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THE EFFECTS OF INCREASED WATER FERTILITY ON TROPICAL SPINOSE PLANKTONIC FORAMINIFERS IN LABORATORY CULTURES

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ABSTRACT

Under controlled laboratory conditions, the influence of increased water fertility on test size was examined in four spinose planktonic foraminifers. Among other things, increased water fertility may be characterized by high prey densities and longer wavelength, low light conditions. Normally, a larger test is formed at higher feeding rates. This is shown most distinctly in *Globigerinella siphonifera* (d'Orbigny). The effect of increased food availability on test size of *Orbulina universa* d'Orbigny is larger at lower temperatures, a condition that prevails during upwelling events. For logistical reasons, the mean final size of *Globigerinoides sacculifer* (Brady) does not show a consistent tendency with feeding rate. *Globigerinoides ruber* (d'Orbigny) does not tolerate high levels of brine shrimp and was thus not cultured at higher feeding levels.

***Globigerinella siphonifera* and *O. universa* reach smaller shell sizes under light conditions that characterize fertile regions (yellow-green) relative to typical open ocean light conditions (blue). In contrast, *G. ruber* attains smaller shell sizes under blue light relative to yellow-green light. Again, *G. sacculifer* does not show a clear trend with respect to final test size under normal and upwelling light.**

The effect of longer wavelength light counteracts and overrules the effect of increased prey capture rates in the investigated symbiont bearing species. This phenomenon is explained by photosynthesis-limited host respiration. The extent to which the light effect counteracts the effect of feeding, probably depends on the habitat to which the species are originally adapted. Quantitative and qualitative pigment analyses suggest that *G. ruber* lives in a shallow, *G. sacculifer* lives in a deeper, and *G. siphonifera* in the deepest habitat. Data from the literature indicate that *O. universa* lives at intermediate depth between *G. siphonifera* and *G. sacculifer*. As *G. siphonifera* is somehow adapted to low intensity longer wavelength light, the negative effect of low intensity and longer wavelength light is minimized in this species. As a result, the effect of increased feeding rate is most pronounced in this species.

Fertile water is found in upwelling settings and in areas where rivers enter into the ocean. Comparison of sediments from fertile regions and neighboring open ocean sites shows that symbiont bearing planktonic foraminifers attain smaller shell sizes in the upwelling area off Benguela but that larger shells are found in the Zaire river plume. Due to the small quantity of reference sediment, statistically significant differences were found only for *O. universa*. The different response is explained as the result of limited respiration in upwelling areas because of lower than usual oxygen levels.

The morphology of the final chamber is influenced by both light quality and feeding rate. At higher feeding rates the number of sac-like phenotypes is decreased. Yellow-green light induces more kummerform morphologies in *G. sacculifer*, *G. ruber*, and *G. siphonifera* and increases second sphere formation in *O. universa*. Light quality effects the terminal morphology to a larger extent than prey capture rates do. Unfortunately, these trends could not be confirmed in our reference sediment due to the low number of kummerforms and sac-like chambers.

Water fertility also influences the fractionation of stable oxygen isotopes. It is concluded that *G. sacculifer* does not secrete carbonate in equilibrium with ambient seawater. Isotopically lighter tests are constructed under longer wavelength light conditions and they tend to get heavier with increasing prey capture rates. Specimens with sac-like chambers are lighter than normalform specimens whereas kummerform types are heavier than normalform types.

INTRODUCTION

Margin processes play a disproportionately important role in the physics and chemistry of the oceans. Regions of high fertility are normally found along the coast where rivers carry nutrients into the ocean or where nutrient-rich deep waters come to the surface. In the open ocean, the thermocline generally prevents the exchange of properties between the mixed layer and the deep water bodies. This barrier breaks down along the coast and nutrient-rich deeper water may enter the photic zone. Water fertility is increased especially where this process is actively generated such as in coastal upwelling regions (Suess and Thiede, 1982; 1983) and along the equator due to divergence (Smith, 1968b). Furthermore, the entrainment of subsurface water is not unusual in the plumes of large rivers. This phenomenon produces river-induced upwelling (Van Bennekom and others, 1978).

When nutrient-rich water enters the photic zone, the specific nutrient uptake rates increase and the phytoplankton grow to maturity faster (e.g., Jones and Halpern, 1981; MacIsaac and others, 1985). Due to the higher productivity in fertile regions, light penetration is lower as a result of scattering and selective absorption (Steeman-Nielson, 1975), and the light quality changes (Jerlov, 1968). In fertile waters longer wavelength light dominates, compared to the adjacent pelagic realm (Jerlov, 1968). Mediated by the

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increase in phytoplankton standing stock, other trophic levels also increase their biomass (e.g., Thiede, 1975; 1983). As a result, abundance, diversity, physiology, and test morphology of planktonic foraminifers may be affected. Typically, coastal upwelling may be characterized by opportunistic species from higher latitudes (Duplessy and others, 1981; Prell and Curry, 1981; Ganssen and Sarnthein, 1983; Wefer and others, 1983; Kroon and Ganssen, 1989). These changes are preserved in the sediment and are useful tools for paleoecological investigations.

Here, we document responses that occur at a species level, and especially those that will be preserved in the sedimentary record. The influence of combined biotic and abiotic factors of high fertility areas on the shell size and shape of planktonic foraminifers is examined in order to trace the fertility of areas through fossil assemblages. Hereto, four species of spinose planktonic foraminifers were kept in laboratory cultures under simulated high fertility conditions. As these species harbor symbionts between their spines and are preferentially carnivorous, we mainly focus on the effects of light quality and intensity and prey availability. The effects of salinity, temperature, and oxygen level on the maximum shell length and the morphological response are also discussed. In addition, a fertility signal may be recognized in the stable isotope composition of planktonic foraminifers. Therefore, the oxygen isotope response and the fractionation behavior of *Globigerinoides sacculifer* (Brady) was also investigated.

In order to maintain comparability with our previous laboratory experiments, and also because of their amenability to culture procedures and their abundance near the field stations, the experiments were carried out with *G. sacculifer, Globigerinoides ruber* (d'Orbigny), *Globigerinella siphonifera* (d'Orbigny), and *Orbulina universa* d'Orbigny. Although these species are not necessarily typical of upwelling regimes, Ganssen (1983) and Ganssen and Sarnthein (1983) documented the summer upwelling activity off northwestern Africa by using *G. sacculifer* and *G. ruber*. Typical upwelling species such as *Globigerina bulloides* d'Orbigny, on the other hand, followed the seasonally shifting latitudinal position of the upwelling cell and thus recorded the lowered sea surface temperature during summer and winter.

MATERIAL AND METHODS

Experiments with *G. sacculifer* were carried out in the summer of 1981 and 1982 at the Bellairs Research Institute, Barbados. At a later stage (1986 and 1987), the experiments were repeated with *G. sacculifer, G. ruber* (pink), *G. siphonifera,* and *O. universa*. The experiments were finished in 1988 at the Caribbean Marine Biological Institute (CARMABI), Curaçao, Netherlands Antilles.

Specimens were collected two miles off the coast by SCUBA divers at approximately 3 to 8 m depth, according to the method described by Alldredge and Jones (1973) and summarized in Hemleben and others (1989). Upon returning to the laboratory, the general condition of each specimen was inspected and the initial shell size was measured.

From 1982 onwards, the surface water salinity off Barbados was frequently low due to freshwater lenses from the Amazon River (Steven and Brooks, 1972; Kidd and Sander, 1979; Deuser and others, 1988). As a result, the *G. sacculifer* population descended to greater depth (35 to 60 m), below the low salinity lens. Consequently, this species was frequently beyond the SCUBA collection depth range. We therefore collected additional specimens by means of plankton tows. Tow specimens were cleaned and transferred to individual culture vessels upon returning to the laboratory. The cleaning procedure has been described in detail by Bé and others (1977).

Only specimens with diameters <340 μm were selected for the experiments. The specimens were kept individually in culture vessels containing approximately 40 ml unfiltered seawater from the collection site and monitored every day. The vessels were covered with translucent plastic covers to prevent evaporation and placed in water baths. The temperature was adjusted to 23.5°C or 26.5°C and kept constant. The salinity of the culture water was controlled at the beginning of the experiments. In the following report, salinities ranging from 32–34.4‰ and 34.5–36.8‰ are quoted as 33‰ and 36‰ respectively. Foraminifers were fed brine shrimps, *Artemia salina* nauplii (BS), at a rate of 1 or 2 BS/day. *Globigerinoides ruber* were kept at a low feeding rate, because it seems to be least adapted for copepod prey (Spindler and others, 1984). At higher feeding rates, *G. ruber* tends to shed its spines and is thus unable to hold and digest prey. This species seems to be adapted for smaller prey.

Two different light environments with a quantum flux of 50–60 $\mu E\ m^{-2}\ sec^{-1}$ were created. The first light regime (L1) was qualitatively adjusted to simulate blue open ocean water. Hereto, we used blue and white light bulbs that emitted mainly light of approximately 430–470 nm wavelength. The second light regime (L2) simulated the light quality of the yellow-green fertile waters. Yellow-orange light bulbs were used with the white and blue light bulbs. Light of approximately 500–550 nm wavelength dominated in this case.

From 1986 onwards, the experimental set-up was slightly modified. Culture water was filtered in order to have a better control on food uptake. Because salinity influenced final test size only to a minor extent, we did not separate the specimens into two salinity groups. The experimental salinities ranged from approximately 32‰ to 36.8‰ and are referred to as 34.5‰. The most significant difference, however, was another approach to create yellow-green light (L3). Instead of using differently colored fluorescent tubes, L1 was filtered with a yellow-green filter that absorbed most light below 500 nm. Longer wavelength light is left almost unaffected (Fig. 1). The reason for this modification was to achieve a better comparability to L1. Although L2 and L3 are perceived as being exactly the same, their physical properties are completely different, as revealed by dissection with a prism. The physiological impact of L2 and L3 on biological processes may be equally different. In the first set-up "high fertility light" was realized by addition of different wavelengths, resulting in an intermediate yellow-green color. In the second set-up, shorter spectral bands were absorbed from "open ocean light," and the reflected colors added to a yellow-green mix color (L3).

Each light environment was regulated to the same level of

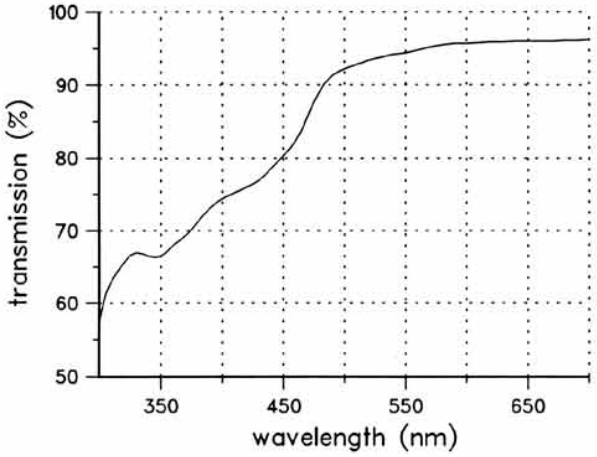

FIGURE 1. Transmission spectrum of the filter used to create L3.

photosynthetic photon flux density by adjusting the distance between light source and water baths. As a consequence, L1, L2, and L3 are characterized by a similar quantum flux but a different spectral composition. For detailed description of the experimental procedures, see Hemleben and others (1987, 1989).

For analysis we chose the same criteria as Hemleben and others (1987). Analysis was based on individuals that constructed at least 2 chambers, were initially <340 μm in diameter, had a final diameter of at least 400 μm (for *G. ruber* ≥ 350 μm), and underwent gametogenesis between 4 to 15 days after onset of the culture. With respect to *O. universa*, we only analyzed adult specimens that had secreted a spherical chamber.

Photosynthesis is a quantum process and differences in symbiont activity thus result from differences in the concentration and composition of the light harvesting pigments. As irradiance increases, the action spectrum becomes progressively flatter, until at complete light saturation, photosynthesis is independent of the spectral composition of the light and, therefore, of the pigment composition of the symbionts (Smith, 1968a). The experiments were thus carried out at low irradiance levels (50–60 μE m^{-2} sec^{-1}) corresponding to the light intensity at 10–30 m water depth in the open ocean (Hemleben and others, 1987). This is well below light saturation but above compensation light intensities reported for the endosymbionts. Spero and Parker (1985) found a saturation intensity of 386 μE m^{-2} sec^{-1} for the symbionts of *O. universa*. Jørgensen and others (1985) reported that photosynthesis in the symbionts of *G. sacculifer* compensated total respiration at 26–30 μE m^{-2} sec^{-1} and was not light limited above 160–170 μE m^{-2} sec^{-1}.

Quantitative and qualitative pigment measurements were carried out on methanol extracts of crushed but not dried foraminifers. Specimens were collected in January 1985 in the Gulf of Elat/Aqaba. The procedure generally followed that of Strickland and Parsons (1972) with modifications reported by Ter Kuile and Erez (1984). Specimens were identified, measured, and divided into three groups (small, medium, and large). The dimensions for these subgroups were chosen differently for each species, depending on preliminary abundance analysis. For *G. sacculifer* the size-intervals for small, medium, and large individuals were <322 μm, 322 μm – 484 μm, and >484 μm respectively. For *G. siphonifera* the size classes were <282 μm, 282 μm – 362 μm, and >362 μm. For *G. ruber* (white) only one group was collected because of low abundance (185 μm –443 μm). Once measured, the foraminifers were transferred to centrifuge tubes and stored in the dark in a −20°C freezer.

For analysis:

1) the foraminifers were crushed with a micro mortar.
2) the pigments were extracted with 5 ml 100% methanol in the dark for 4 hours, mixing with a vortex at the start and after 2 hours.
3) during transfer to the centrifuge, the tubes containing the mixture were wrapped in tin foil.
4) the mixture was centrifuged for 10 minutes at 7000 r.p.m.
5) The optical density (OD) of the supernatant was measured at 665 and 630 nm on a Gilford model 250 spectrophotometer, using a 10 cm cylindrical cell.
6) The chlorophyll *a* concentration in mg l^{-1} was calculated after the equation of Jeffrey (1968): Chlorophyll $a = 13.8 \times OD_{665} - 1.3 \times OD_{630}$.

For qualitative pigment analysis, the OD in the range 350–700 nm was determined in 10 nm steps, starting at the low energy side (700 nm) of the spectrum. Pigment scanning was carried out on the samples with the highest yield. Thus, the spectra were based on 75 medium sized (393 ± 41 μm) *G. sacculifer*, 67 small (289 ± 51 μm) *G. ruber* (white), and 50 large (453 ± 66 μm) *G. siphonifera*. These samples were also used to determine the total carotenoid concentration. Because peridinin is the principal carotenoid in dinoflagellates (Parsons and others, 1977); the following relationship is used to determine the total carotenoid concentration in mg l^{-1}. Carotenoid concentration = $10.0 \times OD_{480}$ (Strickland and Parsons, 1972).

Isotope analysis of empty *G. sacculifer* shells was carried out during the first experiments (1981, 1982). During culture, the vessels were sealed with a lid to minimize evaporation. Consequently, the $\delta^{18}O$ of the culture water did not change drastically during the culture period. After gametogenesis, the specimens were rinsed with fresh water. Each sample for $\delta^{18}O$ analysis contained four to seven gametogenetic tests that had been cultured under similar conditions (e.g., L2; 1 BS/d, 33‰) and had identical morphological features (e.g., 2 normal chambers or 1 normal and 1 sac-like chamber, etc.). The isotope composition of the shells was determined after roasting the sample for 30 minutes in vacuum at 400°C. The CO_2 was extracted with 100% H_3PO_4 at 50°C according to the method of Shackleton (1974). The results are reported in per mil deviations relative to the PDB standard. The precision for oxygen is better than 0.05%. The carbon isotope data are not presented because algal photosynthesis and bacterial activity were not controlled in the culture water.

Our results were compared to surface sediment samples which were taken in areas of different water fertility. During RV "Meteor" cruise 6, leg 6 (1988), a large box corer

was used to obtain three profiles perpendicular to the West African coast (samples kindly provided by Lutz, Pflaumann and Wefer). Profile A was taken in a region that is influenced by the Zaire River discharge. Profile B was taken in a primarily oceanic area that may be slightly influenced by upwelling but not by river runoff. The sites of profile C were in a region of intensive upwelling (Table 1). The mean maximum test size was determined for *G. sacculifer*, *G. ruber*, *G. siphonifera*, and *O. universa* in the fraction >315 μm.

RESULTS

Culture Experiments

Four parameters are examined in this paper (Table 2): 1) Light quality (L1, L2, and L3); 2) Temperature (23.5°C and 26.5°C); 3) Salinity (33‰, 34.5‰, 36‰); 4) Feeding rate (1 BS/day and 2 BS/day). Comparisons between experiments can be made where only one parameter is varied. With respect to feeding rate we compare experiments where less than 1 BS/d or more than 1 BS/d was digested.

Effects of Experimental Variables on Final Shell Size and Growth

Globigerinoides sacculifer

At high temperatures and high salinities, growth is rapid and large average final sizes are reached. The mean final sizes attained under L2 are larger than those attained under L1. Among other reasons, the larger initial size under L2 may be responsible. Under L3, however, smaller final sizes are reached relative to L1, mainly as a result of a smaller chamber size. The effect of feeding rate does not show a consistent trend (Table 2, no. 1–no. 13; Fig. 2A).

Globigerinoides ruber

At high temperatures more chambers are constructed and the average chamber size is large, resulting in a large final shell size. *Globigerinoides ruber* attains a smaller mean shell size under blue water light conditions than under yellow-green light conditions (Fig. 2B), due to a smaller mean chamber size. However, under L1 unfed groups are also included resulting in a lower percentage of specimens that formed at least three chambers and underwent gametogenesis (Table 2, no. 14–no. 16).

Globigerinella siphonifera

At the time the experiments were carried out, we did not distinguish between *G. siphonifera* type I and type II (Faber and others, 1988, 1989). Consequently, the experiments at L3 represent a mixture of both types. The experiments under L1 were run at a later stage when the two types were considered separately. Temperature does not influence growth or final shell size as it does in the other species. Increased growth and large sizes were attained at high feeding rates and under L1. Feeding rate positively affects final

Table 1. Large box corer samples from off West Africa collected on cruise 6/6 of the FS Meteor. Specimens in the size fraction larger than 315 μm for a site influenced by the Zaire River discharge (profile A), for a "normal" location (profile B) and for a site with frequent upwelling off Benguela (profile C) were individually measured. Per profile, the three sites were averaged and the 95% confidence intervals for the means are given. The number of specimens are indicated in brackets. **A)** Mean size in μm. **B)** Averaged distribution in % of chamber morphology at the three sites. The number of specimens are bracketed.

A

Location	Lat. (S)	Long. (E)	Depth (m)	Size SAC	RUB	SIP	UNI
Profile A (Zaire)							
1007-2	06°23.8′	10°56.3′	1533	—	470 (5)	—	630 (5)
1009-3	06°55.1′	08°59.8′	4047	563 (2)	465 (37)	450 (4)	517 (27)
1010-3	07°25.7′	07°25.2′	4474	650 (1)	456 (2)	—	539 (10)
Average				592 (3)	465 (44)	450 (4)	535 (42)
Interval				490–693	446–485	—	511–559
Profile B (normal)							
1014-2	11°47.2′	13°18.3′	701	503 (2)	433 (12)	—	518 (18)
1015-2	11°46.7′	12°50.8′	1638	500 (1)	454 (87)	500 (9)	435 (87)
1017-3	11°44.4′	10°33.0′	3809	517 (23)	448 (14)	—	516 (57)
Average				563 (26)	451 (113)	500 (9)	472 (162)
Interval				528–597	439–463	—	460–485
Profile C (Benguela)							
1023-2	17°09.7′	11°00.6′	1965	—	—	—	—
1025-2	17°09.9′	10°14.5′′	3565	675 (1)	400 (6)	—	436 (88)
1026-3	17°10.2′	08°54.4′	4601	425 (2)	350 (1)	—	463 (105)
Average				508 (3)	393 (7)	—	450 (193)
Interval				407–610	344–441	—	440–462

B

Location	Frequency RUB kum	SIP kum	SAC kum	SAC sac
Zaire (congo)	27 (44)	0 (4)	0 (3)	0 (3)
Normal	16 (113)	0 (9)	8 (26)	12 (26)
Benguela	17 (7)	– (0)	0 (3)	67 (3)

TABLE 2. Four species cultured in 26 different experimental conditions. The light regime, temperature, salinity and feeding rate (FR in brine shrimps per day) are listed. N_1 = total number of specimens. N_2 = observed number of specimens which underwent gametogenesis and formed at least 2 or more chambers in culture. The average initial and final size and growth in culture are given in microns. The percentages of the experimental group that formed 2 (2C) or at least 3 (3C) chambers as well as the number of chambers formed per specimen from culture begin to gametogenesis (CF) are given. Additionally, the size increase per chamber (CS) was calculated. The survival time and the percentage that underwent gametogenesis are listed as ST and GAM respectively. Different phenotypes are reported: sac-like chamber (S), kummerform (K) and for *O. universa* the "biorbulina" (BO). The data reported for no. 1, 2, 4 and 5 are based on Hemleben and others (1987). [1] tow-specimens. [2] tow-specimens included. [3] unfed-specimens included.

#	Species	Light	Temp. (°C)	Sal. ‰	FR (BS/d)	N_1	N_2	Init. (µm)	Final (µm)	Growth (µm)	CF-Rate 2C	CF-Rate 3C	CF	CS (µm)	ST (d)	GAM (%)	S %	K %	BO %
1	*G. sacculifer*	L1	23.5	33.0	0.8	107	80	225	608	383	30	78	3.0	128	8.1	87	72	12	—
2	*G. sacculifer*	L1	23.5	36.0	0.8	65	46	255	637	382	22	78	3.2	119	8.2	93	53	23	—
3 [2]	*G. sacculifer*	L1	23.5	36.0	1.4	32	19	275	610	335	68	32	2.4	140	7.0	94	26	16	—
4	*G. sacculifer*	L1	26.5	33.0	0.7	122	82	233	615	382	27	73	3.0	127	7.9	87	42	21	—
5	*G. sacculifer*	L1	26.5	36.0	0.8	71	57	239	652	413	18	82	3.3	125	8.5	90	43	23	—
6 [2]	*G. sacculifer*	L2	23.5	33.0	0.8	33	24	276	632	356	62	38	2.5	142	7.2	97	38	8	
7 [1]	*G. sacculifer*	L2	23.5	33.0	0.7	49	9	282	554	272	67	33	2.3	116	8.0	36	22	33	—
8	*G. sacculifer*	L2	23.5	36.0	0.8	65	49	244	643	399	27	73	3.0	133	8.0	94	53	8	—
9	*G. sacculifer*	L2	23.5	36.0	1.6	44	25	276	687	411	20	80	2.9	142	7.0	89	40	16	—
10 [2]	*G. sacculifer*	L3	23.5	34.5	0.8	41	27	251	582	331	44	56	2.7	123	7.5	95	7	26	—
11 [2]	*G. sacculifer*	L3	23.5	34.5	1.2	15	15	265	567	302	36	64	2.6	116	6.9	100	27	7	—
12 [2]	*G. sacculifer*	L3	26.5	34.5	0.8	18	13	261	636	375	0	100	3.2	117	7.3	94	23	31	—
13 [2]	*G. sacculifer*	L3	26.5	34.5	1.1	17	8	233	584	351	25	75	3.1	113	6.0	100	0	38	—
14 [3]	*G. ruber*	L1	27.9	36.0	0.2	78	13	228	423	195	54	46	2.5	78	8.1	51	—	15	—
15	*G. ruber*	L3	23.5	34.5	0.5	29	19	255	462	207	53	47	2.5	83	6.9	97	—	16	—
16	*G. ruber*	L3	26.5	34.5	0.7	49	36	235	529	294	36	64	3.0	98	8.0	96	—	47	—
17	*G. siphonifera* (TypeI)	L1	23.5	34.5	0.8	46	42	268	627	359	11	89	3.8	96	10.2	90	—	22	—
18	*G. siphonifera* (mixed)	L3	23.5	34.5	0.7	25	22	249	582	333	0	100	3.6	94	8.4	100	—	28	—
19	*G. siphonifera* (mixed)	L3	23.5	34.5	1.4	37	31	265	697	432	0	100	4.2	105	7.4	100	—	38	—
20	*G. siphonifera* (mixed)	L3	26.5	34.5	0.8	39	31	254	586	332	15	85	3.6	95	7.4	100	—	41	—
21	*G. siphonifera* (mixed)	L3	26.5	34.5	1.4	33	24	270	696	426	3	97	3.7	118	7.6	97	—	30	—
22	*O. universa*	L1	23.5	34.5	0.7	22	22	278	684	406	39	61	3.1	135	11.3	100	—	30	11
23	*O. universa*	L3	23.5	34.5	0.6	69	28	276	541	265	72	28	2.5	111	10.3	84	—	3	25
24	*O. universa*	L3	23.5	34.5	1.1	33	18	275	614	339	67	33	2.7	130	9.8	85	—	6	21
25	*O. universa*	L3	26.5	34.5	0.6	40	19	279	592	313	75	25	2.4	134	9.2	85	—	0	20
26	*O. universa*	L3	26.5	34.5	1.2	25	15	284	613	329	60	40	2.5	136	9.2	84	—	0	19

size particularly through the formation of large chambers and a slightly increased chamber formation rate. On the other hand, light quality influences final sizes through the chamber formation rate rather than through chamber size (Table 2, no. 17–no. 21, Fig. 2C).

Orbulina universa

On a feeding schedule of 1 BS/day, high culture temperatures increase growth and give rise to larger final sizes through an increase in chamber size. At a higher feeding rate the temperature effect is lost. More frequent feeding also leads to increased growth and large final sizes, but the effect decreases with increasing temperature.

Relative to open ocean light conditions, growth and final sizes are smaller in high fertility light conditions. The effect of the light quality overshadows the effect of increased feeding rates, i.e., a larger final size is attained under L1 at 1 BS/d than under L3 at 2 BS/d (Table 2, no. 22–no. 26, Fig. 2D).

EFFECTS OF EXPERIMENTAL VARIABLES ON THE MORPHOLOGY OF THE FINAL CHAMBER

Globigerinoides sacculifer

Under laboratory conditions, *G. sacculifer* produces the same morphotypes as under natural conditions (normalform, kummerform, sac-like chamber). Specimens that secrete at least three chambers produce less normalform morphotypes than specimens that secrete two chambers. The frequency of sac-like chambers is especially increased at higher chamber formation rates (Fig. 3). Although more kummerform chambers are constructed at high temperatures and high salinities, we could not detect a relationship between the formation of sac-like chambers and both temperature and salinity.

Increased feeding leads to the secretion of a higher percentage of normalform chambers, whereas sac-like chamber formation is inversely proportional to feeding frequency (except for the group cultured in L3, fed 2 BS/d at 23.5°C). Kummerform occurrence is also inversely related to food level (except for the group cultured in L2, fed 2 BS/d at 23.5°C). Generally, kummerform phenotypes are more frequent under L3 than under L1 and more frequent under L1 than under L2.

Globigerinoides ruber

The occurrence of kummerform phenotypes increases temperature. L3 induces more kummerforms than L1, especially at higher temperatures. As in the case of *G. sacculifer*, this may be a consequence of increased chamber production (Table 2, no. 14, no. 16; Fig. 4B).

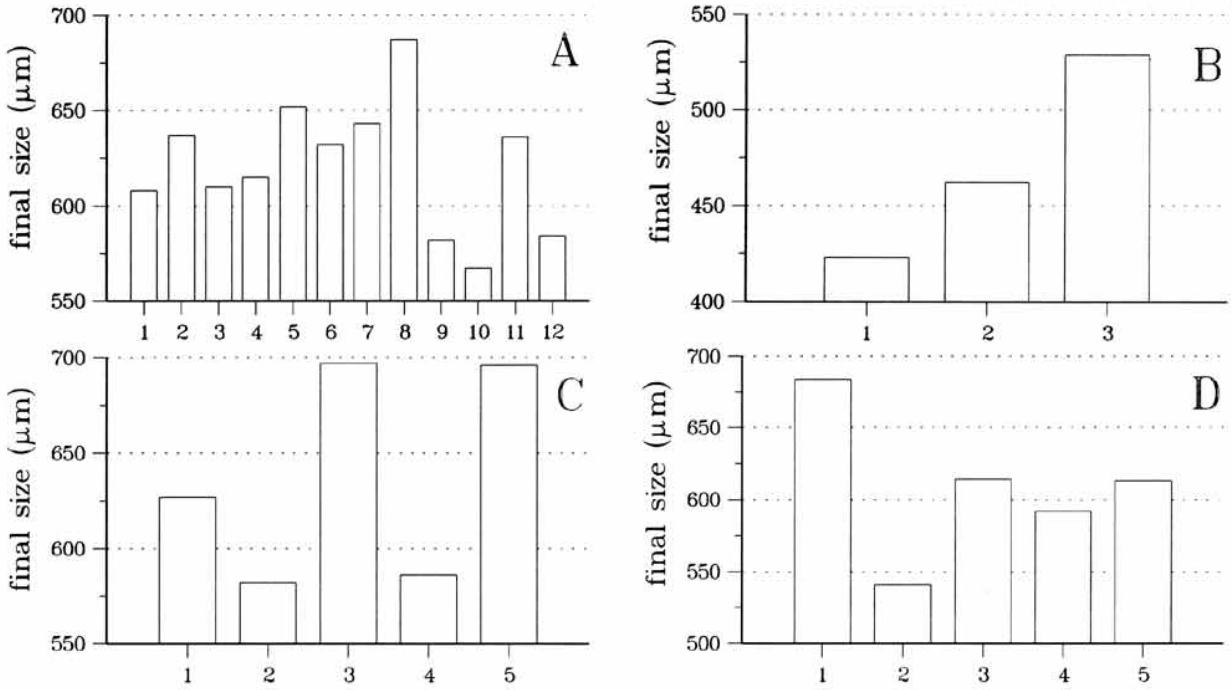

FIGURE 2. Mean final size as a function of different experimental conditions. L1, L2 and L3 indicate the light quality; T and S stand for the experimental temperature and salinity respectively; FR denotes the feeding rate. (A) *Globigerinoides sacculifer:* 1: L1; T = 23.5; S = 33; FR = 0.8; 2: L1; T = 23.5; S = 36; FR = 0.8; 3: L1; T = 23.5; S = 36; FR = 1.4; 4: L1; T = 26.5; S = 33; FR = 0.7; 5: L1; T = 26.5; S = 36; FR = 0.8; 6: L2; T = 23.5; S = 33; FR = 0.8; 7: L2; T = 23.5; S = 36; FR = 0.8; 8: L2; T = 23.5; S = 36; FR = 1.6; 9: L3; T = 23.5; S = 34.5; FR = 0.8; 10: L3; T = 23.5; S = 34.5; FR = 1.2; 11: L31; T = 26.5; S = 34.5; FR = 0.8; 12: L3; T = 26.5; S = 34.5; FR = 1.1; (B) *G. ruber:* 1: L1; T = 27.9; S = 36; FR = 0.2; 2: L3; T = 23.5; S = 34.5; FR = 0.5; 3: L3; T = 26.5; S = 34.5; FR = 0.7; (C) *Globigerinella siphonifera:* 1: L1; T = 23.5; S = 34.5; FR = 0.8; 2: L3; T = 23.5; S = 34.5; FR = 0.7; 3: L3; T = 23.5; S = 34.5; FR = 1.4; 4: L3; T = 26.5; S = 34.5; FR = 0.8; 5: L3; T = 26.5; S = 34.5; FR = 1.4; and (D) *Orbulina universa:* 1: L1; T = 23.5; S = 34.5; FR = 0.7; 2: L3; T = 23.5; S = 34.5; FR = 0.6; 3: L3; T = 23.5; S = 34.5; FR = 1.1; 4: L3; T = 26.5; S = 34.5; FR = 0.6; 5: L3; T = 26.5; S = 34.5; FR = 1.2.

Globigerinella siphonifera

There is no clear relationship between the occurrence of kummerforms and either temperature or feeding rate (Fig. 4C). At a low feeding schedule, kummerforms are more frequent at high temperatures. At high feeding rates, the occurrence is inversely related to temperature. L3 propagates kummerform formation.

Orbulina universa

In the spiral stage, more kummerforms are constructed at low temperatures. More kummerform chambers are also encountered in the spiral stage under L1 than under L3. In the adult stage, more second spheres are secreted under L3 than under L1 (Fig. 4D).

EFFECTS OF EXPERIMENTAL VARIABLES ON THE STABLE OXYGEN ISOTOPE RATIOS IN *G. SACCULIFER*

The $\delta^{18}O$ values scatter between $-0.85‰$ and $-2.04‰$. Within a single experiment, however, the scatter does not exceed 0.63‰ (Table 3). Although, the different experimental conditions do not result in a clear segregation of the isotope ratios, some trends with respect to fractionation are indicated: (1) lighter tests are secreted at high salinity (Fig. 5A), (2) the oxygen isotope ratio gets heavier when more chambers are built in culture (Fig. 5B), (3) heavier tests are formed at higher feeding rates (Fig. 5C), (4) lighter tests are constructed under L2 than under L1 (Fig. 5D), (5) on the average, kummerform phenotypes are heavier and sac-like chambers are lighter than normalform ones. Individuals with normal chambers cover the whole isotopic spectrum (Fig. 5E).

PIGMENT ANALYSIS

The chlorophyll *a* content of the symbionts is positively correlated with the size of the foraminiferal host and demonstrates that the symbiont-number increases with the ontogeny of the host (Fig. 6). The chlorophyll *a* content of *G. siphonifera* and *G. ruber* (white) are roughly 2 and 1.5 times that of *G. sacculifer,* respectively. Relative to the chlorophyll *a* content, *Globigerinella siphonifera* contains 30% more carotenoids than either species of *Globigerinoides* (Fig. 7).

Chlorophyll *a* is the main pigment in the samples of all species, having absorption peaks around 665 and 440 nm (Fig. 8). Peridinin absorbs in the green part of the spectrum roughly from 435 to 625 nm with a peak at 480 nm (Steeman-Nielsen, 1975). The presence of peridinin is shown by the low shoulder at 480 nm. Chlorophyll c (peak absorption at 630 nm) could not be detected in *G. ruber* (white) nor in

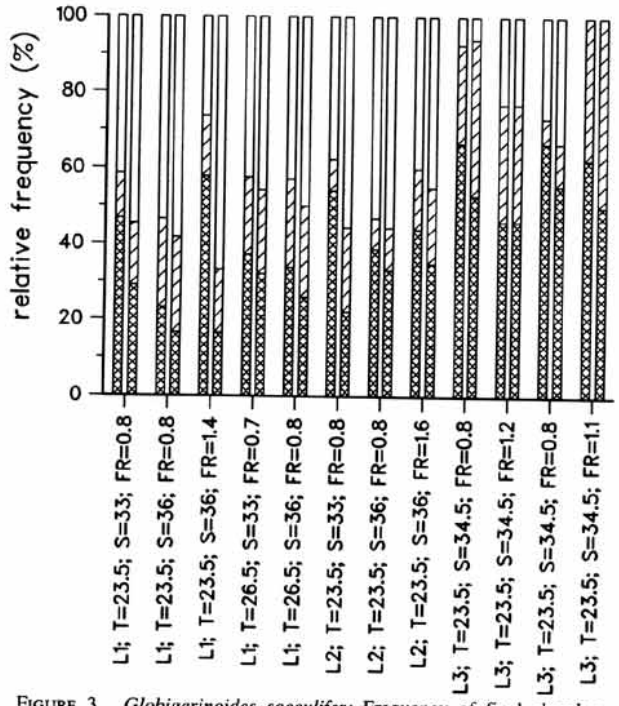

FIGURE 3. *Globigerinoides sacculifer:* Frequency of final chamber morphology within the groups which had formed 2 (left) or at least 3 chambers (right) in culture. Normalform = (▩); Sac-like = (□); Kummerform = (▨). For explanation of the abbreviations see Fig. 2.

G. sacculifer, but is present in *G. siphonifera* as indicated by a slightly increased absorption around 630 nm.

COMPARISON WITH THE SEDIMENT

The mean shell-size of an adult foraminiferal population varies for different geographic locations. In the sediment samples, the mean shell sizes for all species were largest from the region influenced by the Zaire River. Shells reached smallest mean sizes in samples from the upwelling area. Samples from the environment influenced by neither rivers nor upwelling show intermediate sizes. Statistically significant differences were found only for *O. universa* (Table 1a). Due to the low number of specimens, the size differences were not significant for the other species. In agreement with their low salinity tolerance (Bijma and others, 1990a), *G. ruber* is relatively frequent in profile A (Zaire). With respect to the shell morphology, the numbers of observations were also too low to allow conclusions (Table 1b). However, in comparison to the other profiles, the kummerform production in profile A is high.

If a population is normally distributed, the spread and the evenness of the size distribution of this population may be described in terms of the standard deviation. For deviant distributions, the standard deviation only describes the spread but not necessarily the evenness. As the size of populations of planktonic foraminifers are not normally distributed, another measure must be used. Sharp and Pow-Foong Fan (1963) introduced a sorting index that described both the spread and the evenness of the grain-size in the sediment, independent of the type of distribution. Because *O.*

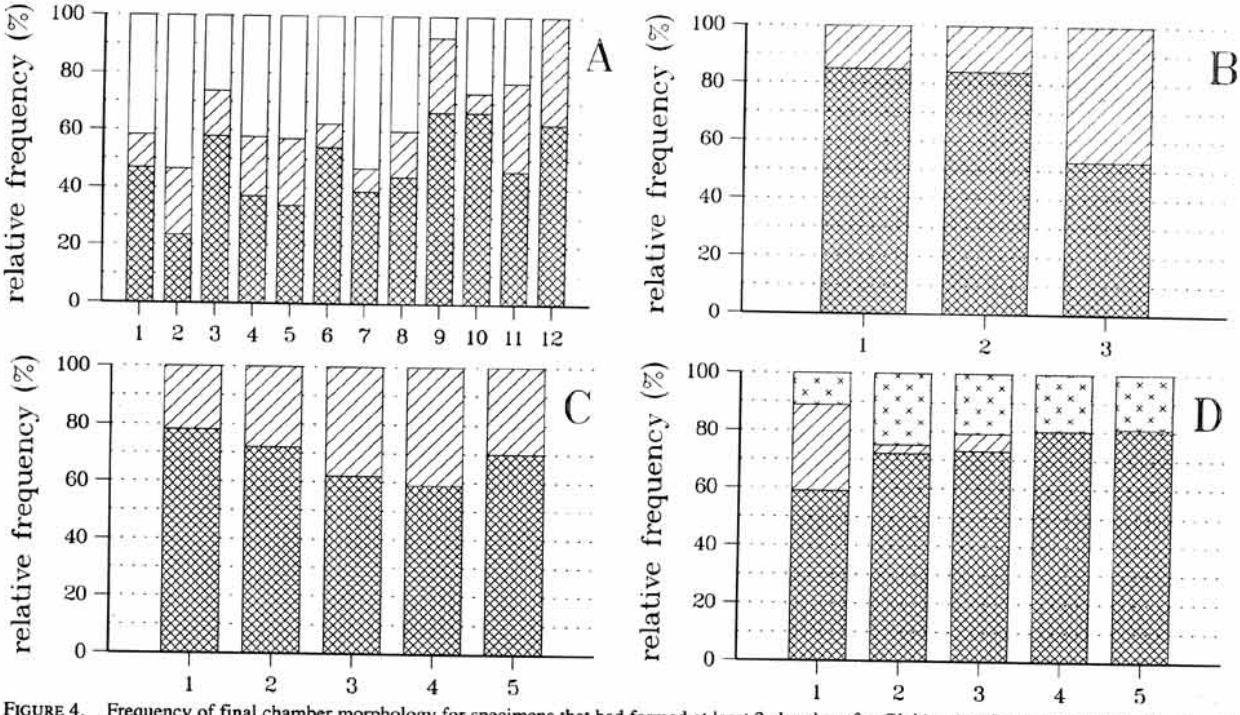

FIGURE 4. Frequency of final chamber morphology for specimens that had formed at least 2 chambers for *Globigerinoides sacculifer* (A), *G. ruber* (B), *Globigerinella siphonifera* (C) and *Orbulina universa* (D). For explanation of the x-axes see Fig. 2 and for explanation of the patterns see Fig. 3; "Biorbulina" = (⊠).

TABLE 3. Stable isotopic data of *Globigerinoides sacculifer* cultured at 23.5°C. Salinity and temperature at the collection site are indicated.

Sample	Salinity (‰)	Temperature (°C)	$\delta^{18}O$ (‰)
Light 1, 2 BS/day, 36‰			
2 chambers, normal	35.7 ± 0.1	28.0	−0.93
2 chambers, kummerform	35.7 ± 0.1	28.0	−0.85
Light 2, 1 BS/day, 33‰			
2 chambers, normal	34.0 ± 0.4	28.0	−1.59
2 chambers, normal	33.1 ± 0.6	28.0 ± 0.2	−1.482
3 chambers, normal	33.2 ± 0.5	27.9 ± 0.3	−1.382
2 chambers, sac-like	33.8 ± 0.2	28.1 ± 0.2	−2.00
2 chambers, sac-like	33.7 ± 0.1	28.0 ± 0.1	−1.37
3 chambers, sac-like	34.0 ± 0.4	28.2 ± 0.2	−1.71
3 chambers, sac-like	33.1 ± 0.6	27.6 ± 0.1	−1.406
3 chambers, sac-like	32.2 ± 0.5	28.0 ± 0.2	−1.592
3 chambers, kummerform	33.1 ± 0.6	28.0 ± 0.2	−1.762
Light 2, 1 BS/day, 36‰			
2 chambers, normal	35.2 ± 0.6	27.9 ± 0.1	−1.79
2 chambers, normal	34.8 ± 0.3	27.8 ± 0.1	−1.60
3 chambers, normal	34.8 ± 0.3	27.8 ± 0.1	−1.71
2 chambers, sac-like	34.9 ± 0.3	27.9 ± 0.1	−2.04
Light 2, 2 BS/day, 36‰			
2 chambers, normal	35.7 ± 0.1	28.0	−1.09
2 chambers, sac-like	35.7 ± 0.1	28.0	−1.51
2 chambers, sac-like	35.7 ± 0.1	28.0	−1.54
3 chambers, sac-like	35.7 ± 0.1	28.0	−1.35
2 chambers, kummerform	35.7 ± 0.1	28.0	−0.97

universa was dominant in our sample, we calculated the sorting index for this species. At upwelling sites it is more than double that of normal or river influenced areas (Fig. 9).

DISCUSSION

The upwelling environment is one of the most extreme biotopes of the pelagic realm. The factors that characterize this environment are manyfold and strongly interconnected. Therefore, we have to extend the discussion a bit beyond our experimental data.

There is a clear relationship between the fertility of a water mass and at least the lower trophic levels of the zooplankton such as planktonic foraminifers. The quantitative link may be obscured because of the time lag caused by the conversion of the phytoplankton into higher trophic levels. In order to understand the response of planktonic foraminifers in upwelling environments we have decoupled the effects of food availability and light quality on test size.

Influence of Increased Prey Density on Test Size

Non-spinose species are preferentially herbivorous and will most likely respond to the increased phytoplankton production. Spinose species, on the other hand, are preferentially carnivorous and will therefore respond to the increased copepod standing stock.

Globigerinoides sacculifer in the tropical Atlantic digests approximately one calanoid copepod per day (Spindler and others, 1984). On the other hand, laboratory experiments have shown that *G. sacculifer, G. siphonifera,* and *O. universa* could digest much more prey if it were offered to them (Bijma and Hemleben, unpublished results). Consequently, increased prey availability in eutrophic areas may lead to a higher feeding frequency. Our data show that increased growth and larger final sizes are attained at higher feeding rates. Especially, *G. siphonifera* form larger shells when they are fed more *Artemia* nauplii. Bé and others (1981) showed that the final test size of *G. sacculifer* increases with increased feeding rate. The reason that the average final test size of *G. sacculifer* was not positively correlated with feeding rate under some conditions in our experiments is probably due to the inclusion of specimens collected with a plankton net. These generally had lower growth rates, remained smaller, and had lower gametogenesis frequencies than SCUBA collected individuals (Table 2, no. 7). We conclude therefore that increased prey availability in high fertility regions tends to increase foraminiferal shell size.

Influence of Light on Test Size

Symbiotic activity may influence the physiology of foraminifers (Caron and others, 1981; Spero and Parker, 1985; Faber and others, 1988, 1989; Spero and Williams, 1989). All spinose species, with the exception of *G. bulloides* and *Hastigerina pelagica* (d'Orbigny), are symbiont bearing (Hemleben and others, 1989). The dinoflagellates that are associated with *G. sacculifer, G. ruber* and *O. universa* were assigned to a new species, *Gymnodinium béii* (Spero, 1987). The symbionts of *G. siphonifera* are much smaller and their fine structure is characteristic for a broad group of yellow-brown algae, collectively known as chrysophycophytes (Faber and others, 1988).

Light intensity

In our experiments the light intensity was kept constant but earlier experiments have shown that the shell size of *G. sacculifer* depends on light intensity (Caron and others, 1981, 1987a). It should be noted that their experiments were carried out under white light and that their high light intensity is 7 to 10-fold stronger than the light intensity used in our experiments. Specimens kept under such high intensities reach final shell sizes that are larger than in natural populations. We may conclude, however, that low light intensities reduce shell size.

Light quality

With the exception of *G. ruber,* smaller tests are formed under high fertility light conditions relative to normal open ocean light conditions (Fig. 2A–D). The comparatively small final size of *G. ruber* under L1 compared to L3 is probably caused by the low food acceptance under L1 (0.2 BS/d) rather than by the difference in light quality.

The larger final sizes found for *G. sacculifer* under L2 as compared to L3 are a result of the slightly larger initial size and may be partly caused by a greater portion of blue-white light that is still present under L2 light conditions. Stunted growth under green or red light as compared to blue or white light of the same photosynthetic photon flux density was also observed in corals (Kinzie and others, 1984). We conclude that the light condition in upwelling environments may reduce shell size.

Pigments

The influence of light depends mainly on the composition and concentration of the light-harvesting pigments such as

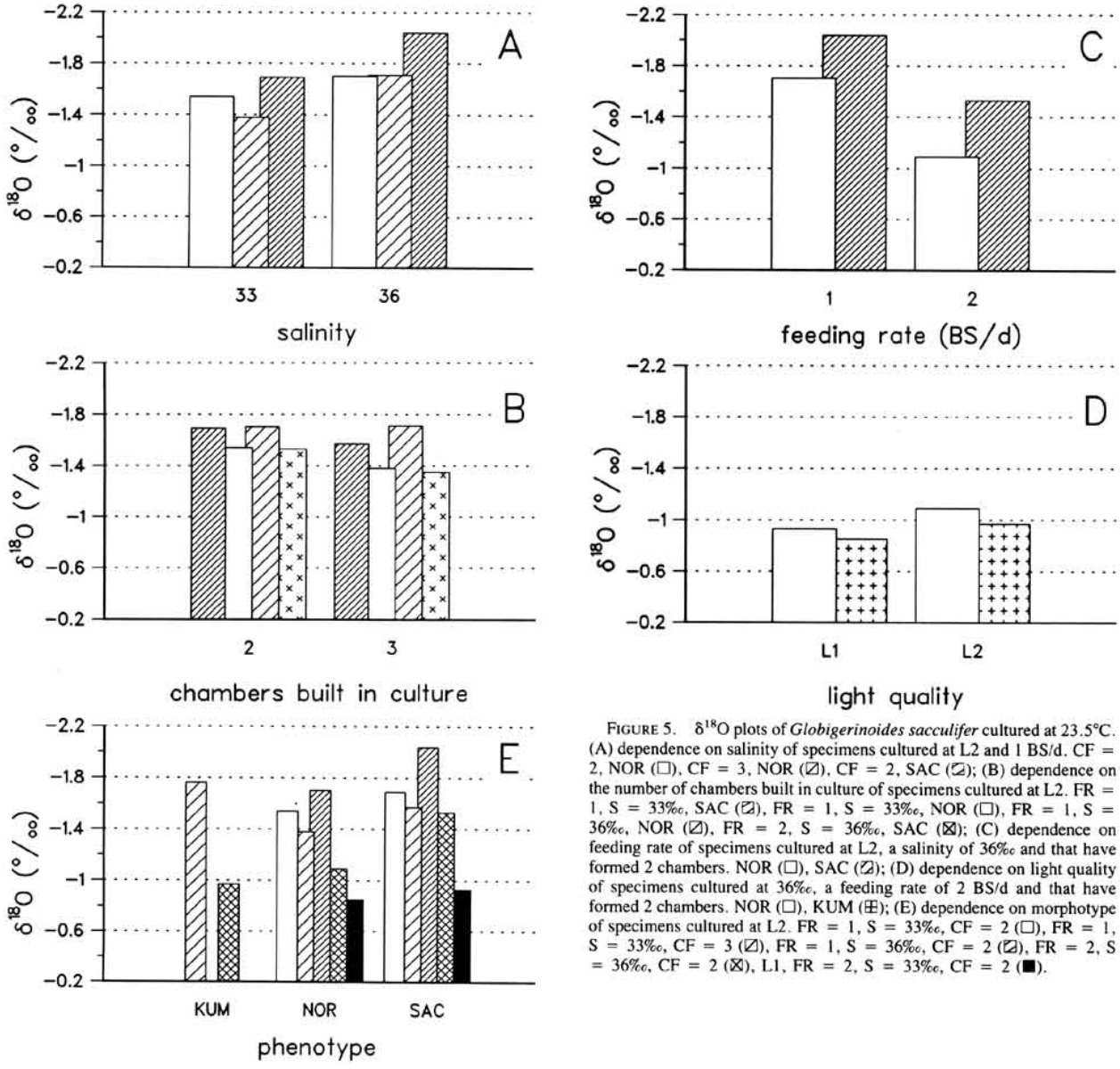

FIGURE 5. $\delta^{18}O$ plots of *Globigerinoides sacculifer* cultured at 23.5°C. (A) dependence on salinity of specimens cultured at L2 and 1 BS/d. CF = 2, NOR (□), CF = 3, NOR (▨), CF = 2, SAC (▨); (B) dependence on the number of chambers built in culture of specimens cultured at L2. FR = 1, S = 33‰, SAC (▨), FR = 1, S = 33‰, NOR (□), FR = 1, S = 36‰, NOR (▨), FR = 2, S = 36‰, SAC (⊠); (C) dependence on feeding rate of specimens cultured at L2, a salinity of 36‰ and that have formed 2 chambers. NOR (□), SAC (▨); (D) dependence on light quality of specimens cultured at 36‰, a feeding rate of 2 BS/d and that have formed 2 chambers. NOR (□), KUM (⊞); (E) dependence on morphotype of specimens cultured at L2. FR = 1, S = 33‰, CF = 2 (□), FR = 1, S = 33‰, CF = 3 (▨), FR = 1, S = 36‰, CF = 2 (▨), FR = 2, S = 36‰, CF = 2 (⊠), L1, FR = 2, S = 33‰, CF = 2 (■).

chlorophyll *a* and carotenoid. Pigment concentrations are influenced by wavelength and may thus indicate a preference for a certain light regime, i.e., depth habitat (e.g., Wallen and Geen; 1971a, 1971b). Among the species studied, the highest chlorophyll *a* content of *G. siphonifera* points to adaptation to the lowest light intensity and thus the deepest habitat. Similarly, the high chlorophyll *a* content of *G. ruber* (white) relative to *G. sacculifer* would indicate that *G. ruber* prefers a deeper habitat. This contradicts the higher light absorption within intact algal cells of *G. sacculifer* as compared to *G. ruber* (pink), which suggests that *G. sacculifer* is adapted to lower light intensities (Hemleben and others, 1989). Field observations also show that *G. sacculifer* lives deeper than both forms of *G. ruber*.

The preference for a certain light environment (depth habitat) may also be inferred from qualitative differences in pigment composition. Although the theory of complementary chromatic adaptation has been criticized (Dring, 1981), the high ratio of carotenoid (absorbing in the green part of the spectrum) to chlorophyll *a* for *G. siphonifera* may also point to a deep habitat of this species. The lower ratio of carotenoid to chlorophyll *a* for both species of *Globigerinoides* suggests optimum absorption in a shallower depth. This is in accordance with reports on the vertical distribution of these species based on plankton tows (e.g., Berger, 1969; Bé and Tolderlund, 1971; Bé, 1977) and on isotope data (e.g., Hecht and Savin, 1970, 1971; Erez and Honjo, 1981; Deuser and others, 1981). *Orbulina universa* lives deeper than *G. sacculifer* (Berger, 1969), but shallower than *G. siphonifera* (Erez and Honjo, 1981). We conclude that *G. siphonifera* is adapted to low intensity and longer wavelength light and that therefore the inhibitory effects of

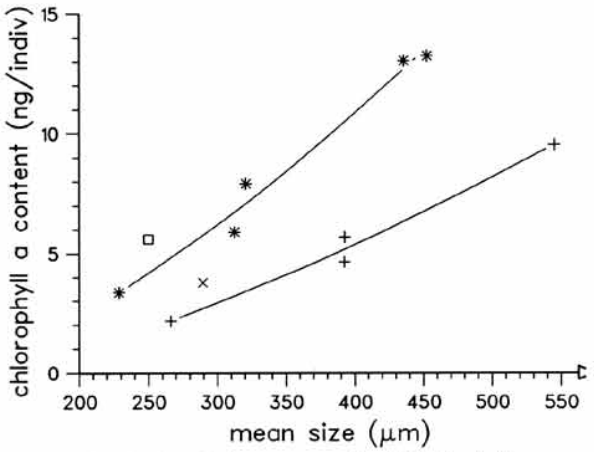

FIGURE 6. Relationship between mean size of *Globigerinoides sacculifer* (+), *G. ruber* (×) and *Globigerinella siphonifera* (*) and the chlorophyll *a* content of their endosymbionts. Gastrich and Bartha (1988) determined for *G. ruber* of 250 μm from the Caribbean Sea a chlorophyll *a* content of 5.6 ng (□).

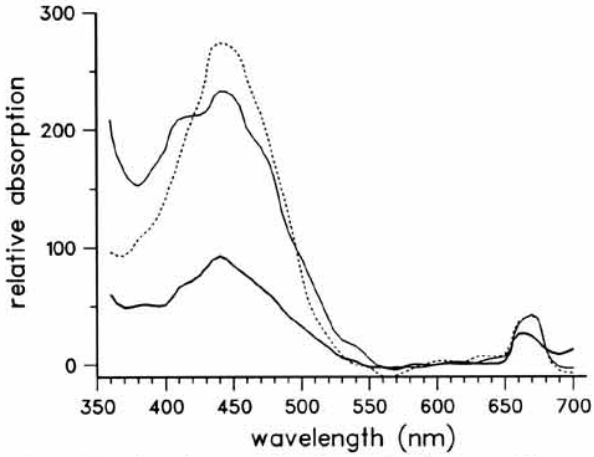

FIGURE 8. Absorption spectra based on methanol extracts of the endosymbionts of *Globigerinoides sacculifer* (−), *G. ruber* (−) and *Globigerinella siphonifera* (. . .). Calibration to zero was done by using the mean absorption between 550 and 650 nm.

high fertility light conditions to increased feeding is smallest in this species.

COMBINED EFFECT OF FEEDING AND LIGHT REGIME ON TEST SIZE

The presence of a species in sediments of upwelling regions, not necessarily implies that it was present in the water column at the time of the year when upwelling occurred. However, the size differences found in this study suggest that the species under investigation grew under different conditions, presumably different water fertilities. Hecht (1974) found anomalously small *G. sacculifer* and *G. ruber* in core-top samples off the coast of West-Africa that he related to the presence of colder waters just beneath the surface, presumably upwelling. Reduction in the shell size of *O. universa* has also been related to upwelling environments (Bé and others, 1973). In agreement with these studies, specimens that have grown in the upwelling region off Benguela are on the average smaller than specimens from areas that are not influenced by upwelling (Table 1).

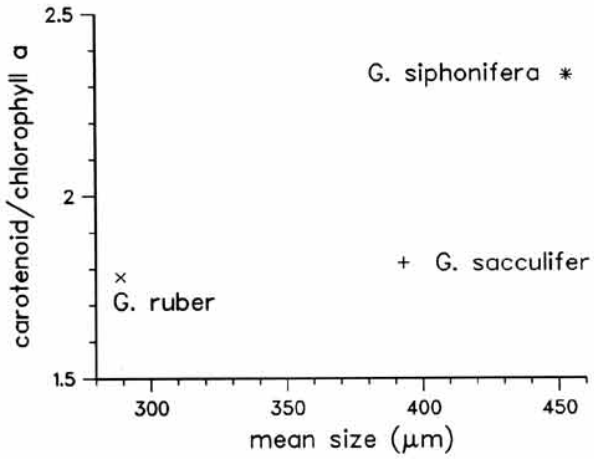

FIGURE 7. Carotenoid to chlorophyll *a* ratio of the endosymbionts as a function of the mean size of the hosts.

In upwelling regions the copepod biomass, is significantly increased relative to open ocean conditions (Weikert, 1982). This food source promotes growth, leading to large shells. The shift to low intensity longer wavelength light, on the other hand, tends to decrease shell size. Consequently, the "light effect" counteracts the effect of high prey densities. At saturation light intensity, *G. sacculifer* is surrounded by an oxygen level of 2.5 times saturation due to photosynthesis of the endosymbionts (Jørgensen and others, 1985). At lower light levels, the oxygen saturation decreases. Thus the hypothesis was raised that symbiont photosynthesis could restrict host respiration and control final test size. Under open ocean conditions, symbiont photosynthesis raises the ambient oxygen concentration and permits fast growth. However, if environmental constrains, such as the light regime in upwelling regions, cut down the photosynthetic activity, the oxygen gradient decreases. As a result, foraminiferal respiration is reduced and specimens remain small. In addition to that, reduced transfer of photosynthates may decrease the biomass of symbiont-bearing species.

Based on the data of Spero and Parker (1985), a photosynthetic quotient of 1.2 (cf. Parsons and others, 1984) and a net photosynthesis to total respiration ratio of 5 (Jørgensen and others, 1985), we calculated that a spherical *O. universa* of 600 μm respires at a rate of about 2 nmol O_2 h^{-1}. This is 30% lower than the total respiration of a *G. sacculifer* of 400 μm (Jørgensen and others, 1985). In other words, these adult symbiont bearing foraminifers require at least 2 nmol O_2 per hour for maintenance and growth.

In the following it will be shown that the photosynthesis of the symbionts cultured under high fertility light conditions proceeds at a rate below the compensation point and that through a decreased oxygen production, the respiration of the host becomes limited under L3. The test is sur-

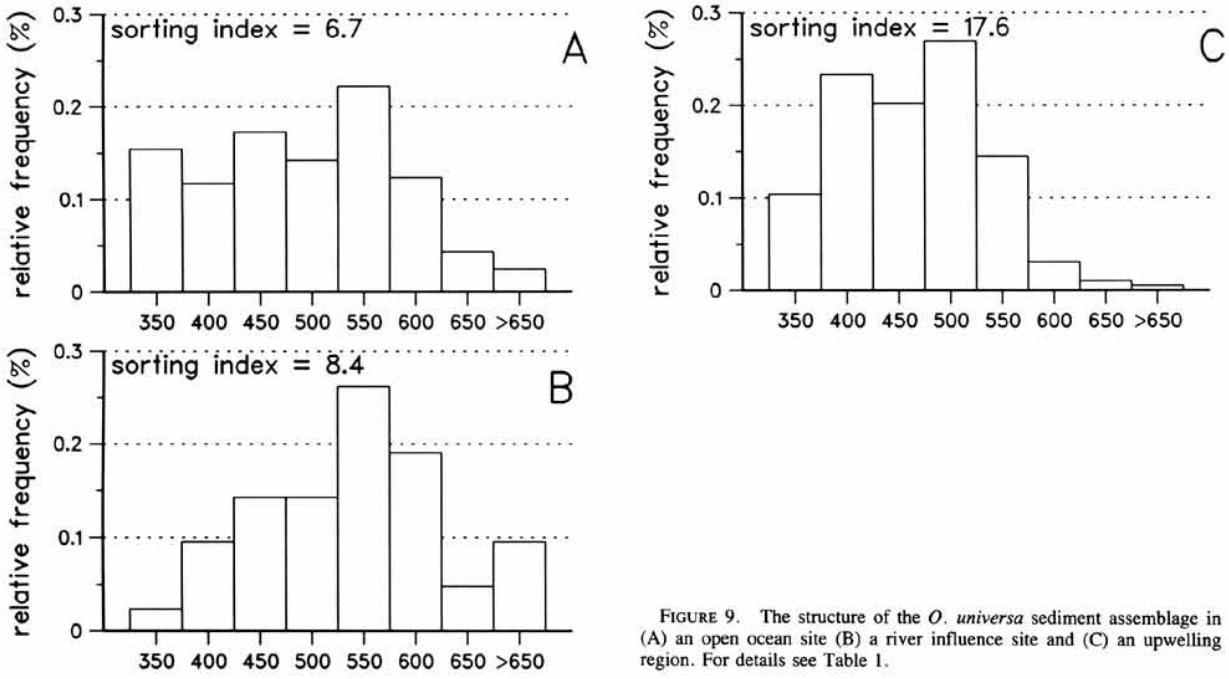

FIGURE 9. The structure of the *O. universa* sediment assemblage in (A) an open ocean site (B) a river influence site and (C) an upwelling region. For details see Table 1.

rounded by spines ($r \approx 1.5$ mm) through which the oxygen diffusion flux F may be calculated: $F = D \times \Delta C/r$. We assume that oxygen is taken up at the highest efficiency, i.e., depletion to zero at the shell surface. Air-saturated water contains only 0.2–0.3 mMol O_2 l^{-1} or 0.25 nMol O_2 mm^{-3}. The O_2 gradient (ΔC) among the spines is then 0.17 nMol O_2 mm^{-1}. The diffusion coefficient (D) of oxygen in seawater of 25°C is 8.46 mm^2 h^{-1} (Broecker and Peng, 1974). The O_2 flux per mm^2 is then: $F = 8.46 \times 0.17/1.5 = 0.96$ nmol O_2 mm^{-2} h^{-1}. The surface area of an *O. universa* of 600 μm in diameter is 1.1 mm^2. The total oxygen flux will thus be 1.06 nmol h^{-1}. This implies that the respiration is limited if the photosynthetic activity of the symbionts does not provide enough oxygen to create a flux of at least 2 nmol O_2 h^{-1}. If, however, oxygen is not taken up 100% efficiently and the ambient water is not saturated, growth may be restricted. We conclude that the light conditions do not limit growth of the host as long as photosynthesis proceeds at rates above the compensation point. The compensation point under yellow-green light is apparently above 50–60 μE m^{-2} sec^{-1}, because at this intensity smaller shells are produced.

Symbiont bearing specimens that grew in the nutrient-enriched vicinity of the Zaire river mouth, reach larger sizes than those that have grown under normal open ocean conditions (Table 1). This observation seems to contradict the mechanism evoked for size control in upwelling areas. Progressive sedimentation of silt in the river plume, increases light transmittance and thus primary productivity. Why then are symbiont bearing foraminifers in these high fertility areas larger than under open ocean conditions? We believe that the reason for this discrepancy lies in the oxygen saturation state of the water. In contrast to upwelled water, which may be markedly undersaturated (Chapman and Shannon, 1985), the oxygen content of the Zaire river is anomalously high (up to 142%) as a result of supersaturation at river rapids (Van Bennekom and others, 1978). This physical supersaturation is not stable but the flow distance from the rapids at Inga to the sea is covered in less than one day and the flushing time of the plume water from 0‰ to 30% salinity is only 2 to 3 days (Eisma and Van Bennekom, 1978; Van Bennekom and others, 1978). Thus, the effects of physical supersaturation could well be detected at some distance from the river mouth where the salinity is high enough to permit growth and reproduction of planktonic foraminifers. The lowest salinities tolerated by planktonic foraminifers are as low as 22‰ to 27‰ (Bijma and others, 1990a). Apparently, the high oxygen content of the plume water permits higher dark respiration rates compared to open ocean conditions and larger shells are constructed despite the low salinity.

The respiration at night normally proceeds at an oxygen level of 50% saturation between the spines of the test (Jørgensen and others, 1985). Because upwelled water may be markedly undersaturated in oxygen, the metabolic rate at night may also be significantly lower in upwelling areas than in open ocean environments, suggesting that symbiont barren species should construct smaller tests under upwelling conditions as well. However, Prell (1984) reported that the average test size of *G. bulloides* increased towards the upwelling maximum in the Arabian Sea. Apparently, the respiration rate of *G. bulloides* in the Arabian Sea is not limited to the extent that higher prey capture rates cannot be converted into additional growth. This phenomenon may explain the opportunistic behavior of this species.

The increased frequencies of herbivorous symbiont-barren species in upwelling regions, such as *Globigerinita glutinata* (Egger) and *Neogloboquadrina dutertrei* (d'Or-

bigny), suggests that their independence of light as well as their higher respiratory quotient (ratio of CO_2 produced to O_2 taken up) that carnivores contribute to their prosperity in those environments.

We conclude that increased food availability increases shell size where the oxygen concentrations do not limit growth and that symbiont-barren, herbivorous, are favored in low oxygen environments.

Other Factors Controlling Test Size

The interplay between the environmental factors that control shell size is complex. For instance, high feeding rates promote growth but under upwelling light conditions, shell sizes remain small. On the other hand, if these dimly lighted eutrophic waters are well oxygenated, shells may again attain larger sizes (Zaire river plume). Other factors such as nutrient concentration, temperature, salinity, life cycle, predation or selective dissolution may control the size of spinose planktonic foraminifers in upwelling regions as well:

(1) The higher nutrient concentrations could increase symbiont productivity and thus contribute to foraminiferal growth as well. However, assuming a photosynthetic quotient of 1 and a Redfield ratio of 106:1 for C:P, Jørgensen and others (1985) calculated that a flux of 0.14 nmol $HPO_4^{=}$ h^{-1} is required to produce balanced growth of the endosymbionts of *G. sacculifer*. Such a flux is reached at an ambient phosphate concentration of 20 μmol l^{-1}. However, even in upwelling areas, reactive phosphorus concentrations do generally not exceed 1.5 μmol l^{-1} (Codispoti and Friederich, 1978). In other words, the endosymbionts are highly diffusion-limited even under eutrophic circumstances.

(2) Temperature departures from the optimum result in a reduction of a final size of *G. sacculifer* (Caron and others, 1987a; Hemleben and others, 1987). A temperature decrease from 26.5°C to 19.5°C and from 25°C to 19.5°C resulted in a reduction of the final test size of 16% (Hemleben and others, 1987) and 13% (Caron and others, 1987a) respectively. A decrease in culture temperature from 25°C to 19.5°C also resulted in a reduction of the final sphere diameter of *O. universa*, by 11% (Caron and others, 1987b). Thus large shell sizes are generally attained under high temperatures. If, however, feeding rates are high, large shells may be secreted under lower temperatures as well.

(3) Spinose planktonic foraminifers from the highly saline Red Sea attain large sizes even though they receive little food. A salinity reduction from 36‰ to 33‰ resulted in a 5% smaller test in *G. sacculifer* (Hemleben and others, 1987).

Thus, the slightly lower salinity as well as the lowered temperatures of upwelled water also contribute to size reduction of planktonic foraminifers in upwelling environments. The other factors that can be evoked to explain size reduction, are discounted here as follows:

(4) In some benthic foraminifers small sizes indicate optimum conditions of growth which cause rapid maturity and the early onset of reproduction (Bradshaw, 1957). However, the life-spans of the planktonic species under investigation are fixed because their reproduction is triggered by certain phases of the moon (Bijma and others, 1990b) and a small average size can thus not be attributed to early onset of reproduction.

(5) Predation might differ in upwelling and non-upwelling areas resulting in the observed size differences. Unfortunately, we have little knowledge of what feeds on foraminifers, so that it is futile to speculate on this subject (Hemleben and others, 1989), but it is difficult to conceive of predators that would produce the degree of size selectivity exhibited for the upwelling area. Because the spheres of *O. universa* which have definitely reached maturity and thus avoided predation, show significant differences in the sphere diameters between the three study areas, we conclude that selective predation does not contribute to the development of the observed size differences.

(6) Selective dissolution might cause the size differences between high fertility areas and open ocean sites. Whereas the sediments below 1533 m depth in profile A, below 1638 m depth in profile B and below 1965 m depth in profile C show strong carbonate dissolution (Wefer and others, 1988), it does not seem likely that selective dissolution removes smaller specimens from the sediment influenced by the Zaire river and larger specimens from the sediment under the upwelling area. Although we cannot exclude the possibility of winnowing, we believe that the disparity between the three profiles can best be ascribed to differences in the respective habitats.

Influence of Water Fertility on Final Chamber Morphology

The average abundance of sac-like chambers was inversely related to the feeding rate but kummerform formation was independent of the feeding rate. The frequencies of sac-like chamber formation, generally below 50%, coincides with those found by Hemleben and others (1987) for experimental as well as for sediment specimens off Barbados. In agreement with Hemleben and others (1987), we could not detect any relationship between sac-like chamber formation and temperature or salinity.

Sac-like chambers are secreted less frequently under high fertility light conditions than under blue-water light conditions. Under yellow-green light conditions all species (except spiral *O. universa*) form more kummerform chambers. *Orbulina universa* secretes a higher percentage of "Biorbulina." *Globigerinoides ruber* is most tolerant of low salinity conditions (Bijma and others, 1990a) and is therefore relatively frequent in the sediment off the Zaire river mouth. There, the kummerform production of *G. ruber* is highest.

In conclusion, planktonic foraminiferal assemblages in sediments under high fertility regions are expected to be characterized by a higher frequency of sac-like chambers, a higher incidence of kummerform chambers, and a higher "Biorbulina" production relative to assemblages from nearby open ocean sediments. The morphological response under high fertility conditions is probably not related directly to the environmental parameters but is a reaction to reproductive constraints under these conditions, because the occurrence of kummerform and sac-like terminal features is

linked to reproduction (Bé, 1965; Berger, 1970; Hemleben and others, 1989; Bijma and others, 1990b).

Influence of Water Fertility on the Population Structure

The sorting index that normally describes a sedimentary grain-size distribution may also be used to characterize the structure of an assemblage with respect to the spread and the evenness of the size distribution (e.g., Kennett, 1968). As the number of *O. universa* in our reference sediment was large enough to produce statistically significant size differences, we used this species to describe the structure of the sediment assemblage at the three sites by means of the sorting index. Because the spread of the size distribution was comparable for the three sites, the differences in the sorting index must be explained by differences in the evenness (Fig. 9). Apparently, populations at the open ocean site and in the region influenced by the Zaire river are more evenly distributed than populations at the upwelling site. This is a direct consequence of the smaller mean size in upwelling areas.

The $\delta^{18}O$ Composition of Foraminifera in Upwelling Environments

The question is raised whether *G. sacculifer* (1) secretes its calcitic tests in isotopic equilibrium or whether (2) its fractionation behavior is influenced by light quality and feeding rate. The tests that were selected for isotope analysis had identical morphological features and comparable final sizes. Thus, the spread of values between the various experiments is neither caused by any morphological criterion nor by the final size reached in culture. As the same culture water was used for the different experiments and evaporation was minimized, the scatter in the $\delta^{18}O$ data may be explained in terms of vital effect.

The mean $\delta^{18}O$ of the culture water was -0.8 ± 0.35 ($n = 8$). The equilibrium value of the calcitic tests is thus -0.58. Obviously, the shells are not secreted in isotopic equilibrium and the observed variation in the $\delta^{18}O$ between the different experimental dispositions originates from differences in fractionation. Additionally, some of the variation may be due to unknown environmental conditions during "pre-culture" growth (e.g., migration through different depth habitats during the juvenile and neanic stages).

Since the variation of the isotopic ratios within an experiment is maximally half of the variation between different experiments, we conclude that *G. sacculifer* discriminates between the two isotopes. Apparently, the biological fractionation of the symbiont-host system is dependent on the culture conditions. In addition to the well established effects of temperature and salinity, at least two other environmental parameters influence the oxygen isotope signal. Tests are isotopically lighter under upwelling light than under blue water light conditions (Fig. 5D). In contrast, higher feeding rates are associated with more positive isotope values (Fig. 5C). In upwelling regions both conditions occur simultaneously.

In our culture experiments kummerforms were generally isotopically heavier than normal morphotypes (Fig. 5E). This is in agreement with the results from core top samples studied by Hecht and Savin (1970; 1971). The fact, however, that the different morphotypes are secreted under identical culture temperature invalidates their environmental stress model (Hecht, 1975). Apparently, the variation results from a different fractionation behavior of the morphotypes.

CONCLUSIONS

It was shown that in addition to temperature and salinity, food availability, light intensity and quality, and the oxygen content of the ambient water influence shell size and morphology of *G. sacculifer, G. ruber, G. siphonifera* and *O. universa* to an important extent. In addition to known paleontological characteristics of sediments in high fertility regions, the following conclusions may help to identify the paleoproductivity and origin of the overlying water on the basis of sediment analysis:

1. Higher prey densities lead to a larger final test size and long wavelength low intensity light conditions lead to a smaller final test size in the species investigated.
2. Light-limited photosynthesis of the endosymbionts reduces the oxygen concentration between the spines which in turn lowers the respiration rate of the foraminiferal host. As a result, symbiont-bearing species reach a smaller final shell size in upwelling areas relative to regions where photosynthesis is uninhibited.
3. Where high fertility is not combined with a low oxygen saturation level such as the region influenced by the Zaire river, larger than normal shells are found (e.g., *O. universa*).
4. The combination of high prey density and long wavelength, low intensity light give rise to smaller than normal tests in upwelling settings but larger than normal tests in the region influenced by the Zaire river.
5. A high frequency of kummerforms, sac-like chambers, and "Biorbulina" may indicate increased fertility.
6. The "sorting-index" of an *O. universa* population from an upwelling region is higher than those for *O. universa* populations from open ocean or river influenced environments.
7. In tropical or subtropical areas an increase of *G. ruber* in a coastal sediment assemblage may indicate the influence of fresh water.
8. *Globigerinoides sacculifer* does not secrete calcite in oxygen isotopic equilibrium ambient seawater. The oxygen isotope ratios of the tests of *G. sacculifer* tend to lighter values in yellow-green light but to heavier values at higher prey capture rates.

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