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# TEMPERATURE AND SALINITY LIMITS FOR GROWTH AND SURVIVAL OF SOME PLANKTONIC FORAMINIFERS IN LABORATORY CULTURES

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ABSTRACT

**The biological response to extreme temperatures and salinities is investigated in the laboratory for seven species of planktonic foraminifera: *Globigerinoides sacculifer* (Brady), *Globigerinoides ruber* (d'Orbigny), *Globigerinoides conglobatus* (Brady), *Globigerinella siphonifera* (d'Orbigny), *Orbulina universa* d'Orbigny, *Neogloboquadrina dutertrei* (d'Orbigny) and *Globorotalia menardii* (d'Orbigny). When one of the vital processes, food acceptance, growth or reproduction is inhibited by a culture variable, the absolute survival limit is reached. The measured *in vitro* temperature ranges compare well with the global temperature distribution patterns of these species, suggesting that this parameter plays a major role in their biogeographical distribution. The salinity ranges that are tolerated in laboratory cultures exceed the range encountered in modern oceans. Thus salinity does not limit the distribution of the species investigated herein.**

**In general, larger mean final shell sizes are attained and the total shell length increase is larger at optimum temperatures and salinities than at extreme culture conditions, but the differences were not always statistically significant. Marginal temperature and salinity conditions do not induce contained growth in expatriated specimens.**

**Under extreme culture conditions, the relative frequency of the different shell morphologies is altered relative to normal conditions. "Abnormal" phenotypes are more frequent under normal conditions and the "normal" morphology is found more often under extreme conditions. As opposed to previous reports, the frequency of kummerform chambers generally decreases toward extreme temperature and salinity culture conditions, indicating that kummerform phenotypes are not indicative of environmental stress. The incidence of sac-like chambers in *G. sacculifer* and the formation of spherical chambers in adult *O. universa* decrease toward extreme temperature and salinity culture conditions, demonstrating that maturation is suppressed in stress situations.**

**SEM investigations show that changes in shell porosity are correlated with treatment variables in culture. The highest porosities are attained at higher temperatures and lower salinities. Generally, an increase in total porosity is achieved by an increase of the pore area accompanied by a reduction of the pore density.**

**The *in vitro* experiments explain the changes that occurred in the Pleistocene foraminiferal assemblages from the Red Sea around 18 thousand years ago and earlier. During glacial periods, salinity approximated or even exceeded the upper thresholds that were tolerated under laboratory conditions. Under these circumstances, species disappeared from the water column. The order of disappearance as recorded in the sediments may be explained with the upper salinity limits found in this study. Also, the recurrent shifts of dominance between *G. sacculifer* and *G. ruber* are well documented for this fossil assemblage. The present experiments support the conclusion that salinity is the driving mechanism behind this phenomenon. Observations in modern oceans suggest that the fertility of the water mass is probably also an important factor behind the shifts of dominance between *G. sacculifer* and *G. ruber*.**

## INTRODUCTION

Murray (1897) recognized that foraminifera are distributed in global belts and faunal provinces. The distributional patterns recognized by various authors (e.g., Vincent and Berger, 1981 and cited literature), have been used to relate abundance to physical and chemical variables. Significant correlations of foraminiferal abundance with temperature and salinity have led to the conclusion that the biogeographical limits of planktonic foraminifera are controlled mainly by these environmental parameters (e.g., Vincent and Berger, 1981 and cited literature). The discrepancy between different authors, however, caused Cifelli (1971) to question a direct, proportional relationship between these physical parameters and species abundance data. Although the relationships between biogeographical ranges and temperature and salinity are well documented for natural populations (e.g., Bé and Hamlin, 1967; Bé and Tolderlund, 1971; Hecht, 1976a, b; Bé, 1977; Bé and Hutson, 1977), few authors considered the effects of these parameters on physiological aspects such as food acceptance, growth, lifespan, and reproduction potential (e.g., Caron and others, 1987a, b; Hemleben and others, 1987, 1988). Empirical examination of the temperature and salinity limits of living planktonic foraminifers in the laboratory will contribute to a better understanding of foraminiferal distribution patterns observed in the world's oceans.

The response of the species investigated herein to temperature and salinity tolerance experiments may help explain their behavior in marginal conditions. During the last glacial maximum, planktonic foraminifera disappeared from the fossil record of the Red Sea (e.g., Berggren and Boersma, 1969; Winter and others, 1983). Knowledge of their survival limits may help to explain the drastic faunal changes that occurred around 18,000 years ago. In addition, such data may

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also help explain the observation that some fossil assemblages (Berggren and Boersma, 1969; Risch, 1976; Oberhänsli and Hemleben, 1984) as well as some recent foraminiferal populations (Auras-Schudnagies and others, 1989) are alternatingly dominated by one or another species or by only a few species. For instance, in the tropical region around Barbados, we observed that surface waters are alternatingly dominated by *Globigerinoides ruber* (d'Orbigny) and *Globigerinoides sacculifer* (Brady).

Generally, the area in which a species can maintain itself through successive life cycles is smaller than the geographical limits that are recorded in the sediments or are indicated by plankton tows. Oceanic currents may carry planktonic foraminifera away from their natural habitats to regions where they continue to live but do not reproduce. This phenomenon is known as expatriation (e.g., Berger, 1970; Auras-Schudnagies and others, 1989). Data presented here may explain some of the observed differences between geographical distribution and the so called autochthonous range (Spoel and Pierrot-Bults, 1979). Many expatriated planktonic organisms are sturdy, have a healthy appearance, and are larger than normal (Spoel and Pierrot-Bults, 1979). Our experiments simulate expatriation and might show the response of planktonic foraminifers to this process. Furthermore, an understanding of expatriation could increase our insight into the mechanism of speciation.

Knowing the temperature and salinity ranges of planktonic foraminifera, a better estimate of the paleotemperature is feasible in some cases. If a species disappears from the sedimentary record because the temperature or salinity of the watermass exceeds the tolerance threshold, then the temperature or the salinity component contributing to the $\delta^{18}O$ of the tests can be calculated using the tolerance limits found in this study (cf. Locke and Thunell, 1988; Thunell and others, 1988).

## MATERIALS AND METHODS

Salinity and temperature tolerances were experimentally determined for *Globigerinoides sacculifer, G. ruber, G. conglobatus* (Brady), *Globigerinella siphonifera* (d'Orbigny), *Orbulina universa* d'Orbigny, *Neogloboquadrina dutertrei* (d'Orbigny) and *Globorotalia menardii* (d'Orbigny). The experiments were carried out at the Bellairs Research Institute, Barbados, between 1985 and 1987, and at the Caribbean Marine Biological Institute (CARMABI), Curaçao, in 1988.

The spinose species were collected individually in glass jars by SCUBA divers, two miles off the west coast of Barbados and Curaçao. The non-spinose species were recovered from depth by means of an open/closing net (202 $\mu$m mesh-size). In the laboratory, the foraminifera were identified and their maximum test diameters were determined. Shell lengths ranged from 110 $\mu$m (the smallest size visible to divers) to approximately 500 $\mu$m. We attempted to place specimens of similar sizes into each treatment. Culture water was obtained from the collection site. Subsequent culturing experiments were conducted at temperatures ranging between 10 to 20°C and 30 to 33°C, and at salinities between 19 to 29‰ and 41 to 50‰ in increments of 1°C and 1‰ respectively. Temperature experiments were carried out at salinities that prevailed during the time of collection. Salinity experiments were conducted at 26°C. The different salinities were obtained by dilution with distilled water or by evaporation of natural seawater at 50°C. Precipitate was never observed following evaporation. Salinities were measured with an EIL (type MC5) salinometer calibrated with a dilution series of standard seawater (IAPO Standard sea-water Service, Charlottenlund Slot, Denmark).

The experiments were carried out under white and blue fluorescent light (Philips TL 40W-55, Osram L 40W-64, light tubes) with an intensity of 60-70 $\mu E\ m^{-2}\ sec^{-1}$ in a 12:12 light/dark cycle. These light conditions closely simulate the quality and the intensity of the underwater light west of Barbados at a depth of 20 to 30 meters (Hemleben and Spindler, 1983).

All specimens were cultured individually in glass vials containing about 40 ml of filtered seawater (0.45 $\mu$m pore size Millipore filter). The foraminifers were fed a single, one-day-old *Artemia* nauplius (brine shrimp) every day, beginning on the day after collection. The individuals were examined daily using a Leitz inverted microscope. Information was recorded on chamber formation, spine length, or—in the absence of spines—on rhizopodial activity. Additional culture procedures were described by Bé and others (1977) and summarized by Hemleben and others (1988).

Over a time period of one to two days, the foraminifers were acclimated to the experimental conditions in increments. In the temperature experiments, the temperature steps never exceeded 5°C and the time intervals were approximately 6 to 12 hr. For example, if the ocean temperature at the time of collection was 26°C and an experimental temperature of 12°C was needed, the following procedure was employed. After initial inspection, the specimens were placed in a temperature bath of 21°C. After 6 hr, the culture vessels were transferred to a temperature bath of 16°C. The next morning, approximately 12 hr later, the temperature was lowered to the final experimental temperature of 12°C.

The salinity difference between consecutive steps was approximately 3‰. Since more steps were generally needed to attain the correct salinity, the time interval between transfers was reduced to 3 hr. In the salinity experiments, the specimens were transferred with a wide-mouth pipette to culture vessels containing water of the desired salinity.

The experiments were continued until the absolute extremes were reached, i.e., where either food acceptance, chamber formation, or the reproductive potential equaled zero. If no cytoplasmic streaming was observed, the individual was considered dead.

Preparations for scanning electron microscopy (SEM) were made in order to determine whether the test microstructure changes under temperature or salinity stress. Measurements of pore density and pore surface area were made on the outside of the test. A Cambridge

scanning electron microscope (type S250) was operated at 1000× (15 kV) to photograph a standard surface area (101 $\mu$m × 68 $\mu$m = 6,868 $\mu$m$^2$). The pore area was determined at the level of the pore plate, and therefore represents the true pore area. With a digitizing tablet (Summagraphics, professional) and a computer program (Tablet, Rolf Ott, Techn. DV.), the number of pores per unit surface area was counted and the total pore area was assessed.

## RESULTS

### Growth and Survival under Normal Conditions

In order to have reference values for food acceptance, growth, and survival, *Globigerinoides ruber* pink, *Globigerinella siphonifera* type I and *Orbulina universa* were cultured under conditions simulating their natural environment (L = 60 $\mu$E m$^{-2}$ sec$^{-1}$ – 70 $\mu$E m$^{-2}$ sec$^{-1}$, T = 23.5°C–26.5°C, S = 33‰–36‰). The physiological response of the species (food acceptance, chamber formation rate, longevity, and survival) to different temperatures and salinities is listed in Tables 1 to 5. Data on percentage chamber formation (CF) and the reproduction frequency (GAM) refer to all individuals in a test population. The other row entries are based on individuals that constructed at least two chambers, did not show chamber resorption, were initially smaller than 340 $\mu$m (for *G. ruber* pink <300 $\mu$m), had a final size of at least 400 $\mu$m (for *G. ruber* pink ≥ 350 $\mu$m) and underwent gametogenesis between 4 to 15 days after onset of the culture. These criteria are the same as those used by Hemleben and others (1987) who investigated the behavior of *G. sacculifer* under normal culture conditions.

TABLE 1. Response of *Globigerinoides sacculifer* to different temperatures (**A**) and salinities (**B**). CF = percentage of test group forming chambers; CF/indiv. = mean number of chambers formed per individual per day; G/indiv./d = mean growth per individual per day in $\mu$m; ST = survival time in days; GAM = percentage of the test group undergoing gametogenesis; BS/indiv. = total number of brine shrimps digested per individual; FR = feeding rate (mean number of BS digested per individual per day).

| **A** | | | | | |
|---|---|---|---|---|---|
| Temperature range (°C) | 11–12 | 13–14 | 15–16 | 31.0 | 32–33 |
| Mean temperature (°C) | 11.6 | 13.9 | 15.6 | 31.0 | 32.9 |
| N | 21 | 21 | 33 | 30 | 12 |
| Mean initial size | 425.7 | 364.3 | 321.9 | 305.7 | 377.3 |
| Mean final size | 425.7 | 420.9 | 398.3 | 539.1 | 383.3 |
| CF (%) | 0.0 | 61.9 | 63.6 | 86.7 | 8.3 |
| CF/indiv. | 0.0 | 0.7 | 0.9 | 2.0 | 0.1 |
| G/indiv./d ($\mu$m) | 0.0 | 11.2 | 14.1 | 36.1 | 3.0 |
| ST (days) | 5.3 | 5.1 | 9.2 | 6.5 | 2.0 |
| GAM (%) | 14.3 | 66.7 | 51.5 | 70.0 | 8.5 |
| BS/indiv. | 0.7 | 2.8 | 4.4 | 4.6 | 1.3 |
| FR (BS/indiv./d) | 0.1 | 0.5 | 0.6 | 0.7 | 0.7 |
| **B** | | | | | |
| Salinity range (‰) | 19–24 | 25–26 | 41–42 | 43–44 | 45–48 |
| Mean salinity (‰) | 21.4 | 25.4 | 41.8 | 43.7 | 46.5 |
| N | 24 | 39 | 42 | 20 | 26 |
| Mean initial size | 345.3 | 345.1 | 394.8 | 334.2 | 421.3 |
| Mean final size | 379.8 | 388.7 | 480.5 | 381.3 | 429.9 |
| CF (%) | 25.0 | 33.3 | 66.7 | 35.0 | 15.4 |
| CF/indiv. | 0.3 | 0.4 | 1.0 | 0.7 | 0.2 |
| G/indiv./d ($\mu$m) | 9.8 | 57.3 | 19.4 | 6.0 | 1.7 |
| ST (days) | 3.3 | 6.8 | 4.6 | 6.6 | 4.2 |
| GAM (%) | 4.2 | 17.9 | 42.9 | 35.0 | 3.8 |
| BS/indiv. | 1.6 | 4.5 | 2.8 | 3.6 | 1.9 |
| FR (BS/indiv./d) | 0.4 | 0.7 | 0.6 | 0.5 | 0.5 |

#### *Globigerinoides ruber* pink

Under normal culture conditions (S = 36‰, T = 27.8°C), only 60% of *G. ruber* accepted a one-day-old *Artemia* nauplius. The comparatively low values for the feeding rate in Table 2A (27.8°C) and Table 2B (36‰) are due to the fact that *G. ruber* is more susceptible to culture procedures than the other species. Consequently, the incidences of chamber formation and gametogenesis also remain low, 51% and 46% respectively. The mean survival time in the laboratory is 7.8 days (Table 2). The mean final shell size and total shell length increase of specimens that constructed one chamber and underwent gametogenesis under normal conditions (T = 23.5°C, S = 33‰), are 309 $\mu$m and 74 $\mu$m respectively (Table 6). The kummerform frequency under normal conditions is 88%.

#### *Globigerinella siphonifera*

Under normal conditions (S = 36‰, T = 23.5°C) and a feeding schedule of 1 BS/day, *G. siphonifera* has a mean acceptance rate of 0.8 BS/indiv./day. From a total of 102 individuals, all constructed chambers and 90% underwent gametogenesis. The survival time of these individuals was 11 days (Table 3). The mean initial and final shell size under normal culture conditions (T = 23.5°C, S = 36‰), after three chamber additions and gametogenesis, are 301 $\mu$m and 613 $\mu$m respectively (Table 6). Under normal conditions, 25% of the population constructed a kummerform last chamber.

#### *Orbulina universa*

Cultured under normal conditions (T = 25.8°C, S = 35.9‰, 1 BS/day), this species has a mean acceptance rate of 0.7 BS/indiv./day. All individuals built spherical chambers and 20% of the population secreted a second sphere, either as a diminutive chamber attached to the larger sphere, as a chamber nearly equal in size to the sphere or as an entire sphere formed concentrically around and encompassing the original sphere (Table 4). After a mean survival time of 10.2 days, 81% underwent gametogenesis (Table 4). Spiral stages with a mean initial length of 317 $\mu$m that constructed only one chamber reached a mean final sphere diameter of 503 $\mu$m (Table 6; T = 26.0°C, S = 35.6‰). Specimens that constructed two chambers reached a mean final sphere size of 527 $\mu$m (Table 6; T = 25.7°C, S = 36.0‰).

### Growth and Survival under Extreme Conditions

In order to get sufficiently large groups of specimens for statistical analysis, adjacent experimental groups (e.g., 15°C and 16°C or 41‰ and 42‰ groups) were combined. Each experimental grouping contains at least

TABLE 2. Response of *Globigerinoides ruber* to different temperatures (**A**) and salinities (**B**). For details see caption Table 1.

| **A** | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Temperature range (°C) | 11–12 | 13–14 | 15–16 | 27.8 | 30–31 | 32–33 | | |
| Mean temperature (°C) | 11.6 | 13.4 | 15.5 | 27.8 | 30.6 | 32.9 | | |
| N | 46 | 15 | 29 | 17 | 24 | 16 | | |
| Mean initial size | 391.0 | 338.8 | 257.4 | 236.1 | 321.9 | 406.3 | | |
| Mean final size | 391.0 | 349.3 | 269.1 | 423.6 | 399.8 | 408.4 | | |
| CF (%) | 0.0 | 6.7 | 10.3 | 53.0 | 62.5 | 6.3 | | |
| CF/indiv. | 0.0 | 0.1 | 0.1 | 2.4 | 1.0 | 0.1 | | |
| G/indiv./d (μm) | 0.0 | 2.3 | 1.5 | 24.0 | 11.5 | 2.3 | | |
| ST (days) | 5.3 | 3.9 | 7.7 | 7.8 | 6.2 | 0.9 | | |
| GAM (%) | 8.7 | 13.3 | 20.7 | 53.0 | 20.8 | 6.3 | | |
| BS/indiv. | 0.2 | 0.7 | 2.8 | 1.8 | 3.2 | 0.1 | | |
| FR (BS/indiv./d) | 0.0 | 0.1 | 0.3 | 0.2 | 0.5 | 0.1 | | |
| **B** | | | | | | | | |
| Salinity range (‰) | 19–22 | 23–25 | 26.0 | 36.0 | 41–42 | 43–44 | 45–48 | 49–50 |
| Mean salinity (‰) | 20.4 | 23.5 | 26.0 | 36.0 | 41.8 | 43.5 | 46.8 | 49.4 |
| N | 22 | 34 | 16 | 17 | 28 | 22 | 32 | 34 |
| Mean initial size | 327.5 | 357.6 | 263.4 | 236.1 | 361.0 | 295.9 | 326.1 | 389.6 |
| Mean final size | 331.4 | 386.0 | 345.3 | 423.6 | 403.9 | 359.4 | 348.8 | 397.5 |
| CF (%) | 18.2 | 29.4 | 50.0 | 53.0 | 39.3 | 63.6 | 37.5 | 11.8 |
| CF/indiv. | 0.2 | 0.4 | 1.1 | 2.4 | 0.8 | 1.2 | 0.4 | 0.1 |
| G/indiv./d (μm) | 1.0 | 4.8 | 8.8 | 24.0 | 10.1 | 11.4 | 4.8 | 2.8 |
| ST (days) | 3.9 | 6.9 | 10.1 | 7.8 | 4.0 | 5.8 | 5.8 | 3.4 |
| GAM (%) | 9.1 | 35.3 | 31.3 | 53.0 | 32.1 | 22.7 | 15.6 | 5.9 |
| BS/indiv. | 2.3 | 5.0 | 7.1 | 1.8 | 2.3 | 3.8 | 3.3 | 0.5 |
| FR (BS/indiv./d) | 0.6 | 0.6 | 0.7 | 0.2 | 0.5 | 0.6 | 0.6 | 0.1 |

20 individuals. The results are shown in Tables 1 to 5. For *G. conglobatus* and *G. menardii* the results are not listed separately because the number of observations is too low. However, we discuss these observations below.

Specimens that secreted chambers during the period of adaptation to an experimental temperature or salinity are not considered in the final analysis. Also specimens that underwent gametogenesis or died during this stage are excluded from analysis. The categories in Tables 1 to 5 represent the mean values of the whole experimental group. We do not distinguish between *G. siphonifera* type I and type II (Faber and others, 1988, 1989) nor between *G. ruber* white and pink. However, it should be noted that *G. siphonifera* type II and *G. ruber* white have relatively low abundances in the surface waters around Barbados and Curaçao. Figures 1 to 4 show graphically how the different statistical catagories in Tables 1 through 5 relate to temperature and salinity.

TABLE 3. Response of *Globigerinella siphonifera* to different temperatures (**A**) and salinities (**B**). For details see caption Table 1.

| **A** | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Temperature range (°C) | 10.0 | 11–12 | 13–14 | 15–16 | 23.5 | 29–30 | 31.0 | 32–33 |
| Mean temperature (°C) | 10.0 | 11.7 | 13.4 | 15.8 | 23.5 | 29.4 | 31.0 | 32.4 |
| N | 12 | 36 | 34 | 30 | 102 | 33 | 24 | 33 |
| Mean initial size | 298.1 | 416.6 | 333.9 | 358.6 | 267.5 | 388.2 | 322.0 | 407.8 |
| Mean final size | 298.2 | 440.9 | 482.7 | 492.3 | 625.4 | 519.8 | 356.3 | 407.8 |
| CF (%) | 16.7 | 36.1 | 100.0 | 73.3 | 100.0 | 81.8 | 33.3 | 0.0 |
| CF/indiv. | 0.0 | 0.4 | 2.4 | 1.8 | 3.7 | 1.5 | 0.4 | 0.0 |
| G/indiv./d (μm) | 0.0 | 5.4 | 16.1 | 19.9 | 32.5 | 13.4 | 4.6 | 0.0 |
| ST (days) | 9.8 | 6.1 | 9.5 | 6.7 | 11.0 | 10.1 | 6.4 | 0.9 |
| GAM (%) | 8.3 | 58.3 | 97.1 | 73.3 | 90.0 | 51.5 | 0.0 | 3.0 |
| BS/indiv. | 1.2 | 1.8 | 7.6 | 4.8 | 8.8 | 7.8 | 2.7 | 0.4 |
| FR (BS/indiv./d) | 0.1 | 0.3 | 0.8 | 0.7 | 0.8 | 0.8 | 0.4 | 0.4 |
| **B** | | | | | | | | |
| Salinity range (‰) | 23–26 | 27.0 | 36.0 | 41–42 | 43.0 | 44–45 | | |
| Mean salinity (‰) | 24.7 | 27.0 | 36.0 | 41.3 | 43.0 | 44.6 | | |
| N | 7 | 27 | 102 | 15 | 14 | 7 | | |
| Mean initial size | 319.4 | 332.0 | 267.5 | 310.1 | 338.6 | 363.9 | | |
| Mean final size | 356.0 | 428.8 | 625.4 | 558.9 | 441.1 | 424.0 | | |
| CF (%) | 42.9 | 89.2 | 100.0 | 86.7 | 92.9 | 42.9 | | |
| CF/indiv. | 0.6 | 1.5 | 3.7 | 2.6 | 1.6 | 0.7 | | |
| G/indiv./d (μm) | 2.7 | 11.2 | 32.5 | 26.6 | 8.8 | 6.9 | | |
| ST (days) | 7.7 | 9.4 | 11.0 | 8.9 | 12.0 | 9.4 | | |
| GAM (%) | 0.0 | 37.0 | 90.0 | 60.0 | 14.3 | 14.2 | | |
| BS/indiv. | 4.9 | 6.8 | 8.8 | 7.2 | 9.6 | 4.6 | | |
| FR (BS/indiv./d) | 0.5 | 0.7 | 0.8 | 0.8 | 0.8 | 0.4 | | |

TABLE 4. Response of *Orbulina universa* to different temperatures (A) and salinities (B). For details see caption Table 1.

| A | | | | | | | |
|---|---|---|---|---|---|---|---|
| Temperature range (°C) | 11–12 | 16.0 | 17.0 | 18.0 | 25.8 | 30–31 | 32–33 |
| Mean temperature (°C) | 11.6 | 16.0 | 17.0 | 18.0 | 25.8 | 30.7 | 32.5 |
| N | 30 | 22 | 33 | 18 | 20 | 40 | 34 |
| Mean initial size | 398.5 | 370.1 | 377.0 | 400.3 | 257.5 | 343.1 | 420.3 |
| Mean final size | 419.3 | 401.6 | 427.1 | 472.1 | 554.9 | 535.9 | 418.1 |
| CF (%) | 30.0 | 45.5 | 42.4 | 66.7 | 100.0 | 92.5 | 11.8 |
| CF/indiv. | 0.3 | 0.7 | 0.5 | 1.1 | 2.4 | 1.5 | 0.1 |
| G/indiv./d (μm) | 2.9 | 2.0 | 6.3 | 4.8 | 29.0 | 25.0 | 1.5 |
| ST (days) | 10.8 | 13.7 | 9.2 | 10.7 | 10.3 | 7.9 | 1.4 |
| GAM (%) | 20.0 | 6.3 | 24.2 | 53.3 | 81.0 | 50.0 | 0.0 |
| BS/indiv. | 1.5 | 2.7 | 4.2 | 7.3 | 6.8 | 5.5 | 0.1 |
| FR (BS/indiv./d) | 0.1 | 0.2 | 0.5 | 0.7 | 0.7 | 0.7 | 0.1 |
| **B** | | | | | | | |
| Salinity range (‰) | 19–23 | 25.0 | 26–27 | 35.9 | 41–42 | 43–44 | 46–47 |
| Mean salinity (‰) | 20.8 | 25.0 | 26.3 | 35.9 | 41.4 | 43.6 | 46.7 |
| N | 13 | 13 | 13 | 20 | 20 | 28 | 38 |
| Mean initial size | 412.4 | 392.5 | 327.2 | 257.5 | 370.9 | 362.7 | 424.7 |
| Mean final size | 412.8 | 379.0 | 366.8 | 554.9 | 486.2 | 397.2 | 423.0 |
| CF (%) | 15.4 | 15.4 | 46.2 | 100.0 | 75.0 | 35.7 | 26.3 |
| CF/indiv. | 0.2 | 0.2 | 0.5 | 2.4 | 1.1 | 0.4 | 0.3 |
| G/indiv./d (μm) | 2.0 | −2.6 | 6.9 | 29.0 | 19.2 | 4.7 | 0.0 |
| ST (days) | 3.0 | 5.2 | 5.8 | 10.3 | 6.1 | 8.1 | 12.5 |
| GAM (%) | 7.7 | 0.0 | 30.8 | 81.0 | 45.0 | 10.7 | 5.3 |
| BS/indiv. | 1.5 | 2.6 | 3.4 | 6.8 | 4.2 | 5.0 | 1.0 |
| FR (BS/indiv./d) | 0.7 | 0.5 | 0.6 | 0.7 | 0.7 | 0.6 | 0.1 |

## GENERAL OBSERVATIONS

In all spinose species studied, the same general responses to extreme temperatures and salinities are observed. The temperatures and salinities at which these phenomena first appear are not the same for all species and gradually become more conspicuous towards the limits of existence of a species.

At extreme high temperatures, the rhizopodia are incapable of holding prey items. They appear to lose their "sticky" character. At extreme low temperatures, the spines become fragile and tend to break when the prey try to escape. Under conditions of extreme low temperature, the spines do not regenerate and the foraminifers are unable to hold prey with their rhizopodial network without the support of spines. This phenomenon is especially obvious in *G. siphonifera.*

At extreme high salinities the rhizopods are retracted, probably as an osmotic response. In this situation, the individuals are incapable of catching prey. All spinose species under investigation gradually resorb the

TABLE 5. Response of *Neogloboquadrina dutertrei* to different temperatures (A) and salinities (B). For details see caption Table 1.

| A | | | | | | | |
|---|---|---|---|---|---|---|---|
| Temperature range (°C) | 13 | 14–15 | 16 | 17–19 | 26–30 | 31–32 | 33 |
| Mean temperature (°C) | 13.0 | 14.4 | 16.0 | 17.9 | 28.6 | 31.5 | 33.0 |
| N | 6 | 19 | 16 | 9 | 14 | 20 | 10 |
| Mean initial size | 433.8 | 307.6 | 283.8 | 285.6 | 268.7 | 340.4 | 409.3 |
| Mean final size | 433.8 | 325.9 | 319.7 | 295.9 | 292.4 | 347.7 | 422.2 |
| CF (%) | 0.0 | 11.0 | 19.0 | 11.0 | 29.0 | 10.0 | 10.0 |
| CF/indiv. | 0.0 | 0.1 | 0.2 | 0.1 | 0.3 | 0.1 | 0.1 |
| G/indiv./d (μm) | 0.0 | 3.9 | 4.6 | 2.6 | 4.0 | 1.8 | 25.8 |
| ST (days) | 2.2 | 4.7 | 7.8 | 3.9 | 5.9 | 4.0 | 0.5 |
| GAM (%) | 33.0 | 74.0 | 81.0 | 44.0 | 7.0 | 10.0 | 10.0 |
| BS/indiv. | 0.2 | 4.1 | 5.0 | 2.1 | 5.0 | 3.7 | 0.0 |
| FR (BS/indiv./d) | 0.1 | 0.9 | 0.6 | 0.5 | 0.9 | 0.9 | 0.0 |
| **B** | | | | | | | |
| Salinity range (‰) | 23 | 25 | 27–219 | 44–45 | 46 | 47 | |
| Mean salinity (‰) | 23.0 | 25.0 | 27.3 | 44.7 | 46.0 | 47.0 | |
| N | 5 | 24 | 13 | 18 | 13 | 9 | |
| Mean initial size | 349.0 | 319.1 | 296.2 | 326.0 | 342.2 | 477.0 | |
| Mean final size | 348.8 | 316.5 | 304.2 | 346.7 | 347.5 | 477.0 | |
| CF (%) | 0.0 | 8.0 | 15.0 | 6.0 | 8.0 | 0.0 | |
| CF/indiv. | 0.0 | 0.1 | 0.2 | 0.1 | 0.1 | 0.0 | |
| G/indiv./d (μm) | 0.0 | −0.3 | 1.2 | 2.7 | 0.9 | 0.0 | |
| ST (days) | 5.0 | 9.9 | 6.5 | 7.7 | 5.7 | 2.2 | |
| GAM (%) | 0.0 | 33.0 | 38.0 | 33.0 | 31.0 | 11.0 | |
| BS/indiv. | 3.4 | 8.0 | 4.5 | 5.8 | 4.8 | 0.1 | |
| FR (BS/indiv./d) | 0.7 | 0.8 | 0.7 | 0.8 | 0.8 | 0.1 | |

TABLE 6. Mean initial size, mean final size and mean growth (all in μm) at extreme and normal temperatures and salinities for specimens that underwent gametogenesis (except *Orbulina universa*) and constructed one chamber. The temperature and salinity range as well as the number of observations (in brackets) is indicated. [1]Two chambers built in culture; [2]three chambers built in culture. The values for *Globigerinoides sacculifer* cultured under normal conditions are based on our data base (Hemleben and others, 1987).

| Species | | Temperature | | | Salinity | | |
|---|---|---|---|---|---|---|---|
| | | Low (n) | Normal (n) | High (n) | Low (n) | Normal (n) | High (n) |
| *G. sacculifer* | range | 14–16 (17) | 26.5 (105) | 31 (3) | 23–26 (5) | 34.8 (154) | 41–47 (11) |
| | init. size | 384 | 402 | 496 | 388 | 402 | 399 |
| | final size | 469 | 525 | 673 | 486 | 525 | 463 |
| | growth | 85 | 123 | 176 | 98 | 123 | 64 |
| *G. sacculifer*[1] | range | 14–16 (6) | 26.5 (89) | 31 (8) | | 34.4 (161) | |
| | init. size | 315 | 332 | 342 | – | 320 | – |
| | final size | 467 | 593 | 581 | – | 579 | – |
| | growth | 152 | 261 | 239 | – | 259 | – |
| *G. ruber* | range | | 23.5 (16) | 30–31 (4) | 22–26 (6) | 33 (16) | 41–45 (7) |
| | init. size | – | 235 | 360 | 346 | 235 | 315 |
| | final size | – | 309 | 449 | 434 | 309 | 360 |
| | growth | – | 74 | 89 | 88 | 74 | 45 |
| *G. siphonifera*[2] | range | 13–16 (20) | 23.5 (46) | 29 (4) | 27 (3) | 36 (46) | 41–45 (8) |
| | init. size | 320 | 301 | 267 | 285 | 301 | 331 |
| | final size | 506 | 613 | 544 | 497 | 613 | 601 |
| | growth | 186 | 312 | 277 | 212 | 312 | 270 |
| *O. universa* | range | 12–18 (29) | 26.0 (131) | 30–31 (19) | 23–27 (6) | 35.6 (131) | 41–47 (25) |
| | init. size | 396 | 317 | 393 | 399 | 317 | 391 |
| | final size | 503 | 503 | 567 | 491 | 503 | 519 |
| | growth | 107 | 186 | 174 | 92 | 186 | 127 |
| *O. universa*[1] | range | 16–18 (7) | 25.7 (21) | 30–31 (7) | | 36.0 (21) | |
| | init. size | 351 | 276 | 309 | – | 276 | – |
| | final size | 571 | 527 | 529 | – | 527 | – |
| | growth | 221 | 251 | 220 | – | 251 | |

last chamber in culture media having a high salinity. In the case of *O. universa,* resorption of the final spherical chamber, a spiral chamber or even the whole spiral stage is observed (Pl. 1, Figs. 1–3). At low salinity, the behavior does not deviate from the normal pattern.

## TEMPERATURE AND SALINITY LIMITS

The tolerance ranges are related to viability and reproductive capacity. Positive criteria are successful feeding (FR), chamber formation (CF), and gametogenesis (GAM). The temperature and salinity limits are summarized in Table 7A–B and Figure 5.

### *Globigerinoides sacculifer* (Table 1)

Although chamber formation does not occur below 14°C, food is accepted at a temperature as low as 11°C. However, gametogenesis is rarely observed at this temperature. Brine shrimps are accepted and subsequent chamber formation occurs at temperatures up to 33°C. However, no reproductive activity is observed above 32°C (Table 1A). The temperature tolerance range is thus 14–32°C (Table 7A, Fig. 5).

Digestion of brine shrimps and chamber formation occur in cultures with a salinity as low as 22‰. Gametogenesis, however, is not observed below 24‰. In cultures with high salinity, gametogenesis and chamber formation occur up to 47‰ whereas brine shrimp are accepted up to 48‰ (Table 1B). The salinity tolerance range is thus 24–47‰ (Table 7B, Fig. 5).

### *Globigerinoides ruber* (Table 2)

Although gametogenesis is observed and *Artemia* are still accepted at 12°C, chamber formation does not occur below 14°C. Up to 31°C, brine shrimp are readily accepted and chamber formation and gametogenesis are frequently observed. At 32°C, brine shrimp are rarely accepted and only one individual constructed a chamber and underwent gametogenesis. Gametes are produced up to 33°C (Table 2A). The temperature tolerance range is thus 14–32°C (Table 7A, Fig. 5).

Although brine shrimps are accepted and digested in a culture medium having a salinity as low as 19‰, neither calcification nor gametogenesis are observed below 22‰. At 49‰, nauplii are still accepted, calcification occurs and gametogenesis is observed. *G. ruber* does not survive a salinity increase to 50‰ (Table 2B). The salinity tolerance range is thus 22–49‰ (Table 7B, Fig. 5).

### *Globigerinoides conglobatus*

Occasionally, *G. conglobatus* was collected by SCUBA divers. A total of 42 individuals were maintained parallel to the primary experimental groups. At 13°C, four *G. conglobatus* were cultured. All digested brine shrimp and underwent gametogenesis, and two individuals formed chambers. Consequently, the lower temperature limit is below 13°C. Food acceptance, chamber formation and gametogenesis are observed at 30°C. One individual, cultured at 31°C, accepted food

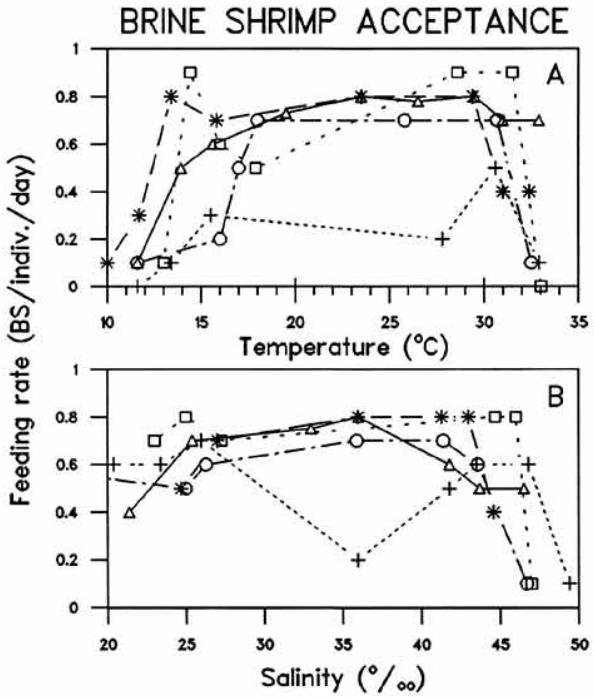



FIGURE 1. Feeding rate as a function of temperature (A) and salinity (B) for *Globigerinoides sacculifer* (△), *Globigerinoides ruber* (+), *Globigerinella siphonifera* (*), *Orbulina universa* (○) and *Neogloboquadrina dutertrei* (□). Values for 33‰ and 36‰ and between 19.5–29.5°C for *Globigerinoides sacculifer* from Hemleben and others (1987).

and formed a chamber but did not undergo gametogenesis. The upper temperature limit for this species is 30°C.

At 27‰, food is accepted, chambers are formed and gametes are produced (n = 8). In contrast, at 25‰, food is accepted and chambers are formed but gametogenesis is not observed (n = 5). At 40‰ (n = 2) and at 45‰ (n = 1), feeding and chamber formation are normal but gametogenesis is not observed. The lower salinity limit for *G. conglobatus* is below 27‰ and the upper salinity limit may be higher than 40‰ (Table 7B, Fig. 5).

*Globigerinella siphonifera* (Table 3)

At 9°C, brine shrimps are accepted but chambers are not formed and gametogenesis is not observed. Although chambers are constructed at 10°C, mean growth is negligible and only one mature individual produced gametes. The lower temperature limit for this species is thus 11°C. *Artemia* are accepted up to 33°C but chamber formation ceases at 31°C. Gametogenesis is observed only once above 30°C (n = 57). However, this individual was already mature and underwent gametogenesis after less than a day (Table 3A). Hence, the upper temperature limit is 30°C.

*Artemia* are accepted and chambers are constructed down to salinities of 26‰. However, *G. siphonifera*

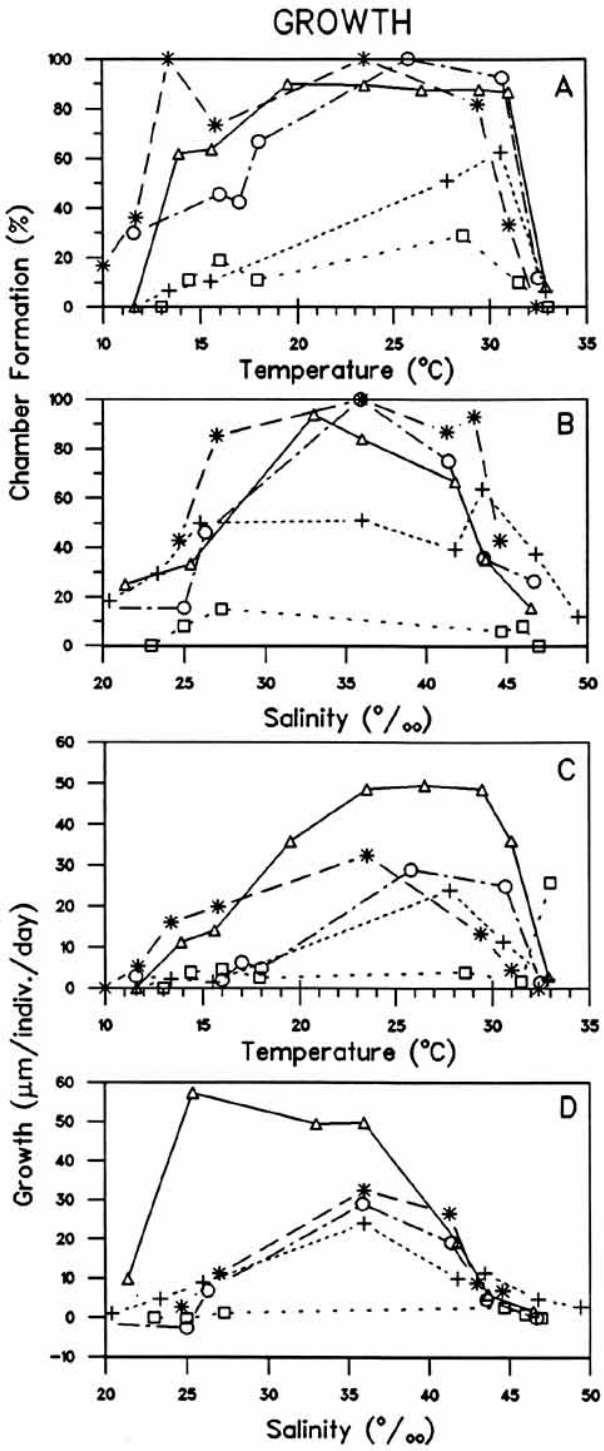



FIGURE 2. Chamber formation in % as a function of temperature (A) and salinity (B). Growth in µm/day as a function of temperature (C) and salinity (D). For explanation see Figure 1.

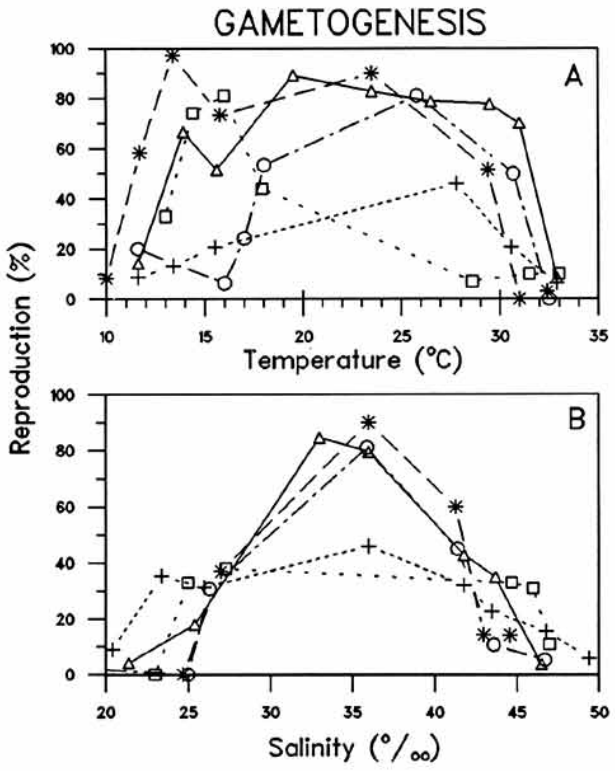



FIGURE 3. Reproduction frequency as a function of temperature (A) and salinity (B). For explanation see Figure 1.

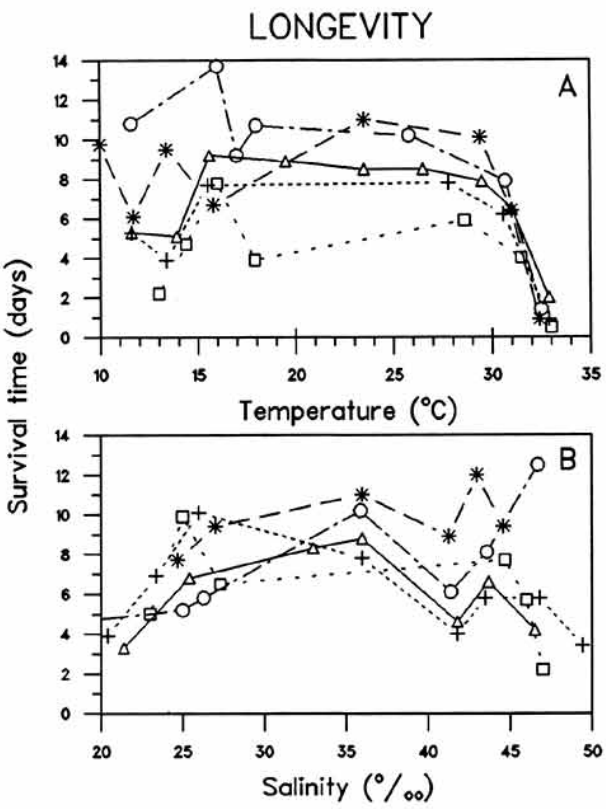



FIGURE 4. Longevity as a function of temperature (A) and salinity (B). For explanation see Figure 1.

does not reproduce below 27‰. In cultures up to 45‰, brine shrimp are accepted, chambers are constructed and gametogenesis is observed. Few individuals survived the transfer to 46‰ and those that did, would not accept *Artemia*, grow chambers or reproduce (Table 3B). The salinity tolerance range is thus 27–45‰ (Table 7B, Fig. 5).

*Orbulina universa* (Table 4)

Brine shrimp are accepted at 11°C while chamber formation and gametogenesis only occur down to 12°C. The upper temperature limit where growth, food acceptance and gametogenesis were observed, is 31°C. In the range of 30 to 31°C, the incidence of gametogenesis is still 50%, whereas between 32°C and 33°C, gametogenesis is not observed (n = 34). In this latter temperature range, however, food is accepted and chambers are formed (0.1 BS/day and 12% respectively; Table 4A). The temperature tolerance range is thus 12–31°C (Table 7A, Fig. 5).

Food acceptance, chamber formation, and gametogenesis occur at salinities as low as 23‰. Below 23‰ *Orbulina* did not survive. Food acceptance and chamber formation are observed at salinities of 47‰ although chamber formation does not result in measurable growth. Zero growth is due to the resorption of chambers or even a whole spiral stage. Gametogenesis is not observed above 46‰ (Table 4B). The salinity tolerance range is thus 23–46‰ (Table 7B, Fig. 5).

*Neogloboquadrina dutertrei* (Table 5)

We cultured 177 individuals of *N. dutertrei* at 11 different temperatures and eight different salinities. Feeding and gametogenesis is observed at 13°C but chamber formation does not occur below 15°C. Cham-

TABLE 7. Temperature (A) and salinity (B) limits and optima (in °C and ‰ respectively). The optima are calculated as the median between the survival limits and on the bases of $Q_{10}$ values where data were available.

| | | Optimum | | |
|---|---|---|---|---|
| | Min. | Mean | $Q_{10}$ | Max |
| **A** | | | | |
| *G. sacculifer* | 14 | 23.0 | 26.5 | 32 |
| *G. ruber* | 14 | 23.0 | 26.5 | 32 |
| *G. conglobatus* | <13 | — | — | 30 |
| *G. siphonifera* | 11 | 20.5 | — | 30 |
| *O. universa* | 12 | 21.5 | 23.5 | 31 |
| *N. dutertrei* | 15 | 23.5 | — | 32 |
| *G. menardii* | <16 | — | — | <31 |
| **B** | | | | |
| *G. sacculifer* | 24 | 35.5 | — | 47 |
| *G. ruber* | 22 | 35.5 | — | 49 |
| *G. conglobatus* | <27 | — | — | >40 |
| *G. siphonifera* | 27 | 36.0 | — | 45 |
| *O. universa* | 23 | 34.5 | — | 46 |
| *N. dutertrei* | 25 | 35.5 | — | 46 |
| *G. menardii* | <27 | — | — | <44 |

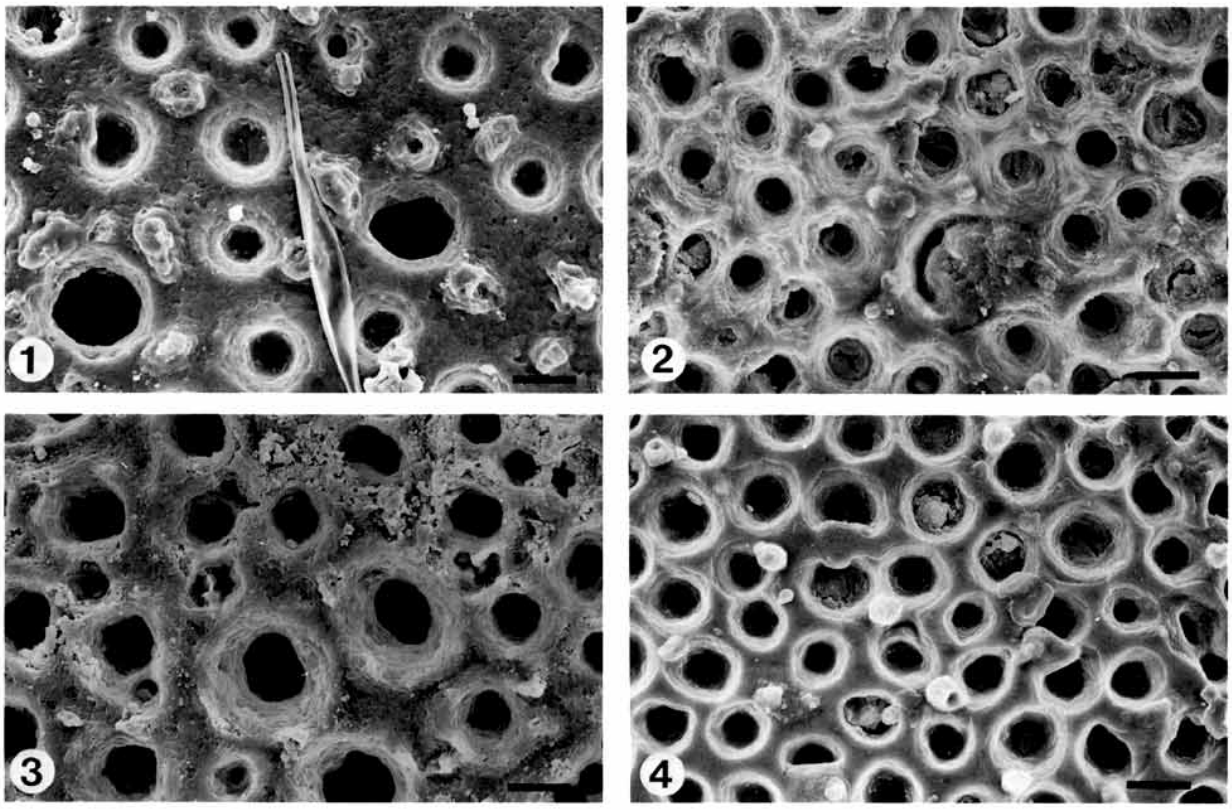



PLATE 1

Wall microstructure of *Orbulina universa* cultured at **1** high temperature, **2** low temperature, **3** high salinity, **4** low salinity. Scale bar is 10 μm.

ber formation and gamete production are recorded up to 33°C but *Artemia* are not accepted at this temperature. The upper limit for food acceptance is 32°C (Table 5A). Consequently, the temperature tolerance range for this species is 15–32°C (Table 7A, Fig. 5).

*Globorotalia menardii*

Since only 18 specimens were cultured at three different temperatures and three different salinities, the absolute environmental limits are not precisely known. The upper temperature limit is below 31°C whereas the lower limit lies below 16°C. The lower and upper salinity limits are below 27 and below 44‰ respectively.

## Maximum Test Size

Mean initial and final sizes and total shell length increase are calculated for *G. sacculifer, G. ruber,* and *G. siphonifera* that constructed chambers and underwent gametogenesis under extreme temperature and salinity conditions. With respect to *O. universa,* all individuals that built a spherical chamber are considered, independent of whether they produced gametes or not (Table 6). In order to test whether or not growth features are statistically different between normal and extreme temperature and salinity conditions, a Scheffé test was performed. Differences with respect to initial size, final size and total shell length increase were tested at a 95% confidence level.

*Globigerinoides sacculifer*

Using our data base (Hemleben and others, 1987), we calculated the mean initial and final size for gametogenetic specimens that had constructed only one chamber at 26.5°C and 34.8‰. The mean initial size is 402 μm and the mean final size is 525 μm. After two chamber additions at 26.5°C, 34.4‰, the mean final

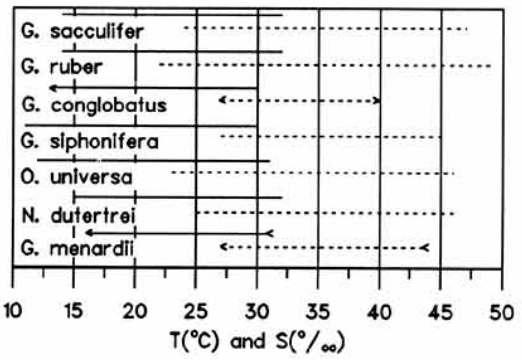



FIGURE 5. The temperature (solid line) and salinity (dashed line) ranges for seven species of planktonic foraminifera.

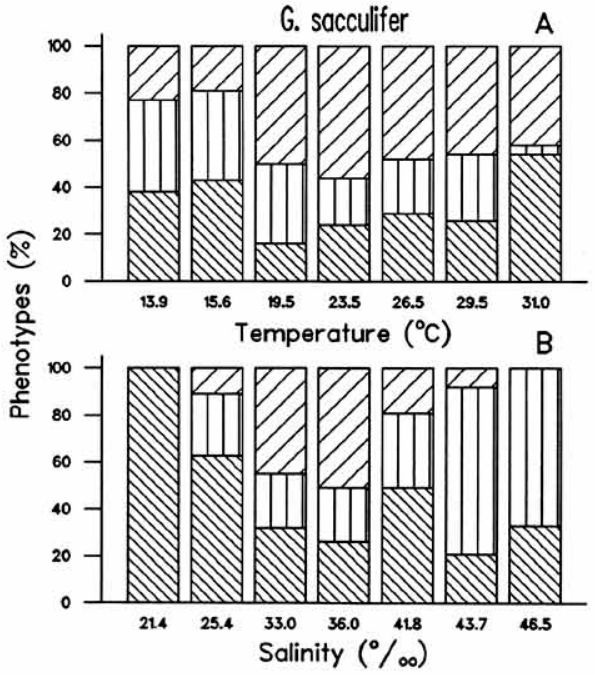



FIGURE 6. Distribution of last chamber morphology for *Globigerinoides sacculifer* at different temperatures (A) and salinities (B). Normalform (▨), Kummerform (□) and sac-like (▨) chambers are distinguished. Values for 33‰ and 36‰ and at 19.5–29.5°C for *Globigerinoides sacculifer* from Hemleben and others (1987).

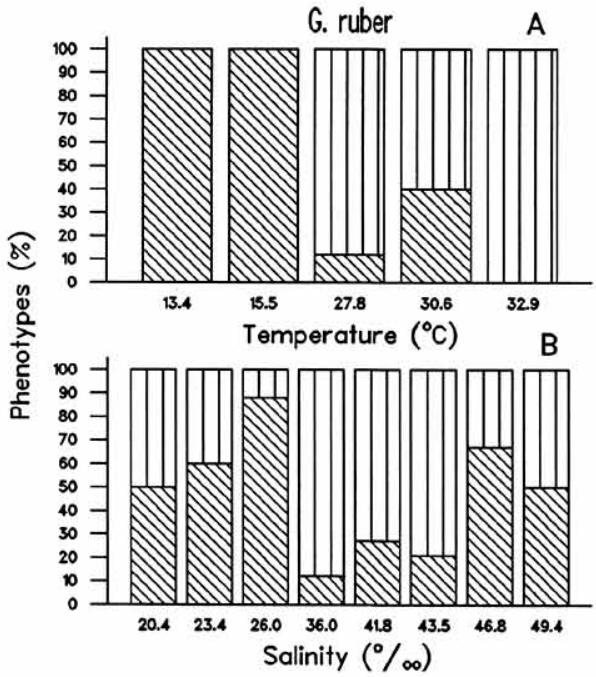



FIGURE 7. Distribution of last chamber morphology for *Globigerinoides ruber* at different temperatures (A) and salinities (B). For explanation see Figure 6.

size of gametogenetic specimens is 593 μm and the mean initial size is 332 μm (Table 6).

On the bases of two chamber additions, larger shells are built at 26.5°C than at 14–16°C or at 31°C. With respect to salinity, larger shells are formed at 34.8‰ than at 23–26‰ or at 41–47‰ (on the basis of one chamber addition). However, none of the differences between initial size, final size or total shell length increase of specimens grown under different culture conditions are statistically significant.

*Globigerinoides ruber*

The final sizes of specimens grown at 30–31°C or 22–26‰ are significantly larger than the final size of specimens grown under normal conditions (23.5°C, 33‰). However, the initial sizes of specimens grown at 30–31°C or 22–26‰ also are significantly larger than the initial size of specimens grown under normal conditions.

The total shell length increase does not differ significantly between the different experimental treatments, but is smaller for specimens grown under high salinity (41–45‰) than for specimens grown under other experimental conditions.

*Globigerinella siphonifera*

The initial shell lengths differ maximally 64 μm among the different culture treatments. However, the differences are not statistically significant.

The final test size is reduced under all extreme situations in comparison to normal conditions. Only the final size of specimens grown at low temperature (13–16°C) is significantly smaller than specimens grown under normal culture conditions (23.5°C, 36‰) or high salinity conditions (41–45‰).

The total shell length increase is reduced under all extreme situations in comparison to normal culture conditions. However, only the total shell length increase of specimens cultured at 13–16°C or at 27‰ is significantly smaller relative to normal conditions (23.5°C, 36‰). The total shell length increase of specimens cultured at 29°C or at 41–45‰ is significantly larger than the total shell length increase at 13–16°C.

*Orbulina universa*

On the basis of one chamber addition, the initial size of specimens grown at 12–18°C, at 30–31°C and at 41–47‰ is significantly larger than specimens grown under normal conditions (25°C, 35.7‰). The initial size of specimens grown at 23–27‰ is also larger than the initial size of specimens cultured under normal conditions, but not significantly. On the basis of two chambers formed in culture, the initial size of specimens cultured at normal temperatures (25.7°C) is smaller than those cultured under extreme temperature conditions. However, only specimens cultured at extreme low temperatures (16–18°C) are significantly larger in initial size than specimens cultured at 25.7°C.

The differences in final size between the different culture treatments are neither statistically significant

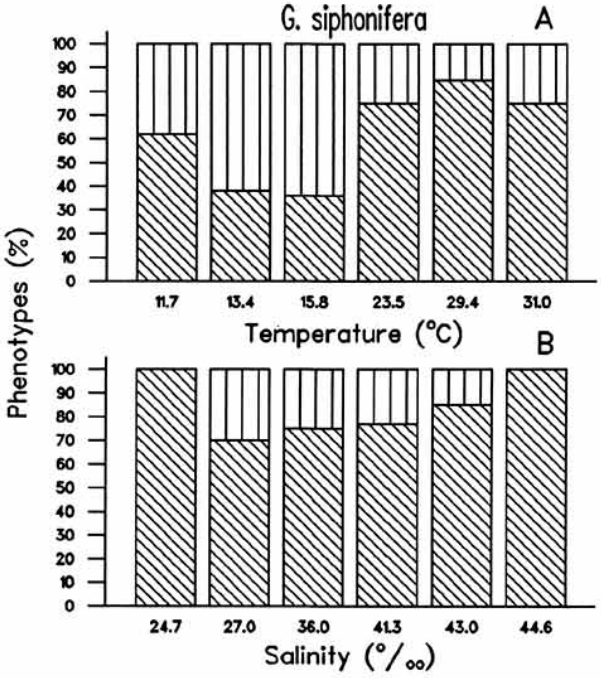



FIGURE 8. Distribution of last chamber morphology for *Globigerinella siphonifera* at different temperatures (A) and salinities (B). For explanation see Figure 6.

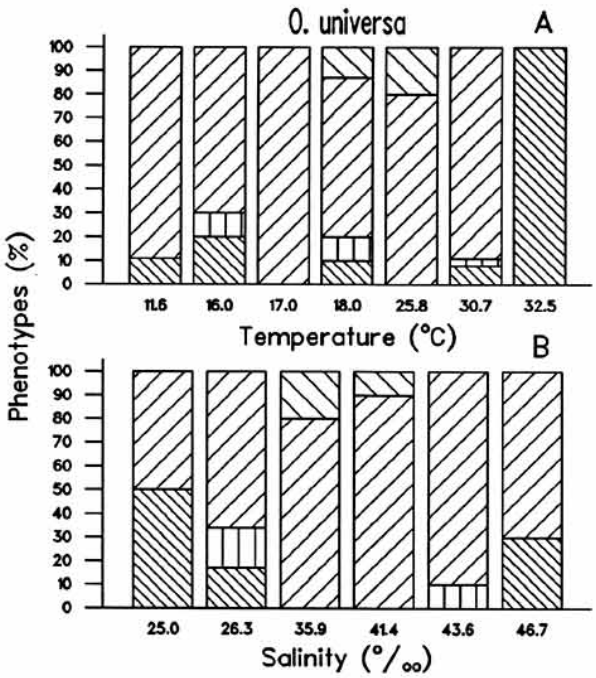



FIGURE 9. Distribution of last chamber morphology for *Orbulina universa* at different temperatures (A) and salinities (B). Spherical chamber (▨) and biorbulinas (▧); Kummerform (□) and normalform (▩) last chambers where no sphere was constructed.

on the basis of one chamber formed in culture nor on the basis of two chambers formed in culture.

The total shell length increase is larger under normal than under extreme temperature or salinity conditions. However, only the total shell length increase of specimens cultured at 12–18°C or at 41–47‰ is significantly smaller than that of specimens cultured at 25°C and 35.7‰ (on the basis of one chamber addition).

## Distribution Of Phenotypes

The phenotype distribution for *G. sacculifer, G. ruber, G. siphonifera,* and *O. universa* grown under extreme temperatures and salinities is shown in Figures 6 to 9. It should be noted that the number of observations these graphs are based on is low because few individuals constructed chambers under extreme culture conditions. As the number of observations is even lower for *G. conglobatus, N. dutertrei* and *G. menardii,* we did not account for the distribution of phenotypes within these species.

### *Globigerinoides sacculifer* (Fig. 6)

The frequency of sac-like chambers diminishes slightly in cultures under high temperatures but decreases markedly in cultures maintained at low temperatures relative to 23.5°C. Sac-like chambers are absent at both salinity extremes.

Kummerform chambers are more frequent under cold conditions than at 23.5°C, but the frequency decreases towards extreme warm conditions relative to 23.5°C. Under high salinity conditions, high relative frequencies of kummerform chambers are found as compared to 36‰. In a low salinity environment, however, no or few kummerform chambers are formed.

### *Globigerinoides ruber* (Fig. 7)

A higher percentage of kummerform chambers are constructed under high temperature than at 27.8°C or under low temperature conditions. Under low temperature culture conditions a lower frequency of kummerform chambers is observed than at 27.8°C. In cultures under low or high salinity, fewer kummerform chambers are secreted than at 36‰. The incidence of kummerforms at the low salinity range, however, increases towards lower salinities. At the high salinity side of the survival range, kummerform chambers are formed less frequently as salinity increases.

### *Globigerinella siphonifera* (Fig. 8)

More kummerform chambers are secreted at low temperatures than at normal (23.5°C) or higher temperatures. However, the frequency of kummerform chambers at the low temperature side of the survival range decreases as temperature decreases. The frequency at the high temperature extreme is comparable to the frequency at 23.5°C. Fewer kummerform phenotypes are recorded towards both extreme salinities relative to 36‰.

TABLE 8. Pore density (number of pores/$10^4$ $\mu m^2$), pore area ($\mu m^2$) and calculated porosity (%) at low and high temperatures (**A**) and low and high salinities (**B**). The temperature and salinity ranges and the number of observations are indicated.

| A | Pore density | | Pore area | | Porosity | |
|---|---|---|---|---|---|---|
| Species | Low T (n) | High T (n) | Low T | High T | Low T | High T |
| *G. sacculifer* | 14–15 (2) | 32 (4) | | | | |
| | 47 | 48 | 8 | 20 | 4 | 10 |
| *G. ruber* | 14 (1) | 30 (1) | | | | |
| | 100 | 80 | 6 | 14 | 6 | 11 |
| *G. siphonifera* | 13 (2) | 30–31 (3) | | | | |
| | 131 | 122 | 4 | 7 | 6 | 8 |
| *O. universa* | 16 (4) | 31 (4) | | | | |
| | 58 | 23 | 22 | 26 | 12 | 6 |

| B | Pore density | | Pore area | | Porosity | |
|---|---|---|---|---|---|---|
| Species | Low S (n) | High S (n) | Low S | High S | Low S | High S |
| *G. sacculifer* | 25–26 (3) | 44 (2) | | | | |
| | 54 | 32 | 16 | 40 | 9 | 13 |
| *G. ruber* | 22–25 (4) | 43–44 (4) | | | | |
| | 86 | 55 | 12 | 12 | 10 | 6 |
| *G. siphonifera* | 27 (2) | 41–44 (2) | | | | |
| | 167 | 99 | 6 | 7 | 10 | 7 |
| *O. universa* | 23–27 (4) | 43 (3) | | | | |
| | 55 | 41 | 25 | 26 | 15 | 11 |

*Orbulina universa* (Fig. 9)

Kummerform chambers in the spiral stage are found between 16 and 31°C and between 26 and 44‰ but not at the temperature or salinity extremes of the survival range.

Under normal conditions, adult specimens secrete a terminal spherical chamber. Under extreme temperature or salinity conditions the frequency of spherical chamber formation decreases markedly. At extreme high temperatures spherical final chambers are not formed. The frequency of second sphere formation also is decreased under extreme conditions relative to normal culture conditions (25.8°C, 35.9‰). Second spheres are observed only between 18–25.8°C and between 35.9–42‰.

### POROSITY

Pore concentration and pore diameter were determined for *G. sacculifer, G. ruber, G. siphonifera,* and *O. universa.* Individuals were selected from the limits of the temperature and salinity tolerance ranges, where chamber formation was still observed. Irregularly calcified individuals, or those with chambers formed during the period of stepwise acclimation, were not considered (Table 8; Pl. 2, Figs. 1–4).

For spherical *O. universa,* smaller and larger pores are distinguished. In living specimens, the smaller pores possess an inner organic lining and pore plates (Bé and others, 1980). The larger pores typically lack such a structure and are thus defined as apertures. The porosities listed for *O. universa* in Table 8 include these apertures.

To allow direct comparison with other studies we have converted the pore densities to $10^4$ $\mu^2$. The mean number of pores per $10^4$ $\mu^2$ varies from 23 to 167 and the pore area from 4 to 40 $\mu m^2$. In ascending order, the greatest number of pores per unit surface area occurs in *G. siphonifera, G. ruber, O. universa,* and *G. sacculifer.* For all species, the greatest number of pores is observed in cultures of low temperature (except for *G. sacculifer*) and low salinity. Pore areas are larger under high temperatures than under low temperatures. With the exception of *G. sacculifer,* the pore areas are similar under low and high salinities. Generally, pore density and pore area are inversely related. The highest porosities are observed at higher temperatures (except for *O. universa*) and, at lower salinities (except for *G. sacculifer*).

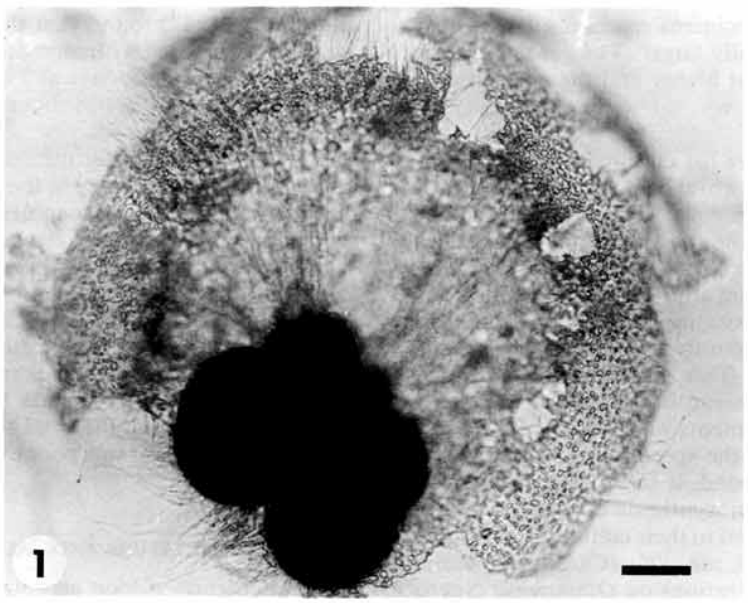
## DISCUSSION

### GROWTH AND SURVIVAL UNDER NORMAL CONDITIONS

Recently, Faber and others (1989) cultured *G. siphonifera* at 26°C, normal salinity, and at a feeding schedule of 1 BS/day. If we combine their results of *G. siphonifera* type I cultured at a light intensity of 20–50 $\mu E\ m^{-2}\ sec^{-1}$ and at 100–200 $\mu E\ m^{-2}\ sec^{-1}$, we find a mean initial and mean final size of 250 $\mu m$ and 595 $\mu m$. The chamber formation rate was 3.6 CF/indiv. and after 11.7 days, 76% of the specimens produced gametes. These data compare well with our results. In

PLATE 2

Dissolution in *Orbulina universa*: **1** a spherical chamber, **2** a spiral chamber, **3** a whole spiral stage. Scale bar is 100 $\mu m$.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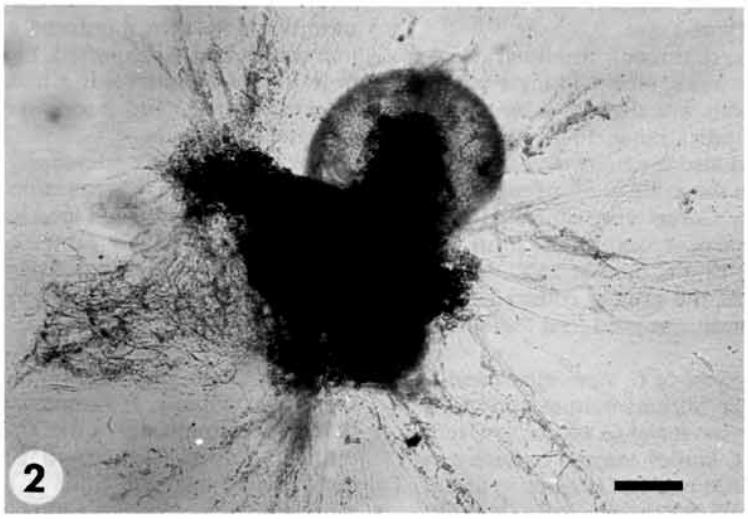
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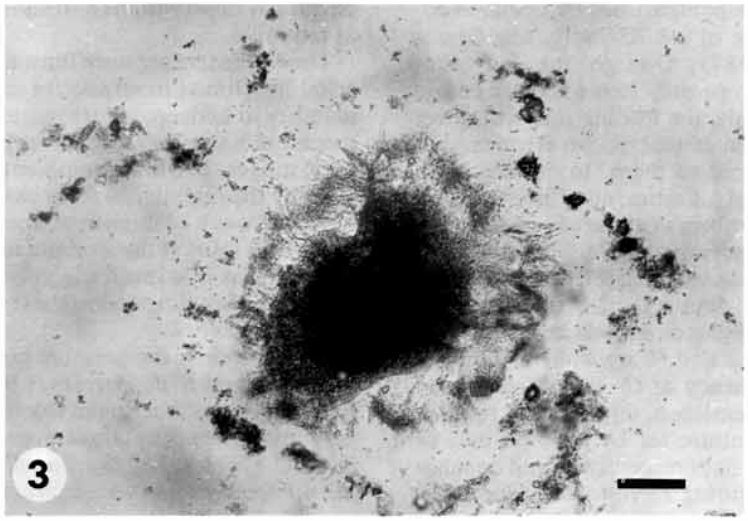
3

our experiments the specimens reached a larger final size but also were initially larger. The gametogenesis frequency was somewhat higher and the incidence of kummerform formation was slightly lower in our cultures.

Caron and others (1987b) cultured *O. universa* at normal salinities, under white light of a relatively high intensity (200–400 $\mu$E $m^{-2}$ $sec^{-1}$), at 1 BS/day and at temperatures that span the range at which this species is abundant in the ocean. They reported a mean final sphere diameter of 669 $\mu$m after 1.7 chamber additions at 25°C. The mean maximum size of *O. universa* in our cultures at 25.7°C was only 527 $\mu$m after two chamber additions (Table 6). This discrepancy could have two reasons. First, the mean initial size of the specimens used in our experiments was 88 $\mu$m smaller than the mean initial size of the specimens used by Caron and others (1987b). Second, it could be attributed to increased symbiont photosynthesis due to the higher light intensity they applied to their cultures. It is known from earlier studies on *G. sacculifer* (Caron and others, 1982) and recent investigations on *O. universa* (Spero and DeNiro, 1987) that light intensity and quality affect terminal morphology and size.

In our experiments, the chamber formation rate was higher, the survival time was somewhat longer but the frequency of gametogenesis was slightly lower than in their cultures. In both studies the incidence of sphere formation was 100% and also the frequency of second sphere formation was on the same order of magnitude (10 to 20%). However, Caron and others (1987b) showed that the incidence of second sphere formation was five times higher at 19.5°C than at 25°C. In contrast, our data show that the groups cultured under sub-optimum growth conditions produced less second spheres.

The physiological response of *G. siphonifera* and *O. universa* is similar under normal culture conditions and comparable to the behavior of *G. sacculifer* (Hemleben and others, 1987). Under normal culture conditions the food acceptance rate of *O. universa* and *G. siphonifera* is high, 0.7 BS/indiv./day and 0.8 BS/indiv./day, respectively. In comparison, *G. sacculifer* accepted *Artemia* at a rate of 0.8 BS/indiv./day (Hemleben and others, 1987). Due to the fact that foraminifers do not accept prey items shortly before and during gametogenesis, the feeding rate will never be 1 BS/indiv./day even if that is the frequency at which *Artemia* are offered to them. In cultures with normal temperatures and salinities, all *O. universa* and *G. siphonifera* form chambers at a rate of one chamber every 3 and 4 days respectively. The chamber formation rate for *G. sacculifer* was slightly higher, about one chamber every 2.6 days (Hemleben and others, 1987). The incidence of gametogenesis is 80–90% respectively for *O. universa* and *G. siphonifera.* Equally, the gametogenesis frequency of *G. sacculifer* was between 80% and 90% (Hemleben, unpublished results). The survival time in culture for *O. universa* and *G. siphonifera* is 10 and 11 days respectively and depends primarily on the size during recruitment. Hemleben and others (1987) found that the survival time of *G. sacculifer* decreased with increasing temperature, from 9 days at 19.5°C to 8 days at 29.5°C.

In contrast, *G. ruber* is more sensitive to manipulations than the other species used in this investigation and it is therefore rather difficult to maintain in laboratory cultures. Contrary to the other spinose species, *G. ruber* tends to shed its spines relatively easily and rarely floats in the culture vessel. The fact that the brine shrimp acceptance rate is low under normal conditions supports earlier observations indicating that the food requirements of this species differ from the other spinose species used in this investigation (Hemleben and others, 1988). *Globigerinoides ruber* seems to be least adapted to feed on copepods (Spindler and others, 1984). Consequently, the total shell length increase is reduced and survival was poor even under normal culture conditions.

### Temperature and Salinity Limits

The incidence of food acceptance, chamber formation, and gametogenesis under severe temperatures and salinities is drastically reduced when compared to normal conditions. As expected, Figures 1 to 4 show more or less parabolic curves in which low food acceptance, reduced growth, and poor survival correspond with extreme conditions.

The temperature and salinity ranges for the investigated species were determined by the highest and lowest extremes at which food was accepted, chambers were constructed and gametogenesis was observed. Spinose planktonic foraminifera that do not acquire particulate food are unable to construct additional chambers (Bé and others, 1981). If chamber formation is inhibited through refusal of food or other causes, pre-adult stages cannot grow to maturity and will not reproduce. Finally, if gametogenesis is suppressed in mature specimens, there will also be no progeny. Consequently, if one of these vital processes is inhibited, the absolute survival limit is reached. The survival ranges of *G. conglobatus* and *G. menardii* are based on only a few observations and should thus be considered as tentative.

The upper temperature limit and the upper and lower salinity limits in all species are primarily set by the inability to undergo gametogenesis. Calcification is the second most important factor that restricts these survival ranges. The lower temperature limit in all species is set by the inability to form chambers. In *N. dutertrei* further growth at higher temperatures is limited because they refused the *Artemia* nauplii offered to them. However, as this species is primarily herbivorous under natural circumstances, the upper temperature limit may be higher.

Based on their temperature preferences, *G. ruber, G. sacculifer,* and *N. dutertrei* may be characterized as true tropical species that do not tolerate extremely low temperatures. The upper temperature limit for these species is 32°C (Tables 7A, B). For *O. universa* and *G. siphonifera,* the upper temperature limit lies 1°C and 2°C

TABLE 9. Upper and lower limits and optimum conditions for the planktonic foraminifera under consideration. The data from this study are experimentally derived. The literature data are based on in situ measurements in the North Atlantic and Indian Ocean. (**A**) temperature in °C and (**B**) salinity in ‰.

**A**

| | This study | | | Bé and Hamlin (1967) | | | Bé and Tolderlund (1971) | | | Tolderlund and Bé (1971) | | | Bé (1977); Bé and Hutson (1977) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Min. | Opt. | Max. | Min. | Opt. | Max. | Min. | Opt. | Max. | Min. | Opt. | Max. | Min. | Opt. | Max. |
| *G. sacculifer* | 14 | 26.5 | 32 | 18 | >21 | 26 | 15 | >24 | 30 | 15.0 | >22.1 | 29.5 | — | 25.2 | — |
| *G. ruber* | 14 | 26.5 | 32 | 18 | >23 | 27 | 14 | 21–29 | 30 | 13.3 | 21.3 | 29.5 | — | 24.4 | — |
| *G. conglobatus* | <13 | — | 30 | 21 | >25 | 27 | 15 | 21–29 | 30 | 19.2 | 22.5–28.7 | 29.5 | — | 24.4 | — |
| *G. siphonifera* | 11 | — | 30 | 15 | 20–23 | 27 | 12 | 19–28 | 30 | 10.5 | 17.4–25.3 | 29.5 | — | 23.5 | — |
| *O. universa* | 12 | 23.5 | 31 | 12 | — | 26 | 10 | 17–23 | 30 | 10.5 | >18.2 | 29.5 | — | 21.7 | — |
| *N. dutertrei* | 15 | — | 32 | — | — | — | 9 | 16–24 | 30 | 17.2 | — | 27.0 | — | 23.2 | — |
| *G. menardii* | <16 | — | <31 | — | — | — | 16 | 20–25 | 30 | 17.2 | — | 29.5 | — | 23.1 | — |

**B**

| | This study | | | Bé and Tolderlund (1971) | | | Tolderlund and Bé (1971) | | | Bé (1977); Bé & Hutson (1977) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Min. | Opt. | Max. | Min. | Opt. | Max. | Min. | Opt. | Max. | Min. | Opt. | Max. |
| | | | | | | | 35.75 | | | | | |
| *G. sacculifer* | 24 | — | 47 | — | 34.5–36.0 | — | 35.75 | >36.43 | 36.63 | — | 34.94 | — |
| *G. ruber* | 22 | — | 49 | — | <34.5; >36 | — | 35.75 | — | 36.63 | — | 35.25 | — |
| *G. conglobatus* | <27 | — | >40 | — | — | — | 35.75 | 36.63 | 36.63 | — | 34.99 | — |
| *G. siphonifera* | 27 | — | 45 | — | — | — | 35.75 | >36.56 | 36.63 | — | 35.34 | — |
| *O. universa* | 23 | — | 46 | — | 35.4–35.9 | — | 35.75 | — | 36.63 | — | 35.40 | — |
| *N. dutertrei* | 25 | — | 46 | — | — | — | 35.75 | — | 36.63 | — | 35.19 | — |
| *G. menardii* | <27 | — | <44 | — | — | — | 35.75 | — | 36.63 | — | 34.99 | |

lower respectively. These species also have the lowest lower temperature limit and prefer somewhat colder conditions. Based on the temperature range, *O. universa* and *G. siphonifera* may be considered the least typical for the tropical assemblage. On the basis of sediment assemblages from the South China and Java Seas, Rottman (1978) distinguished three groups of planktonic foraminifera. *Globigerinoides sacculifer, G. ruber,* and *N. dutertrei* tolerated temperatures up to 31.35°C. *Globigerinella siphonifera* withstood temperatures up to 30.47°C. *Orbulina universa* and *G. conglobatus* were not found in areas where the temperatures exceeded 30.45°C. Her conclusions are in good agreement with our results.

*Globigerinella siphonifera* shows the narrowest salinity tolerance range and the lowest upper salinity limit, followed by *N. dutertrei.* The salinity ranges of *O. universa* and *G. sacculifer* are comparable, but both are narrower than the range of *G. ruber. Globigerinoides ruber* has the widest salinity tolerance range and the highest upper salinity limit among the species examined. Hence, this species appears to be the most flexible with respect to salinity changes. In general, the higher the upper salinity limit, the higher also the upper temperature limit. This seems reasonable, as higher salinities are to be expected at higher temperatures.

Planktonic foraminifera may be considered eurythermal and euryhaline. However, their tolerance ranges are relatively small compared to most benthic foraminifera. Deep-sea benthos live at temperatures ranging from 1°C (polar region) to 20°C (Red Sea) and shallow-living benthic foraminifera from temperate latitudes withstand temperatures between at least −1°C (winter) and >40°C (summer). Agglutinated foraminifers inhabit tide pools where temperature and salinity fluctuations span a much wider range than that in this investigation.

Using plankton tows, Bé and Hamlin (1967) and Bé and Tolderlund (1971) derived temperature limits and optima for various species from the observed geographic distributions. The latter authors also deduced optimum salinities. Bé (1977) and Bé and Hutson (1977) correlated maximum abundances with temperature and salinity preferences. As a result, 27 species of Recent planktonic foraminifera were grouped into five faunal provinces. The ranges and optima of the seven species considered here are summarized in Table 9.

The salinity tolerance range for all the species under investigation is wider than the variation encountered in present oceans. With respect to the biogeographical distribution, salinity *per se* appears to be of subordinate importance. However, as one of the determining factors of density, salinity may play a role in the vertical distribution of the population and thus indirectly influence their geographical borders.

The in vitro temperature limits for the species under investigation closely match the temperatures that were measured at the periphery of their distribution in the natural environment. This suggests that temperature plays a major role with respect to the biogeographical distribution. The upper temperature limits that were tolerated in the laboratory are slightly higher than those measured in situ. The lower temperature limits that were measured in the laboratory are generally somewhat lower than those indicated by field studies. On the other hand, Tolderlund and Bé (1971) found *G. ruber, O. universa,* and *N. dutertrei* in the field at temperatures that were lower than those tolerated in laboratory cultures (Table 9).

These small differences may be due to stress under laboratory conditions or may result from differences in physiological response between populations of the same species at different locations. The tolerance range

of Caribbean populations may be shifted to higher temperatures as compared to their relatives at higher latitudes. In general, organisms from warm waters have higher lethal temperature limits than organisms of the same species from colder environments (Prosser, 1961). The same rule applies for salinity tolerance. Specimens of *G. sacculifer,* which were collected from the highly saline Gulf of Elat/Aqaba (41–42‰) and subsequently grown in the laboratory at 48‰, produced gametes (Reiss and Hottinger, 1984). They did not survive salinities of about 50‰ (Halicz and Reiss, 1981). *Globigerinoides sacculifer* collected in waters of lower salinity (this study) produced gametes only up to 47‰. We conclude that the life history of the juveniles may slightly alter the survival range of the adult.

Even in the same geographical locality, the survival ranges of a species may not be consistent. Different physiological phenotypes may be present depending on the chemical and physical parameters of the water mass. For instance, the salinity tolerance range of the bryozoan *Electra crustulenta* in the harbor of Cochin (India) changed from 16–32‰ before the monsoon season to 0–21‰ during the monsoon season. This salinity tolerance shift corresponded with a mean seawater salinity change of 21.6 to 1.5‰ respectively (Menon and Nair, 1972). Apparently, it is possible that the same species demonstrates different tolerance ranges in the same locality, depending on the conditions that prevail. With respect to planktonic foraminifers, this phenomenon is best demonstrated by *G. ruber.* Around Bermuda, the summer population includes both the white and pink variety. The winter population, however, consists mainly of the white variety which has a lower optimum temperature. Tolderlund and Bé (1971) found optimum temperatures of 21.3 and 24.4°C for the white and pink varieties respectively. Based on the hypothesis that largest test sizes are found in regions of optimum temperature and salinity, Hecht (1976a, b) also distinguished slightly different preferences between the two varieties. Optimum temperatures for *G. ruber* white ranged from 20 to 25°C whereas the pink phenotype preferred temperatures between 22 and 26°C.

The primary difference between our results and field observations is that we measured the survival range of late neanic to adult individuals (Brummer and others, 1987), whereas in the field, the overall survival range was obtained, i.e., the survival range of all ontogenetic stages together. Although a significant portion of the life cycle took place under controlled conditions (under normal conditions, up to 90% of the calcite may be added in the laboratory), we were unable to maintain planktonic foraminifers in culture through successive generations. Bé and Hamlin (1967), Bé and Tolderlund (1971), Tolderlund and Bé (1971) and Bé and Hutson (1977), on the other hand, investigated the in situ assemblages. If the tolerance ranges of the different ontogenetic stages (including the gametes) vary, the species' distribution will be constrained by the least tolerant stages, e.g., the stage with the highest lower limit and the stage with the lowest upper limit. Consequently, our laboratory results should be considered as maximum limits for the species in question. The actual ranges may be narrower than the ones that we find empirically for the neanic and adult stages, never wider. Table 9 shows that the in situ temperature and salinity tolerance ranges are mostly narrower than the empirical ranges, except for the lower temperature limit of *G. ruber, O. universa,* and *N. dutertrei.* It should be noted that the autochthone range of a species is very often smaller than the distribution that is indicated by plankton tows (Spoel and Pierrot-Bults, 1979).

The differences observed between in vivo and in vitro temperature and salinity survival ranges might also be a function of a synergistic effect of temperature and salinity on survival. It is known that salinity, temperature, and osmotic pressure are related empirically by the equation of Miyake (1939). Thus, if the salinity limits were measured at a different temperature, the resulting salinity interval may have shown a different range (e.g., Kinne, 1956, 1957). For instance, some marine animals are known to migrate to higher salinity environments when the temperature falls in winter and vice versa. Such a response is thought to keep the difference between the osmotic pressures of blood and medium at a constant value (e.g., Broekema, 1941; Verwey, 1957, 1958).

Several methods have been devised for comparing quantitatively the effect of temperature upon the condition of organisms. The most widely used technique is the $Q_{10}$ approximation. The metabolic rate, expressed as a $Q_{10}$-value, relates the growth rates at different temperatures according to the equation of Prosser (1961). Values for $Q_{10}$ of 1 to 4 have been reported for protozoans (Finlay, 1977; Baldock and others, 1980; Stoecker and Guillard, 1982; Sherr and others, 1983). Caron and others (1987a, b) estimated a $Q_{10}$ value of 1.6 for *O. universa* and about 1.0 for *G. sacculifer.* Since the rate of enzymatic reactions is not a linear function of temperature, $Q_{10}$ varies over a temperature range (Prosser, 1961). We calculated $Q_{10}$ values for *G. sacculifer, G. ruber,* and *O. universa* between 19.5°C and 29.5°C (Table 10). Where not enough data were available the median temperature and salinity of the survival ranges were calculated (Table 7). A $Q_{10}$ value larger than 1 indicates that the growth rate increases, while a $Q_{10}$ value smaller than 1 indicates that the growth rates slows down. A $Q_{10}$ value of 1 indicates that the growth rates are equal between the two temperatures. From Table 10 we conclude that the optimum temperature for *G. sacculifer, G. ruber,* and *O. universa* are 26.5°C, 26.5°C, and 23.5°C respectively. Apparently, the median temperature underestimates the optimum growth temperature calculated in the basis of $Q_{10}$ values (Table 10).

### Maximum Test Size

Because under extreme conditions only a few chambers were constructed, the Scheffé test was run with a low number of data points. Consequently, the differences with respect to size or growth had to be large in order to be significant. As a result, statistically significant differences were found only in a few cases.

The final size reached in culture is biased by the initial size. The size of each consecutive chamber is progressively larger. Thus, the growth potential is a function of size. Specimens with a larger initial size construct larger chambers and reach a larger final size. For example, the small final size of *G. ruber* that is reached under normal conditions as compared to cultures with marginal temperature and salinity conditions is caused by the relative small initial size of this group (Table 6).

At extreme high temperatures, the final chamber size and growth of *G. siphonifera* is larger (but not significantly) than at extreme low temperatures, even though the mean initial size—and thus the growth potential—is smaller at high temperatures. On the basis of equal initial size, the final size reached in high temperatures might have been significantly larger.

On the basis of two chamber additions, the final size of *O. universa* grown under conditions of low temperature was larger than the final size of specimens grown under normal or under high temperature conditions. Field studies in the Indian Ocean and the western Atlantic have shown a relationship between the size of *O. universa* and climatic changes, whereby higher temperatures corresponded with larger spheres (e.g., Bé and others, 1973; Colombo and Cita, 1980). In contrast, our observations agree with Malmgren and Healy-Williams (1978) and Caron and others (1987b), who found that the main effect of rising temperature was a reduction in sphere diameter. This contradiction may indicate that temperature is not the most important factor controlling the test size in this species. In a recent laboratory study on *O. universa* we observed that increased feeding frequency resulted in larger sphere sizes. This effect was more pronounced at lower temperatures (unpublished data).

*Globigerinella siphonifera* and *O. universa* show larger final sizes at high salinities than at low salinities. The final sizes, however, are within the size range of specimens cultured under normal conditions. *Globigerinoides sacculifer* and *G. ruber* on the other hand reach larger sizes under low, rather than under high, salinity conditions. This is in contrast to the observation that planktonic foraminifera from Red Sea sediments are larger than their counterparts from normal saline habitats in the same latitude (unpublished data).

Our data indicate that growth under extreme temperature and salinity conditions is generally restricted and that smaller average final tests are constructed under extreme conditions than under normal circumstances. This is in agreement with earlier culture experiments which have shown that *G. sacculifer* reached the largest mean final size between 23.5 and 26.5°C and that the mean final size decreased towards both higher and lower temperatures (Hemleben and others, 1987; Caron and others, 1987a). Also, the observation that largest final shell sizes are found in areas of maximum abundance where optimum conditions prevail supports our results (Hecht, 1976a, b).

Expatriated planktonic foraminifers are individuals that are displaced with respect to their autochthonous range. It has been argued that displaced specimens delay their reproduction or are unable to reproduce in marginal environments and therefore grow larger shells (e.g., Sliter, 1970; Malmgren and Kennett, 1976). In our experiments, they did not continue to grow and the final sizes reached under marginal conditions did not exceed final sizes attained under normal conditions. In contrast, the mean final size reached under unfavorable conditions is very often small relative to optimum growth conditions. This observation is supported by previous laboratory cultures of *G. sacculifer* (Caron and others, 1987a; Hemleben and others, 1987) and *O. universa* (Caron and others, 1987b) which showed that sub-optimum growth conditions result in a smaller average final test size. Apparently, expatriated planktonic foraminifera do not reach larger final sizes.

TABLE 10. Mean growth rates in μm per day between 19.5°C and 29.5°C. $Q_{10}$ values were calculated with the equation of Prosser (1961). Temperature in °C; Growth rate in chambers per day; $Q_{10}$ is dimensionless. Data for *G. sacculifer* are from Hemleben and others, 1987.

| Species | Temperature | Growth rate | $Q_{10}$ |
|---|---|---|---|
| *G. sacculifer* | 19.5–23.5 | 35.9–48.6 | 2.13 |
| *G. sacculifer* | 23.5–26.5 | 48.6–49.6 | 1.07 |
| *G. sacculifer* | 26.5–29.5 | 49.6–48.6 | 0.93 |
| *G. ruber* | 19.5–23.5 | 12.4–16.9 | 2.17 |
| *G. ruber* | 23.5–26.5 | 16.9–28.2 | 5.51 |
| *G. ruber* | 26.5–27.5 | 28.2–20.3 | 0.04 |
| *G. ruber* | 27.5–29.5 | 20.3–17.4 | 0.46 |
| *O. universa* | 19.5–23.5 | 10.8–27.1 | 9.97 |
| *O. universa* | 23.5–26.5 | 27.1–16.7 | 0.20 |
| *O. universa* | 26.5–29.5 | 16.7–15.8 | 0.83 |

## DISTRIBUTION OF PHENOTYPES

In *G. sacculifer* the pre-gametogenic chamber shows three morphologies (Fig. 6). Fewer sac-like chambers are built at both extremes of temperature and salinity. At high temperatures and low salinities fewer kummerform phenotypes are formed than under normal conditions. Caron and others (1987a) also concluded that high temperature (28°C) and low salinity (34.25‰) had an adverse effect on sac-like chamber formation. In contrast, Hemleben and others (1987) could not establish any relationship between the occurrence of normalform, kummerform, and sac-like chambers within a temperature range of 19.5 to 29.5°C and a salinity range of 33 to 36‰. This discrepancy could be attributed to increased symbiont photosynthesis due to the higher light intensities used by Caron and others (1987a). High light intensities promote the occurrence of sac-like phenotypes and induce the formation of a second (and occasionally a third) sac-like chamber in a higher percentage of individuals than low light intensities (Caron and others, 1982).

*Globigerinoides ruber* shows decreased formation of kummerform phenotypes in cultures of low temperature and high and low salinities. At high temperatures only one specimen secreted a new chamber (Fig. 7).

The formation of kummerform phenotypes in trochospiral *O. universa* seems to be controlled by the same constraints as in *G. siphonifera*, where the frequency of kummerform chambers decreased with increasing temperature and salinity stress (Figs. 8–9). In general, the "abnormal" morphologies are more frequent under normal conditions and the "normal" phenotype is found more often under marginal conditions. We conclude that kummerform chambers are not induced by temperature or salinity stress, as suggested in earlier reports (Berger, 1968; 1969a, b; Hecht and Savin, 1970, 1971, 1972). As concluded elsewhere, the formation of kummerform chambers and sac-like chambers is closely tied to the reproductive process (Hemleben and Spindler, 1983; Anderson and Faber, 1984; Hemleben and others, 1988; Bijma and others, 1990). The observed trends may thus indicate that it becomes more difficult to reproduce under severe conditions. Also, *O. universa* constructs fewer spherical chambers and the incidence of second sphere formation is reduced under extreme conditions, indicating that it becomes more difficult to reach maturity.

Expatriated species are reported to show an increased production of kummerform phenotypes (Berger, 1970; Malmgren and Kennett, 1976). In our experiments, this does not hold for *O. universa* and *G. siphonifera* and applies only to *G. sacculifer* in low temperature or high salinity environments and to *G. ruber* in high temperature or low salinity environments. Thus the concept of a higher kummerform output at the margins of the biogeographical range of some planktonic foraminifers may neither apply to all species nor result from unfavorable temperature or salinity conditions.

## Porosity

Comparing test porosity and derived parameters between consecutive growth stages within the same specimen yields an interesting relationship. The number of pores per unit surface area increased markedly with size while the pore area decreased. This resulted in a slight reduction of the shell porosity with shell size. The trend was consistent for all species and independent of the culture conditions. We hypothesize that the reduction in porosity with ontogeny is the result of decreasing metabolic activity with age. For this reason, we used only final chambers in the porosity measurements.

In cultures of extreme high temperatures and salinities, the pore densities for all species except *G. ruber* are relatively low compared to the pore concentrations reported for natural populations (Bé, 1968; Frerichs and others, 1972). With the exception of *O. universa*, pore diameters are small relative to data reported by Bé (1968) for plankton tow specimens, but are larger than diameters reported by Frerichs and others (1972). The latter investigators, however, measured the minimum pore diameter of sediment specimens. In addition, the porosities of cultured material are lower than those reported by Bé (1968) but higher than the porosities recorded by Frerichs and others (1972).

The function of pores is probably comparable in planktonic and benthic foraminifers. The observed concentrations of mitochondria below the inner pore entrances in benthic species indicates a function related to gas exchange and respiration (Berthold and others, 1976; Leutenegger and Hansen, 1979). We believe that the porosity in planktonic foraminifers, in combination with the surface area to biomass ratio, is a function of either metabolic or growth rates. At higher temperatures, growth rates and respiration are accelerated, accompanied by higher oxygen consumption. In order to compensate for the enhanced oxygen requirements at higher temperatures, physiological and/or morphological adaptations may take place to increase the shell porosity.

With the exception of *O. universa*, we find a positive relationship between temperature and porosity. This supports data from earlier studies that reported increasing test porosity with decreasing latitude in planktonic foraminifers from plankton tows and sediments (Bé, 1968; Frerichs and others, 1972; Bé and others, 1973, 1976). The shells of *G. sacculifer* were 2.5 times more porous at 32°C than at 14–15°C. This value is on the same order of magnitude as the measurements of Caron and others (1987a). They reported that the test porosity of *G. sacculifer* cultured at 28°C increased by a factor of 2.8 as compared with specimens cultured at 19.5°C. For *O. universa* cultured at extreme low and high temperatures, the porosities show the reverse of the expected relationship. However, this observation is not in agreement with previous studies (Bé and others, 1973; Colombo and Cita, 1980; Haenel, 1987) and is not clearly understood.

Although the salinity experiments were carried out at a constant temperature, the porosities varied considerably. With the exception of *G. sacculifer*, the porosities were between 1.4 to 1.7 times higher at low salinity than at high salinity. Also, the pore concentration was between 1.3 to 1.7 times higher at low salinities than at high salinities. The same phenomenon was observed in *Globorotalia scitula* (Brady) from piston cores of a Pleistocene sequence in the eastern Mediterranean that included three sapropel intervals (Baumfalk and others, 1987). Using palynological evidence, these investigators eliminated temperature and concluded that low salinity was the driving mechanism behind the increase in pore concentration.

Changes in the oxygen solubility caused by salinity are trivial in comparison to temperature effects, and are not likely to influence porosity to any great extent. Moreover, the solubility of oxygen is higher in waters of low salinity. The variation in porosity at the same temperature for high and low salinities, as displayed by the different species, is not well understood. At this stage, we suggest that either a higher metabolic activity is required at low than at high salinities to keep a certain osmotic balance between internal and external environment or that high salinity conditions restrain respiration.

The pore area, the number of pores per unit surface area, or both may increase to give a higher total po-

rosity. Previous studies showed that a higher porosity is generally achieved by an increase in pore diameter, accompanied by a reduction of the pore concentration (Bé, 1968; Frerichs and others, 1972; Bé and others, 1973, 1976). In the temperature experiments, this strategy is followed by *Globigerinoides ruber* and *G. siphonifera.* They increased their porosity by an expansion of the pore area (233 and 175% respectively) and a reduction of the pore concentration (80 and 93% respectively). In contrast, *O. universa* increased the pore density and reduced the pore diameter, while *G. sacculifer* increased the pore area (250%) but kept the pore density constant to achieve a higher test porosity. Remarkably, Caron and others (1987a) observed the same strategy for *G. sacculifer.* In the salinity experiments *G. sacculifer* followed the normal pattern, while *G. ruber, G. siphonifera,* and *O. universa* increased the number of pores per unit surface area but kept the pore area constant in order to increase their porosity.

## Paleoecological Implications

If we assume that no physiological changes have occurred within planktonic foraminifers since the last glacial maximum and that the populations of species collected off Barbados and Curaçao are the norm for all populations of species, we may apply the currently established tolerance ranges to paleoenvironments. The Red Sea forms an ideal locale to test the results of our temperature and salinity experiments for two reasons. First, Red Sea sediments are dominated by *O. universa, G. siphonifera, G. ruber,* and *G. sacculifer* (Berggren and Boersma, 1969), the same species that are dominant in the waters around Barbados and Curaçao where this study was carried out. Second, the salinity increased to more than 50‰ and the winter temperatures of the surface waters fell between 2 and 5°C during the last glacial maximum as compared to the present (Reiss and others, 1980; Ivanova, 1985; Thunell and others, 1988). Salinity is controlled by water exchange dynamics at the shallow Hanish Sill in the Strait of Bab el Mandeb and temperature variations are caused by global climate fluctuations.

No planktonic foraminifers are found in the Gulf of Elat/Aqaba during the last glacial maximum; *G. ruber* disappears shortly after *G. sacculifer* and prior to the glacial maximum (Winter and others, 1983). Berggren and Boersma (1969), reported the following sequence of elimination during the same interval: *O. universa* → *G. siphonifera* → *G. sacculifer* → *G. ruber.* The order of disappearance from the sediments differs slightly from the sequence predicted by our investigation. Using the upper salinity limits that were established in this study, the sequence of elimination of species should be *G. siphonifera* → *O. universa* → *G. sacculifer* → *G. ruber.* Comparison of the two series could indicate that early ontogenetic stages of *O. universa* are more sensitive to high salinity than late neanic stages or adults. On the other hand, perhaps salinity alone cannot be held responsible.

Anticyclic fluctuations between *G. ruber* and *G. sacculifer* have been reported in late Pleistocene sediments from the Red Sea (Berggren, 1969; Berggren and Boersma, 1969; Risch, 1976; Reiss and others, 1980). According to Reiss and others (1980), the dominance of *G. sacculifer* in the hypersaline Gulf of Elat/Aqaba proves that the near absence of this species in glacial intervals cannot be attributed to high salinity alone. They concluded that minimum winter temperatures below 17°C prevented *G. sacculifer* from surviving, while *G. ruber* withstood temperatures down to 13°C. We found identical lower temperature limits for *G. sacculifer* and *G. ruber,* thus excluding a temperature controlled mechanism. Reiss and Halicz (1976) pointed out that present day densities of the Gulf of Elat/Aqaba are far above the sigma-t range suggested to restrict the distribution of *G. sacculifer* or *G. ruber.* Berggren and Boersma (1969) supposed that lowered temperature superimposed on high salinity controls the responses of *G. ruber* in the Red Sea sediments and interpreted the behavior of *G. sacculifer* as salinity-sensitive. Among other suggestions, Yusuf (1978) proposed salinity changes to be of prime importance. Also, Risch (1976) concluded that the differences between late Quaternary synchronous faunal assemblages from the Red Sea and the Gulf of Aden can be more convincingly attributed to differing salinity than to temperature. On the basis of oxygen isotopes, Deuser and others (1976), calculated 4 to 5°C higher temperatures in the Red Sea than in the Gulf of Aden during the last glacial maximum. Such temperature differences, nowadays, occur only for a brief period in late summer, suggesting that the foraminiferal tests were formed only during a short period of maximum temperature difference. Because this possibility is not very likely, the $\delta^{18}O$ data probably reflect salinity changes leaving temperature changes subordinate in importance (Risch, 1976; Deuser and others, 1976). These conclusions are supported by the present study. The anticyclicity between the two globigerinoids in the Pleistocene Red Sea sediments may also be explained as a consequence of different upper salinity limits (see Locke and Thunell, 1988; Thunell and others, 1988).

Although the anticyclic changes observed in the Pleistocene sediments of the Red Sea may be conveniently explained by the species-specific upper salinity limits, shifts in dominance in present day oceans must have a different basis. The classical concept is that *G. ruber* dominates the lower and higher salinity areas, whereas *G. sacculifer* dominates water masses of intermediate salinity (e.g., Bé and Hutson, 1977). For instance, fresh water lenses, originating from the Amazon River, lower the salinity of the surface waters off Barbados temporarily from 36 to 31‰ and force most *G. sacculifer* to deeper, normal saline habitats below the fresh water lenses, while *G. ruber* remains in the low saline surface waters (Hemleben and others, 1987; Deuser and others, 1988). On the other hand, *G. ruber* is also a typical inhabitant of the more saline water mass of the southern Sargasso Sea (36‰) as well as the eastern Mediterranean, where salinities exceed 39‰ (Berggren and Boersma, 1969; Bé and Tolderlund,

1971; Thunell, 1978; Vergnaud Grazzini and others, 1986). *Globigerinoides sacculifer* is the most important species in many intermediate salinity regimes (34–36‰). However, *G. sacculifer* is also found in high salinity environments. The assemblage in the Gulf of Elat/Aqaba (>41‰) is dominated by *G. sacculifer* (Reiss and others, 1980). These contradictions leave room for an alternative but yet tentative explanation.

We found that *G. sacculifer* and *G. ruber* have the same "optimum" salinity, suggesting that the anticyclicity in present day oceans may not be controlled by salinity. Other factors may contribute to the regulation of the planktonic foraminiferal community. All species under investigation live associated with endosymbionts. We believe that the nutrient level of the water mass might play an important role in the population dynamics of these species and may control their anticyclicity in present day oceans. Several studies support this concept. *Globigerinoides sacculifer* was found to be a low-fertility associated species, whereas *G. ruber* has an affinity to water masses of higher productivity (Halicz and Reiss, 1981). Since the Gulf of Elat/Aqaba is oligotrophic, the dominance of *G. sacculifer* (Reiss and others, 1980) may indicate that it tolerates low nutrient environments better than *G. ruber* does and that *G. ruber* is more dependent on the symbiotic relationship and responds more as an "autotroph" with respect to environmental parameters. The fresh water lenses that pass Barbados originate from the Amazon and are enriched in nutrients and phytoplankton (Deuser and others, 1988). These lenses are dominated by *G. ruber*. The oligotrophic northern part of the Red Sea is dominated by *G. sacculifer*. The more fertile southern water masses of the Red Sea are controlled by *G. ruber*, often in association with *G. siphonifera* (unpublished data). *Globigerinoides ruber* and *G. siphonifera* contain respectively 1.5 and 2 times more chlorophyll *a* than does *G. sacculifer* (Bijma, 1986). Although a smaller chlorophyll *a* content does not necessarily imply a more moderate need for nutrients, it may partly explain the more "heterotrophic" character of *G. sacculifer*.

Another factor should be considered when studying the anticyclic fluctuations between *G. sacculifer* and *G. ruber*. *Globigerinoides sacculifer* reproduces according to the synodic lunar cycle, whereas *G. ruber* has a biweekly (semi-lunar) reproduction cycle (Bijma and others, 1990). Consequently, *G. ruber* is twice as productive with respect to the empty shell output. Compared with the standing stock, therefore, the sediments show a twofold increase of *G. ruber* over *G. sacculifer* (Almogi-Labin, 1981, cited in Reiss and Hottinger, 1984). In other words, even if *G. ruber* dominates the sediment, it may not have been the dominant species in the water column.

Using the upper salinity limits, we may differentiate between temperature and salinity effects on the oxygen isotopic composition at the time of the disappearance of a species from the Red Sea sedimentary record (Locke and Thunell, 1988; Thunell and others, 1988). The relationship between $\delta^{18}O$ and salinity in the Red Sea may thus be empirically verified.

## CONCLUSIONS

1. The temperature ranges of *G. sacculifer, G. ruber, G. siphonifera, O. universa,* and *N. dutertrei* that were experimentally determined in this investigation are comparable to the temperature ranges that are derived from their distribution in the oceans. Hence, temperature is an important factor in the establishment of biogeographic boundaries.
2. The salinity ranges of *G. sacculifer, G. ruber, G. siphonifera, O. universa,* and *N. dutertrei* are much wider than salinity fluctuation observed under normal ocean conditions. We conclude that salinity per se does not limit the biogeographic distribution of planktonic foraminifera.
3. Under conditions of extreme temperatures or salinities, stunted growth leads to smaller average final sizes. Expatriation does not induce continued growth in planktonic foraminifers.
4. The incidence of kummerform and sac-like morphotypes is reduced under adverse culture conditions. We conclude that the increased kummerform output of expatriated planktonic foraminifers is not the result of marginal temperature or salinity conditions.
5. The upper salinity limits of *G. sacculifer* and *G. ruber* could explain their anticyclic fluctuations in late Pleistocene sediments of the Red Sea.
6. Nutrient gradients seem to be of importance for planktonic foraminiferal distribution. The effect of nutrients should be investigated.

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