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Marine Micropaleontology 50 (2004) 319–338
MARINE MICROPALEONTOLOGY
www.elsevier.com/locate/marmicro

Size distribution of Holocene planktic foraminifer assemblages: biogeography, ecology and adaptation

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Received 17 March 2003; received in revised form 28 July 2003; accepted 30 July 2003

Abstract

The size of any organism is influenced by the surrounding ecological conditions. In this study, we investigate the effects of such factors on the size spectra of planktic foraminiferal assemblages from Holocene surface sediments. We analyzed assemblages from 69 Holocene samples, which cover the major physical and chemical gradients of the oceans. On a global scale, the range of sizes in assemblages triples from the poles to the tropics. This general temperature-related size increase is interrupted by smaller sizes at temperatures characteristic of the polar and subtropical fronts, at 2°C and 17°C, respectively, as well as in upwelling areas. On a regional scale, surface water stratification, seasonality and primary productivity are highly correlated with the size patterns. Such environmentally controlled size changes are not only characteristic for entire assemblage, but also for the dominant single species.

Keywords: planktic foraminifera; morphometrics; size; biogeography; Holocene; paleoenvironment

1. Introduction

Size is an obvious morphological characteristic, readily preserved in fossils, easy to measure, conspicuous, ecologically important, comparable across taxa and extremely variable in time and space. Consequently, this parameter has been studied for several groups of organisms (Peters, 1983; Skelton, 1993; Futuyma, 1998). Much of this work has focused on terrestrial animals, showing both the role of ecology (Bergmann's rule, i.e. increase in body-size towards high latitudes) and evolution (Cope's law, i.e. increase in body-size along a lineage). Fewer studies have addressed the factors influencing size of marine organisms. Recent examples have identified oxygen availability as controlling size in amphipods (Chapelle and Peck, 1999; Peck, 2001), benthic foraminifers (Kaiho, 1998), and gastropods (McClain and Rex, 2001).

Planktic foraminifers, because of their wide

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doi:10.1016/S0377-8398(03)00098-7

geographical occurrence, allow global studies of ecological and evolutionary influences on size. Size changes in modern planktic foraminiferal species have been related to ecological factors such as temperature (Bé et al., 1973; Hecht, 1976) and upwelling intensity (Naidu and Malmgren, 1995). From an evolutionary point of view, foraminifers as a group have undergone at least three periods of diversification since their origin in the Mid-Jurassic (Loeblich and Tappan, 1985), each of which is thought to have involved a general increase in test size (Arnold et al., 1995).

Understanding the repetitive morphological evolutionary radiation of foraminifers in the Cenozoic demands a test of various ecological factors influencing test size. The goal of this study is to provide a calibration which will allow to quantify and attempt to understand the paleoecological, paleobiogeographical and evolutionary significance of size variability in planktic foraminiferal in the past.

Most studies of evolutionary size changes in planktic foraminifers focused on single species or lineages (e.g. Malmgren and Kennett, 1981; Arnold, 1983; Malmgren et al., 1983; Spencer-Cervato and Thierstein, 1997; Kucera and Malmgren, 1998; MacLeod et al., 2000). Single species or lineages have provided regional ecological and stratigraphic information on size change. Analyses of entire planktic foraminiferal assemblages, which integrate information of all individual species, hold the potential for giving insights into long-term macro-evolutionary processes or potential global environmental changes. The only attempt to study Cenozoic size variation of the entire group of planktic foraminifers (Arnold et al., 1995; Parker et al., 1999) was based on analyses of one specimen per species, restricting the reliability of the results.

In order to understand the ecological significance of size variability we have studied planktic foraminifer assemblages in a Holocene data set as an important step towards an analysis of size changes of planktic foraminifers in Quaternary (Schmidt et al., 2003) and the late Phanerozoic. We can expect test sizes of total planktic foraminiferal assemblages to be the result of various processes acting on at least three different scales. (1) They have been found to be influenced by the physical and chemical properties of the ambient sea water, such as temperature, salinity, nutrient availability, carbonate saturation, and oxygen availability (e.g. Berger, 1969; Bé and Tolderlund, 1971; Caron et al., 1981; Caron et al., 1987a; Bijma et al., 1992; Schiebel et al., 2001). If so, size ought to depend on these factors on a global scale. (2) Biogeographic differences in species composition and diversity have been well documented (Bé and Tolderlund, 1971; Hemleben et al., 1989). Since individual species show distinct size variability (Hecht, 1976), biogeographic changes in species composition may lead to size changes of the entire assemblages. (3) Test sizes of populations of individual species are known to vary with environmental factors (Hecht, 1976; Ortiz et al., 1995; Naidu and Malmgren, 1996) with size maxima at distinct environmental conditions. Size changes of the entire planktic foraminiferal assemblages may therefore represent a composite of size spectra of various species, which may have lived at or outside their environmental optima.

2. Materials and methods

2.1. Materials

We have selected a set of 69 surface sediment samples (Fig. 1) covering all biogeographic zones which were defined based on the species composition of planktic foraminifers (Bé and Tolderlund, 1971; Hemleben et al., 1989). A large subset of these samples has previously been used for the Holocene calibration of the CLIMAP study (CLIMAP, 1981). The samples are from water depths of 808–4825 m (mean of 3000 m) and show no signs of dissolution and few non-foraminiferal particles. The samples cover the major physical and chemical gradients of the world's oceans (Table 1, an extended version of Table 1 is available at http://www.pangaea.de/PangaVista?query=@Ref25175). The selection is biased towards the Atlantic, since the greater water depth, and hence dissolution, prevents us from using samples from large areas of the Pacific and Indic.

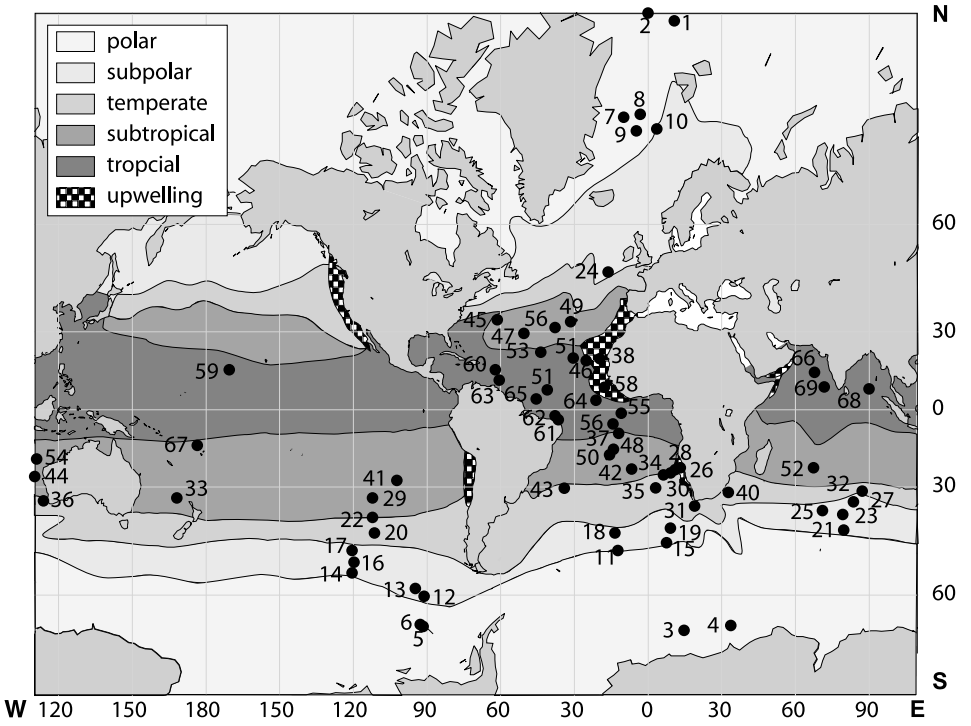

Fig. 1. Sample locations. Biogeographic areas are based on Bé and Tolderlund (1971) and Hemleben et al. (1989).

The fraction larger than 150 μm was used for analysis to allow for species recognition on digitized images and to exclude pre-adult ontogenetic changes in test form (Brummer et al., 1987). Using the same size fraction as the global taxonomic data set of Prell et al. (1999) also allows direct comparison with their relative abundance data.

2.2. Size measurements

To characterize the size distribution within an entire assemblage, a complete split of each sample was analyzed, a mean of 1667 individuals (minimum 685, maximum 3797 individuals), in total 114 991 measurements. The assembly of such a large morphometric data set was possible by applying a system for automated test outline extraction (Bollmann et al., in press) The system consists of a CCD video camera attached to an incident light stereomicroscope equipped with a motorized stage (Bollmann et al., in press). Foraminifers are strewn on a glass tray, and are hence not oriented. A predefined area was scanned and all images were saved. The maximum diameter of the object was chosen as the most suitable size estimator, because it is least affected by random orientation. The resolution of the images at the applied magnification of 160× is 3.31 μm per pixel.

In order to test the accuracy and the reproducibility of size measurements, standard glass microbeads have been analyzed (mean diameter with standard deviation of 168 ± 7.4 μm, 331 ± 14.1 μm, and 655 ± 29.0 μm, Duke Scientific co-operation). Repeated preparations and measurements of these microbeads showed a good reproducibility and an accuracy (172 ± 5.1 μm; 330 ± 3.51 μm; 636 ± 24.2 μm) of mean diameter for all microbeads. The reproducibility of 10 times repeated measurements of a natural foraminiferal sample of the mean size of the distribution is ± 4.1 μm, that of the median is ± 3.9 μm and that of the 95-percentile is ± 9.71 μm, which represents an error range of 1.5–2.2%.

Aggregates, detrital grains, pteropods and sponge spicules could be identified based on their

Table 1
Station numbers and characteristics of samples

Sta. No.	Label	Zone	Lat (deg)	Long (deg)	Depth (m)	dbsf (cm)	N	Sr	Size (μm)	T_0 (°C)	T_{seas} (°C)	ΔT (°C)	PP (g C m^{-2} a^{-1})	PP_{seas} (g C m^{-2} a^{-1})
1	PS2192	1	88.3	9.9	4375	0–1	1670	2	330	−1.2	1.3	−0.90	86.5	45.5
2	PS2190	1	90.0	0.0	4240	0–1	2051	2	318	−1.1	2.5	−0.60	77	36
3	PS1815	1	−65.2	34.3	1526	0–1	1435		352	0.2	2.8	0.04	20.5	13.5
4	PS1829	1	−65.8	14.1	2859	0–1	1208	2	339	0.3	3.3	−0.23	20.5	13.5
5	PS2690	1	−65.4	−90.8	2404	0–1	3306		317	0.6	3.1	−0.01	42	19.5
6	PS2695	1	−65.2	−92.7	3316	0–1	1226		319	0.7	3.5	0.09	51	19.5
7	PS1893	1	74.9	−10.1	3247	0–1	2418	3	277	0.8	4.5	0.48	50	22.5
8	PS1901	1	75.9	−3.7	3569	0–1	2496	5	281	1.1	4.5	0.66	63.5	36
9	PS1736	1	74.3	−5.2	3460	0–1	1763	5	289	1.6	4.9	1.19	63.5	36
10	PS1912	2	74.6	3.0	3704	0–1	2893	3	268	2.7	4.8	1.61	77	36
11	PS1778	2	−49.0	−12.7	3380	0–1	1226	9	380	3.9	2.2	1.68	43.5	15.5
12	PS2703	2	−59.4	−91.2	2747	0–1	1955	4	420	4.2	2.1	1.13	59	15.5
13	PS2676	2	−58.2	−94.6	2700	0–1	2032		380	4.7	2.5	1.13	58	16.5
14	E33-22	2	−54.9	−120.0	2743	0–3	1849		441	5.6	2.4	1.18	57	17.5
15	PS1754	2	−46.8	7.6	2471	0–1	1506	9	418	6.4	4.0	2.37	61	15.5
16	E21-15	2	−52.0	−120.0	2999	4–7	2230		420	6.6	3.1	1.08	61	15.5
17	E21-14	2	−49.0	−120.1	3319	0–3	2398		420	8.9	2.9	1.59	66	15.5
18	PS2498	2	−44.2	−14.20	3782	0–1	1137	10	492	10.1	5.2	3.12	47.5	11
19	PS2489	2	−42.8	9.0	3795	0–1	776	6	517	10.1	3.8	2.61	76.5	13.5
20	E20-18	3	−44.3	−111.2	2868	6–8	3163	20	441	11.2	6.7	3.95	72	18
21	RC11-120	2	−43.5	79.9	3193	0–1	2127	14	409	11.4	2.1	0.90	76.5	13.5
22	E21-11	3	−39.9	−112.2	2798	0–3	2627		445	14.0	6.1	5.21	72	6.5
23	E48-27	2	−38.3	79.5	3283	1–4	1417	15	374	14.4	5.4	1.87	85.5	13.5
24	MC 440	3	49.0	−16.5	4825	0–0.5	3011	17	369	14.5	5.8	3.12	166	51.5
25	RC11-118	3	−37.8	71.5	4354	0–1	727	16	389	15.4	4.8	2.36	86	18.5
26	GeoB1710	6	−23.4	11.7	2987	0–1	973	13	392	17.6	4.2	5.65	128	22.5
27	E48-31	2	−34.5	84.1	3639	3–5	1405	17	397	17.8	8.4	5.10	85.5	9
28	GeoB1709	6	−23.6	10.8	3837	0–1	685	12	387	18.0	4.4	5.83	114.5	17.5
29	RC 8-91	4	−33.4	−111.9	2723	1–5	677	26	414	18.2	5.6	4.69	58.5	4.5
30	GeoB1212	6	−24.2	8.1	4669	0–1	2629	21	377	19.1	5.0	6.16	92	7
31	PS2487	3	−35.8	18.1	2942	0–1	1536	17	436	19.4	4.4	6.15	81	9
32	E48-36	3	−30.9	87.8	1366	2–4	1713	22	393	19.4	7.5	6.09	72	9
33	RC 9-126	4	−33.2	168.7	2060	1–5	2621	18	402	19.5	5.0	8.47	116	9.5
34	GeoB1204	3	−25.0	5.5	2241	0–1	2680	22	539	19.8	5.1	6.12	97	12
35	V27-215	3	−29.5	2.2	2692	2–3	946	20	464	20.0	5.2	5.57	81	9
36	RC 9-150	4	−31.2	114.3	2703	0–2	2031	20	521	20.2	3.5	5.01	113.5	9.5
37	INDM 65	3	34.4	−29.6	1959	0–1	1585	20	556	20.4	7.1	4.72	81	9
38	GeoB1048	6	20.9	−19.7	3635	0–1	1640	17	391	21.1	4.7	6.08	441	54
39	INDM 51	4	31.6	−37.8	3895	0–1	1587	17	463	21.7	6.9	4.11	81	4.5
40	RC17-69	4	−31.3	32.4	3380	0–1	1127	24	479	22.2	4.7	5.30	113.5	9.5
41	RC 8-94	4	−27.3	−102.1	3074	2	1889	19	531	22.4	5.2	4.85	67.5	9
42	V12-66	4	−22.9	−7.0	2760	0–1	1345	19	419	22.4	5.0	7.17	81	9
43	INDM127	4	−29.9	−34.0	2509	0–1	1300	20	516	22.5	5.7	6.45	72	9
44	RC11-145	4	−25.5	110.0	3869	0–1	645	19	519	22.6	3.4	5.34	111	9.5
45	V 7-67	4	34.7	−61.5	4308	6–7	990	19	640	22.8	7.9	4.63	110.5	13.5
46	V23-101	5	19.5	−25.3	4482	1–2	1322	19	544	23.0	4.0	6.99	182.5	29
47	V16-209	4	30.0	−51.5	4673	0–1	2875	19	536	23.4	6.9	5.09	81	4.5
48	INDM115	4	−17.6	−16.2	3452	0–3	1457	24	534	23.7	3.7	7.81	94.5	4.5
49	INDM110	4	−10.0	−13.4	3063	1–2	2122	22	595	23.7	3.1	10.85	94.5	4.5
50	GeoB5142	4	−19.1	−17.2	3946	0–1	1413	24	445	23.8	4.5	7.40	76.5	9
51	V22-211	4	20.4	−31.3	4402	0–1	811	22	669	23.8	3.5	6.23	101	11
52	V20-175	4	−22.2	68.0	3526	0–1	1032	19	564	24.1	4.9	5.54	81	9
53	V10-89	4	23.0	−43.8	3523	0–1	1057	21	492	24.8	3.8	5.72	76.5	9
54	RC11-147	4	−19.0	112.5	1953	0–1	2716	20	592	25.7	4.2	7.26	115	13.5
55	GeoB1104	5	−1.2	−10.7	3755	0–1	1314	19	515	25.8	5.1	12.61	217	32
56	INDM109	5	−5.5	−16.0	3659	1–2	1123	18	635	26.2	3.8	14.50	204	35.5
57	V22-26	5	8.7	−41.2	3720	0–1	1245	18	578	26.4	2.2	15.76	127	9
58	V26-46	6	9.6	−18.2	2898	5–6	1802	21	508	26.4	7.1	6.82	81	4.5
59	V28-195	5	16.6	−169.8	2439	0–1	2602	25	739	26.6	2.3	8.47	85.5	4.5

Table 1 (*Continued*).

Sta. No.	Label	Zone	Lat (deg)	Long (deg)	Depth (m)	dbsf (cm)	N	Sr	Size (μm)	T_0 (°C)	T_{seas} (°C)	ΔT (°C)	PP (g C m^{-2} a^{-1})	PP_{seas} (g C m^{-2} a^{-1})
60	M35006	5	16.3	−62.3	808	0–2	1162	10	534	27.1	2.7	7.64	113	2.5
61	V20-228	5	−2.5	−36.4	3676	2–3	1389	15	630	27.2	1.9	14.10	103.5	13.5
62	GeoB3915	5	−2.3	−38.0	3127	0–1	784	15	533	27.2	1.9	13.80	103.5	13.5
63	M35003	5	12.1	−61.1	1301	0–1	1040	14	514	27.3	2.4	11.08	211	29
64	INDM104	5	4.3	−21.3	3247	0–1	1174	21	688	27.5	1.6	14.18	159.5	20.5
65	RC11-10	5	4.6	−45.6	3834	3–4	1281	16	631	27.5	1.0	14.86	106	7
66	MC 398	5	15.6	68.6	3837	0.5–1	1003	19	573	28.0	4.0	11.61	182	33
67	RC13-38	4	−14.2	177.1	2867	5	4231	24	474	28.3	2.2	6.99	90	0
68	RC12-339	5	9.1	90.0	3010	4–5	842	18	628	28.4	2.3	14.50	131	6.5
69	RC17-125	5	9.6	72.8	1734	0–1	1816	23	550	28.7	2.6	13.96	163	9.5

Station number (Sta. No.) (see Fig. 1), sample label ordered by increasing temperature, biogeographic zone (1 = polar, 2 = subpolar, 3 = temperate, 4 = subtropical, 5 = tropical, 6 = upwelling), geographic latitude (lat) and longitude (long), negative values refer to southern latitude respectively western longitude, water depth (depth), depth below sea floor (dbsf), number of size measurements (N), species richness (Sr) (Niebler, 1995; Prell et al., 1999; Schmuker, 2000), $size_{assemblage5}$ (size) (i.e. size measure separating the largest 5% of the assemblage from the rest), average annual sea surface temperature (T_0), maximum seasonal temperature difference (T_{seas}), difference between average annual temperature at 0 and 200 m water depth (ΔT), average primary productivity (PP), maximum seasonal difference in primary productivity (PP_{seas}). All physico-chemical environmental data have been taken from Levitus et al. (1994), and primary productivity from Antoine et al. (1996).

distinct gray values and shape factors (perimeter to area ratio) and discharged from the data set. Based on these parameters, planktic foraminifers could not be distinguished from benthic foraminifers and carbonate grains of comparable size and shape. Since benthic foraminifers usually make up less than 1% in a well-preserved deep-sea sample, their contribution is minimal.

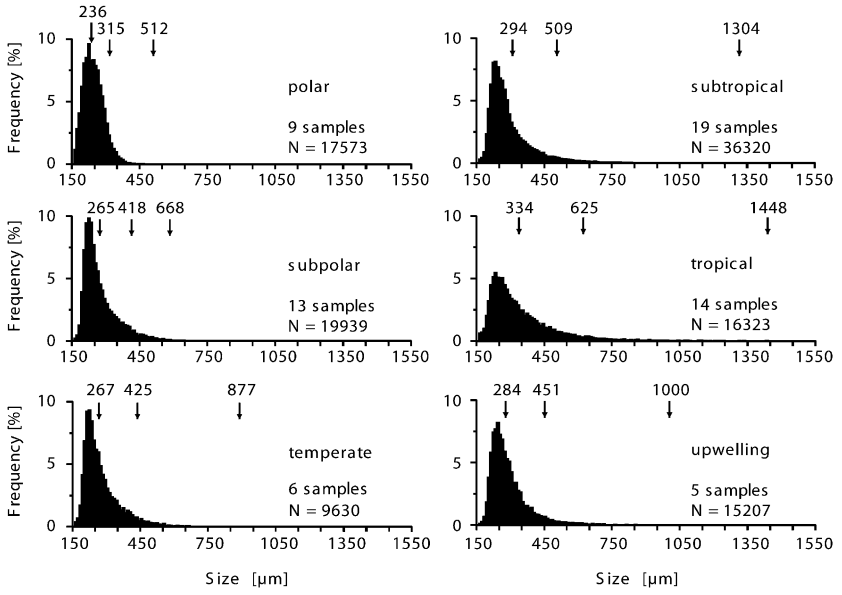

Fig. 2. Size distribution within biogeographic zones. Each histogram shows measurements of all individuals within a biogeographic zone. The arrows indicate, from the left to the right, average, 95-percentile (i.e. size separating the 5% largest tests from the rest) and maximum of the zonal size distribution with the corresponding values (N = number of measurements, bin widths = 10 μm).

Table 2
Mean and maximum sizes (μm) of dominant species found within the largest 5% of the Holocene assemblages analyzed

Sta. No.	Label	T_0	PP_{ann}	pachy count	pachy sp_5	pachy max	bulloides sp_5	bulloides max	trunc sp_5	trunc max	inflata sp_5	inflata max	hirsuta sp_5	hirsuta max	menardii sp_5	menardii max
1	PS2192	-1.2	86.5			397										
2	PS2190	-1.1	77			369										
3	PS1815	0.3	20.5	69	379	475										
4	PS1829	0.3	20.5			410										
6	PS2695	0.7	51			393										
7	PS1893	0.8	50			319										
8	PS1901	1.1	63.5			348										
9	PS1736	1.6	63.5			329										
10	PS1912	2.7	77	106	264	317	291	301								
11	PS1778	3.9	43.5					520				482				
12	PS2703	4.2	59					598		557		568				
13	PS2676	4.7	58					549				539				
14	E33-22	5.6	57	88			516	668	541	591	500	614				
15	PS1754	6.4	61					644				611				
16	E21-15	6.6	61					625		556		644				
17	E21-14	8.9	66					582				512				
18	PS2498	10.5	47.5	57			582	718		567	525	579				
20	E20-18	11.2	72					645		692						
21	RC11-120	11.4	76.5			591		625				669				
22	E21-11	14.0	72					649		567		574				
23	E48-27	14.4	85.5	70			402	442	454	548	420	533		490		
24	MC 440	14.5	166					554		633		564				
26	GeoB1710	17.6	128									557				948
27	E48-31	17.7	85.5	69				301	455	558	430	470	535	678		
29	RC 8-91	18.2	58.5							654		664				
31	PS2487	19.4	81									583		638		587
32	E48-36	19.4	72					482		628		479				
33	RC 9-126	19.5	116							668						
34	GeoB1204	19.8	97							837						1000
35	V27-215	20.0	81	43					563	711	493	545	590	696		
36	RC9-150	20.2	114													1024
37	INDM 65	20.4	81							763				744		
38	GeoB1048	21.1	441									694		522		546		689
39	INDM 51	21.7	81									800				761		
40	RC17-69	22.2	114									737				741		755
41	RC8-94	22.4	67.5									727						
42	V12-66	22.4	81	66								528	792	449	517	480	499	818
43	INDM127	22.5	72									787						983
44	RC11-145	22.6	111															1096
45	V7-67	22.8	111	46								741	835		662	24	889	853 1071
46	V23-101	23.0	183															944
47	V16-209	23.4	81									835						861
48	INDM115	23.7	94.5									765						1108
49	INDM110	23.7	94.5															1106
50	GeoB5142	23.8	76.5	70								555	759	540	549			596 694
51	V22-211	23.8	101	40			754	843				708						859 1080
52	V20-175	24.1	81									821						
53	V10-89	24.8	76.5									765						
54	RC11-147	25.7	115														634	1383
55	GeoB1104	25.8	217	59	529	601	674					548						841 1216
56	INDM109	26.2	204															
57	V22-26	26.4	127															1286
58	V26-46	26.4	81															1029
59	V28-195	26.9	85.5	95														936 1340
60	M35006	27.1	113									809						796
61	V20-228	27.2	104															1322
62	GeoB3915	27.2	104															845
63	M35003	27.3	211	47														762 1103
64	INDM104	27.5	160	162				528										1044 1323
65	RC11-10	27.7	106															1448
66	MC 398	27.9	182	192														942 1298
67	RC13-38	28.3	90															840
68	RC12-399	28.4	131	41			726	779										1086 1430
	Present in # of samples			12			21		31		26		11		30			

Station number (Sta. No.), core designation (label), number of taxonomically identified specimens/individuals in 17 environmental representative samples (count), their average size (sp_5) and maximum size (max), for: *N. pachyderma* (pachy), *G. bulloides* (bulloides), *G. truncatulinoides* (trunc), *G. inflata* (inflata), *G. hirsuta* (hirsuta), *G. menardii* (menardii), *G. tumida* (tumida), *G. ruber* (ruber), *G. sacculifer* (sacculifer), *G. conglobatus* (conglob), *O. universa* (universa), *P. obliquiloculata* (pull). The (max) refers also to the maximum size of a species within the 12 largest individuals of an assemblage for all samples. For abbreviations see Table 1.

2.3. Data analysis

To characterize the size distribution in an assemblage, the mean, median, the 95-percentile ($size_{assemblage5}$), and the maximum were determined. Natural foraminifer populations, because of their serial chamber additions, must start with the largest number of individuals in the size class of the first chamber, which ranges from 7 to 54 μm (Hemleben et al., 1989). Because of differential mortality, the size distribution may deviate from an exponentially decreasing size distribution. The minimum size in our data set, as given by the mesh size of 150 μm, represents an artificial cut-off of the natural size distribution, and therefore does not have any biological significance. Since the distributions are highly skewed towards large sizes (Fig. 2), the most suitable descriptor is the

Table 2 (*Continued*).

		tumida		ruber		sacculifer		conglob		universa		pull	
Sta. No.		sp_5	max	sp_5	max	sp_5	max	sp_5	max	sp_5	max	sp_5	max
1	PS2192												
2	PS2190												
3	PS1815												
4	PS1829												
6	PS2695												
7	PS1893												
8	PS1901												
9	PS1736												
10	PS1912												
11	PS1778												
12	PS2703												
13	PS2676												
14	E33-22						519						
15	PS1754		570										
16	E21-15												
17	E21-14												
18	PS2498				609								
20	E20-18										656		
21	RC11-120												
22	E21-11												
23	E48-27		391		380		402				601		
24	MC 440										668		
26	GeoB1710										607		
27	E48-31										515		
29	RC 8-91								644				
31	PS2487						668						
32	E48-36										527		
33	RC 9-126												
34	GeoB1204												
35	V27-215					545	612			533	533		
36	RC 9-150		818						782				
37	INDM 65				647				729		710		
38	GeoB1048						588						
39	INDM 51												
40	RC17- 69								655				
41	RC 8-94								722				
42	V12-66				605				475	496	601		
43	INDM127				809						746		
44	RC11-145												
45	V 7-67										716		
46	V23-101										923		
47	V16-209												
48	INDM115				743						996		
49	INDM110				1024						999		
50	GeoB5142							489	512	590	885		
51	V22-211									739	785		
52	V20-175				771						780		
53	V10-89								765		802		
54	RC11-147												
55	GeoB1104-5	578		604						600	798		
56	INDM109												
57	V22- 26				1196						916		
58	V26-46										701		
59	V28-195				1075					827	1228	848	1110
60	M35006				991				789		727		
61	V20-228										1139		
62	GeoB3915				845						896		
63	M35003				649	593	694	619	726			612	720
64	INDM104	802	1177				974	820	1142				
65	RC11- 10				1072						976		
66	MC 398						619	717	936				
67	RC13- 38								805		824		
68	RC12-399				1253						901	748	851
Present in # of samples		17		13		28				21		5	

measured size value separating the largest 5% of the assemblage from the smaller 95% ($size_{assemblage5}$) and the maximum. Of these two, $size_{assemblage5}$ showed higher correlation with means, medians, and maxima (for the mean $r = 0.942$, median $r = 0.817$, maximum $r = 0.886$, for all correlations $P < 0.001$) than the maximum, which is more dependent on random sampling bias. Consequently we consistently use the diameter separating the 5% largest specimens from the rest of the assemblage as size parameter (Chapelle and Peck, 1999). To evaluate the potential effects of species changes, the largest 5% of the assemblage were taxonomically classified in 17 environmentally representative samples covering a mean annual temperature range of 0.25–28.38°C and a productivity range of 20.5–217 g C m^{-2} a^{-1}. The mean size for each species '$size_{species5}$' in the largest 5% of the assemblage was calculated (Table 2). Additionally, in 64 assemblages the 12 largest individuals were taxonomically classified to determine the environmental conditions for maximum size development of individual species (Table 2).

The environmental data used in our analyses are sea surface temperature and primary productivity. The importance of these two parameters was confirmed in multivariate statistical analyses

of numerous parameters (annual mean temperature, maximum seasonal temperature difference at sea surface; salinity; nitrate, and phosphate (annual means at sea surface and 200 m and the difference between these depths) as well as primary productivity (annual mean, seasonal minima and maxima) all taken from Levitus et al. (1994) and Antoine et al. (1996).

The relationship between $size_{assemblage5}$ and the environmental parameters was analyzed by linear correlation and by forward multiple linear regression. The lowest probability tolerated in the analysis was $P = 0.05$. A probability larger than $P = 0.05$ is considered not statistically significant. The differences within biogeographic zones were tested by ANOVA (analysis of variance). Within a biogeographic zone the relationship between size and environmental parameters was reanalyzed by linear correlation analysis. As an estimator for changes in diversity the species richness was chosen. Species richness is defined as the number of species in the assemblage (Table 1).

2.4. Environmental setting

The structure of all environmental data was analyzed by PCA (principal component analysis). The first unrotated principal component (44% of total variance) showed the highest correlations with sea surface temperature (annual mean and annual maximum: $r = 0.95$) and the second unrotated axis (21% variance) by primary productivity (annual mean, $r = 0.61$; maximum, $r = 0.76$). The analyses of the size response to environmental change consequently were focused on mean annual sea surface temperature and primary productivity.

The biogeographic zones were defined based on the changing species composition of living planktic foraminifers (Bé and Tolderlund, 1971; Hemleben et al., 1989). The zones are structured, with only small overlaps, along the global temperature gradient (Fig. 3). The relationship between temperature and primary productivity in polar to temperate biogeographic zones differs from those in subtropical and tropical zones. Superimposed are the effects of primary productivity, describing two different temperature–fertility relationships

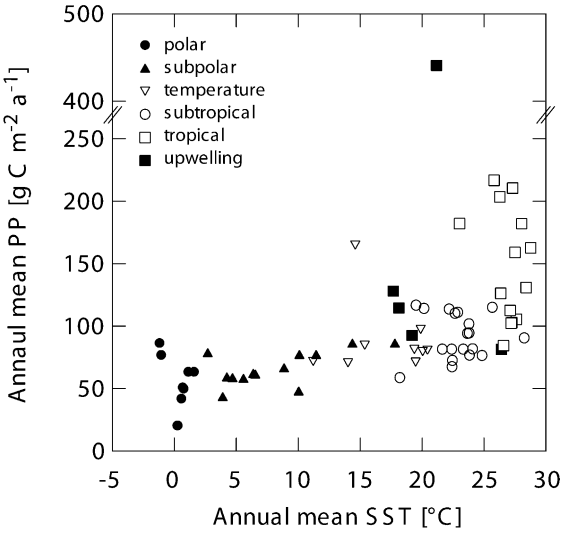

Fig. 3. Temperature (°C) versus primary productivity (g C m^{-2} a^{-1}) for all 69 samples. Biogeographic zones are polar (9 samples, filled circle), subpolar (13 filled triangles), temperate (9 open triangles), subtropical (19 open circles), tropical (14 open squares), upwelling (5 filled squares).

(Fig. 3). From the subpolar to temperate zones, fertility only gradually increases with temperature, whereas in the subtropical and tropical zones variability of primary productivity increases significantly. A large fertility gradient characterizes the upwelling zone.

3. Results and interpretation

3.1. General size distribution

The size distributions of all analyzed planktic foraminiferal assemblages are strongly skewed towards larger sizes (Fig. 2). From the polar to the tropical zone, the $size_{assemblage5}$ doubles, from 315 to 625 μm and the maximum test size almost triples from 512 to 1448 μm. The upwelling assemblages have size distributions most similar to the temperate and subtropical ones.

To analyze these patterns in more detail, the relationship of the $size_{assemblage5}$ with the main environmental parameters is further investigated. The means of the $size_{assemblage5}$ for the six biogeographic zones are highly correlated ($r = 0.926$,

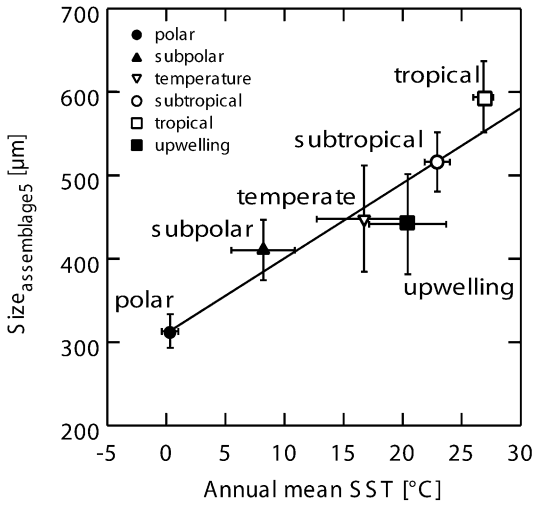

Fig. 4. Mean of the $size_{assemblage5}$ per biogeographic area (µm) plotted against annual average sea surface temperature (SST in °C) (Levitus et al., 1994). Error bars represent the 95%-confidence intervals for the average. The full line corresponds to the regression line ($r = 0.938$, $P = 0.006$).

$P = 0.008$) with temperature (Fig. 4). However, compared to the general linear increase of the means of the $size_{assemblage5}$ from the polar to the tropical zones, the upwelling group is an outlier and shows a smaller size than expected. Globally, the highest correlations between size and environmental parameters are those with mean annual temperature at the sea surface and 200 m depth and the difference of these, i.e. the thermal stratification of the surface waters (Table 3).

An examination of the size/temperature relationship of all analyzed samples shows that the increase of the $size_{assemblage5}$ is not linear but shows two distinct minima at sea surface temperatures of around 2°C and 17°C (Fig. 5a). These minima do not occur in the linear correlation of stratification and size (Fig. 5b).

We performed a multiple linear regression analysis of the $size_{assemblage5}$ versus all environmental parameters available. The highest proportion of size variance (68%) was explained by mean sea surface temperature (63%), followed by seasonality of temperature (+4%), and fertility (+1%):

$$size_{assemblage5} = 9.626 t_0 - 14.297 t_{seas} - 0.945 \times PP_{winter} + 391.671;\ r = 0.833,\ P < 0.001).$$

On the global scale surface water stratification and maximum primary productivity also show a strong positive correlation with size (Table 3). To

Table 3
Coefficients of correlation (r) between $size_{assemblage5}$ and environmental parameters for the global data set and for the different biogeographic zones

	Global	Polar	Subpolar	Temperate	Subtropical	Tropical	Upwelling
T_0 0 m	**0.793**	−0.546	0.273	0.489	0.380	0.159	**0.919**
Sal 0 m	**0.499**	−0.112	−0.330	0.328	0.198	−0.193	0.324
PO_4 0 m	**−0.404**	**0.857**	0.243	−0.517	−0.022	−0.414	−0.270
NO_3 0 m	**−0.439**	0.590	0.292	−0.071	−0.297	−0.451	−0.668
T_0 200 m	**0.683**	−0.192	0.260	0.380	0.230	−0.080	−0.114
PO_4 200 m	−0.071	**0.714**	0.255	−0.463	−0.200	−0.322	−0.317
ΔT 0–200 m	**0.740**	**−0.673**	0.203	0.444	0.019	0.143	**0.855**
T_{seas}	−0.140	**−0.749**	−0.100	0.076	−0.032	−0.426	**0.936**
PP_{ann}	**0.283**	−0.408	−0.252	−0.323	0.325	−0.448	−0.282
PP_{seas}	**−0.378**	−0.382	**−0.716**	−0.512	0.372	−0.293	−0.402
PP_{max}	0.103	−0.385	**−0.654**	−0.426	**0.500**	−0.451	−0.326
PP_{min}	**0.504**	0.099	0.371	0.436	0.389	**−0.631**	−0.260
PP_{spring}	**0.472**	0.099	0.357	−0.040	0.389	**−0.592**	−0.219
PP_{winter}	0.059	−0.588	**−0.654**	−0.232	0.243	−0.438	−0.362

Average annual sea surface temperature [°C] (T_0), maximum seasonal temperature difference [°C](T_{seas}), difference between average annual temperature at 0 m and 200 m water depth [°C] (ΔT), salinity (Sal), phosphate (PO_4), nitrate (NO_3) in surface waters (0 m) and 200 m depth, average (PP_{ann}), maximum (PP_{max}), minimum (PP_{min}), spring (PP_{spring}) and winter (PP_{winter}) primary productivity [g C m^{-2} a^{-1}], maximum seasonal difference in primary productivity [g C m^{-2} a^{-1}] (PP_{seas}). For references see Table 1. Significant correlations ($P < 0.05$) are marked in bold.

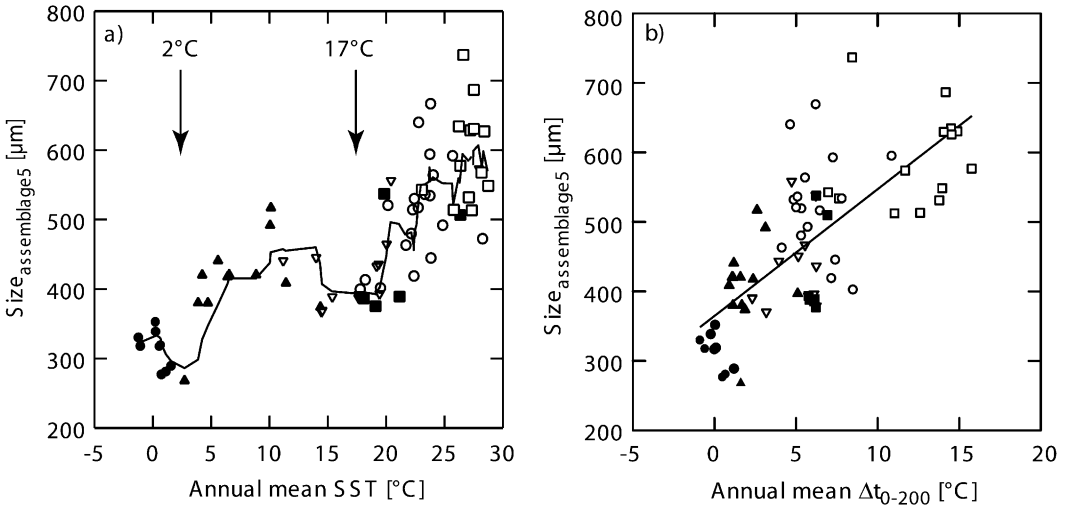

Fig. 5. $Size_{assemblage5}$ per sample (µm) plotted against (a) mean annual sea surface temperature (SST in °C) and (b) surface water stratification, given as the difference between mean annual sea surface temperature and temperature at 200 m depth (Levitus et al., 1994). Arrows indicate the areas of minimum size at 2°C and 17°C, corresponding to the polar and the subtropical front, respectively. The black line represents the five-point moving average in panel a and the regression line in panel b. Biogeographic zones as in Fig. 3.

reduce the globally dominant influence of temperature, the data set was split into biogeographic zones, within which the effects of secondary factors, such as primary productivity, might be better recognizable.

3.2. Size patterns within biogeographic zones

The mean $size_{assemblage5}$ of the upwelling assemblage is distinctly smaller than expected from the global size/temperature correlation (Fig. 4), suggesting a negative effect of fertility on size. On the other hand, an increase in mean test sizes of several planktic foraminiferal species in Pleistocene cores have been linked to higher paleofertility in the Arabian Sea (Naidu and Malmgren, 1995).

There is little correlation between primary productivity and temperature within the individual biogeographic zones except in one (Table 4). The exception is the subpolar zone with a positive correlation between estimates of primary productivity and temperature. Therefore, any size trend in this zone could be caused by either parameter. Within all other zones, a size dependency on fertility, which is unrelated to temperature, might be identifiable.

A linear correlation analysis of size and environment within individual biogeographic zones shows that in subpolar and tropical assemblages size is negatively correlated to primary productivity (Table 3). In the polar assemblage there is no statistically significant correlation with primary productivity, but there is a strong positive correlation with another fertility parameter: phosphate. In the temperate zone, no environmental parameter correlates with size.

Within the upwelling zone, $size_{assemblage5}$ shows the highest correlation coefficient not with a fertility parameter, but with temperature (Table 4). Most species, defining biogeographic zones, are temperature dependent. In contrast, the upwelling assemblage is defined by the dominance of the species *Globigerina bulloides*, which has an affinity to high nutrients in a wide range of water temperatures (Schiebel et al., 1997). Because fertility is the defining characteristic for these assemblages, temperature is the dominant variable within this geographically heterogeneous zone.

The inconsistent size relationship with fertility among the biogeographic zones defies a simple explanation. Since biogeographic zones are defined by the dominance of a few species, it is likely

that successive adaptational optima of these might strongly influence the observed assemblage patterns through replacement of dominant species.

3.3. Size effects related to changing species abundances

3.3.1. Size variation and diversity

Changing $size_{assemblage5}$ is a composite result of size variability within species and among species as well as the number of species, and their changing relative abundance (Hecht, 1976). It has repeatedly been documented that species richness, i.e. number of species in an assemblage, in planktic foraminifers generally increases from low to high temperatures (Bé and Tolderlund, 1971; Rutherford et al., 1999). In our data set, assemblage size is positively correlated with species richness ($r = 0.598$, $P < 0.001$). This correlation could be the expected result of two different effects. Firstly, there might be a direct correlation of species richness and size, because a larger number of species in an assemblage also increases the probability of large species to be included (statistical effect). Secondly, subtropical/tropical assemblages include many more species, which are known to become larger than species adapted to other environments and consequently their increasing abundance can influence assemblage size indirectly. This question requires an examination of size distribution patterns in individual species.

3.3.2. Size variation at the species level

We have investigated in our subset of 17 representative samples the $size_{species5}$ of the largest 5% of the assemblages. This fraction included an average of 80 specimens per sample, in which we found a total of 23 species. These species are polar *Neogloboquadrina pachyderma* sinistral, subpolar and temperate *Globigerina bulloides*, *Globorotalia truncatulinoides*, *Globorotalia inflata*, *Orbulina universa*, and the subtropical to tropical species *Globorotalia hirsuta*, *Globorotalia menardii*, *Globorotalia tumida*, *Globigerinoides ruber*, *Globigerinoides sacculifer*, *Globigerinoides conglobatus* and *Pulleniatina obliquiloculata*.

A global plot of all means of these species sizes (Fig. 6) shows a similar temperature-related increase as observed in the assemblage sizes. Size patterns of individual taxa also marginally reproduce the two assemblage size minima at 2–3°C and 17°C. Apparently three levels of maximum size development can be distinguished. Small species, such as *Neogloboquadrina pachyderma* sinis-

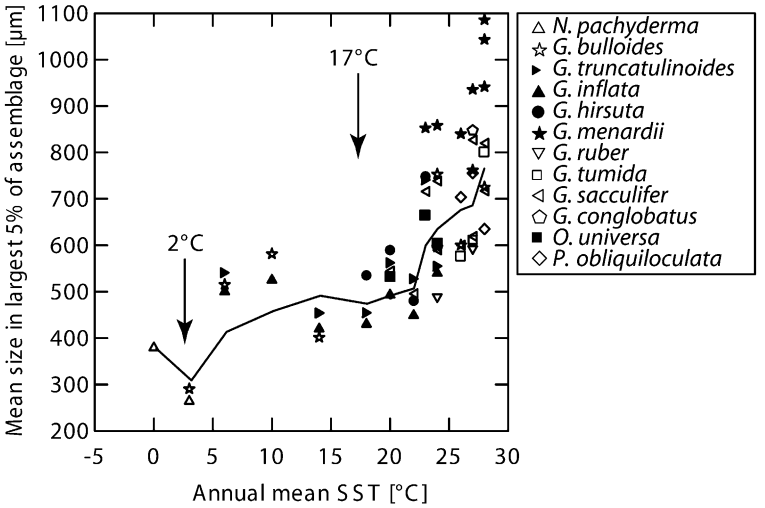

Fig. 6. Mean size (µm) of the dominant species within the largest 5% of the assemblages ($size_{species5}$) plotted against mean annual sea surface temperature (SST in °C)(Levitus et al., 1994). Arrows indicate the areas of minimum size at 2°C and 17°C, corresponding to the polar and subtropical front, respectively. The black line represents the five-point moving average.

Table 4
Correlation coefficients (r) among environmental parameters within the different biogeographic zones

	T_0 0 m	PO_4 0 m	T_0 200 m	PO_4 200 m	ΔT 0–200 m	T_{seas}	PP_{ann}	PP_{seas}	PP_{max}	PP_{min}	PP_{spring}
Polar											
T_0 0 m	1.000										
PO_4 0 m	−0.320	1.000									
T_0 200 m	**0.839**	0.142	1.000								
PO_4 200 m	0.021	**0.926**	0.477	1.000							
ΔT 0–200 m	**0.946**	−0.544	0.617	−0.252	1.000						
T_{seas}	**0.915**	−0.566	0.630	−0.253	**0.948**	1.000					
PP_{ann}	−0.373	−0.515	−0.617	**−0.761**	−0.174	−0.196	1.000				
PP_{seas}	−0.309	−0.603	−0.599	**−0.814**	−0.093	−0.163	**0.948**	1.000			
PP_{max}	−0.299	−0.558	−0.562	**−0.774**	−0.100	−0.172	**0.964**	**0.994**	1.000		
PP_{min}	0.180	0.569	0.498	0.590	−0.036	−0.030	−0.155	−0.360	−0.255	1.000	
PP_{spring}	0.180	0.569	0.498	0.590	−0.036	−0.030	−0.155	−0.360	−0.255	1.000	1.000
PP_{winter}	−0.107	−0.633	−0.423	**−0.797**	0.095	0.060	**0.947**	**0.928**	**0.947**	−0.121	−0.121
Subpolar											
T_0 0 m	1.000										
PO_4 0 m	**−0.725**	1.000									
T_0 200 m	**0.974**	**−0.691**	1.000								
PO_4 200 m	**−0.759**	**0.957**	**−0.756**	1.000							
ΔT 0–200 m	**0.671**	−0.535	0.485	−0.457	1.000						
T_{seas}	**0.697**	**−0.739**	0.550	**−0.707**	**0.888**	1.000					
PP_{ann}	**0.638**	**−0.818**	**0.658**	**−0.897**	0.309	0.546	1.000				
PP_{seas}	**−0.625**	−0.049	**−0.620**	0.000	−0.383	−0.141	0.074	1.000			
PP_{max}	0.049	**−0.651**	0.047	**−0.639**	0.036	0.298	0.722	**0.676**	1.000		
PP_{min}	**0.893**	−0.532	**0.885**	**−0.587**	0.552	0.466	**0.563**	**−0.736**	0.001	1.000	
PP_{Spring}	**0.891**	−0.540	**0.880**	**−0.590**	0.556	0.472	**0.566**	**−0.729**	0.009	**0.998**	1.000
PP_{winter}	0.049	**−0.651**	0.047	**−0.639**	0.036	0.298	**0.722**	**0.676**	1.000	0.001	0.009
Temperate											
T_0 0 m	1.000										
PO_4 0 m	−0.491	1.000									
T_0 200 m	0.919	−0.369	1.000								
PO_4 200 m	−0.329	0.976	−0.183	1.000							
ΔT 0–200 m	0.634	−0.470	0.277	−0.443	1.000						
T_{seas}	−0.100	−0.035	−0.148	−0.028	0.046	1.000					
PP_{ann}	−0.155	0.894	0.027	0.956	−0.430	−0.168	1.000				
PP_{seas}	−0.433	0.947	−0.211	0.954	−0.640	−0.051	0.934	1.000			
PP_{max}	−0.317	0.915	−0.107	0.948	−0.562	−0.122	0.974	0.980	1.000		
PP_{min}	0.586	−0.172	0.524	−0.043	0.399	−0.354	0.192	−0.111	0.088	1.000	
PP_{Spring}	0.191	0.594	0.270	0.712	−0.063	−0.251	0.849	0.633	0.768	0.668	1.000
PP_{winter}	−0.250	−0.002	−0.194	−0.063	−0.229	−0.496	0.055	0.128	0.187	0.299	0.143
Subtropical											
T_0 0 m	1.000										
PO_4 0 m	0.104	1.000									
T_0 200 m	**0.711**	0.152	1.000								
PO_4 200 m	0.125	**0.526**	−0.088	1.000							
ΔT 0–200 m	0.267	−0.077	−0.378	0.277	1.000						
T_{seas}	−0.422	0.297	−0.023	−0.003	**−0.510**	1.000					
PP_{ann}	0.053	−0.185	0.057	−0.201	0.191	−0.225	1.000				
PP_{seas}	−0.148	−0.263	0.012	−0.074	−0.153	0.221	0.431	1.000			
PP_{max}	0.187	−0.187	0.160	−0.156	0.201	0.015	**0.739**	**0.562**	1.000		
PP_{min}	0.143	−0.108	0.047	−0.228	0.256	−0.309	**0.873**	0.041	**0.650**	1.000	
PP_{Spring}	0.143	−0.108	0.047	−0.228	0.256	−0.309	**0.873**	0.041	**0.650**	1.000	1.000
PP_{winter}	−0.020	−0.136	0.131	−0.142	−0.005	0.053	**0.891**	**0.561**	**0.642**	**0.654**	**0.654**

Table 4 (*Continued*).

	T_0 0 m	PO_4 0 m	T_0 200 m	PO_4 200 m	ΔT 0–200 m	T_{seas}	PP_{ann}	PP_{seas}	PP_{max}	PP_{min}	PP_{spring}
Tropical											
T_0 0 m	1.000										
PO_4 0 m	0.013	1.000									
T_0 200 m	−0.026	−0.101	1.000								
PO_4 200 m	−0.182	**0.804**	−0.207	1.000							
ΔT 0–200 m	0.503	0.091	**−0.876**	0.086	1.000						
T_{seas}	−0.484	0.414	0.134	**0.619**	−0.353	1.000					
PP_{ann}	−0.251	0.441	−0.108	0.458	−0.034	**0.723**	1.000				
PP_{seas}	−0.390	0.331	−0.167	0.369	−0.053	**0.703**	**0.875**	1.000			
PP_{max}	−0.356	0.411	−0.120	0.459	−0.075	**0.764**	**0.965**	**0.955**	1.000		
PP_{min}	−0.202	0.458	−0.003	0.512	−0.098	**0.688**	**0.890**	**0.632**	**0.834**	1.000	
PP_{Spring}	−0.173	**0.566**	0.027	0.396	−0.105	0.504	**0.839**	**0.559**	**0.743**	**0.899**	1.000
PP_{winter}	−0.124	**0.554**	−0.376	**0.638**	0.257	**0.648**	**0.870**	**0.804**	**0.847**	**0.714**	**0.637**
Upwelling											
T_0 0 m	1.000										
PO_4 0 m	0.031	1.000									
T_0 200 m	0.259	**0.923**	1.000								
PO_4 200 m	−0.017	**0.999**	**0.914**	1.000							
ΔT 0–200 m	**0.954**	−0.117	0.192	−0.160	1.000						
T_{seas}	**0.955**	−0.251	0.021	−0.296	**0.978**	1.000					
PP_{ann}	0.007	**0.999**	**0.906**	**0.998**	−0.149	−0.277	1.000				
PP_{seas}	−0.184	**0.954**	0.768	**0.961**	−0.370	−0.466	**0.966**	1.000			
PP_{max}	−0.056	**0.992**	0.869	**0.994**	−0.222	−0.341	**0.997**	**0.984**	1.000		
PP_{min}	0.043	**1.000**	**0.928**	**0.998**	−0.103	−0.238	**0.998**	**0.950**	**0.990**	1.000	
PP_{Spring}	0.072	**0.998**	**0.916**	**0.994**	−0.090	−0.216	**0.998**	**0.954**	**0.991**	**0.998**	1.000
PP_{winter}	−0.094	**0.989**	0.859	**0.993**	−0.256	−0.376	**0.994**	**0.987**	**0.999**	**0.987**	**0.986**

For abbreviations and references see Table 1. Significant correlations ($P < 0.05$) are marked in bold.

tral (and likely *Turborotalita quinqueloba*) live in polar waters and reach a maximum diameter of less than 500 μm. Medium-sized species reach 500–1000 μm in subpolar to tropical zones: *Orbulina universa*, *Globorotalia truncatulinoides*, *Globorotalia inflata*. Comparable maximum sizes of *Globigerinoides ruber*, *Globorotalia hirsuta* and *Globigerinoides conglobatus* are only observed in the subtropics and tropics. The largest species, characteristic of the tropical zone, may grow to 1250 μm (*Globorotalia tumida* and *Globigerinoides sacculifer*) or even 1450 μm (*Globorotalia menardii*). Because the tropics host species that may grow to large and intermediate sizes, the total variability of $size_{assemlbage5}$ is also large. In temperate waters, the maximum sizes obtained for all species and thus assemblages present are more or less similar.

Our globally distributed data also allow us to identify characteristic temperatures at which the largest size and relative abundance of individual species coincide (Fig. 7). This confirms earlier observations by Kennett (1976) and Hecht (1976) that abundance and size maxima of many taxa tend to occur at specific temperatures. We note that the species with characteristic ecological optima occur in three groups at temperatures, corresponding to the polar, temperate and subtropical/tropical biogeographic zones. The taxa in these groups are the polar species *Neogloboquadrina pachyderma* (sinistral) with an optimum around 0°C; typical temperate species *Globigerina bulloides* and *N. pachyderma* (dextral) around 12°C, subtropical (20–25°C) (with deep-dwelling species *G. inflata*, *G. truncatulinoides*, *G. hirsuta* and additionally *Orbulina universa*, and tropical (> 25°C) with the surface dwellers *Globigerinoides ruber*, *G. sacculifer*, *G. conglobatus* and the deeper dwelling *Globorotalia menardii* and *G. tumida*. No species found in our assemblages has its optimum

size development at temperatures characteristic of frontal areas at 2° and 17°C. The size minima observed in frontal zones suggest that these assemblages consist of species living outside their ecological optima. *G. bulloides* and *G. inflata* display two optima expressed by maximum size and abundance, which we interpret to be likely caused by cryptic speciation with distinct adaptation (Kucera and Darling, 2002). It is likely that other species may also display multiple optima, but these cannot be detected in our current data set, due to the limited number of samples and taxonomic resolution of size measurements.

Additionally, we explored the potential influence of changing primary productivity on the size of species (Fig. 8). Despite the stated limitations of our data set, a general relationship between size of the species present and productivity is still visible. In general, maximum sizes of individual species encountered tend to increase up to a primary productivity of 150 g C m^{-2} a^{-1}. Above this threshold value, the size of species decreases with increasing primary productivity, indicating that these species may be outside their optimum primary productivity conditions.

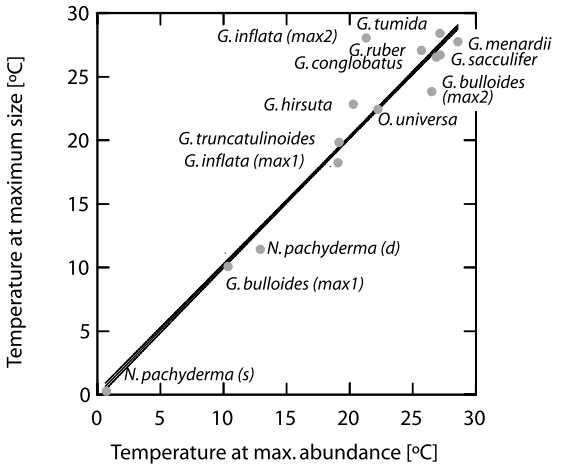

Fig. 7. Correlation ($r = 0.966$, $P < 0.001$) between the temperatures at which species populations show their maximum relative abundance (Prell et al., 1999) and their maximum sizes (this study) in our data set. (s) refers to *Neogloboquadrina pachyderma* sinistral and (d) to the dextral form. Note that *Globorotalia inflata* and *Globigerina bulloides* have two optima each in both size and abundance.

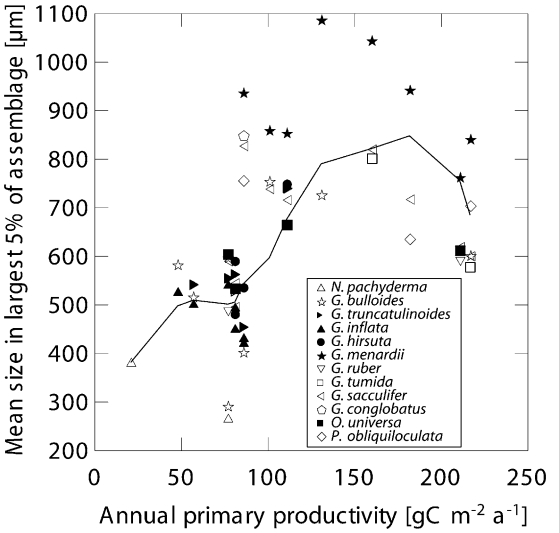

Fig. 8. Mean size (µm) of the dominant species within the largest 5% of the assemblage ($size_{species5}$) plotted against annual primary productivity (g C m^{-2} a^{-1})(Antoine et al., 1996).

4. Discussion

4.1. Latitudinal size variations: possible factors causing the general size increase – abiotic versus biotic

4.1.1. Temperature

The most important trend emerging from our results is the general increase in planktic foraminiferal test size from the poles to the tropics (Figs. 4 and 5). Besides the possible direct influence of water temperature, many other ecological parameters co-vary with temperature. Cell physiology in general is known to accelerate with temperature and enzymatic activity has been shown to approximately double when temperature increases by 10°C in different species of planktic foraminifers (Caron et al., 1987a; Caron et al., 1987b; Bijma et al., 1990b; Spero et al., 1991). The increasing enzymatic activity with rising temperature will lead to faster growth by enhanced calcification and cytoplasm synthesis, both of which are highly correlated (Spero et al., 1991).

4.1.2. Calcium supersaturation

Shell calcification processes not only depend on

the enzymatic activity, but also on the availability of Ca^{2+} ions and the amount of dissolved inorganic carbon (Gattuso et al., 1998; Bijma et al., 1999). Calcium carbonate supersaturation is known to increase from the poles to the tropics (Buddemeier and Fautin, 1994), because CO_2 is less soluble in warmer waters. Enhanced calcification in foraminifer tests could be a direct consequence of higher carbonate supersaturation. To our knowledge, no global data set of calcium carbonate supersaturation with appropriate spatial resolution and depth penetration exists. Such a data set may allow disentangling the effects of carbonate supersaturation and temperature and could complement the experimental results of (Lea et al., 1999).

Temperature can influence planktic foraminifers directly via physiology, but also indirectly. Temperature gradients in the surface water affect the number of pelagic niches. Increased stratification, i.e. a larger vertical temperature gradient, provides more niches. Ecological partitioning may minimize interspecific competition and allow growth to large size as is indicated by the positive correlation between size and stratification (Fig. 5b). Conceivable direct biotic effects include changing species richness, replacement of species with different ontogenetic size trajectories, and intraspecific size changes, all of which can be evaluated with our data.

4.1.3. Diversity

The increase in species richness from the poles to the tropics shows the same trend as the $size_{assemblage5}$. The $size_{assemblage5}$ in any single sample is the cumulative result of distinct environmental adaptations of individual species. Hence, the increase of taxa with distinct, temperature-dependent size and abundance maxima, from the polar to tropical areas, could lead to the observed, stepped global size increase. The intra- and interspecific size variability in the tropics and subtropics is considerably larger than in the subpolar and temperate assemblages (Figs. 5 and 6) and could be the result of enhanced fine-scale or short-term environmental variability related to the stronger thermal gradients in the upper part of the water column (Fig. 5a). Over evolutionary timescales this may have led to an efficient ecological segregation of planktic foraminiferal species and thus to larger diversity (Rutherford et al., 1999).

4.1.4. Species replacement

The subtropical and tropical environments apparently allow for growth to larger test sizes by the single or combined effects of higher temperatures, increased surface water stratification, enhanced calcium carbonate supersaturation, and high light intensity. All of these may promote photosynthesis of symbionts and thus more efficient resource harvesting. Interestingly, symbiont-bearing species, such as *Globigerinoides ruber*, *G. sacculifer*, and *G. conglobatus*, reach indeed larger maximum sizes than the asymbiotic species *Neogloboquadrina pachyderma*, *Globigerina bulloides*, *Globorotalia inflata*, and *G. truncatulinoides*. Symbiont-bearing species are also the most frequent components of subtropical and tropical assemblages (Hemleben et al., 1989). This by itself could explain the larger sizes observed in these zones, because enhanced symbiotic activity was experimentally shown to increase the shell size (Bé et al., 1982). In addition, other groups of symbiont-bearing organisms, such as corals, are also known to increase their size with increasing carbonate supersaturation (Gattuso et al., 1998).

4.1.5. Size variation within populations

The test size of planktic foraminifers increases during their lifetime. Final size is determined by reproduction, during which gametes are released and the empty test sinks to the ocean floor. In most planktic foraminiferal species reproduction is known to be triggered by the synodic lunar cycle (Spindler et al., 1979; Bijma et al., 1990a; Schiebel et al., 1997) and the time allotted to growth is little influenced by local environmental conditions. However, a single specimen can grow to different adult sizes, depending on environmentally controlled growth rate (Caron et al., 1981; Caron et al., 1987a; Bijma et al., 1990b). From these observations we infer that larger size and high abundance define optimum conditions whereas small sizes and fewer numbers of individ-

Table 5
Temperatures of samples with largest sizes (this study) and highest relative abundances (from Prell et al., 1999) of dominant planktic foraminifera species encountered in the largest 5% of our Holocene assemblages

Species name	Maximum size[a] (μm)	T_{opt}[a] (°C)	Maximum relative abundance[b] (%)	T_{opt}[b] (°C)
N. pachyderma (s)	475	0.3	97.99	0.7
N. pachyderma (d)	591	11.4	48.38	12.9
G. bulloides	718	10.5	60.11	10.4
	843	23.8	47.1	26.6
O. universa	920	22.4	32.33	22.2
G. truncatulinoides	837	19.8	18.78	19.2
G. inflata	804	27.9	26.7	21.4
	664	18.2	56.83	18.5
G. tumida	1253	28.4	11.85	27.2
G. menardii	1448	27.7	42.54	28.6
G. sacculifer	1139	27.2	38.07	27.2
G. ruber	974	27.5	81.01	25.8
G. hirsuta	889	22.8	8.69	20.3
G. conglobatus	1110	26.9	11.29	27.0

T_{opt} = temperatures at respective optima; (s) refers to *N. pachyderma* sinistral and (d) to the dextral form. Note that *G. inflata* and *G. bulloids* have two optima in both size and abundance.
[a] This study.
[b] Prell et al. (1999).

uals of a species population result from less favorable conditions. For example, *Globigerina bulloides* populations show largest sizes around 50°N whereas the subtropical to tropical *Globigerinoides ruber* attain their maximum sizes around 10°N (Hecht, 1976) (Table 5). Malmgren and Kennett (1976) also have described the correlation of size and abundance of *G. bulloides* in surface sediments with optimum conditions between 6 and 10°C, similar to our results. A correlation of size and accumulation rates of several species was documented for *Neogloboquadrina dutertrei*, *G. ruber*, *G. sacculifer* and *G. bulloides* in the Arabian Sea (Naidu and Malmgren, 1995). Their data showed that increased production and accumulation of tests and not merely changing relative abundances controlled their size-frequency relationship.

4.2. Deviations from the latitudinal trend: frontal systems and upwelling areas

The general $size_{assemblage5}$ increase towards the tropics is not monotonous (Fig. 5). Instead deviations from the general trend indicate the influence of secondary factors interfering with the global temperature-related effects. Smaller sizes are found at annual mean sea surface temperatures around 17°C and 2°C. These temperatures define two of the most important frontal systems, the subtropical fronts, which are associated with 15–18°C sea surface temperatures, and the northern and southern polar fronts, which are defined by the 2°C isotherm. The mean sizes in the seasonally dynamic coastal upwelling zone are also smaller than expected from the global size–temperature trend (Fig. 4).

Test sizes of foraminiferal species have been previously documented to be smaller in frontal and upwelling areas (Ortiz et al., 1995). These environments are characterized by high turbulence along different water masses, frequently appearing eddies (Beckmann et al., 1987), and storm events (Schiebel et al., 1995), all of which lead to expatriation (Berger, 1970; Weyl, 1978) and vertical displacement of biota. Fronts appear to function as environmental barriers (Berger, 1971; Schiebel et al., 2001) between the three stable ecosystems of the polar, subpolar and temperate respectively subtropical and tropical regions, each harboring groups of well-adapted species able to grow to large sizes. Frontal and upwelling

areas may inhibit growth directly by their high environmental variability, but also indirectly by light attenuation, caused by high plankton standing stocks. The resulting lowered symbiotic activity of the few symbiont-bearing species living in these environments (Bijma et al., 1992; Ortiz et al., 1995) may also lead to size reduction. At very high primary productivity rates, a decrease in test sizes suggests that there is a global foraminiferal productivity optimum at primary productivity rates of about 150 g C m^{-2} y^{-1}.

The smaller $size_{assemblage5}$ observed in upwelling assemblages is influenced by the absence of many subtropical species that leads to a dominance of temperate *Globigerina bulloides*, a comparably small species. Some species, such as *Globorotalia inflata* and *G. truncatulinoides* show several abundance optima with respect to global temperature variability (Prell et al., 1999). *G. inflata* has been considered a species with specific adaptation to frontal environments (Schiebel et al., 2002). Our analyses, however, demonstrate that two temperature-related optima in abundance and size exist, both on either side of the subtropical front (Fig. 7). The increase in relative abundance seems to result mostly from the absence of other species. *G. truncatulinoides* and *G. inflata* are known to be deep-dwelling species (Hemleben et al., 1989) and might therefore be affected in a more complex way (Renaud and Schmidt, 2003).

4.3. Local influence of primary productivity

Within most of the biogeographic zones (polar, subpolar, subtropical, tropical) size is linked to fertility (Table 3). These relationships seem, however, to be complex, with an apparent positive correlation in the subtropical and negative correlations in the subpolar and tropical zones. The limited number of samples within each individual zone, however, makes reliable analyses difficult. A larger and more detailed database will be required to better characterize the potential effects of shifting abundances and sizes with respect to primary productivity optima and the interfering variability in frontal zones. The two effects may balance each other in different ways among the various biogeographic zones.

5. Conclusions

(1). On a global scale, planktic foraminifers as a group increase in size from the poles to the tropics. This pattern can be attributed to the covariation of several temperature-related effects such as metabolic efficiency, carbonate supersaturation, niche richness, diversity, species replacement, and intraspecific size variation.

(2) The close global temperature correlation of maximum size and relative abundance of individual species allow definition of environmental optima, beyond which decreases in both size and abundance can be expected.

(3). The increase of assemblage test sizes with increasing temperature is not monotonous. Rather it shows two local minima, one at 2°C the other around 17°C, where polar and subtropical fronts are found. Fronts represent major environmental perturbations and act as biogeographic barriers for shallow dwelling planktic foraminifers. They lead to unfavorable conditions resulting in a lower diversity and smaller sizes. A few persisting species, e.g. *Globorotalia inflata*, become dominant in these areas and show little size reaction.

(4). Assemblages from upwelling areas also show smaller sizes. Here, the additional effects may include decreased numbers of symbiont-bearing species, leaving, e.g., *Globigerina bulloides* dominant, and lower symbiont activity caused by turbidity.

(5). On a regional scale, where temperature ranges are reduced, the secondary effect of primary productivity may come to bear. A better understanding of these effects would require size spectra of single species in many additional samples.

The ecological relevance of our hypotheses has been tested in the late Quaternary records (Schmidt et al., 2003). This study shows that the ecological preferences of the investigated species did not change much during the last 300 kyr. As in the Holocene, assemblage size variability in the Quaternary is primarily affected by paleotemperature. The hypotheses developed for the Holocene will be used to analyze the repetitive evolutionary size patterns in the Cenozoic.

Acknowledgements

We acknowledge the generosity of B. Donner, A. Mackensen, Ch. Hemleben, R. Spielhagen, and G. Wefer to share their material with us. We are grateful to U. Gerber, R. Hoffmann, and M. Mettler for their skillful technical help. We thank J. Bijma, H. Hilbrecht, and J. Ortiz for discussion during the various stages of the work, as well as Helen Williams for linguistic improvements. This paper has benefited from the comments of J. Cullen, M. Spindler, R. Thunell and A. Mackensen. The research was funded by a grant of the Swiss National Science Foundation. The raw data is available at http://www.pangaea.de/PangaVista?query=@Ref25175.

Taxonomic appendix

The taxonomic appendix lists all taxa cited in the paper. The taxonomy follows Parker (1962); Bé (1967); Stainforth et al. (1975) and Hemleben et al. (1989).

Globigerina bulloides d'Orbigny, 1826

Globigerinoides conglobatus (Brady) = *Globigerina conglobata* Brady, 1879

Globigerinoides ruber (d'Orbigny) = *Globigerina rubra* d'Orbigny, 1839

Globigerinoides sacculifer (Brady) = *Globigerina sacculifera* Brady, 1877

Globorotalia hirsuta (d'Orbigny) = *Rotalina hirsuta* d'Orbigny, 1839

Globorotalia inflata (d'Orbigny) = *Globigerina inflata* d'Orbigny, 1839

Globorotalia menardii (d'Orbigny) = *Rotalia (Rotalie) menardii* d'Orbigny, 1826

Globorotalia crassaformis (Galloway and Wissler) = *Globigerina crassaformis* Galloway and Wissler, 1927

Globorotalia truncatulinoides (d'Orbigny) = *Rotalia truncatulinoides* d'Orbigny, 1839

Globorotalia tumida (Brady) = *Pulvinulina menardii* (d'Orbigny) var. *tumida* Brady, 1877

Neogloboquadrina pachyderma (Ehrenberg) = *Aristerospira pachyderma* Ehrenberg, 1861

Orbulina universa d'Orbigny, 1839

Pulleniatina obliquiloculata (Parker and Jones) = *Pullenia sphaeroides* (d'Orbigny) var. *obliquiloculata* Parker and Jones, 1865

Turborotalita quinqueloba (Natland) = *Globigerina quinqueloba* Natland, 1938

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