

Seasonal production and morphologic variation of *Neogloboquadrina pachyderma* (Ehrenberg) in the northeast Pacific

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ABSTRACT: A high resolution study of seasonal variation in the flux of the planktonic foraminifer *Neogloboquadrina pachyderma* to the sea floor has been carried out in the northeast Pacific (50°N, 145°W). Using an automated time series sediment trap moored at 3858 m, a total of 24 consecutive two-week samples were taken from September 1982 to September 1983. Two distinct morphologic groups of *N. pachyderma* were recognized, based on textural and coiling differences. Variations in the shell flux of each *N. pachyderma* group are directly related to seasonal changes in water temperature and structure and depth of the thermocline. Group A, predominantly sinistral forms with a crystalline, heavily calcified test, is most abundant when surface water temperatures are less than 8°C and the upper 100 m of the water column are well mixed. In contrast, the less calcified, reticulate forms of Group B are predominantly dextrally coiled and are most abundant when surface water temperatures are greater than 8°C and the thermocline is well established at depths between 5 and 20 m. The association of each *N. pachyderma* group with different near-surface water conditions suggests they are strongly dependent on specific thermal environments. By examining the variation in the shell flux of *N. pachyderma* as it relates to seasonal changes in local hydrography, it is possible to better understand the ecology of this important paleoclimatic indicator.

INTRODUCTION

In the past 25 years, considerable emphasis has been placed on the study of the planktonic foraminifer *Neogloboquadrina pachyderma* (Ehrenberg). Ericson (1959) and Bandy (1960) were the first to recognize that coiling direction in *N. pachyderma* could be used as a paleoclimatic indicator. Several workers (Bé 1960, 1977; Kennett 1968; Malmgren and Kennett 1972) have described its Recent geographic distribution, particularly in the Southern Hemisphere. Kennett (1970) compared arctic with antarctic *N. pachyderma*; he, Stehman (1972), Vilks (1975), and Keller (1978) are among the few who have studied the morphology and distribution of this species in surface sediments from the Northern Hemisphere. Several authors (Malmgren and Kennett 1972; Srinivasan and Kennett 1974a, 1974b; Kennett 1976; Kennett and Srinivasan 1980) have examined the test ultrastructure of *N. pachyderma* and identified two textural forms: crystalline and reticulate.

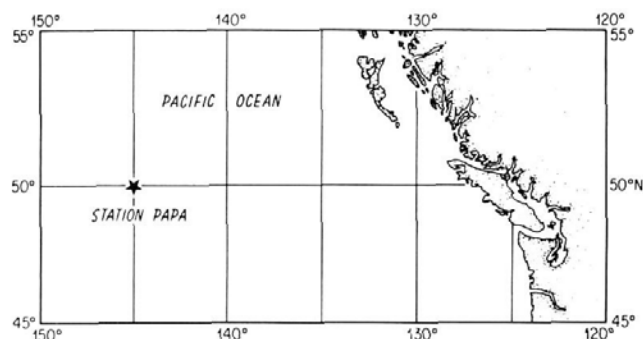
In the present study, the seasonal production of *N. pachyderma* was studied at Station PAPA (Ocean Station P) in the northeast Pacific (50°N, 145°W) (text-fig. 1) near the northern edge of the North Pacific Drift (NPD). Hydrographic conditions and surface nutrient chemistry have been researched extensively at this site, rendering it an ideal location to study the relationship between the shell flux of *N. pachyderma* and changes in surface water conditions in a sub-polar environment.

Using a Mark V PARFLUX (Particulate Flux Experiment) sediment trap (Honjo et al. 1980) moored at 3858 m, 412 m off the sea floor, empty tests of *N. pachyderma* were collected during their descent through the water column. This time series sediment trap collected 12 consecutive samples, each for approximately two weeks. Two successive trap deployments provided 24 consecutive samples for the period from September 1982 to September 1983 (table 1).

The ecology of *N. pachyderma* is still only poorly known, though its behavior may be similar to that of other nonspinnose foraminifera (Bé 1977; Berger 1971; Arikawa 1983; Thunell and Reynolds 1984). In order to evaluate the ecology of *N. pachyderma*, the environment in which it lives must be understood, and the factors controlling its distribution must be identified. Ericson (1959) and Bandy (1960) emphasized the importance of temperature in determining the coiling direction of *N. pachyderma*. Kennett (1968) discussed latitude and, in general, surface water temperature as a controlling factor in the morphological variation seen in this species in the Southern Hemisphere. Stehman (1972), who studied *N. pachyderma* from Baffin Bay in the North Atlantic, concluded that latitude is not the primary controlling factor in either morphologic variation or the distribution of *N. pachyderma*, particularly in hydrographically restricted regions. Instead, he pointed out that different morphotypes of *N. pachyderma* prefer and are geographically distributed in association with specific surface water masses. These "upper water masses" are a function of local and seasonal surface circulation patterns and can be identified by their surface temperatures and salinities (Bradshaw 1959). Stehman's (1972) conclusions agree with earlier concepts of faunal association with specific water masses (Russell 1939; Phleger 1954).

The NPD, which brings warm westerly waters from the Kuroshio Current across the Pacific Ocean, fluctuates its latitudinal position annually in response to seasonal changes in atmospheric pressure and the resultant wind patterns. The position of the NPD greatly influences seasonal surface temperatures at Station PAPA, creating distinct seasonal changes in the thermal structure of the upper 50 m of the water column.

A comparison of seasonal changes in the near-surface hydrography with shell flux patterns of different morphoforms



TEXT-FIGURE 1
Location map of Station PAPA (50°N, 145°W), North Pacific Ocean.

should supply new information concerning the ecology of *N. pachyderma* and will aid future studies of both Recent and ancient marine environments.

REGIONAL HYDROGRAPHY

Surface current circulation in the North Pacific

A winter low-pressure zone centered over the Aleutian Islands produces a counterclockwise movement of the associated winds. Strong south-southwesterly winds produced by the low pressure zone divert currents from the NPD toward the coast of Alaska (Livingstone and Royer 1980) (text-fig. 2A). The land-mass configuration then sets up a cyclonic surface current gyre in the Gulf of Alaska. Mass movement away from the center of the gyre due to Ekman Transport (Livingstone and Royer 1980) creates upwelling of deeper, nutrient-rich waters. Station PAPA is on the southeastern portion of this gyre. The low-pressure zone also draws cold arctic air southward, strengthening water flow through the Bering Strait. These arctic currents are incorporated into the stronger currents of the winter NPD and subsequently flow into the Gulf of Alaska gyre, thereby lowering surface temperature.

The summer warming of surface waters produces a large high-pressure zone centered directly south of Station PAPA along the 40°N parallel. The associated winds circulate in an anti-cyclonic gyre and are weaker than winter winds (Livingstone and Royer 1980). The south and south-easterly winds of the western portion of this clockwise gyre cause a northward shift of the NPD to its northernmost position at approximately 50°N (text-fig. 2B). The cold arctic waters from the Bering Strait are no longer drawn southward, and the warm, weakened NPD currents pass over Station PAPA, dramatically increasing surface water temperatures during the summer. The general decrease in ocean-current energy during this time of year disrupts the circulation of the Gulf of Alaska gyre, and upwelling intensity decreases.

Near-surface seasonal hydrography at Station PAPA

Seasonal salinity, dissolved oxygen content, temperature, and density data for Ocean Station P (Station PAPA), collected in 1980 by the Institute of Ocean Sciences (IOS), are illustrated in text-figure 3 and are considered to be representative

of a typical year. The near-surface layer at Station PAPA is defined as the upper 30 m of the water column, since seasonal events affect mainly this region. Surface salinities (text-fig. 3A) vary by only 0.3‰ throughout the year, and an average change of only 0.2‰ occurs in the near-surface layer. Between 30 and 50 m, salinities increase significantly from 32.8 to 33.8‰. This major salinity increase is a permanent feature and is not affected by seasonal hydrographic changes. Throughout the year, dissolved oxygen content (text-fig. 3B) varies by only 1.0 ml/l in the upper 30 m, drops from approximately 6 at the surface to 3.5 ml/l at 30 to 50 m, and continues to decrease to the oxygen minimum, below 100 m.

Seasonal variability in the near-surface layer is more pronounced for temperature (text-fig. 3C) than for either salinity or dissolved oxygen content. Surface temperatures fluctuate from approximately 6 to 14°C, and the near-surface layer changes seasonally from well mixed to thermally stratified. During the months of January through May the upper 30 m of the water column are essentially isothermal and surface temperatures range from 5.8 to 8°C, with the annual surface temperature minimum occurring in April (text-fig. 3C). These winter near-surface conditions are characterized by cold, nearly isothermal, nonstratified water.

In contrast, the summer near-surface water conditions are identified by surface temperatures exceeding 8°C and have strong thermal stratification within the upper 30 m. As summer solar radiation warms cold winter surface waters, stratification increases. By June, the thermocline is well established at a depth just below 5 m, and surface temperatures are 9.5°C. The annual surface temperature maximum of approximately 14°C is reached in September, when the thermocline is best developed. During this time of year, the temperature gradient is strongest between 5- and 15-m depth, producing intense stratification in the near-surface layer. Surface water temperatures decrease after September, and by November the weakened thermocline is positioned at a depth of between 15 and 20 m. During January the near-surface layer is only slightly stratified and the upper 25 m of the water column are isothermal, indicating a return to the winter near-surface conditions. Throughout the year, temperatures are colder than 7°C at depths greater than 30 m.

Water density, a function of temperature, salinity and pressure, also varies seasonally within the near-surface layer. Sigma-t profiles are illustrated in text-figure 3D. At Station PAPA, only temperature varies substantially within the upper 30 m, producing a temperature-dependent seasonal pycnocline. A permanent pycnocline, one not affected by seasonal events, is found at Station PAPA between 30 and 40 m. Since temperature varies little at these depths, the permanent pycnocline is salinity-dependent. The breakdown of the seasonal thermocline/pycnocline allows for increased mixing of the near-surface waters, and by April the upper 50 m is well mixed. The presence of a permanent pycnocline at Station PAPA suggests that seasonal upwelling caused by mass movement away from the center of the Gulf of Alaska gyre (Livingstone and Royer 1980) must affect only the near-surface waters of this region, and is not of the intensity of coastal upwelling observed in many parts of the world, such as in the Panama Basin (Stevenson 1970).

TABLE 1

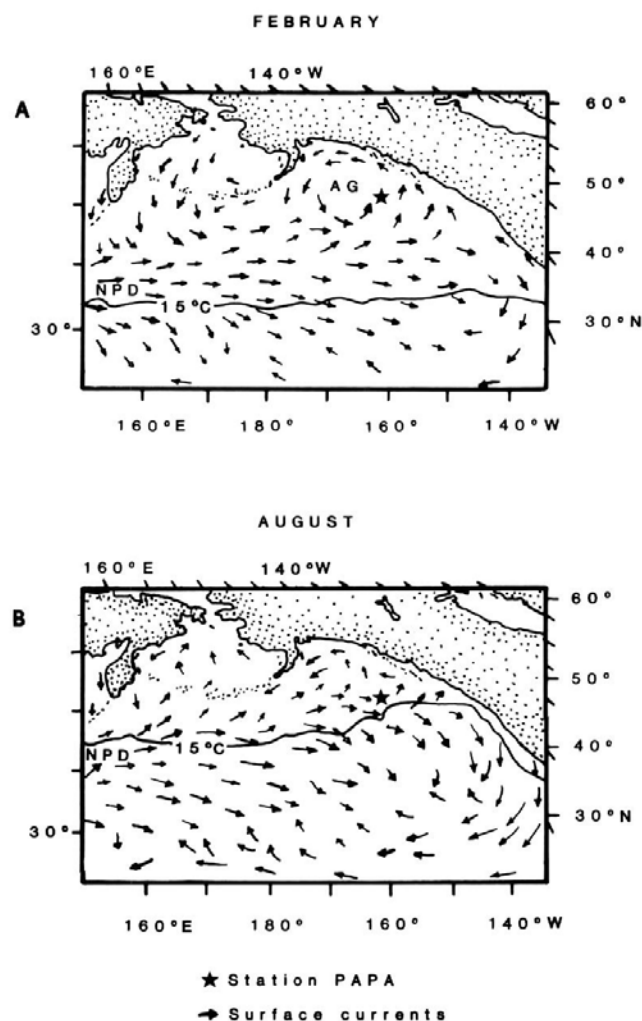
Station PAPA sampling periods with their durations, shell fluxes (# specimens/m²/day) and mass fluxes (mg/m²/day) of *Neogloboquadrina pachyderma*.

Sample No.	Dates	Duration (# days)	Shell Flux	Mass Flux
PAPA I				
1	Sept. 23 - Oct. 8, 1982	15	534	2.18
2	Oct. 8 - Oct. 23	15	174	.65
3	Oct. 23 - Nov. 7	15	64	.25
4	Nov. 7 - Nov. 22	15	445	2.15
5	Nov. 22 - Dec. 7	15	1552	7.58
6	Dec. 7 - Dec. 22	15	634	2.51
7	Dec. 22 - Jan. 6, 1983	15	1025	4.13
8	Jan. 6 - Jan. 21	15	1029	3.16
9	Jan. 21 - Feb. 5	15	481	1.47
10	Feb. 5 - Feb. 20	15	103	.22
11	Feb. 20 - Mar. 7	15	100	.27
12	Mar. 7 - Mar. 18	11	87	.22
PAPA II				
1	Mar. 27 - Apr. 12, 1983	16	520	1.67
2	Apr. 12 - Apr. 28	16	786	2.34
3	Apr. 28 - May 14	16	997	3.30
4	May 14 - May 30	16	2365	7.47
5	May 30 - Jun. 15	16	796	2.50
6	Jun. 15 - Jul. 1	16	539	1.83
7	Jul. 1 - Jul. 17	16	60	.20
8	Jul. 17 - Aug. 2	16	1503	6.27
9	Aug. 2 - Aug. 18	16	326	1.09
10	Aug. 18 - Sep. 3	16	96	.22
11	Sep. 3 - Sep. 19	16	87	.08
12	Sep. 19 - Oct. 5	16	69	.40

Nutrient concentrations

Seasonal surface-water concentrations of nitrate, silicate, and phosphate at Station PAPA were continuously measured by IOS from 1974 to 1981. Similar seasonal patterns are exhibited by each nutrient and are repeated annually (text-fig. 4). From December to late March/early April nutrient con-

centrations increase to their annual maximum owing to the upwelling of deeper, nutrient-rich waters. Following this maximum, concentrations decrease rapidly as environmental conditions (i.e. light intensity) improve for photosynthetic uptake by phytoplankton. Photosynthetic uptake depletes surface nutrient concentrations, which consequently reach



TEXT-FIGURE 2

Surface current circulation in northeast Pacific Ocean (Tchernia 1980). (A) North Pacific Drift (NPD) is at its southernmost extent in February. North American continent deflects these eastward-flowing currents to the south and north and, owing to the land-mass configuration, the northward deflection of the NPD creates a cyclonic surface-current gyre in the Gulf of Alaska (AG). (B) In August, the NPD migrates northward, nearing the region of Station PAPA. Gulf of Alaska gyre is disrupted because of this migration and the general decrease in surface current energy.

an annual minimum in late June or early July. At that time nutrient replenishment is reduced by the increased stratification. Nutrients are present in low concentrations from July to September. After September, the gradual weakening of the seasonal thermocline allows for an increase in nutrient influx to the surface. Concentrations increase slowly with only minor fluctuations from October to December.

METHODS

Samples collected in the Mark V sediment trap (Honjo et al. 1980) were split using a precision rotary splitter (Honjo 1978). A 1/64 split of each Station PAPA sample was soaked for

48 hr in a sodium hydroxide-buffered solution of hydrogen peroxide (pH 7.7) in order to dissolve organic matter. The samples were then wet-sieved through a 125- μ m mesh screen onto millipore filter paper. After being dried at 50°C, planktonic foraminiferal tests were removed from the filter paper and dry-sieved through 500-, 250-, and 125- μ m mesh screens. Foraminiferal specimens smaller than 125 μ m were not counted owing to both the difficulty in preserving the delicate tests and the abundance of juvenile specimens. Individual species were identified, separated, counted, and weighed for each size fraction. Calculations of shell flux (specimens/m²/day) and mass flux (mg/m²/day) were made taking into account the sample split (1/64), the trap area (1.2 m²), and the sample duration (table 1). In this paper we focus on the seasonal flux and morphological variation of the species *Neogloboquadrina pachyderma*.

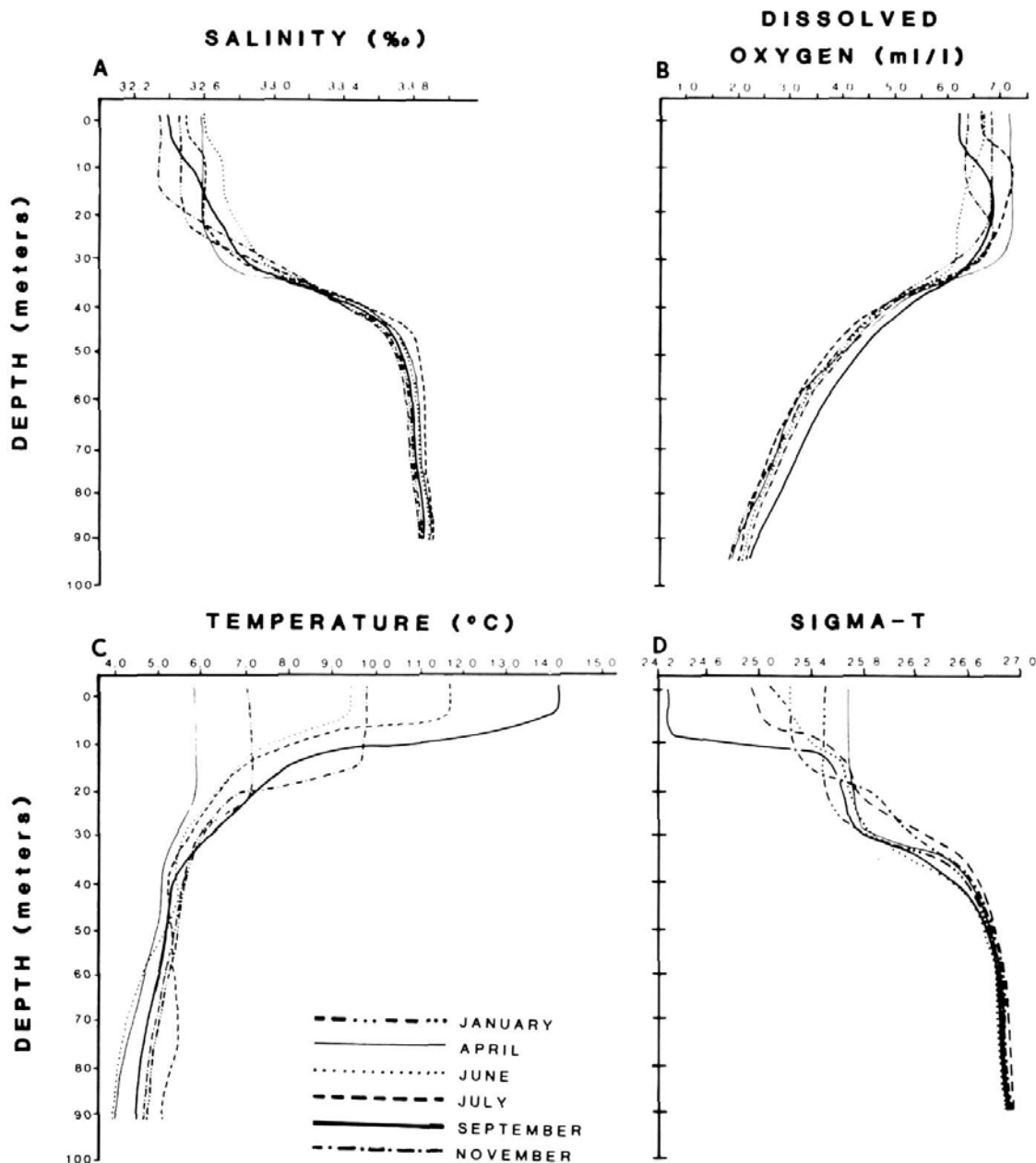
In order to understand the relationship between surface-water conditions and the abundance of *N. pachyderma* in the sediment trap samples, the settling velocity of the empty foraminiferal tests through the 3858-m water column must be taken into account. Several authors have discussed settling velocities of planktonic foraminifera (Berger and Piper 1972; Fok-Pun and Komar 1983) and Radiolaria (Takahashi and Honjo 1983). Curry and Takahashi (unpubl. data) measured sinking speeds for several foraminiferal species including *Neogloboquadrina dutertrei*, which were collected in a sediment trap in the Panama Basin. Based on the morphologic similarity of *N. dutertrei* to *N. pachyderma*, their estimates, which were determined for both test diameter and mass, were used for the prediction of *N. pachyderma* settling velocities.

Recognition of *Neogloboquadrina pachyderma* morphotypes

Using the textural classifications of Srinivasan and Kennett (1974a), *Neogloboquadrina pachyderma* was initially separated into two groups, A and B, according to the surface texture of each specimen. Group A consists of the crystalline forms; Group B forms have reticulate textures.

Under a light microscope, Group A crystalline forms have a coarse, heavily encrusted appearance. Euhedral calcite crystals cover most or all chambers, obscuring the pores and producing a thick "calcite crust" (Bé and Ericson 1963). Plate 1, figures 1, 2 and 3 illustrate two Group A specimens and the detail of the crystalline texture. The crystalline texture is formed from a secondary calcification process over a primary reticulate surface texture (Srinivasan and Kennett 1974a). This crust can break off, exposing the initial reticulate surface (pl. 1, fig. 4). The gradual increase in calcite overgrowth with successively older chambers suggests a nondiagenetic cause for this secondary calcification (Bé 1965). The foraminifer adds the euhedral crystals to each chamber over a period of time that begins with the chamber's formation (Srinivasan and Kennett 1974a).

Group B is composed of forms with a reticulate texture (pl. 1, figs. 5, 6, 8). Many specimens of Group B have the classic, clean texture (pl. 1, fig. 7) of the *Neogloboquadrina* genus, similar in appearance to *N. dutertrei* recovered in Panama Basin sediment traps (pl. 1, fig. 9). Broken calcite ridges commonly surround individual microcrystalline pore pits (pl. 1, fig. 10). Other specimens from Group B have well-



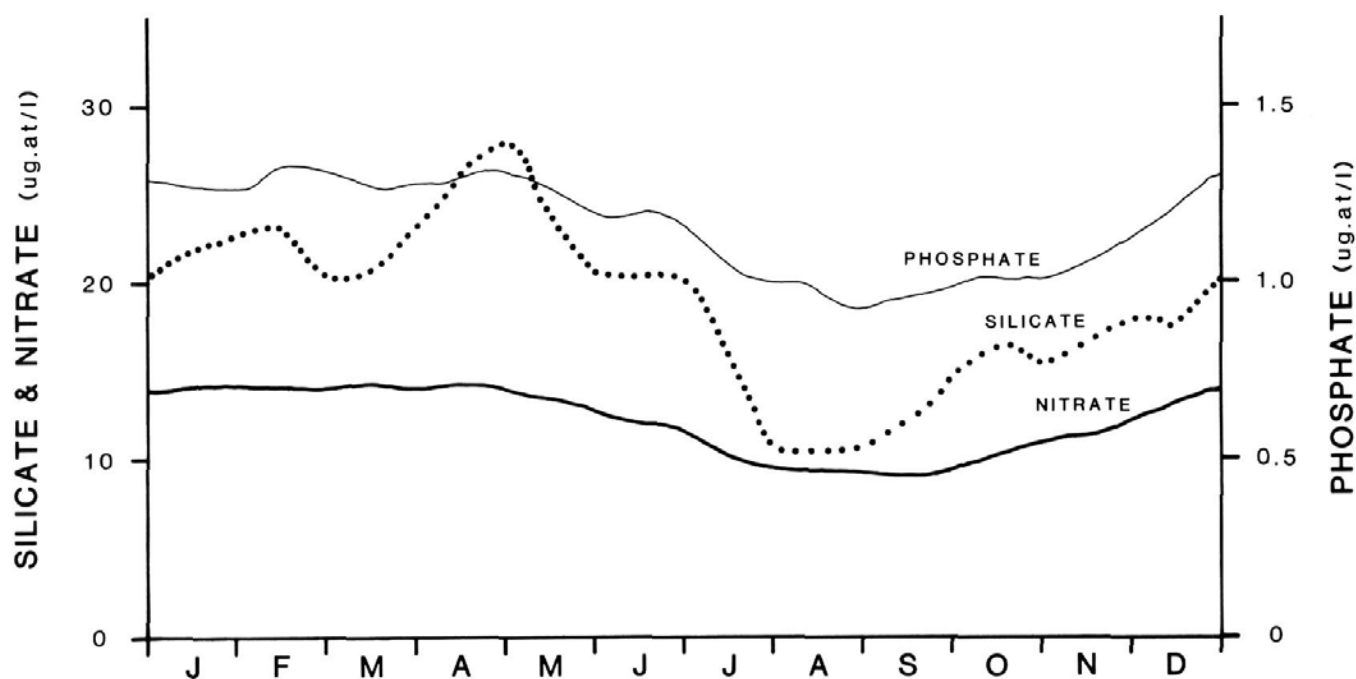
TEXT-FIGURE 3

Seasonal hydrography of upper 90 m of water column at Station PAPA (Institute of Ocean Sciences, Sidney, British Columbia data base, 1980). Salinity (A) and dissolved oxygen content (B) profiles show little seasonal variation in the upper 30 m of the water column, defined as the near-surface layer at Station PAPA, compared with temperature (C) and sigma-t (D) profiles.

developed calcite ridges that may cover most of the primary surface (pl. 1, figs. 11, 12). Under a light microscope this texture appears less coarse than that of crystalline forms, as the development of euhedral calcite crystals has not occurred and the pores remain visible. Although texture was the only criterion used in the initial separation of Groups A and B, other morphological differences are present and will be discussed in detail in the following section.

Other workers (Stehman 1972; Keller 1978) have identified three morphotypes of *Neogloboquadrina pachyderma* (Forms

1, 2 and 3). The characteristics of Form 1 are similar to those of the Group A, crystalline forms. Group B, as used in this study, is a combination of Forms 2 and 3. Owing to the gradational differences observed between the reticulate-texture individuals, further subdivision within Group B was difficult. The separation of *N. pachyderma* morphotypes based solely on the presence or absence of a "calcite crust" may have greater reproducibility for future studies and is sufficient for the interpretation of the environmental factors controlling the distribution of each.



TEXT-FIGURE 4

Seasonal changes in relative surface nutrient concentrations at Station PAPA, estimated from data collected by the Institute of Ocean Sciences (Sidney, B.C.) from 1974 to 1980.

RESULTS

The *N. pachyderma* shell fluxes and mass fluxes from the 24 Station PAPA samples are listed on table 1. These data represent the total *N. pachyderma* population before separation into morphologic groups.

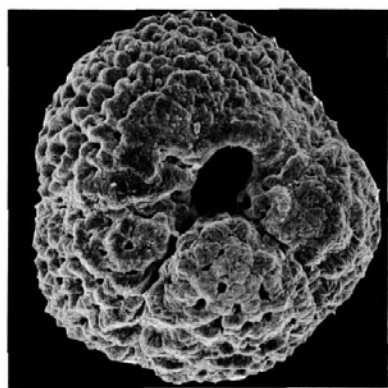
Morphologic variation in *Neogloboquadrina pachyderma*

There are distinct morphological differences between Groups A and B other than the major textural differences that were used to separate them initially. These characteristics are similar to those outlined by Srinivasan and Kennett (1974a) with

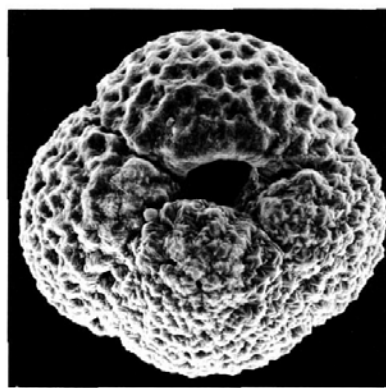
the exception of coiling direction. Group A is dominantly sinistrally coiled in all samples and is primarily responsible for the sinistral coiling nature of 44% of the total *N. pachyderma* population in the combined 24 samples. Seasonal variation in the percentage of sinistrally coiled *N. pachyderma* displays a pattern similar to that for the Group A specimens of the total *N. pachyderma* shell flux (text-fig. 5). Group B is predominantly dextrally coiled in all samples with the exception of those collected during May. Based on these results, coiling direction is a viable method for morphotype separation of *N. pachyderma* at Station PAPA and could be used in place of differences in surface ultrastructure.

PLATE 1

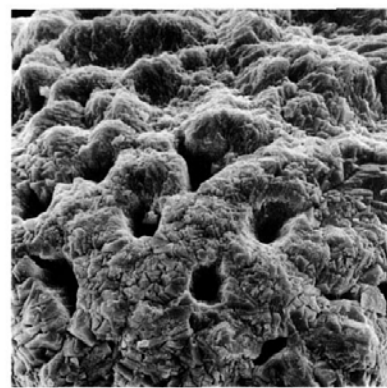
- 1, 2 *Neogloboquadrina pachyderma* Group A forms (scale bars = 100 μ m). Note heavy encrustation of crystalline surface and sinistral coiling.
- 3 Textural detail of Group A form (scale bar = 1000 μ m). Note euhedral calcite crystals of the crystalline surface.
- 4 Broken secondary reticulate surface, exposing primary surface underneath (scale bar = 1000 μ m).
- 5, 6, 8 *Neogloboquadrina pachyderma* Group B forms (scale bars = 100 μ m). Note reticulate surface texture, less calcified than crystalline surfaces of Group A forms. Note dextral coiling direction.
- 7 Textural detail of Group B form (scale bar = 1000 μ m). Note calcite ridges surrounding individual pore pits.
- 9 *Neogloboquadrina dutertrei* specimen collected in a sediment trap from the Panama Basin. Note similarity of form and surface texture to *N. pachyderma* specimen (fig. 8) from Station PAPA (scale bar = 100 μ m).
- 10-12 Stages of calcite ridge development around pore pits from Group B reticulate-texture forms (scale bars = 1000 μ m).



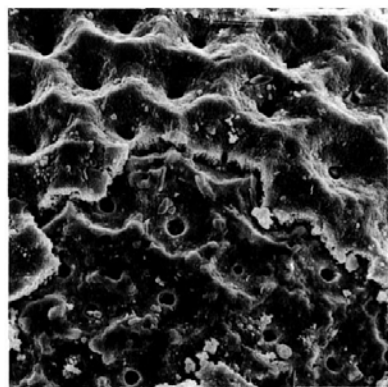
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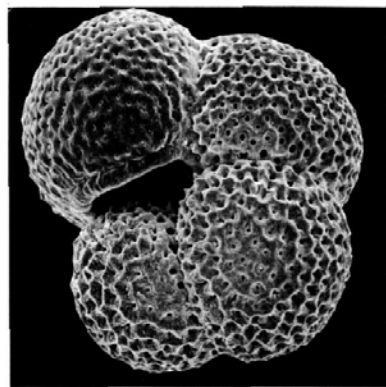
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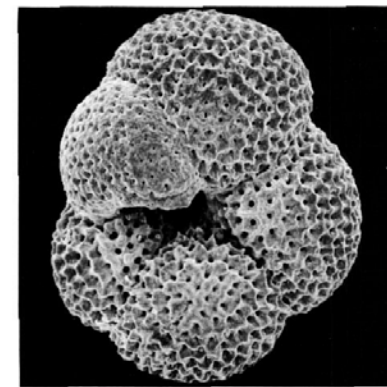
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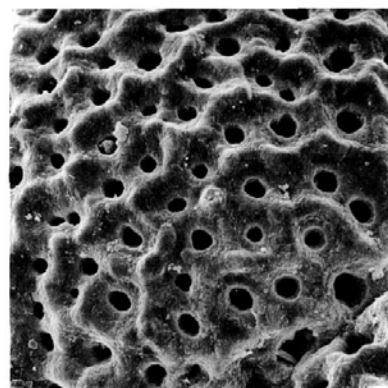
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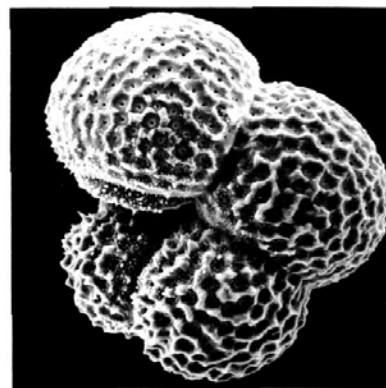
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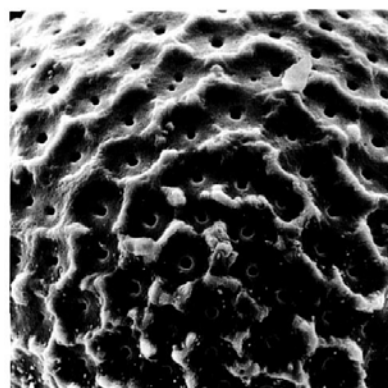
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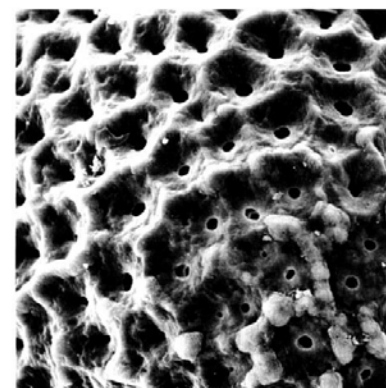
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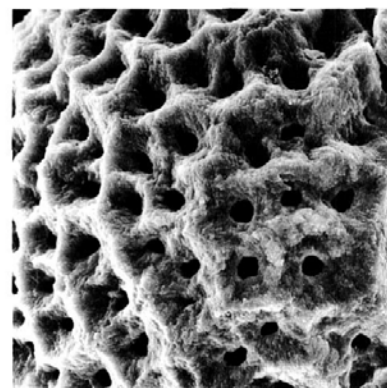
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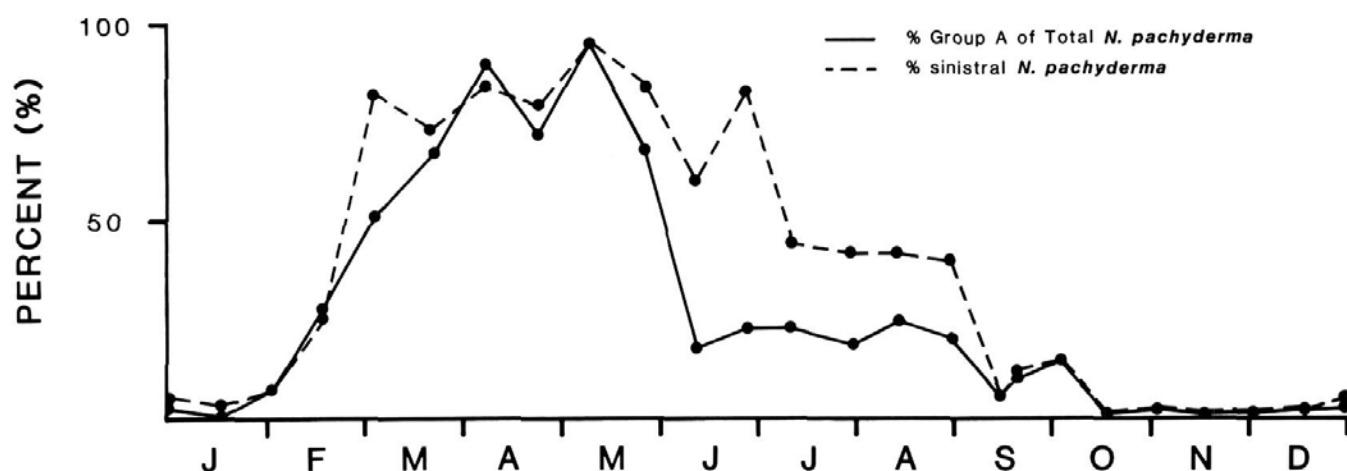
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11



12



TEXT-FIGURE 5

Comparison of the percent Group A specimens of the *Neogloboquadrina pachyderma* shell flux with that of sinistral coiled forms of the total shell flux at Station PAPA.

In contrast, Srinivasan and Kennett (1974a) found no correlation between texture and coiling direction.

Two previous studies (Banerji et al. 1971; Lipps 1976) suggest an association between planktonic foraminiferal coiling ratios and nutrient concentrations. Although neither study discusses *N. pachyderma* or sub-polar planktonic foraminifera, there appears to be a direct association between the patterns of percent sinistral coiled *N. pachyderma* (text-fig. 5) and surface nutrient concentrations at Station PAPA (text-fig. 4). These seasonal patterns are inversely related to the seasonal surface temperature curve (text-fig. 6). Sinistral coiled forms are most abundant when nutrient concentrations are high while the *N. pachyderma* population is predominantly dextrally coiled when nutrient concentrations are relatively low.

At Station PAPA, Group A forms have a mean diameter of approximately 0.15 mm. Specimens from this group larger than 0.2 mm were not found in the sediment trap samples. In comparison, Group B forms have a mean diameter of approximately 0.2 mm, with few specimens exceeding 0.25 mm.

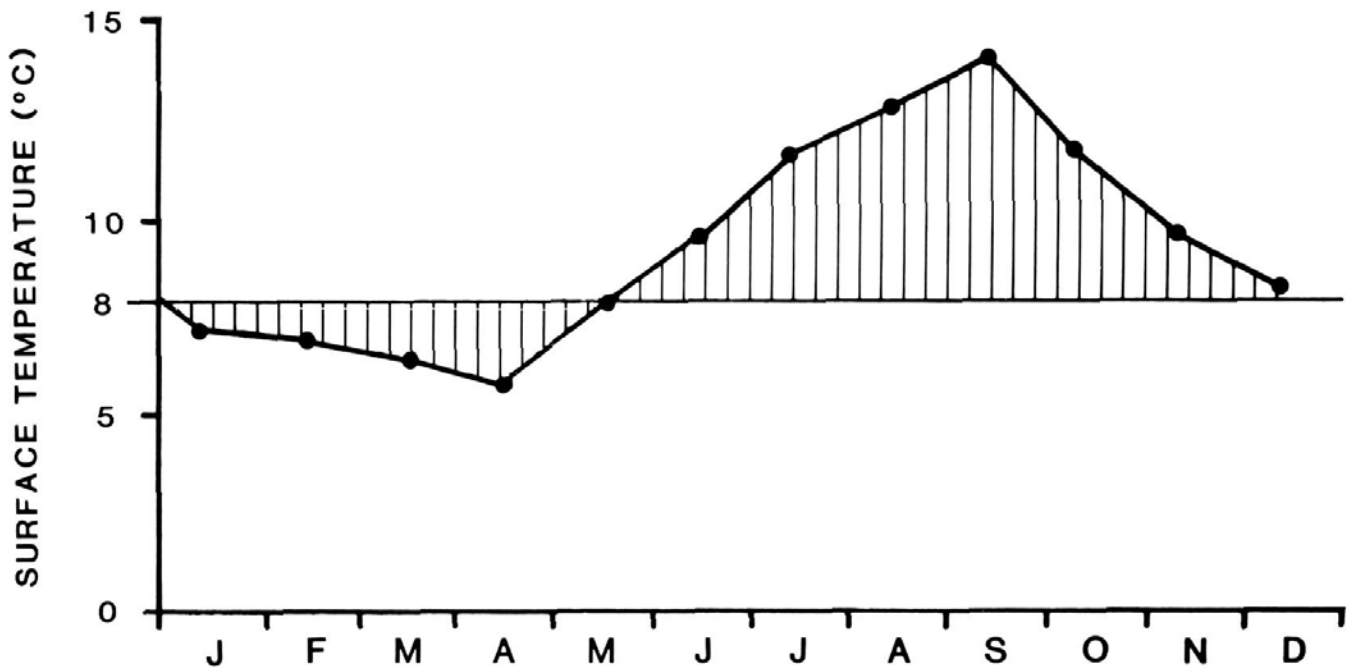
There also exists a certain amount of morphologic variation within each group of *N. pachyderma*. Plate 2, figures 1 through 6 illustrate several Group A morphotypes. During periods of low shell flux, most Group A forms have rounded apertures with distinct rimlike lips, and only four chambers in a compact arrangement (pl. 1, figs. 1, 2; pl. 2, figs. 1, 2). During times of high shell flux, a majority of the individuals have 4½ chambers and are less compact (pl. 2, figs. 5, 6). These two variant forms account for all the Group A individuals.

Variability of forms within Group B is greater than within Group A. Plate 2, figures 7 through 12 illustrate several Group B morphotypes. Individuals have apertures ranging from either umbilical to umbilical-extraumbilical, and are with or without thickened lips. They may be four-chambered with a quadrate periphery (pl. 2, figs. 7-9) or they may be more lobulate with four (pl. 2, fig. 10), four and a half (pl. 2, fig.

11) or five chambers with an open umbilical region (pl. 2, fig. 12). At Station PAPA, there is a complete gradation of variants between these "end-members," though all individuals are distinctly different from Group A forms.

Settling velocities

The average lengths of the individuals in Groups A and B are approximately 150 and 200 μm , respectively. Using the settling velocities estimated for *Neogloboquadrina dutertrei* (Curry and Takahashi, unpubl. data), a species similar to *N. pachyderma*, sinking rates of 250 m/day and 330 m/day are predicted for Groups A and B, respectively. Using the calculated average masses of 0.003 and 0.004 mg for Group A and B individuals, the sinking velocities obtained (400 and 500 m/day, respectively) are faster than those determined for test length. The *N. pachyderma* specimens from Station PAPA appear to have greater masses than *N. dutertrei* specimens of comparable sizes. This difference is undoubtedly due to the heavy "calcite crust" of Group A individuals and the additional calcification on many Group B specimens. Settling velocity estimates have yet to be made for specimens in varying densities of sea water. Since water density increases with depth as salinity increases and temperature decreases, the settling velocities measured by Curry and Takahashi can be considered as maximum values. These estimates for *N. pachyderma* correspond to descent times of 10 to 15 days for Group A specimens and 8 to 12 days for those of Group B. Since sample collection durations average 15.3 days and the descent times represent minimum estimates, a "correction factor" of one sampling period has been applied to each of the *N. pachyderma* shell flux values. This correction factor accounts for the lag-time between initiation of descent and entrapment. With such an adjustment for seasonal shell flux patterns, a better assessment can be made of the relationship between the seasonal production pattern of living *N. pachyderma* and changes in the upper part of the water column (text-fig. 7).



TEXT-FIGURE 6
Seasonal changes in surface water temperature at Station PAPA. The 8°C isotherm is shown.

Seasonal variation in the shell flux of *Neogloboquadrina pachyderma*

By incorporating this correction factor of one sample period, the seasonal shell flux of *N. pachyderma* from the surface can be estimated. The adjusted annual shell flux pattern of each *N. pachyderma* group (text-fig. 7) illustrates the seasonal differences in the production of Group A and Group B individuals. Group A, the crystalline forms, dominates the *N. pachyderma* population from March to May, reaching a maximum shell flux in May of 2218 specimens/m²/day. During May, the total *N. pachyderma* shell flux is at an annual maximum of 2365 specimens/m²/day. Group A accounts for 94% of this maximum *N. pachyderma* shell flux. Soon after this maximum, the Group A shell flux decreases to 560 specimens/m²/day in June. For the remainder of the year, the Group A shell flux is fewer than 65 specimens/m²/day, with the exception of a small increase in July (334 specimens/m²/day).

In contrast, the reticulate forms (Group B) dominate from June to February, and are most abundant from July to early January (text-fig. 7). There are several major oscillations in the Group B shell flux pattern. Significant increases in shell flux occur during July (1146 specimens/m²/day), September (534 specimens/m²/day), and November (1552 specimens/m²/day), and from mid-December to mid-January (1025 specimens/m²/day). During the period from late January to March, the Group B shell flux decreases to a winter minimum of fewer than 100 specimens/m²/day. In March when Group A begins to dominate the *N. pachyderma* population, the Group B shell flux remains lower than 300 specimens/m²/day.

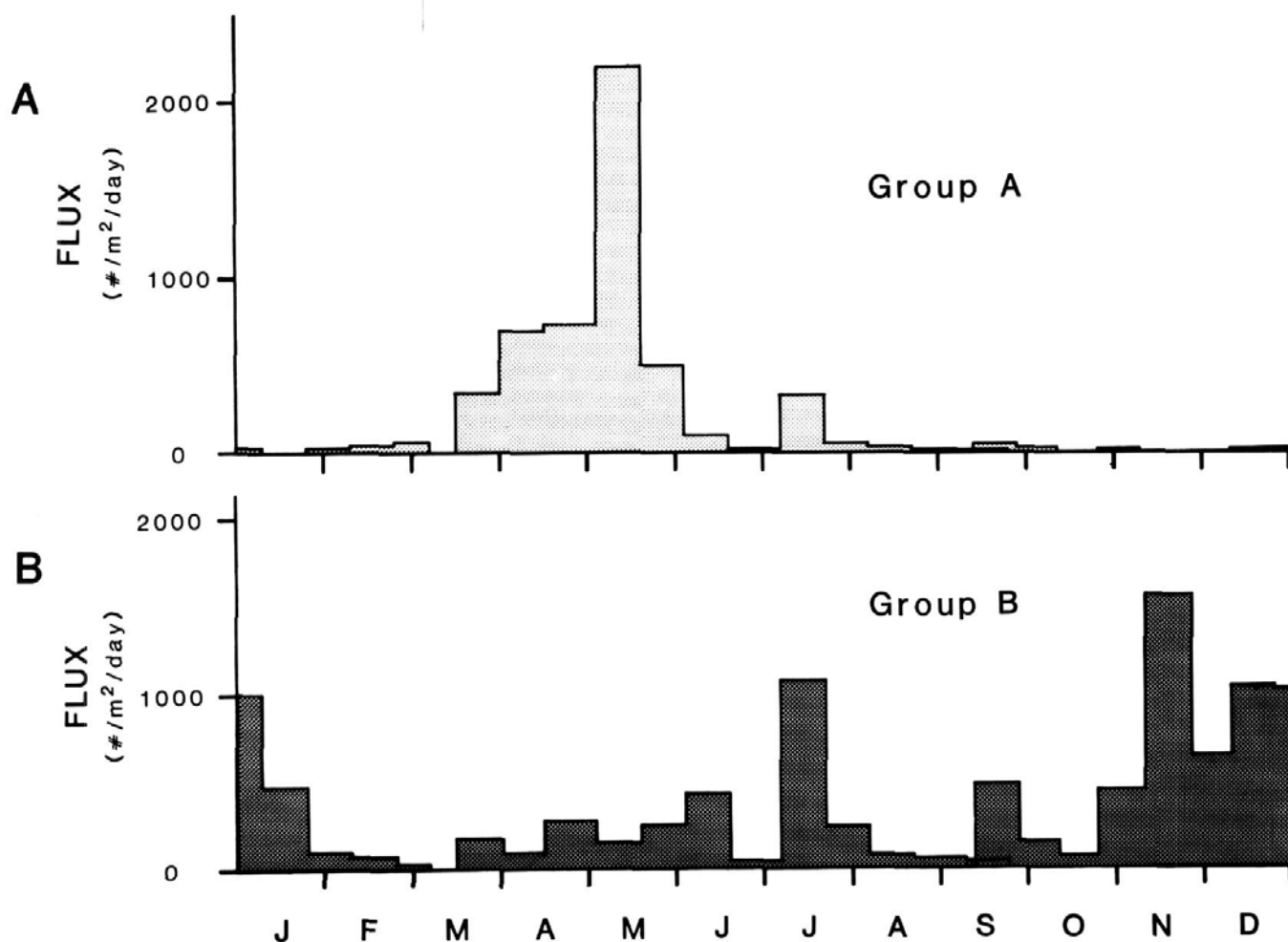
A comparison of the mass flux patterns of each *N. pachyderma* group (text-fig. 8) shows that the larger Group B specimens account for the maximum mass flux of calcite for any sampling period despite their lower shell flux (text-fig. 7).

The total *N. pachyderma* shell flux and mass flux patterns (text-fig. 9) are similar, though the influence of the greater mass of Group B specimens is evident in the total mass flux pattern, causing the May and November peaks to be of similar height. These patterns are cumulative and illustrate the seasonal changes in the shell flux at a water depth of 3858 m. They are not adjusted by a "descent time" correction factor. A comparison of both the total shell flux and total mass flux of *N. pachyderma* (text-fig. 9) with total shell flux and mass flux of all planktonic foraminiferal species (text-fig. 10) clearly illustrates the importance of *N. pachyderma* to the overall foraminiferal population and biomass in this region.

Neogloboquadrina pachyderma constitutes 36% of the annual foraminiferal shell flux, ranging from a minimum of 6% during July to a maximum of 80% during January (text-fig. 11). Surface sediments from this region should approximate this percentage if dissolution has not greatly altered the assemblage. Our value of 36% is comparable to Keller's (1978) observation that *N. pachyderma* constitutes approximately 40% of the faunal assemblage in surface sediments from 47°N, 132°W.

DISCUSSION

Our results compare well with previous studies concerning the distribution of *Neogloboquadrina pachyderma* in both



TEXT-FIGURE 7

Seasonal shell flux patterns for the two morphologic groups of *Neogloboquadrina pachyderma*, with the correction factor for settling velocity applied (see text). Group A, the crystalline form, is dominant during the months of March through May. Group B is present throughout the year at Station PAPA, and is the dominant *N. pachyderma* group from June to February. Group B is most abundant from June to January.

Recent and ancient sediments. At Station PAPA, *N. pachyderma* is dominantly sinistral only between March and May (text-fig. 5). During those months, surface water temperatures are less than 8°C, and at depths greater than 10 m, temper-

atures are less than 7.2°C (text-fig. 3C). Bé (1960) observed that the sinistrally coiled form of *N. pachyderma* from the Arctic occurs primarily in waters cooler than 8°C, and for the North Atlantic, Bé and Hamlin (1967) demonstrated that

PLATE 2

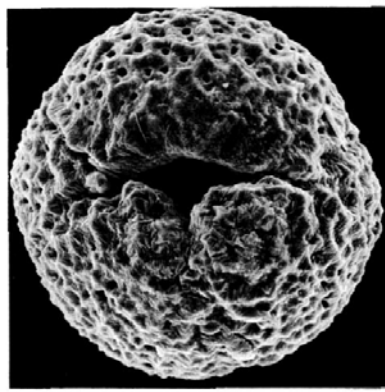
Neogloboquadrina pachyderma (scale bars = 100 μ m)

- 1, 2 Umbilical views of Group A forms. Note compact arrangement of chambers.
- 3, 4 Spiral views of compact Group A forms.
- 5, 6 Umbilical views of 4½-chambered morphotypes of Group A.

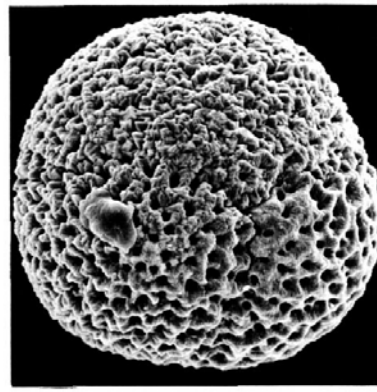
- 7-9 Quadrate morphotypes of Group B forms.
- 10 Four-chambered lobulate morphotype from Group B.
- 11 Four and one-half-chambered lobulate morphotype from Group B.
- 12 Five-chambered lobulate morphotype from Group B. Note open umbilical region.



1



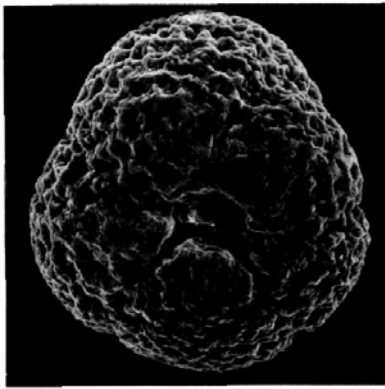
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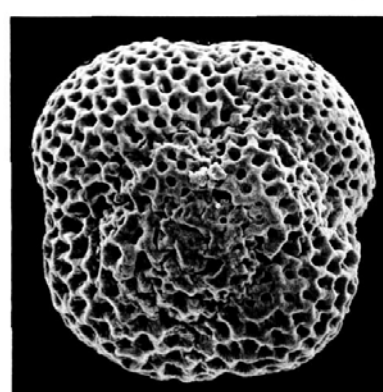
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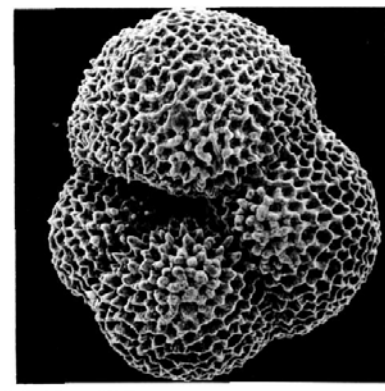
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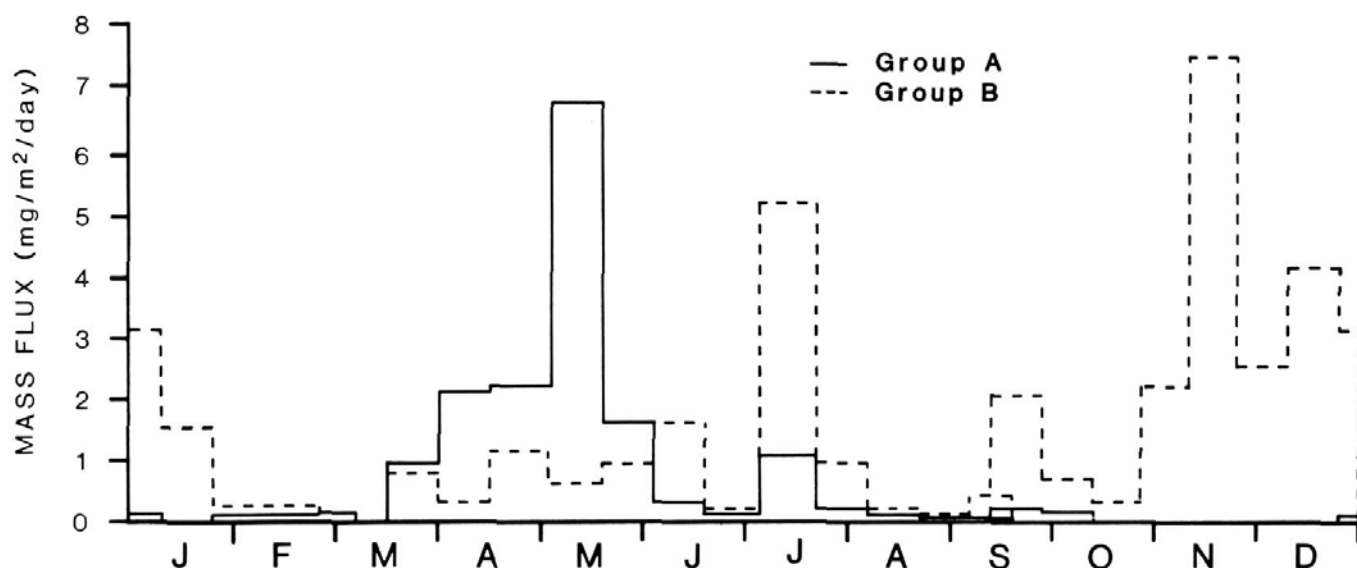
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11



12



TEXT-FIGURE 8

Comparison of the mass flux of each *Neogloboquadrina pachyderma* group, with the correction factor for settling velocity applied (bar heights are not cumulative). Despite a higher number of specimens fluxing to the sea floor (text-fig. 7), the maximum Group A mass flux is smaller than that of Group B.

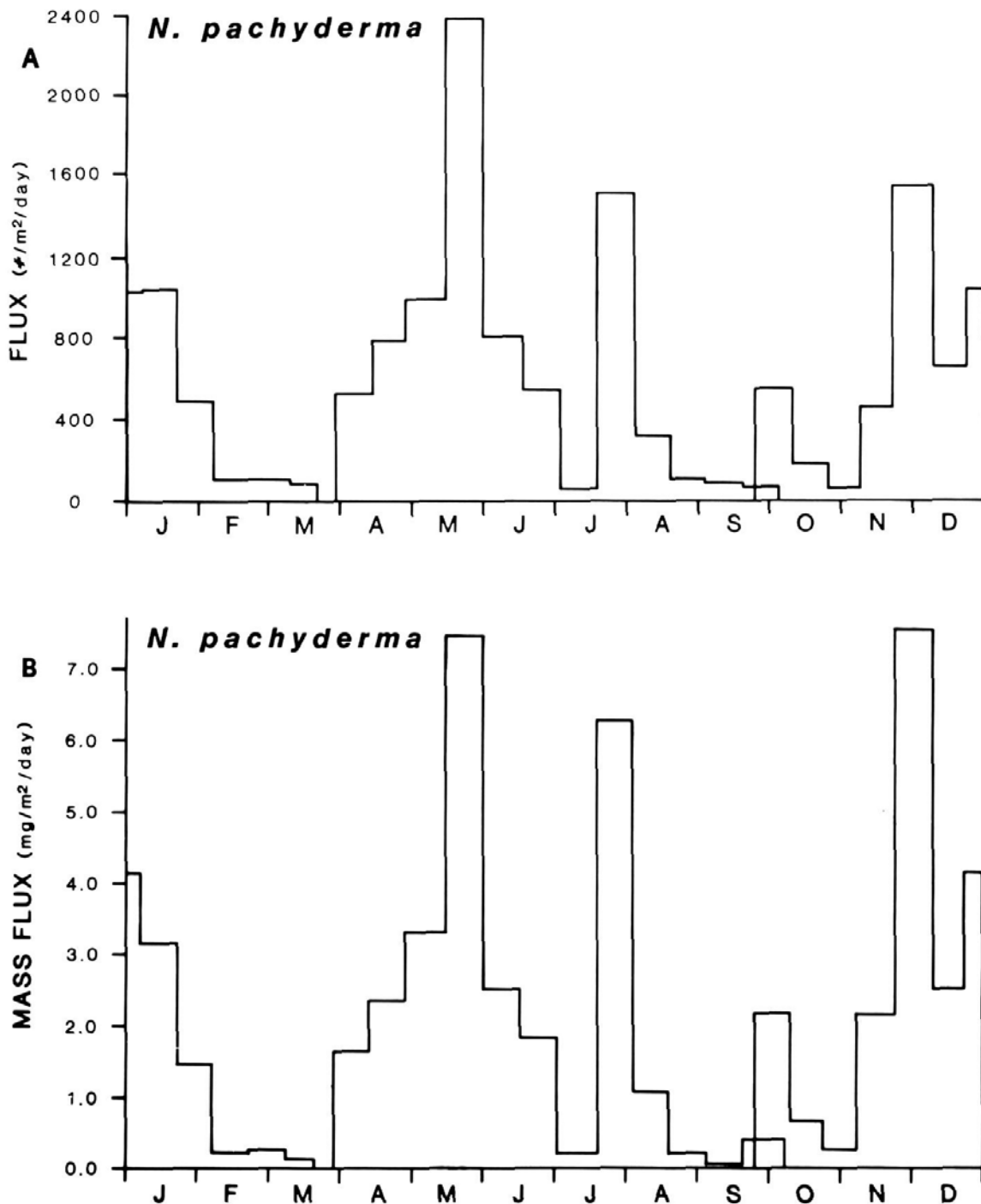
the boundary between dextral and sinistral forms is associated with the 7.2°C surface isotherm. Similarly, Kennett (1968) found a sharp increase in the percent sinistral specimens at latitudes poleward of 52°S, with dextrally coiled *N. pachyderma* dominating the lower latitude sediment assemblages.

Srinivasan and Kennett (1974b) found the abundance of reticulate forms to be high in the Southern Hemisphere during interglacial episodes of the last several hundred thousand years. In contrast, during glacial episodes when frequencies of *N. pachyderma* are high, assemblages from the Southern Hemisphere are dominated by crystalline forms (Srinivasan and Kennett 1974b). A similar trend was also observed in Recent surface sediments from the same region (Kennett 1968). Keller (1978) found that morphotypes similar to those in Group B dominate *N. pachyderma* assemblages during warm periods in the Northern Hemisphere. At Station PAPA, Group A forms, which correspond to both the crystalline forms defined by Srinivasan and Kennett (1974b) and Form 1 of Keller (1978), are dominant when surface waters are coldest and the shell flux of *N. pachyderma* is highest. The Group B reticulate forms correspond to Forms 2 and 3 (Keller 1978) and are dominant during months when surface temperatures in the northeast Pacific are relatively warm.

Tolderlund and Bé (1971) have shown that in sub-arctic regions of the North Atlantic, *N. pachyderma* has a distinct bimodal seasonal occurrence with maximum abundances during the spring (April through June), and a secondary peak in November. In the North Atlantic transitional water mass, the maximum *N. pachyderma* abundance occurs in the fall (Tolderlund and Bé 1971). Although morphotypes of this species were not separated, Tolderlund and Bé (1971) reported an abundance of sinistrally coiled forms in the sub-arctic water mass during the spring, and a predominance of

dextrally coiled forms in the transitional water mass during the late summer and fall. These observations suggest that the bimodal distribution of *N. pachyderma* in the North Atlantic may reflect the relative abundances of the Group A and Group B morphotypes.

Knowledge of the depth at which a species lives is important in determining the ecology of the species and its response to seasonal hydrographic changes. Bé (1960) suggested that in the Arctic *N. pachyderma* inhabits the upper few tens of meters of the water column during early life stages and then migrates to depths greater than 200 m during late ontogeny. Bé and Ericson (1963) noted that a test thickening or the addition of a calcite crust accompanies this migration. These studies imply that *N. pachyderma* individuals with a calcite crust inhabit deeper waters than those without a crust. At Station PAPA, however, the abundance of heavily encrusted forms of *N. pachyderma* appears to be primarily controlled by seasonal changes in the thermal structure of the upper water column and is temperature-dependent. This is in agreement with the earlier work of Srinivasan and Kennett (1974b). *Neogloboquadrina pachyderma* individuals from Station PAPA that possess calcite crusts (Group A members) are most abundant when cold, nearly isothermal conditions, are present in the near-surface layer, whereas individuals lacking a crust (Group B members) are most abundant when warmer summer conditions exist. This would explain the high percentage of heavily encrusted forms in the antarctic surface sediments (Kennett 1968, 1970), but contradicts Kennett's (1970) observation that less encrusted *N. pachyderma* specimens dominate arctic waters, and that heavily encrusted forms dominate the sub-arctic region. The sub-arctic *N. pachyderma* population found at Station PAPA over a year-long period is dominated by reticulate, less encrusted forms,



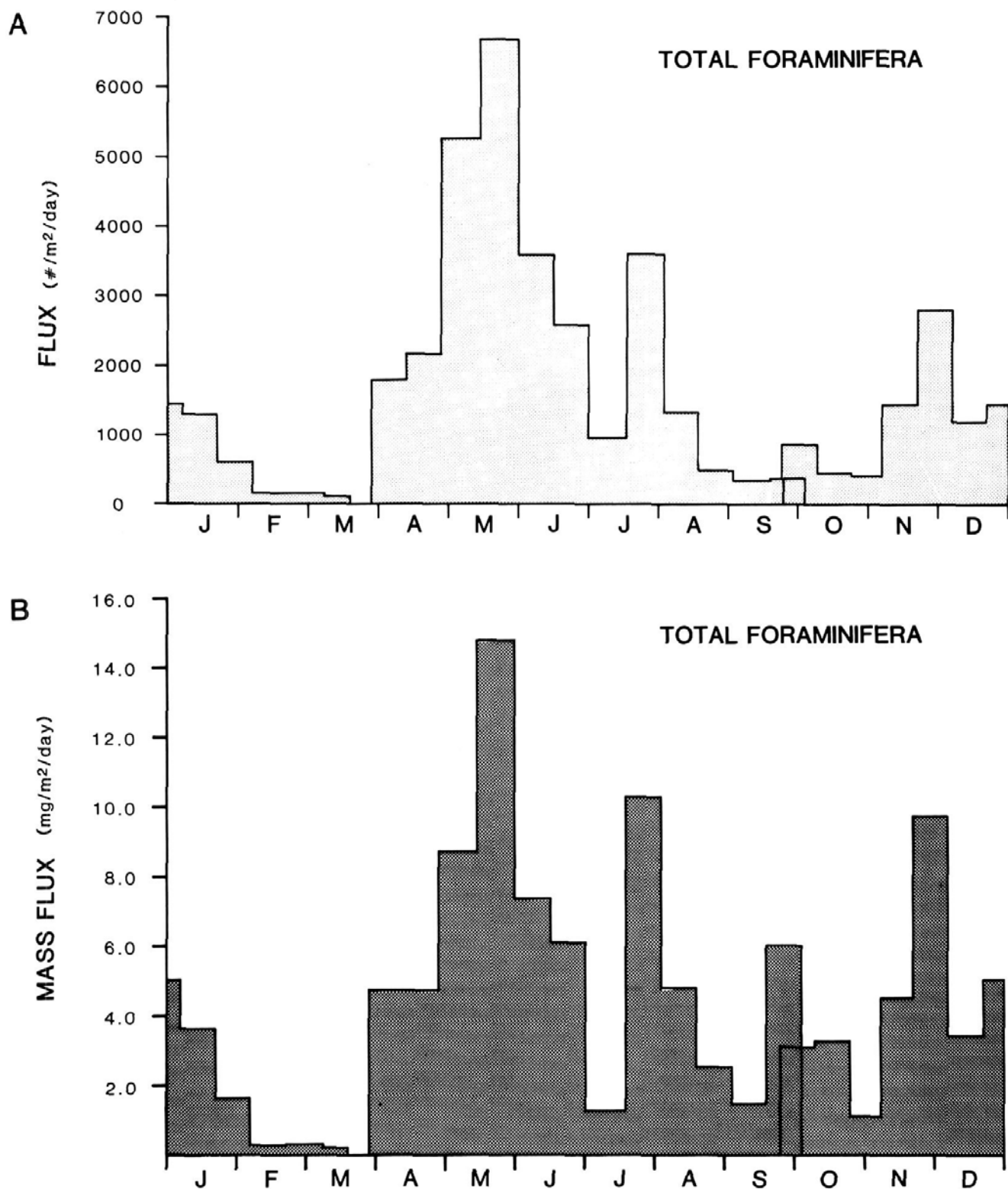
TEXT-FIGURE 9

Comparison of shell flux and mass flux patterns for all *Neogloboquadrina pachyderma* specimens. No correction factor for settling velocity was used. Note accentuated July and November peaks in the mass flux pattern (B) in comparison with those of the shell flux pattern (A).

which account for approximately 64% of the annual *N. pachyderma* shell flux.

The depth habitat of members of each *N. pachyderma* group may be dependent on maximum food source concentrations. At Station PAPA, where winter near-surface waters are nearly isothermal, the Group A crystalline forms are most likely

present at the depth within the photic zone where their food source is most concentrated. During months when the Group B reticulate forms are most abundant, a strong thermocline exists in the upper 30 m of the water column. Recent studies (Fairbanks and Wiebe 1980; Fairbanks et al. 1982) have shown that several nonspinose planktonic foraminiferal

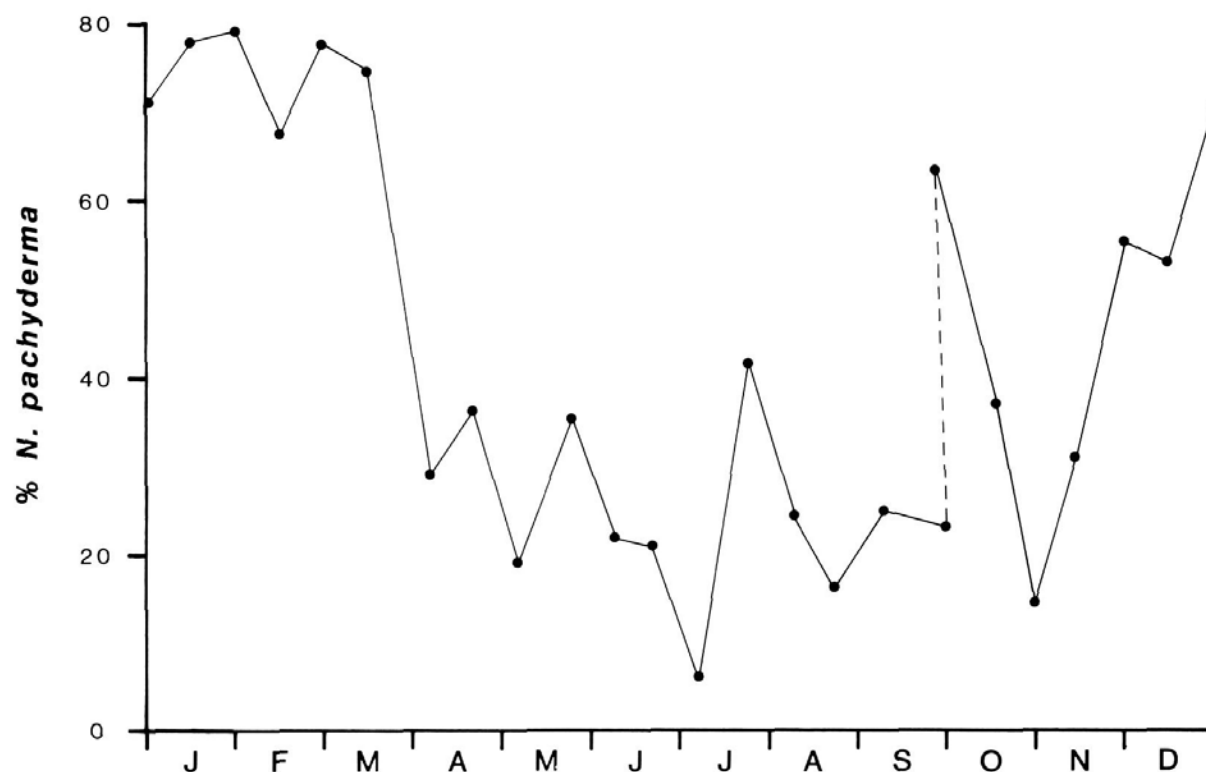


TEXT-FIGURE 10

Seasonal patterns of total foraminiferal shell flux (A) and total foraminiferal mass flux (B). Note similarity of these patterns to those of the total *Neogloboquadrina pachyderma* shell flux (text-fig. 9A) and mass flux (text-fig. 9B).

species live at or below the thermocline where food concentrations within the chlorophyll maximum are high. Plankton tows taken for six days at Station PAPA in late June/early July of 1971 revealed a preferred depth range for *N. pachy-*

derma of 50 to 100 m (Miles 1973). During that sampling period the upper 30 m of the water column were nearly isothermal (8.5°C) and the overall thermal structure of the water column was similar to conditions found in May of



TEXT-FIGURE 11

Percentage of *Neogloboquadrina pachyderma* of total foraminifera in the trapped assemblages.

1980 (text-fig. 3C) during the transition from the winter to summer near-surface conditions. The study by Miles (1973) was not a seasonal study, and thus the observed depth habitat of *N. pachyderma* does not necessarily apply to all forms of this species. The proposed depth habitat for Station PAPA *N. pachyderma* (Miles 1973), however, may relate to the forms associated with nearly isothermal waters.

In sediment trap samples from the Panama Basin, Thunell and Reynolds (1984) found a close similarity in the seasonal shell flux patterns of *N. pachyderma* and *N. dutertrei*. A morphologic similarity is observed between Group B forms from the northeast Pacific and the dextrally coiled *N. pachyderma* specimens from Panama Basin trap samples. Similar surface textures are also found on both Group B *N. pachyderma* from Station PAPA and Panama Basin *N. dutertrei* tests (pl. 1, figs. 8 and 9, respectively). Group A forms of *N. pachyderma* were not found in Panama Basin trapped assemblages. The shell flux of both *Neogloboquadrina* species in the Panama Basin is greatest when intense seasonal upwelling (Stevenson 1970) positions the thermocline within the photic zone, thereby enabling the development of a chlorophyll maximum and a subsequent increase in *Neogloboquadrina* species populations. Fairbanks et al. (1982) have demonstrated that peak abundances of *N. dutertrei* in the water column of the Panama Basin are associated with the chlorophyll maximum, and isotopic work by Curry et al. (1983) indicates that this species adjusts its depth habitat to the changing position of the thermocline. The similarities in

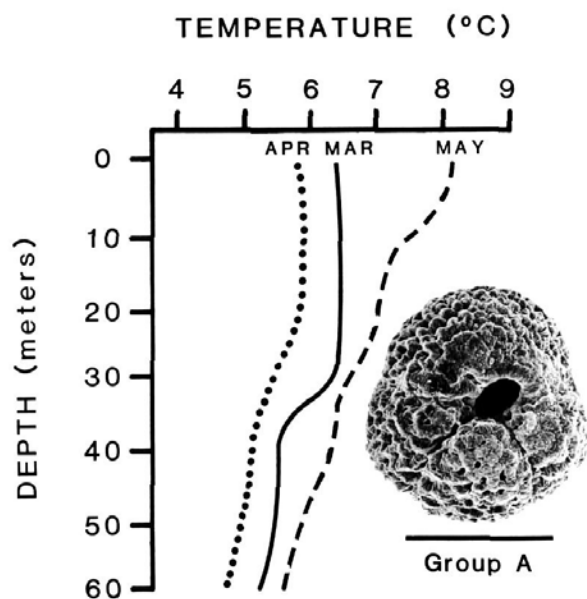
morphology and seasonal shell flux pattern observed of Group B forms of *N. pachyderma* from Station PAPA and both *N. pachyderma* and *N. dutertrei* from the Panama Basin suggest that the depth habitat of *N. pachyderma* Group B individuals at Station PAPA may also be associated with the position of the seasonal thermocline and the chlorophyll maximum.

For each morphotype group of *N. pachyderma* at Station PAPA there exists a close association between surface ultrastructure and coiling direction. An initial separation of *N. pachyderma* morphotypes by coiling direction rather than by surface ultrastructure would have produced similar results and conclusions.

CONCLUSIONS

Two morphologically different groups of *Neogloboquadrina pachyderma*, collected in sediment traps deployed in the subarctic northeast Pacific, display distinctly different seasonal shell flux patterns. The abundance of each group varies synchronously with the seasonal warming and cooling of near-surface waters and with the seasonal migration of the North Pacific Drift. The thermal structure and the relative nutrient concentrations of the upper 50 m of the water column at Station PAPA (50°N, 145°W) are altered by these changes and influence the *N. pachyderma* population.

Several morphotypes of *N. pachyderma* were initially separated into two groups, A and B, based on their surface tex-



TEXT-FIGURE 12
Thermal structure of the upper water column at Station PAPA during the period when the Group A crystalline forms dominate the *Neogloboquadrina pachyderma* shell flux. High surface nutrient concentrations are associated with these seasonal near-surface water conditions. (Scale bar = 100 μ m.)

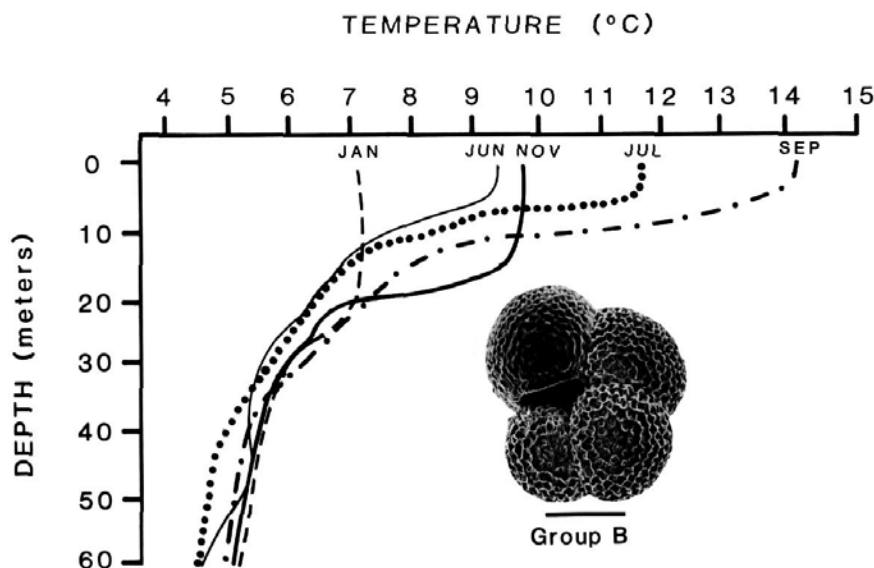
tures. Group A, the crystalline, heavily encrusted forms, are distinctly different from the reticulate, less calcified forms of Group B. Based on the seasonal shell flux patterns observed at Station PAPA, each group dominates the *N. pachyderma*

population under different thermal and nutrient conditions. Group A forms of *N. pachyderma* appear to prefer habitats with cold (colder than 8°C) waters that have little or no stratification (text-fig. 12). Such conditions are found at Station PAPA during the sub-polar winter months March through May when upwelling within the upper water column mixes the near-surface layer and increases surface nutrient concentrations. Group B forms are most abundant when the near-surface layer is well stratified and relatively warm (warmer than 8°C). A strong thermocline is present at Station PAPA during the months between May and December (text-fig. 13). During these months, nutrient concentrations are lower than when Group A forms dominate.

Other distinct differences between Group A and Group B morphotypes include predominant coiling direction and size. Group A individuals are generally sinistrally coiled and are smaller than the predominantly dextrally coiled Group B individuals. An initial separation of *N. pachyderma* morphotypes by coiling direction would have produced similar results and conclusions. Using coiling direction as a means for morphotype separation is less subjective than using textural differences and thus in the future may result in more consistency and better comparability among authors.

ACKNOWLEDGMENTS

We thank Dr. Susumu Honjo (Woods Hole Oceanographic Institution) for generously providing the sediment trap samples. Drs. William Curry and Kozo Takahashi (Woods Hole Oceanographic Institution) provided us with unpublished data on planktonic foraminiferal settling velocities. The critical reviews of Drs. William Curry, Richard Fairbanks, Richard Fillon, James Kennett, and Douglas Williams are appreciated. Special thanks are extended to Dr. C. Wylie Poag and



TEXT-FIGURE 13
Thermal structure of the upper water column at Station PAPA during the period when Group B reticulate forms are most abundant and dominate the *Neogloboquadrina pachyderma* shell flux. Presence of the seasonal thermocline and relatively high surface temperatures are characteristic of the near-surface summer conditions. Relatively low surface nutrient concentrations are associated with this thermal make-up. (Scale bar = 100 μ m.)

Judith Commeau of the U.S. Geological Survey, Woods Hole, for their SEM work. This research was supported in part by NSF Grants OCE81-10161 and OCE85-00663.

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ANNOUNCEMENT

WORKSHOP ON FORAMINIFERA

The Second International Conference on Paleooceanography will be held at Woods Hole from September 8-13, 1986. Two days of workshops are scheduled for the weekend prior to the formal meeting (September 6-7). Among those planned will be a workshop devoted to "FOSSIL AND RECENT FORAMINIFERA."

Depending upon the level of interest, the workshop will be either a half day or full day in length, composed of informal presentations from the participants. Preliminary plans call for the workshop to be divided into two parts. The general topics and themes that we have considered emphasizing include the following.

Topic A: Recent Foraminifera (C. Hemleben)

1. Experimental approaches in foraminiferal research
2. Ontogeny of benthic and planktonic foraminifera
3. Ecologic niches of foraminifera
4. Distribution of Recent foraminifera

Topic B: Fossil Foraminifera (R. Thunell)

1. Evolutionary rates and trends in fossil foraminifera
2. Paleooceanographic-paleobathymetric reconstructions using benthic and planktonic foraminifera
3. Paleobiogeography of foraminifera
4. Stratigraphic resolution: new data on faunal, paleomagnetic and isotopic calibrations

Individuals interested in participating in the workshop should contact either:

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