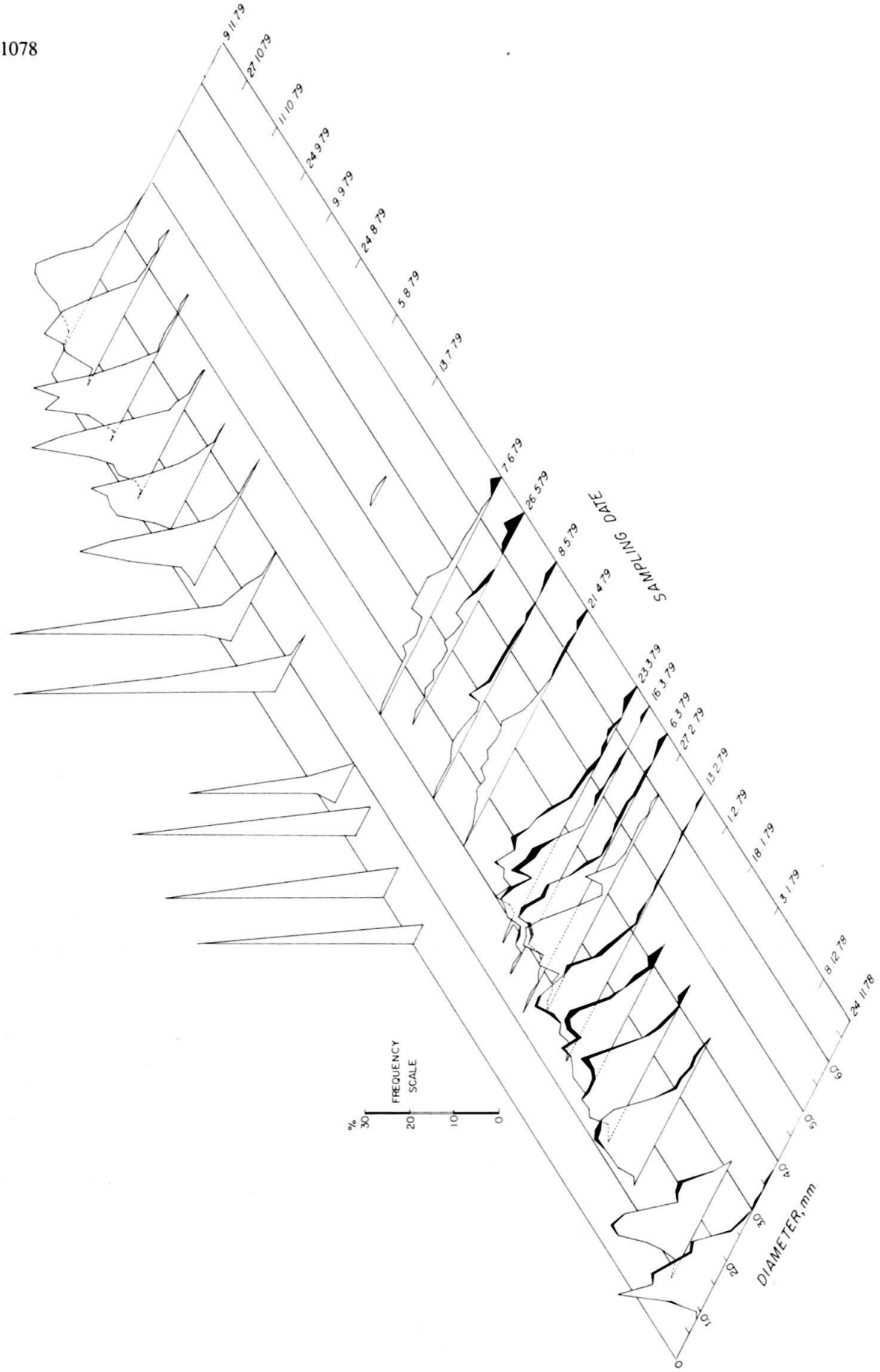

Fig. 5. Size frequency distributions of *A. hemprichii* populations over a one-year period. (Black areas = microspheric specimens.)

the leaves only in June, after water temperature went up to their normal spring values (>23 °C).

Microspheric specimens comprised only an average of 6% of the total first generation. Upon maturity they reached larger sizes than the megalospheric specimens. Microspheric individuals were, however, not detected in the second generation, between April and November 1979, although more than 3000 specimens were examined. It may be noteworthy that in August 1979 a depth profile between 0 and 40 m yielded no microspheric specimens either. Only later, in March and April 1980, such specimens were found again in the populations at the sampling site.

Living *Amphisorus* retrieved from the sediment samples comprised only 10–20% of the total standing crop (see appendix 1, 2). Their size distributions followed a pattern similar to that of the plant populations, but their standing crops were too small for statistical analysis.

Growth rates

In order to show that diameter can be regarded as a measure of test growth in *Amphisorus*, the relationship between the number of cyclical chambers, or "rings", produced at consecutive growth steps, on one hand, and test diameter, on the other, were examined in thin-sectioned individuals. Figure 6 shows examples of this relationship in three randomly chosen individuals from different samples. The diameter:number-of-rings relationship observed is close to linear, although deviations from linearity occur in earliest and in latest growth stages. Addition to diameter can, therefore, be regarded as a direct measure of growth during most of the life span of *Amphisorus*, but neither in specimens smaller than 1 mm (when the same number of growth steps is represented by relatively small addition to diameter), nor in largest ones (where the opposite is true of latest growth stages) (see also Ross' (1972) similar results on *Marginipora vertebralis*).

Figure 7 demonstrates the temporal changes of the mean diameter (in mm) of megalospheric and microspheric *Amphisorus* generations. Growth rates (Table 1), taken as addition to diameter in μm/week, were calculated as mean addition with time to average diameter, from Figure 7.

Table 1: *Average growth rates of megalo- and microspheric forms of A. hemprichii expressed in μm/week and μm/day. Values from Figure 7, as mean addition diameter, with time.*

Form	Period	Generation	Diameter increase μm/week	μm/day
Megalospheres	November 1978–February 1979	I	90.1	12.9
Megalospheres	March–June 1979	I	60.2	8.6
Megalospheres	August–November 1979	II	105.7	15.1
Microspheres	November 1978–June 1979	I	148.7	21.2

Megalospheric specimens grew steadily during winter 1978/9 (November–February), with an average diameter increase of 90 μm/week. For that period the standard deviation is also constant, indicating that the whole population was growing at about the same rate, i.e. synchronously. A change, both in growth rate and in standard deviation is observable in late February–March 1979: the average

addition to diameter slowed down to 60 μm/week, which, according to the diameter: number-of-rings relationship, means a remarkable slowdown in growth of large shells. The standard deviation increased markedly, indicating that growth of individuals was not synchronous any longer: some continued their relatively fast growth, while others slowed down, or stopped growing. Thus, in large specimens the diameter is not a measure of the biological age of the individual.

An average of 4.0 mm diameter was the typical size of adult megalospheric individuals in spring (April–May) 1979.

Microspheric forms grew at a much faster rate as compared to the megalospheric forms (Table 1). During winter 1978/9 their average growth rate reached nearly 150 μm/week. Unlike megalospheric forms, this rate did not slow down in late February–March, and as a result microspheric forms reached larger sizes (up to 10 mm in diameter).

A new generation of *Amphisorus* appeared in spring 1979. As mentioned above, at earliest growth stages the addition to diameter yields underestimates of growth

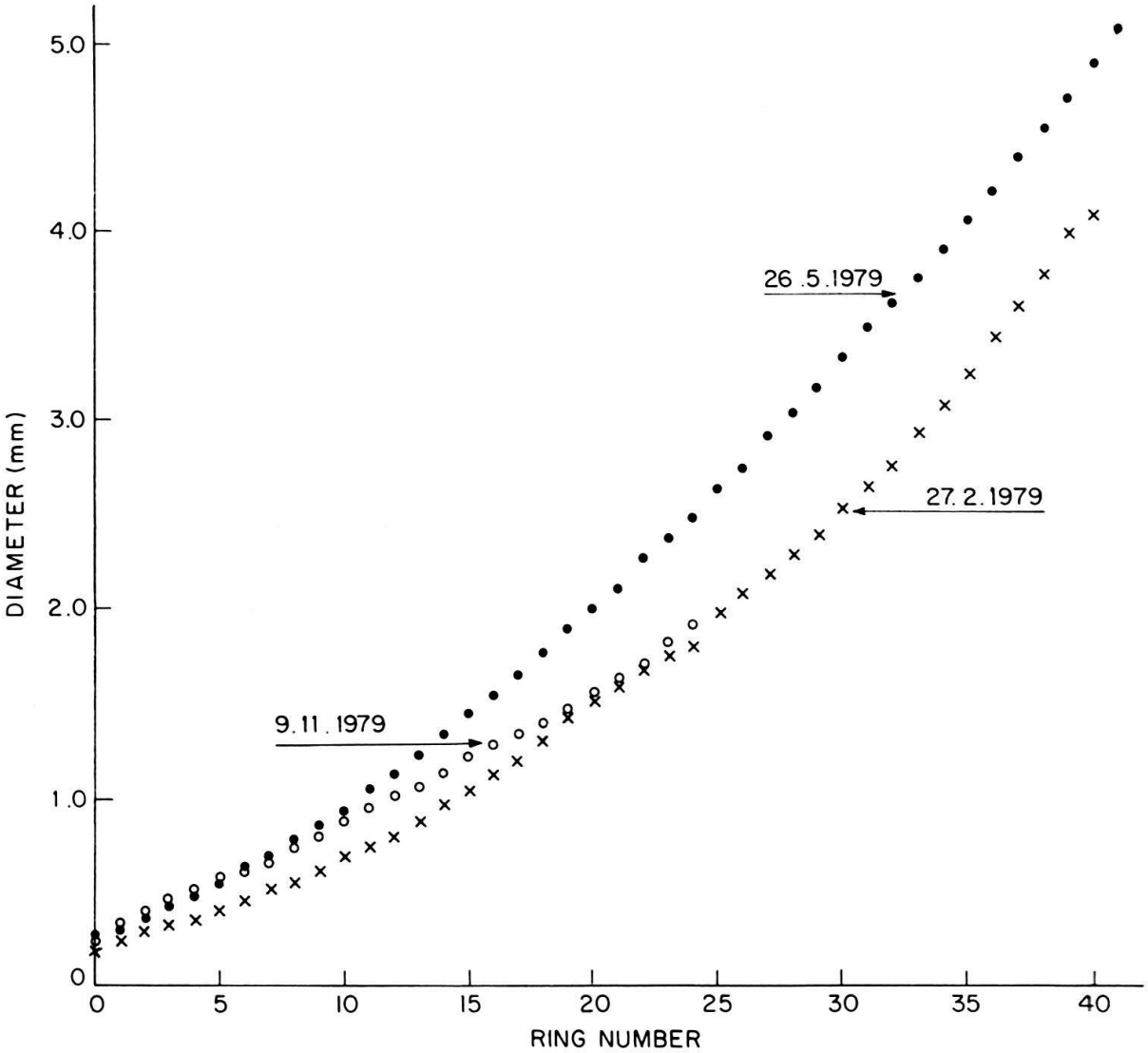

Fig. 6. Relationsship between number of rings (chambers) and diameter of test in three thin-sectioned specimens of *A. hemprichii*, belonging to two generations. Dates of collection are indicated.

rates (Fig. 6). Starting with sizes larger than 1 mm, diameter increases proportionally with growth. For this new generation, an average growth rate of 105 μm/week was observed, which is, therefore, higher than that of the former generation. The standard deviation of the second generation's mean diameter increases slowly with time, suggesting increasing variability of environmental effects on individual growth (Fig. 7).

Biometry

Differences between the two consecutive generations are expressed not only in standing crop, growth rates and occurrence of microspheric specimens, but also in measurable biocharacters of the shell. Equatorial sections were prepared from 53 specimens, chosen at random from both generations. Diameters of proloculus and flexostyle canal, of the deuteroconch, and the diameter of first five rings were measured in all sectioned individuals, and the number of chamberlets in the first

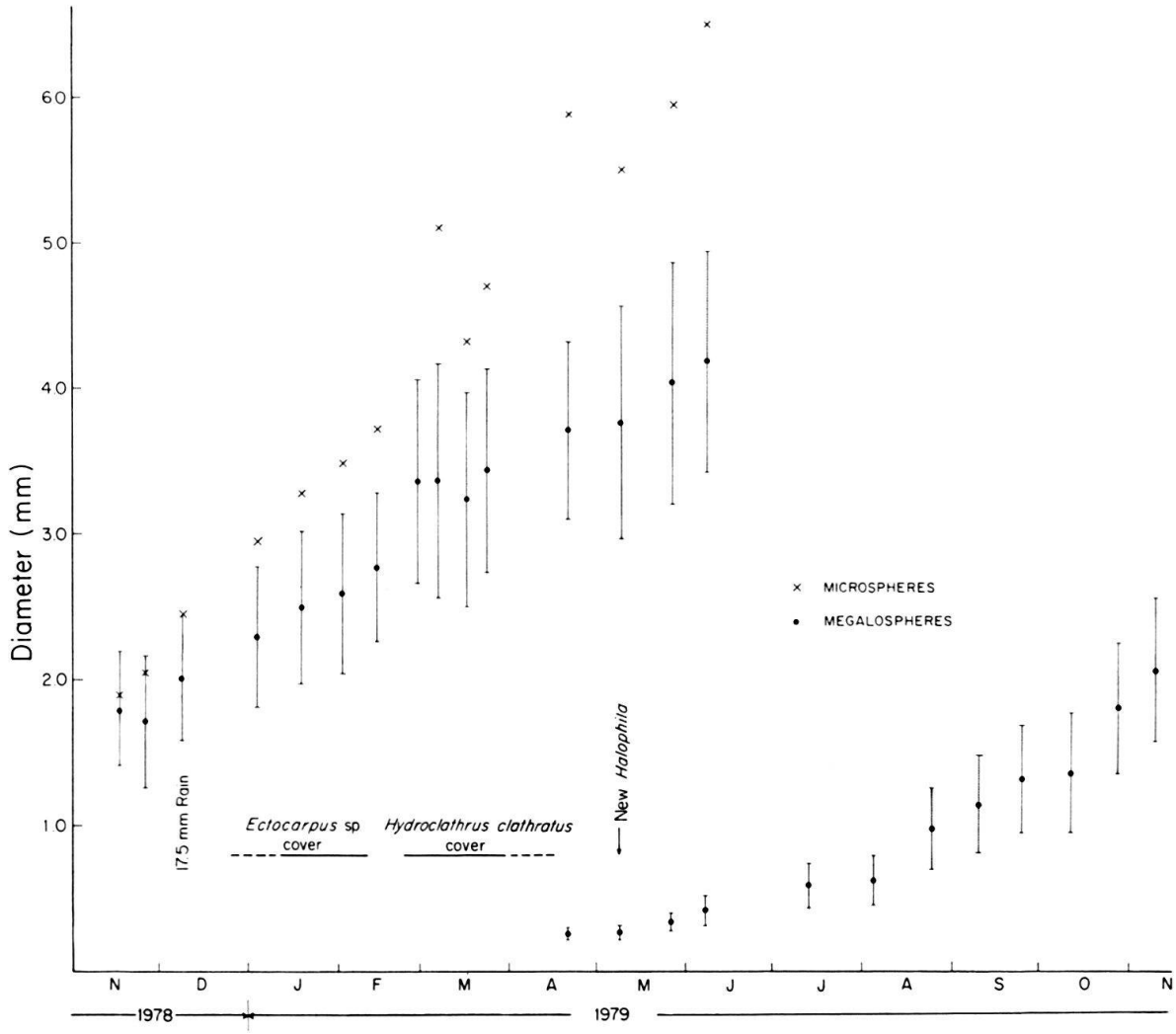

Fig. 7. Annual growth cycle of megalospheric and microspheric *A. hemprichii* generations, expressed by temporal changes in mean diameter (standard deviations of microspheric forms' mean diameter are not included, because of their low frequency in the population). Seasonal algal cover over the *Halophila* meadow is indicated.

whorl was counted (parameters are indicated in Figure 8). The results are summarized in Table 2 and show differences between the two generations in the size of the embryonal apparatus: the mean diameter of the proloculus + flexostyle canal and of the deuteroconch are larger in the second generation; the average number of chamberlets in first whorl is larger, and so is the average radius of the first five rings. Figure 9 shows the relationship between these parameters: the larger the embryonal apparatus, the more chamberlets in the first ring and the wider the following five growth steps.

Table 2: *Biocharacters of A. hemprichii embryonal apparatus, measured in thin-sectioned individuals, from two consecutive generations (two samples from each generation).*

	Generation I			Generation II		
	27.2.79	26.5.79	Average 2 samples	27.10.79	9.11.79	Average 2 samples
Number of specimens	15	12		10	16	
Average number of chamberlets in first whorl	6.3	7.4	6.7	8.3	8.6	8.5
Mean diameter in µm of proloculus + flexostyle	124.1	143.3	132.8	141.3	149.9	146.8
Mean diameter in µm of deuteroconch	80.0	100.5	89.2	112.9	113.2	113.1
Mean total diameter in µm of embryo	204.1	243.8	223.2	254.2	263.1	261.1
Mean diameter in µm of first five whorls	108.8	114.3	112.4	137.6	141.2	140.0

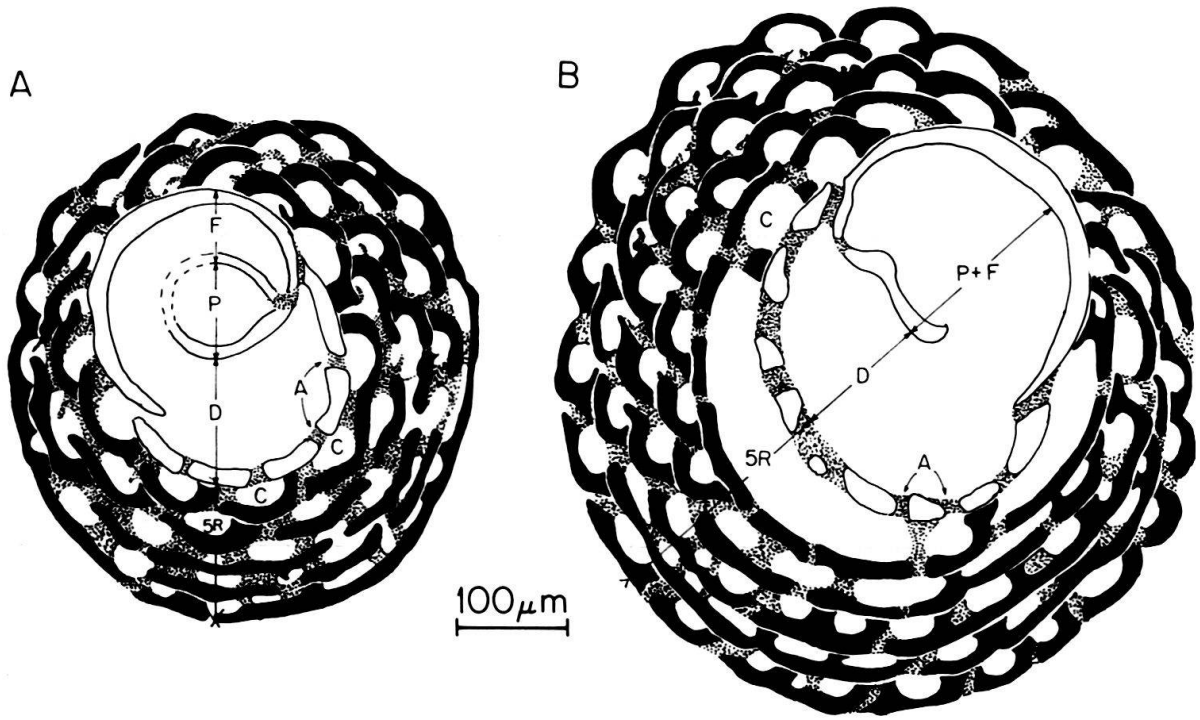

Fig. 8. Variations in dimensions of embryonal apparatus and first five rings (chambers) in megalospheric *A. hemprichii* individuals. Equatorial sections, camera lucida drawings. *A* = specimen from generation I, small embryonal apparatus, narrow first five rings. *B* = specimen from generation II, large embryonal apparatus, wide first five rings. P = proloculus; F = flexostyle; D = deuteroconch; A = aperture; C = chamberlet; 5R = five rings (width of five chambers).

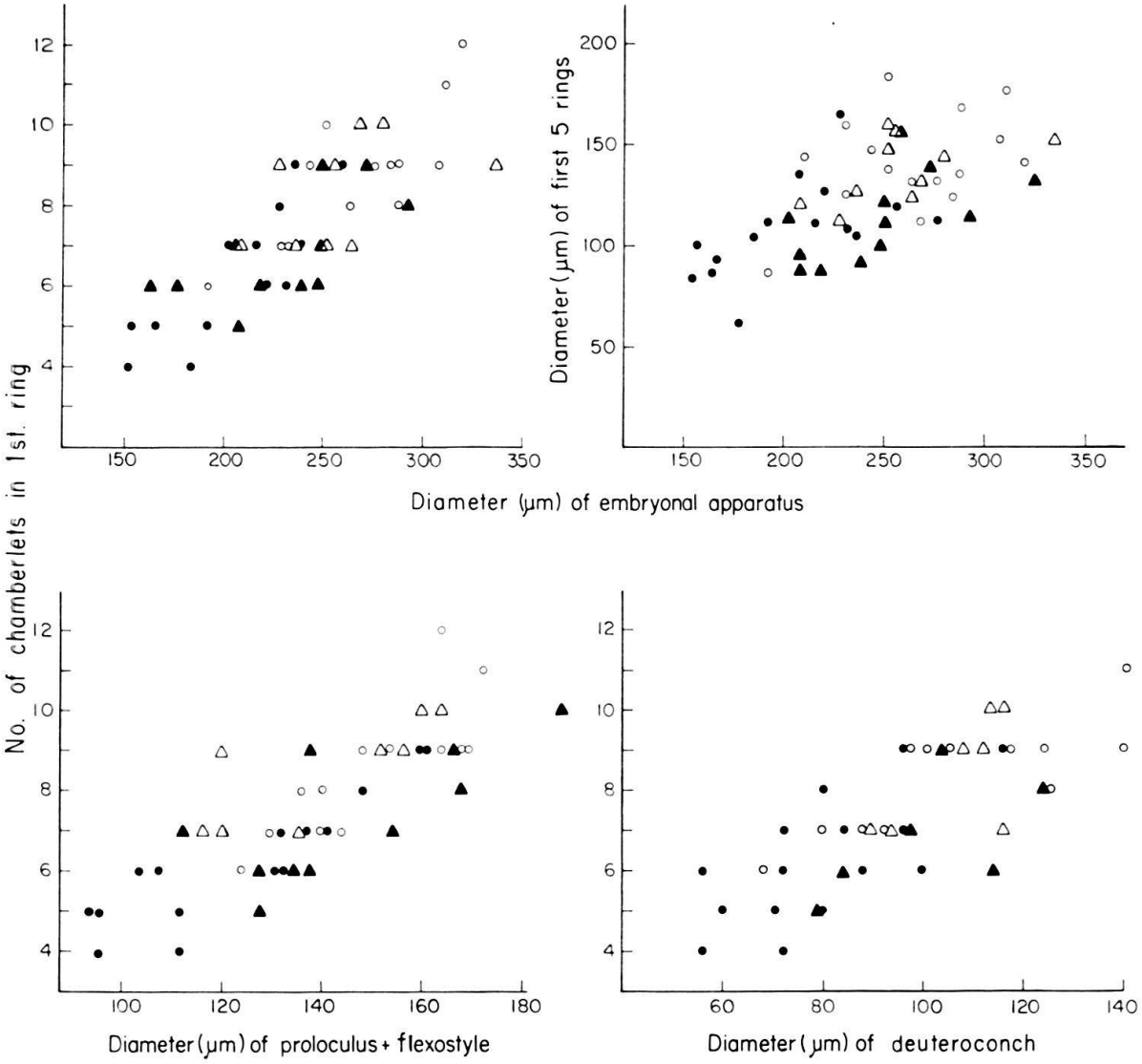

Fig. 9. Variations in dimensions of embryonal apparatus and first five rings (chambers) in megalospheric *A. hemprichii* individuals from two generations. Black marks = first generation; empty marks = second generation (specimens from four samples).

Dead assemblages

Comparison of dead counts from different sediment symples must take into account the total weight of the sample. For this reason, a standard of 100 g sediment was arbitrarily chosen, and all dead counts were fitted to this standard. The standardized values are presented in Figure 4.

Dead assemblages during November 1978 through May 1979 were rather stable, both in counts (Fig. 4 and appendix 2), and in sizes (appendix 3), suggesting that not many dead foraminifera were added to the sediment during that period. A large average diameter with a large standard deviation, both of which do not change markedly from one sample to another also characterize these dead assemblages. This indicates a stable situation in which the sediment is being continually mixed by bioturbation.

A remarkable change in the dead assemblages was noticed in August 1979, when shells of mature specimens were added to the sediment. At the same time masses of dead juvenile tests of megalospheric forms occurred in the sediment, apparently because of high mortality rate soon after their release from the mother cell (see also MULLER 1977). The time lag between the reproduction in April–May and the dead assemblage peak in August reflects the time it takes for recently dead foraminifera to fall off the leaves and may be dependent on the frequency of storms and their intensity.

Figure 10 summarizes the size-frequency distributions of all dead *Amphisorus* shells collected from 14 sediment samples over an entire year. A bimodal distribution is observable: the highest peak at a diameter of 0.5 mm is made up of juveniles which probably died shortly after their release. The second peak, at 4.5 mm, represents accumulation of shells of fully grown individuals. The largest shells (>6 mm, grouped in the largest size-group in Fig. 10) are contributed almost exclusively by microspheric forms. Medium sized shells (1.5–3.5 mm in diameter) are least frequent in the thanatocoenose and are probably a result of death due to predation, disease or cover by sand after storms (see MURRAY 1967). Shells of smallest size groups were most numerous in the sediment for a short period after their production, but during most of the year they were missing in the upper sediment layer, probably as a result of turbation by several abundant sediment dwellers such as *Holothuria* sp., *Clypeaster* sp. or the garden eel *Gorgazia*.

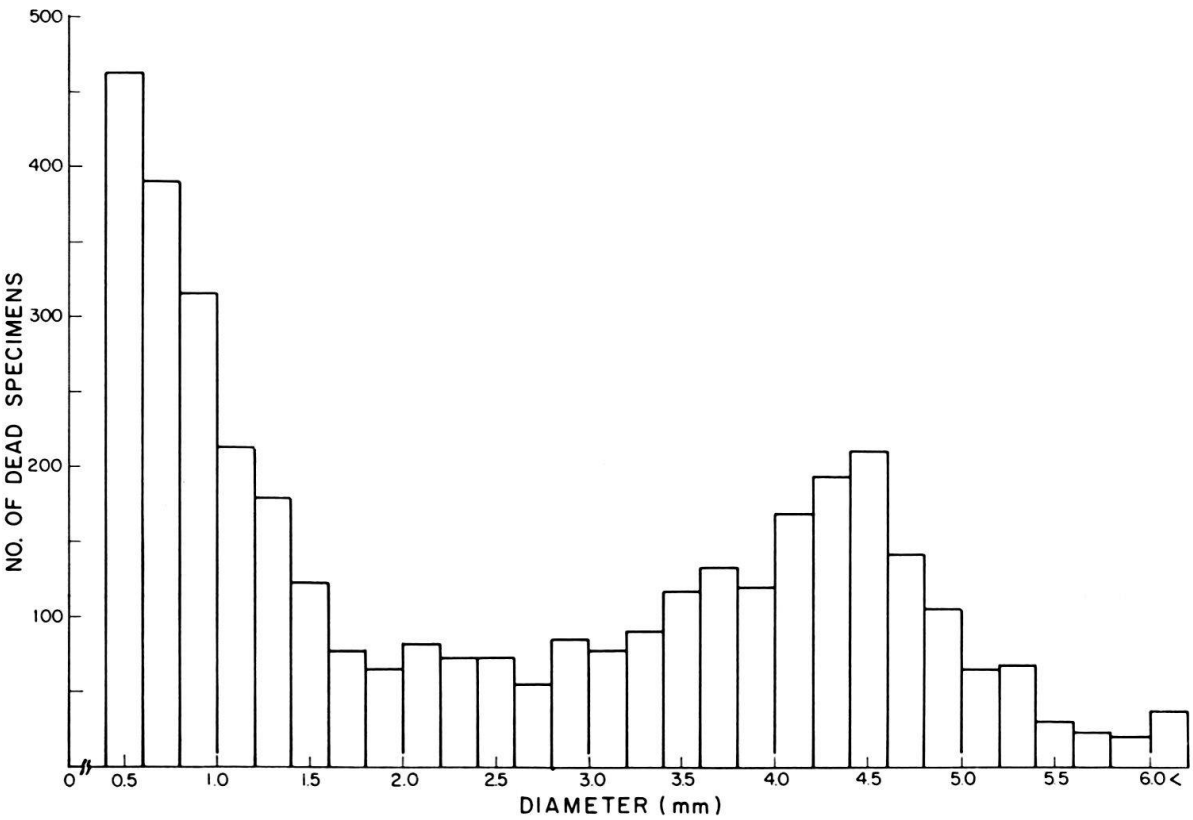

Fig. 10. Size (diameter, in mm) frequency distribution of dead *A. hemprichii* assemblages from 14 samples (after fitting specimen-frequencies to a 100-g sediment standard). Samples were collected between November 1978 and November 1979.

Carbonate production

Annual carbonate production is defined as the amount of $CaCO_3$ produced per unit area, during the course of one year. In practice, carbonate production by foraminifera is taken to be (after MULLER 1977, with slight modifications) the dry weight of carbonate shells per unit area, added to the sediment by loss of living individuals from the population. Loss of $CaCO_3$ by dissolution is neglected, bearing in mind the high pH in the Gulf of Aqaba (between 8.2 and 8.6, FRIEDMAN 1968). Carbonate production is discussed in terms of g $CaCO_3$ m^{-2} yr^{-1}.

Diameter:weight relationship (Fig. 11) was determined by calculating average individual dry weight and average individual diameter for each of the samples. Plotting diameter against weight values resulted in a third degree regression line, with extremely high coefficient of correlation ($r = 0.99$), indicating that at any stage of the life cycle, weight could be computed from diameter, according to the best-fit formula:

$$\overline{Wt} = -0.48 + 1.15\,\bar{D} - 0.44\,\bar{D}^2 + 0.13\,\bar{D}^3$$

where $\overline{Wt}$ is the average individual weight and $\bar{D}$ is average diameter. A similar relationship was obtained when samples were subdivided into size classes by means

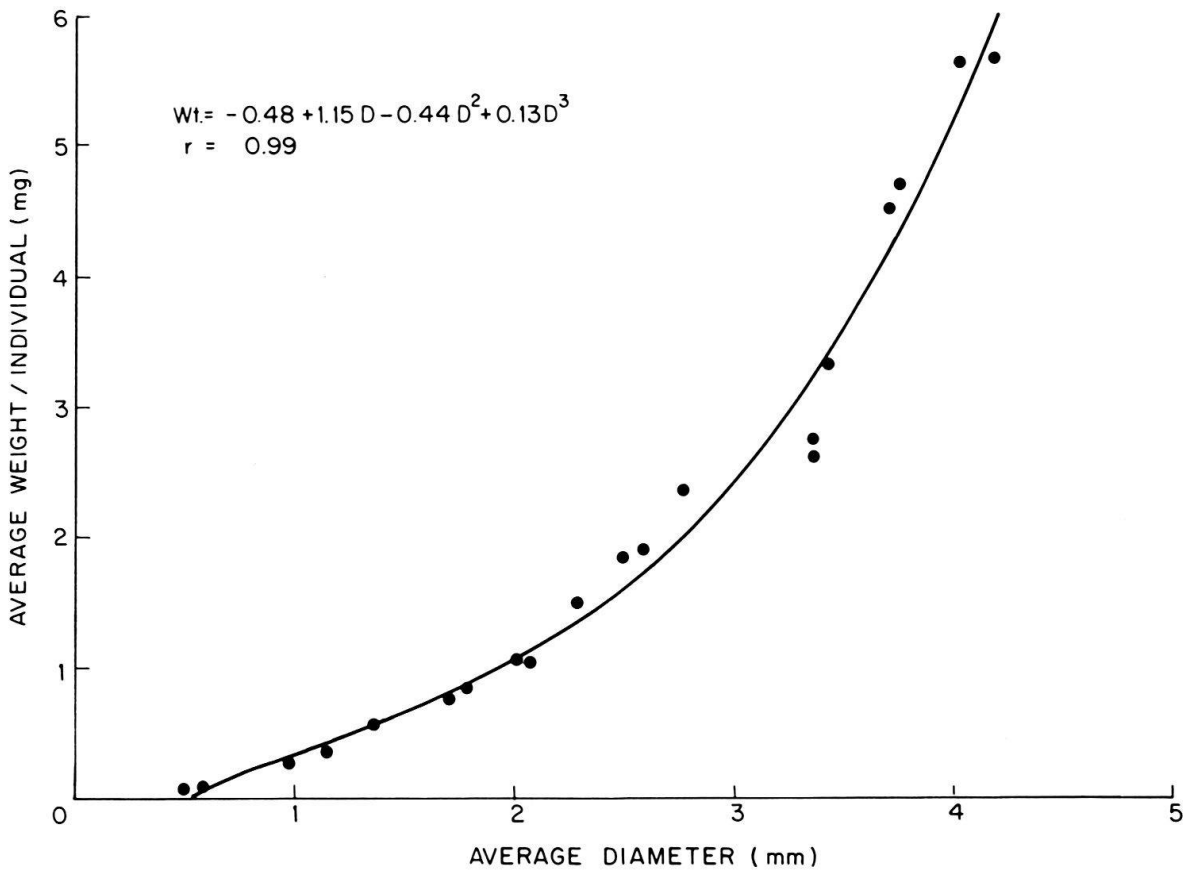

Fig. 11. Relationship between average diameter and average individual weight of *Amphisorus* in each of the samples examined. In samples where two generations co-occur, each generation was treated separately.

of standard mesh sieves and relation between weight and diameter of individuals in each single size class was computed. Therefore, the above equation can be rewritten:

$$Wt = -0.48 + 1.15\,D - 0.44\,D^2 + 0.13\,D^3$$

where Wt is individual weight and D is diameter.

Annual carbonate production (CP) was then estimated from the following formula:

$$CP = \overline{SC} \times \overline{W}_i \times R \times 44.445$$

where $\overline{SC}$ is mean standing crop, from both *Halophila* and sediment; $\overline{W}_i$ is mean weight of an average-sized, mature *Amphisorus;* R is the number of reproductions per year (= 1 for *Amphisorus*); and 44.445 is the conversion factor from 225 cm^2 sampling unit area to 1 m^2 (see also WEFER & LUTZE 1978).

Bearing in mind the more or less stable standing crop of the first generation prior to reproduction (Fig. 4), we can assume that most megalospheric individuals reached maturity, with an average size of 4 mm (Fig. 7). This size corresponds to an average weight of 5.2 mg per individual. The relative small contribution to carbonate production of infrequent medium sized shells (Fig. 9) is compensated by the relatively large contribution of the - albeit rare - "giant" microspheric specimens.

Juveniles were not taken into account, due to their short residence time in the upper sediment layers, as was indicated above. Still, a potential (as distinguished from actual) contribution to carbonate production by juveniles in the order of 5-10% of that of the adult carbonate production is most likely.

Carbonate production was calculated separately for each generation. Calculations for the first generation provide a low estimate: average standing crop was relatively low that year, and also the contribution of individuals which died prior to beginning of sampling is not included. Calculation for the second generation, on the other hand, yielded a high estimate: here, average standing crop from relatively early stages of the life was taken as the average annual standing crop. (This is true only if there was no mortality in the populations before next reproduction and is by no means an overestimate.) The average of both estimates is taken as the annual carbonate production by *Amphisorus hemprichii.* Results are presented in Table 3.

Table 3: *Mean standing crop and annual carbonate production by A. hemprichii in the Gulf of Elat.*

Generation	Mean standing crop in sampled unit area (225 cm^2)	in 1 m^2	Annual carbonate production (g $CaCO_3$ m^{-2} yr^{-1})
I	265	$1.14 \cdot 10^4$	59.3
II	1108	$4.92 \cdot 10^4$	256.1
Average for two generations	686	$3.03 \cdot 10^4$	157.7

Carbonate production by three other common species of larger foraminifera (*Sorites orbiculus, Amphistegina lessionii* and *A. lobifera*) should be borne in mind

when coming to examine the productivity of the study area. In fact, remarkable calcification rates by *Amphistegina*, in the Gulf of Elat, were demonstrated by EREZ (1978).

Discussion

Life cycle

Megalospheric individuals are known in various species of foraminifera to be either mononucleate gamonts (A2-forms) or plurinucleate schizonts (A1-forms). In such species, proloculus size is no indication of the sexual or asexual nature of the individual. LEUTENEGGER (1977*a*, *c*) has demonstrated by electron microscopy of the cytoplasm of *Amphisorus hemprichii* from the Gulf of Elat (Aqaba), that nearly all megalospheric individuals examined were plurinucleate, hence A1-schizonts. In our study, at least 94% of all specimens in each sample were megalospheric. It is therefore most possible that most of these megalospheric individuals were the product of apogamic schizogony (by A1-forms), within a paratrimorphic cycle, as suggested by LEUTENEGGER.

Dominance of the megalospheric generation is typical of at least two other Soritids: *Marginopora vertebralis* from the Great Barrier Reef (ROSS 1972) and *Sorites orbiculus* from the Gulf of Elat (LEUTENEGGER 1977*a*, *c*), and from Curaçao (KLOOS & MAC GILLAVRY 1978). It could be that a paratrimorphic cycle is typical of the family.

Production of A2-forms and consecutively gametogenesis happens apparently only rarely in *Amphisorus*, thus explaining the scarcity of microspheric (B-forms) and the seasonality in their occurrence in the populations. It is possible that gametogenesis occurs some months later than the production of A-forms by schizogony: the faster growth rate displayed by microspheric specimens (as compared to the megalospheric ones) would then compensate for the shorter growth period, and enable B-forms to attain their typical large sizes.

An additional explanation of the scarcity of microspheric individuals could be a high rate of predation upon the free floating, flagellated gamets.

Another possibility was suggested by KLOOS & MAC GILLAVRY (1978). They interpreted LEUTENEGGER's results in a new light and suggested the existence of a plurinucleate, megalospheric schizont/gamont generation (instead of A2-gamonts). Such individuals would be capable of producing both megalospheric embryos and gamets. The results obtained by us could agree with such a dual model only, if it is further assumed that in a given individual schizogony and gamogony occur at different times. This could perhaps explain the absence of microspheric individuals during part of the year and their appearance later.

Growth cycle

The present study indicates that in the Gulf of Elat, *Amphisorus hemprichii* has an annual growth cycle. Asexual reproduction, by multiple fission occurs in spring, within a short time interval (1–2 months): first, individuals grow brood chambers which can be identified morphologically by having relatively thin chamber walls and large chamber volume. Soon afterwards, masses of juveniles occur on the

Halophila leaves. These individuals grow steadily and synchronously during summer, autumn and early winter. Towards the following reproduction period, average growth rate slows down. Such slowdown in growth was described by MURRAY (1967) as a general phenomenon in Foraminifera (see also RÖTTGER 1974; RÖTTGER & SPINDLER 1976, with regard to *Heterostegina depressa*). This slowdown could also be affected, at least partially, by local environmental factors. Such a factor may be the thick filamentous, brown algal mat, which covered the *Halophila* during winter 1978/9, restricting light penetration and affecting the microenvironment of the leaves. Irregularities in growth were demonstrated also on an individual scale, in axially sectioned specimens, where volume of additional rings (chambers) fluctuates only at certain growth stages, while it is continuous in others.

The synchroneity in reproduction of *Amphisorus* individuals and, consequently, in growth of individuals during most of their life, is remarkable. Such synchroneity was also reported to occur in *Sorites orbiculus* from Curaçao (KLOOS & MAC GILLAVRY 1978) where more than 50% of all specimens collected at one date had brood chambers, of which many contained brood.

Correlation between reproduction and spring temperature rise in the Gulf may point to temperature as an environmental trigger for reproduction in *Amphisorus:* in a cold year reproduction was postponed by two months relative to a "normal" year and occurred only when water temperature reached normal spring temperature (23 °C).

Length of day and amount of sunshine do not change significantly from one year to another in the desert-enclosed Gulf of Elat, and therefore probably do not affect the difference in timing of reproduction between the years.

It is noteworthy that reproduction of the other soritid, *Sorites orbiculus,* was also delayed in the cold year by about two months relative to the "normal" year.

Life span and growth rates are known for only few tropical benthic species, mostly from laboratory growth experiments: *Marginopora vertebralis* QUOY & GAIMARD, 1-3 years (ROSS 1972); *Heterostegina depressa* D'ORBIGNY, six months (RÖTTGER 1974; RÖTTGER & SPINDLER 1976). Field observations by MULLER (1977) showed that the life span of *Calcarina spengleri* GMELIN, *Amphistegina lessonii* D'ORBIGNY and *A. lobifera* LARSEN, is 3-4 months in Palau (West Pacific), but varies with changes of physicochemical conditions and in *A. lobifera* is one year in Hawaii. LARSEN (1976) also suggested that the life span of *Amphistegina* in the Gulf of Elat is one year. *Amphisorus hemprichii* and *Sorites orbiculus* were observed in this field study to live one year.

Since there is a good correlation between diameter and weight of individual *Amphisorus* specimens, either of these parameters can be used for measuring growth rates in the population. Since these rates change with ontogenesis, diameter is not indicative of the biological age, in specimens larger than 3 mm.

Examination of dead assemblages added only little to our knowledge of the living epiphytic populations: the rate of bioturbation in the sediments far exceeded the dynamics of the populations, and the record preserved in the upper sediment layer seems to be determined mainly by grain size. Changes of size distribution with time, in the dead assemblages was in this case uniformative.

Biometry

The distinct differences between generations in biocharacteristics of the embryonal apparatus are of major importance for taxonomical considerations in larger foraminifera: the dimensions of the proloculus and of the deuteroconch serve as diagnostic taxonomic criteria for establishing phylogenetic relationships and distinguishing between related species, especially when dealing with fossil material. The existence of wide range intraspecific variability in such biocharacters must be taken into consideration.

HOTTINGER (1977) and FERMONT (1977*a*, *b*) have indicated similar intraspecific variations in shell biocharacters and dimensions of protoconch in *Heterostegina* and in *Operculina* from the Gulf of Elat. This variability was found to be partially depth-related, over a 150 m range. Considering the present study, it is obvious that variations in size of embryonal apparatus in consecutive generations of *Amphisorus* are by no means depth-related. The possibility is not excluded that populations with larger proloculi were produced by schizogony from microspheric (B-forms), 6–10 mm-in-diameter mother cells, while the smaller ones were produced by schizontic, megalospheric (A1-forms), 4–5 mm mother cells. Such a suggestion is supported by the fact that brood chambers (HOTTINGER 1977) were seen clearly – mostly in microspheric forms from generation I. These may have reproduced to form the relatively large embryos of generation II. On the other hand, microspheric specimens were extremely rare both on plants and in the sediments, during generation I. KLOOS & MAC GILLAVRY (1978) checked megalospheric *Sorites orbiculus* individuals containing brood in their brood chambers, and reported no clear difference between the mean diameter of the protoconchs of a brood and that of its parent. However, they did not check the brood of microspheric individuals. Further investigation is necessary in order to explain the variability of the embryonal apparatus size.

Carbonate production

According to MURRAY (1967), sea-floor regions having a total foraminiferal standing crop of more than 10^6 shells/m^2 must be regarded as regions of high fertility and high productivity, while regions where standing crop is less than 10^4 shells/m^2 are of extremely low productivity. Our values (for one species only!) fall inbetween these extremes, despite the low nutrient content, low biomass and low primary productivity in the Gulf of Elat (KLINKER et al. 1978; LEVANON et al. 1979). This may point to the important role of the symbiotic algae in larger, shallow water foraminifera (like *Amphisorus*) both in regard to host metabolism and carbonate production (see also ROSS 1972).

MULLER has shown that symbiont-bearing foraminifera from Palau, West-Pacific, are capable of producing carbonate at rates measured in kg $CaCO_3$ m^{-2} yr^{-1}, i.e. comparable to other major reef carbonate producers, such as corals, coralline algae and macrobenthos. In other places, e.g. Hawaii, foraminifera are secondary to corals in their carbonate production.

In the Gulf of Elat *Amphisorus* by itself, with its average addition of one growth ring per week, contributes about 160 g $CaCO_3$ m^{-2} yr^{-1}, hence, not much less than the 500 g produced by two species of *Amphistegina* in Hawaii.

Conclusions

1. In the Gulf of Elat (Aqaba), *Amphisorus hemprichii* has an annual growth cycle, with only one main reproduction period, in spring.
2. Growth of *Amphisorus* individuals, within the populations studied, proceeds synchronously and at relatively constant rates, during early and intermediate growth stages. Average growth rates slow down a few months prior to reproduction.
3. The main pattern of reproduction in *Amphisorus hemprichii* is by multiple fission, resulting in dominance of megalospheric forms.
4. The rare microspheric forms grow at faster rates, compared to the megalospheric ones, and reach larger shell sizes. During part of the year, these forms are completely absent from the epiphytic and sediment populations.
5. Because of the growth pattern exhibited by *Amphisorus*, diameter size is not indicative of biological age in large individuals (> 3 mm).
6. In the case of epiphytic foraminiferal populations, quantitative analysis of associated dead (sediment) assemblages adds little to the understanding of the living populations.
7. The annual carbonate production by *Amphisorus hemprichii* in the Gulf of Elat is estimated to be 160 g $CaCO_3$ per m^2 per year.

Appendices

Appendix 1: *Amphisorus hemprichii standing crop, in Halophila samples.*

Date of sampling	Water temp. (°C)	*Halophila* dry weight in g	Generation	Standing crop Megalospheres	Standing crop Microspheres	Standing crop Total	Standardized total standing crop, on 225 cm² leaves
16.11.1978			I	268	3	271	
24.11.1978		1.75	I	180	10	190	98
8.12.1978		2.01	I	266	4	270	122
3.1.1979	22.5	0.99	I	220	11	231	210
18.1.1979	21.7	1.85	I	267	21	288	140
1.2.1979	21.6	1.09	I	116	12	128	106
13.2.1979	21.8	1.65	I	350	34	384	209
27.2.1979	21.4	1.16	I	125	-	125	97
6.3.1979	21.3	1.50	I	276	22	298	179
16.3.1979	21.3	1.24	I	150	12	162	117
23.3.1979	21.8	1.72	I	205	14	219	115
21.4.1979	22.0	1.40	I	162	8	370	230
			II	>200	-		
8.5.1979	23.1	2.29	I	120	20	140	
			II	>200	-		

Appendix 1: Continued.

Date of sampling	Water temp. (°C)	*Halophila* dry weight in g	Generation	Standing crop Megalospheres	Standing crop Microspheres	Standing crop Total	Standardized total standing crop, on 225 cm² leaves
26.5.1979	23.6	1.86	I	43	12	203	94
			II	148	-		
7.6.1979	25.1	2.92	I	161	9	470	145
			II	>300	-		
13.7.1979	25.6	0.64	I	2	-		
			II	606	-	608	858
4.8.1979	26.0	2.42	II	1263	-	1263	470
24.8.1979	26.2	0.86	II	1783	-	1783	1855
9.9.1979	26.0	2.90	II	1554	-	1554	501
24.9.1979	25.9	0.80	II	667	-	667	750
11.10.1979	25.7	1.33	II	453	-	453	308
27.10.1979	25.5	1.43	II	658	-	658	414
9.11.1979	25.3	1.09	II	728	-	728	621
27.11.1979	25.0	2.46	II	1680	-	1680	615

Appendix 2: *Living and dead A. hemprichii in sediment samples.*

Date of sampling	Weight of sediment sample (g)	Number of dead shells collected	Standardized number of dead shells (in 100 g sediment)	Number of living megalospheric forms	Number of living microspheric forms	Total living
24.11.1978	64.26	135	210.0	18	-	18
8.12.1978		141		32	3	35
3.1.1979	46.13	84	181.7	12	2	14
18.1.1979	70.43	72	102.2	59	-	59
1.2.1979	28.56	18	70.4	19	2	21
13.2.1979	49.28	41	81.2	24	2	26
27.2.1979	68.22	72	105.5	10	-	10
6.3.1979	34.22	27	79.0	32	5	37
16.3.1979	20.13	13	64.4	8	1	9
23.3.1979	60.20	14	23.3	24	2	26
21.4.1979	80.10	71	89.0	39	2	41
8.5.1979	94.29	49	52.0	51	1	52
26.5.1979	148.22	154	104	59	10	69
7.6.1979	155.60	293	188	17	2	19
13.7.1979	105.00	325	309.5	32	1	33
4.8.1979	58.75	753	1280	188	-	188
24.8.1979	63.46	157	247	537		537
9.9.1979	76.80			259	-	259
24.9.1979	35.03	143	409	128		128
11.10.1979	57.91	395	682	94	-	94
27.10.1979	137.22	344	924	147	-	147
9.11.1979	48.90	183	374	108	-	108
27.11.1979	58.61	130	222	150	-	150

Appendix 3: *Mean diameter and standard deviation of living Amphisorus hemprichii (megalo- and microspheric forms) from Halophila samples and of dead A. hemprichii from sediment samples.*

Date of sampling	Living Megalospheric forms		Microspheric forms	Dead Total	
	$\bar{D}$ in mm	Standard deviation	$\bar{D}$ in mm	$\bar{D}$ in mm	Standard deviation
16.11.1978	1.79	0.40	1.9		
24.11.1978	1.71	0.45	2.10	3.37	1.40
8.12.1978	2.01	0.43	2.45	3.62	-
3.1.1979	2.29	0.48	2.95	3.44	1.34
18.1.1979	2.49	0.52	3.28	3.70	1.31
1.2.1979	2.59	0.55	3.48	3.38	1.24
13.2.1979	2.77	0.51	3.72	3.33	1.33
27.2.1979	3.36	0.67	-	3.82	1.37
6.3.1979	3.36	0.80	5.1	3.23	1.45
16.3.1979	3.23	0.73	4.12	3.50	1.24
23.3.1979	3.43	0.70	4.50		
21.4.1979	3.71	0.61	5.88	3.36	1.26
8.5.1979	3.76	0.80	5.50	3.33	1.20
	(0.25)		(-)		
26.5.1979	4.03	0.84	5.95	3.18	1.61
	(0.36)		(-)		
7.6.1979	4.18	0.76	6.50		
	(0.42)		(-)		
13.7.1979	(0.59)	(0.15)	(-)	3.26	1.41
4.8.1979	(0.63)		(-)		
24.8.1979	(0.98)	(0.28)	(-)	2.75	1.60
9.9.1979	(1.15)	(0.34)	(-)		
24.9.1979	(1.32)	(0.37)	(-)	1.96	
11.10.1979	(1.36)	(0.41)	(-)	2.22	1.80
27.10.1979	(1.80)	(0.45)	(-)	2.03	
9.11.1979	(2.07)	(0.49)	(-)	1.73	

Numbers in parentheses indicate diameters and standard deviations of living specimens from the second generation.

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