

Planktic foraminifera as North Atlantic water mass indicators

Planktic foraminifera
Water masses
Frontal zones
Diversity
NE Atlantic

Foraminifères planctoniques
Masses d'eau
Région frontale
Diversité
Atlantique NE

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ABSTRACT

Distribution patterns of planktic foraminifera, collected from Eastern North Atlantic surface waters during August and September 1986, are related to measured hydrographical parameters. Three main water masses, Subpolar Water (SW), the North Atlantic Current (NAC), and the Azores Current (AC) are all characterized by distinct faunal assemblages. A fourth, distinct water mass is here referred to as North Atlantic Transitional Water (NATW). The distinction, based on species clusters, between the NATW and the southern AC, is less evident than between the NATW and the northern SW and the NAC. This is the combined result of low absolute frequencies, a high number of species and a superimposed complex hydrography in the southern water masses.

The oceanic frontal zones between the NAC, NATW and the AC coincide with faunal boundaries. Along the boundaries, broad mixing zones can be recognized by their highly diverse foraminiferal assemblages of relatively low equitability.

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RÉSUMÉ

Les foraminifères planctoniques comme indices des masses d'eau de l'Atlantique Nord

Des modèles de répartition des foraminifères planctoniques prélevés dans les eaux superficielles à l'est de l'Atlantique Nord en août et septembre 1986, sont comparés aux paramètres hydrologiques mesurés à la même époque. Trois masses d'eau importantes, l'eau subpolaire (SW), le courant nord-atlantique (NAC), et le courant des Açores (AC) sont caractérisés par des associations de foraminifères distinctes les unes des autres. Une quatrième masse d'eau distincte peut être mentionnée : l'eau intermédiaire nord-atlantique (NATW). La distinction entre la NATW et le AC du Sud, d'après les groupes d'espèces, est moins évidente que celles entre la NATW, la SW du Nord et le NAC. Ceci est dû aux faibles fréquences absolues, au nombre élevé d'espèces et à l'hydrologie complexe dans les masses d'eau australes.

Les zones océaniques frontales entre le NAC, la NATW et le AC coïncident avec les limites faunistiques, au long desquelles des zones de mélange étendues peuvent être identifiées par des associations de foraminifères très diverses et d'une équitabilité relativement basse.

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INTRODUCTION

Paleoceanographic and paleoclimatic reconstructions based on planktic foraminifera (*e.g.*: CLIMAP, 1976; 1981; Vincent and Berger, 1981) make use of the traditional distinction between "arctic", "subarctic", "transitional", "subtropical" and "tropical" faunal provinces (Bé and Tolderlund, 1971). However these provinces do not necessarily match the planktic foraminiferal patterns in surface waters. Faunal frequency patterns as well as the peak frequencies of different species in fact undergo substantial changes throughout the year, induced by seasonally changing hydrographic conditions (*e.g.*: Cifelli and Smith, 1974; Cifelli and Benier, 1976; Pujol *et al.*, 1976; Brummer and Kroon, 1988). A detailed knowledge of hydrography can clarify the controls on the differences between surface water and bottom assemblages. For example, water circulation can create and maintain water bodies with particular species groups. Information concerning the seasonal effect in sediment assemblages can be obtained from water samples collected at identical stations during different seasons. By quantitatively determining specific living seasonal assemblages and their horizontal variation, it can be established to what extent a particular season is represented in the annual shell accumulations on the sea floor and we can consequently determine average paleotemperatures. For example, if a certain species is solely present during summer in a certain area, an average summer temperature for the sedimentary assemblage in that area can be reconstructed from the oxygen isotope ratio in the foraminiferal shell of this particular species (Ganssen, 1983).

The objective of this paper is to characterize water masses in terms of planktic foraminifera (frequency distributions, cluster analyses and information indices) in conjunction with recorded hydrographical parameters such as temperature, salinity and density. The study covers the Subpolar Water, the North Atlantic Transitional Water and the North Atlantic and Azores Currents. The author calculated information indices for use as a research tool on sediment assemblages comprising extinct species, as they do not depend on the assumption of a temporally invariant species ecology or of a particular species composition. The described material was collected during the R/V *Tyro* APNAP-I cruise (August and September 1986) in the Central North Atlantic (Ganssen *et al.*, 1986). APNAP (Actuomicropaleontology Paleoceanography North Atlantic Project) investigates an area east of the Mid-Atlantic Ridge from 60° N to 27° N (Fig. 1 *a, b*) during several seasons. In the course of this cruise, planktic foraminifera were collected from surface waters, the watercolumn and the seafloor.

The present paper concerns the study of 93 surface water samples with the aim of applying derived foraminiferal water mass characteristics to bottom sediments.

METHODS

With the research vessel under way, surface water (0-5 m) was continuously filtered through 75 µm mesh nylon plankton nets by means of a deckwash pump with an attached flow meter. A collecting interval of between three and six hours was used, depending on productivity. Upon recovery, part of the samples were examined under a light microscope to verify that the amount of filtered water was sufficient to obtain a valuable data set. The temperature and salinity of the surface waters were logged at the time of recovery using continuous CTD recording, when available, or were measured using hand methods (Tab. 1). Additionally, 14 CTD profiles were recorded. Only patterns are used for the reason that the CTD data underwent no calibration. The plankton samples were stored in an alcohol compound (95 % ethanol, 5 % methanol). In the laboratory the samples were washed over a 63 µm sieve to remove the alcohol. The residue was dried at 50° C and then combusted in a Low Temperature Asher, which oxidizes organic matter, concentrating the non-organic contents (*e.g.* calcareous shells). Species were counted separately for the 125-250 µm and 250-500 µm fractions. Although the coarse fraction (250-500 µm) adds only less than one per cent to the total sample (>125 µm; Tab. 2 *a* and *b*) and its signals will therefore be obscured, we did separate it, because it permits rapid determination and is commonly used for isotopic measurements. Therefore its very variable and low absolute frequencies are not considered in quantitative data analysis such as cluster analysis on samples and equitability computations. For each fraction, large samples were split into suitable aliquots of at least 200 specimens; sample fractions containing less than 200 specimens were counted completely. Matrices of planktic foraminiferal relative frequencies were clustered both for samples and for species. A Principal Component Analysis (PCA) did not result in a significant variation reduction and is considered no further in this paper. In addition, information indices of Shannon-Wiener for diversity and Buzas-Gibson for equitability (Lipps *et al.*, 1979) were computed for this dataset. Since equitability values depend in great measure on the number of specimens, especially when the species count is low (Sheldon, 1969), the coarse fraction with its low and variable frequencies is not considered in the equitability computations. The resulting values of the fine fraction were been contoured on the track chart. Computer contouring of these and of surface temperature and salinity data used the weighted mean method and an adjustable digital Butterworth filter (Slootweg, 1978). The material has been filed in the collection of the Geomarine Center, Amsterdam.

Hydrography

GENERAL

Surface water temperatures of the Eastern North Atlantic are closely related to latitude and currents, and to a with

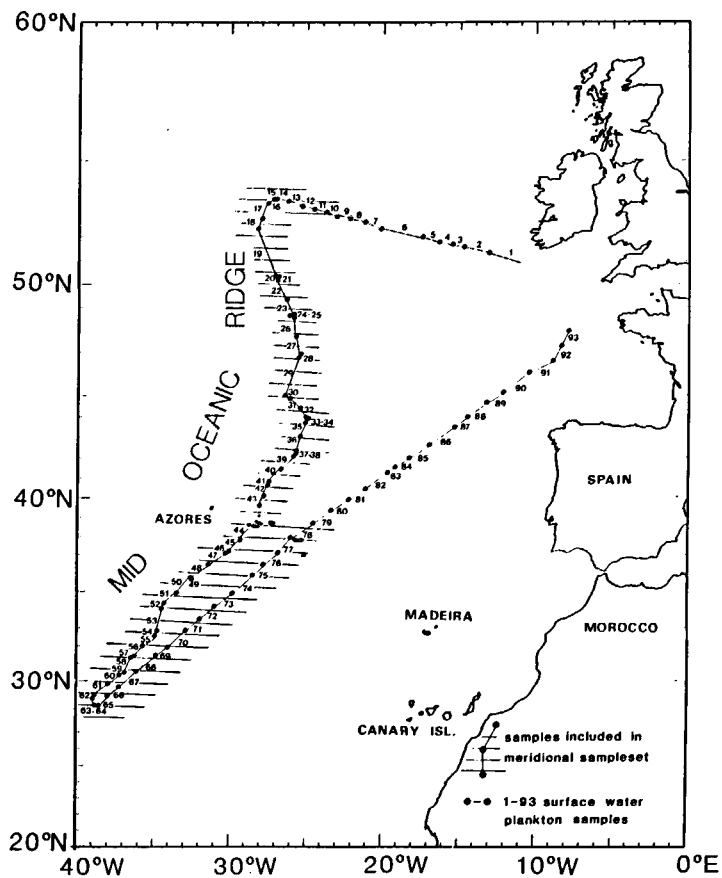
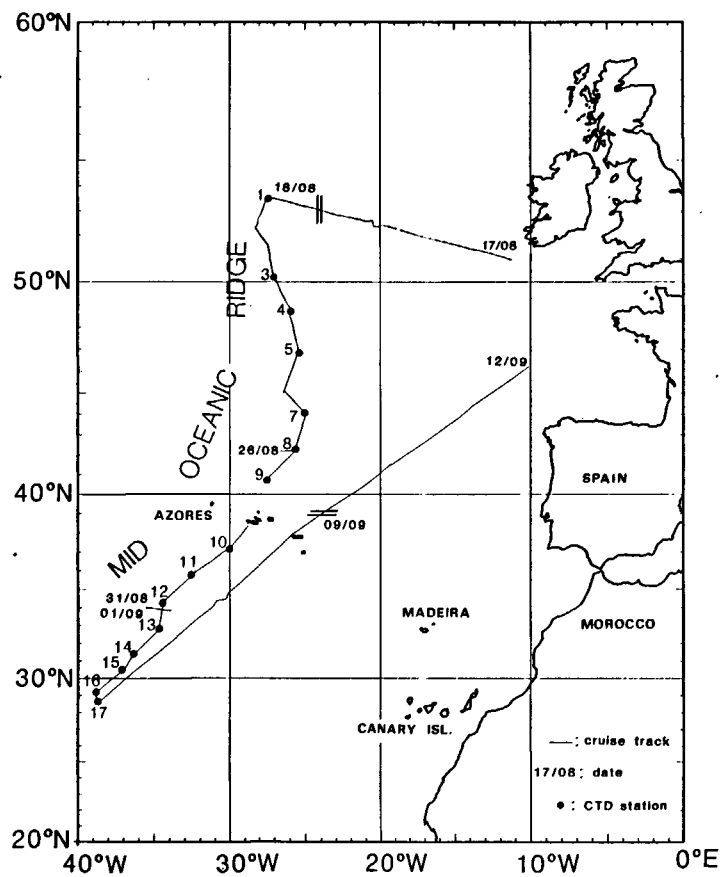


Figure 1

a) R/V Tyro track of cruise APNAP I (August and September, 1986) showing CTD stations and dates.
 b) Idem showing numbers and intervals of surface water sampled. Dots at the end of each sampling interval also indicate samples used for temperature and salinity measurements.

superimposed cyclonic and anticyclonic gyre system which creates and maintains distinct water masses (Williams *et al.*, 1968 *a*; Tchernia, 1980; Käse *et al.*, 1985). An overview of the water masses is given in Figure 2.

Strong seasonal variations in temperature are encountered especially at the higher latitudes, while salinity remains relatively constant throughout the year. North of the subtropical convergence at about 33° N, with a seasonal shift of 3° (Käse and Siedler, 1982), salinities and temperatures primarily depend on currents of Gulf Stream origin (Tchernia, 1980). In the north, the Subarctic Front (SF), associated with strong horizontal

temperature gradients, separates cold Subpolar Water (SW) from warmer Gulf Stream waters (Krauss and Käse, 1984). The Gulf Stream branches in the vicinity of 40° N-40° W into a strong North Atlantic Current (NAC) and the Azores Current (AC; Käse *et al.*, 1986). The northern boundary of the NAC is also formed by the so-called Subarctic Front, although temperature gradients are less distinct in the eastern basin (Krauss, 1986). The NAC dies out southward, yet strong current regions (NAC s.s.) are separated by frontal jets from regions with indistinct currents (Krauss, 1986), referred to as North Atlantic Transitional Water (NATW) in this paper. At about 34° N the perpetual, basically west-east meandering Azores Frontal Zones (AFZ) is associated

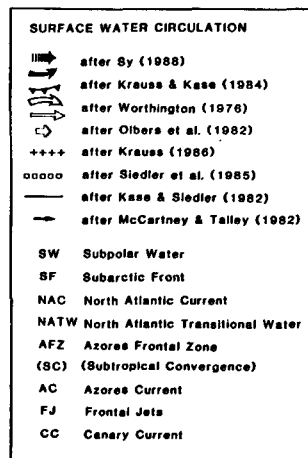
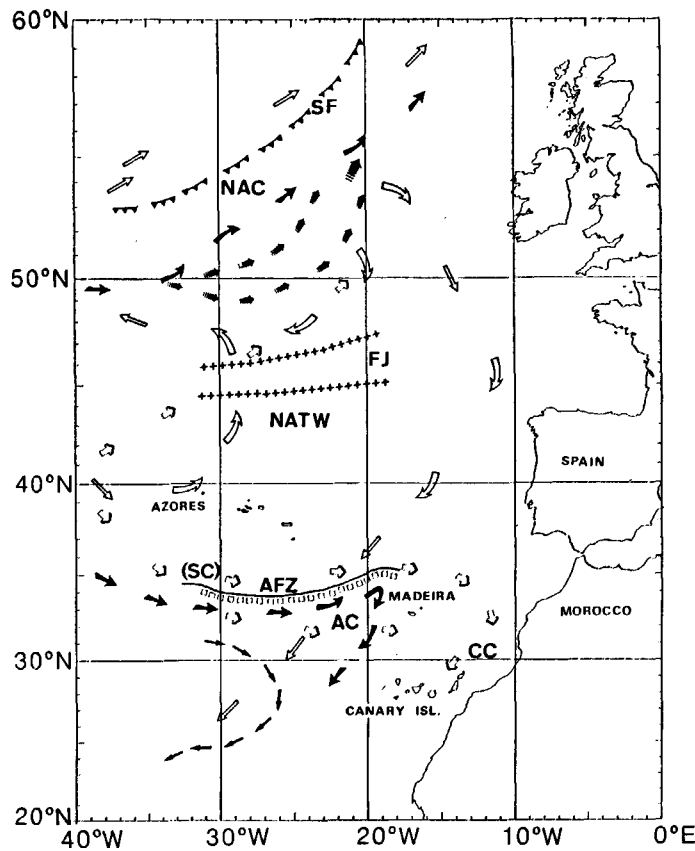


Figure 2

Surface water masses as described in the literature for the North East Atlantic Basin.

with the eastward AC (Siedler *et al.*, 1985). The AFZ separates southern regions with a permanent thermohaline mixed layer and a subtropical thermocline from northern regions with a seasonal thermocline formation, comprising water masses of the NAC, which show winter convective and advective mixing (Käse and Siedler, 1982). The AC branch of the Gulf Stream (Käse *et al.*, 1986; Käse and Zenk, 1987), also forms the northern boundary of the subtropical gyre, which encompasses the Subtropical Mode Water (McCartney and Talley, 1982; Käse *et al.*, 1985).

APNAP I HYDROGRAPHY

To determine the representativity of the APNAP I temperature data, we compared our data with temperature values derived from long-term mean August and September isotherms, averaged over a period of 25 years by Robinson *et al.*, 1979 ($r = 0.98$, see also Fig. 3 *a*, *c* and *d*).

APNAP I salinity data are compared with salinity values derived from interannual mean isohalines (Robinson *et al.*, 1979 give no record of monthly mean isohalines), giving a lower correlation ($r = 0.93$) than temperature. Our August salinities are generally lower than the annual average, but still fall within the normal annual variation (see also Fig. 3 *b* and *e*). These excellent correlations confirm that we sampled during a representative summer. Comparison of our patterns of surface water isotherms and isohalines (Fig. 3 *a* and 3 *b*) with the patterns of the mean August and September isotherms over the same period (Fig. 3 *c* and *d*) and the annual mean isohalines (Fig. 3 *e*; Robinson *et al.*, 1979) reveals the following differences. From 47° N to 44° N our surface water isotherms show a sudden increase in density of the isolines absent from the Robinson *et al.*, 1979 map. A north-south meridional isotherm cross-section along about 30°W (Fig. 4 *a*) shows that this column down to 800 m, forming an uplift of deeper isolines. The

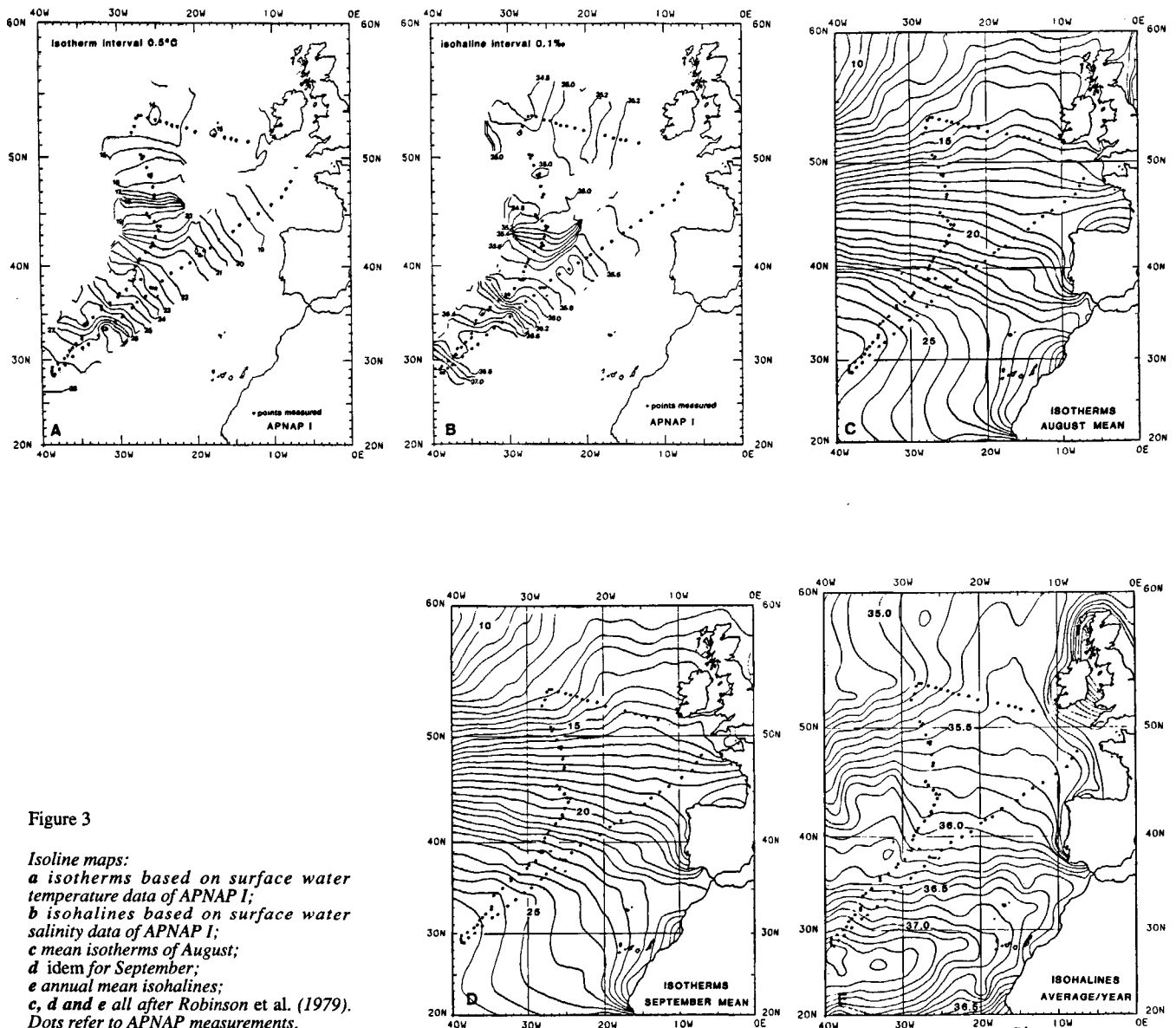


Figure 3

Isoline maps:
a isotherms based on surface water temperature data of APNAP I;
b isohalines based on surface water salinity data of APNAP I;
c mean isotherms of August;
d idem for September;
e annual mean isohalines;
c, *d* and *e* all after Robinson *et al.* (1979).
 Dots refer to APNAP measurements.

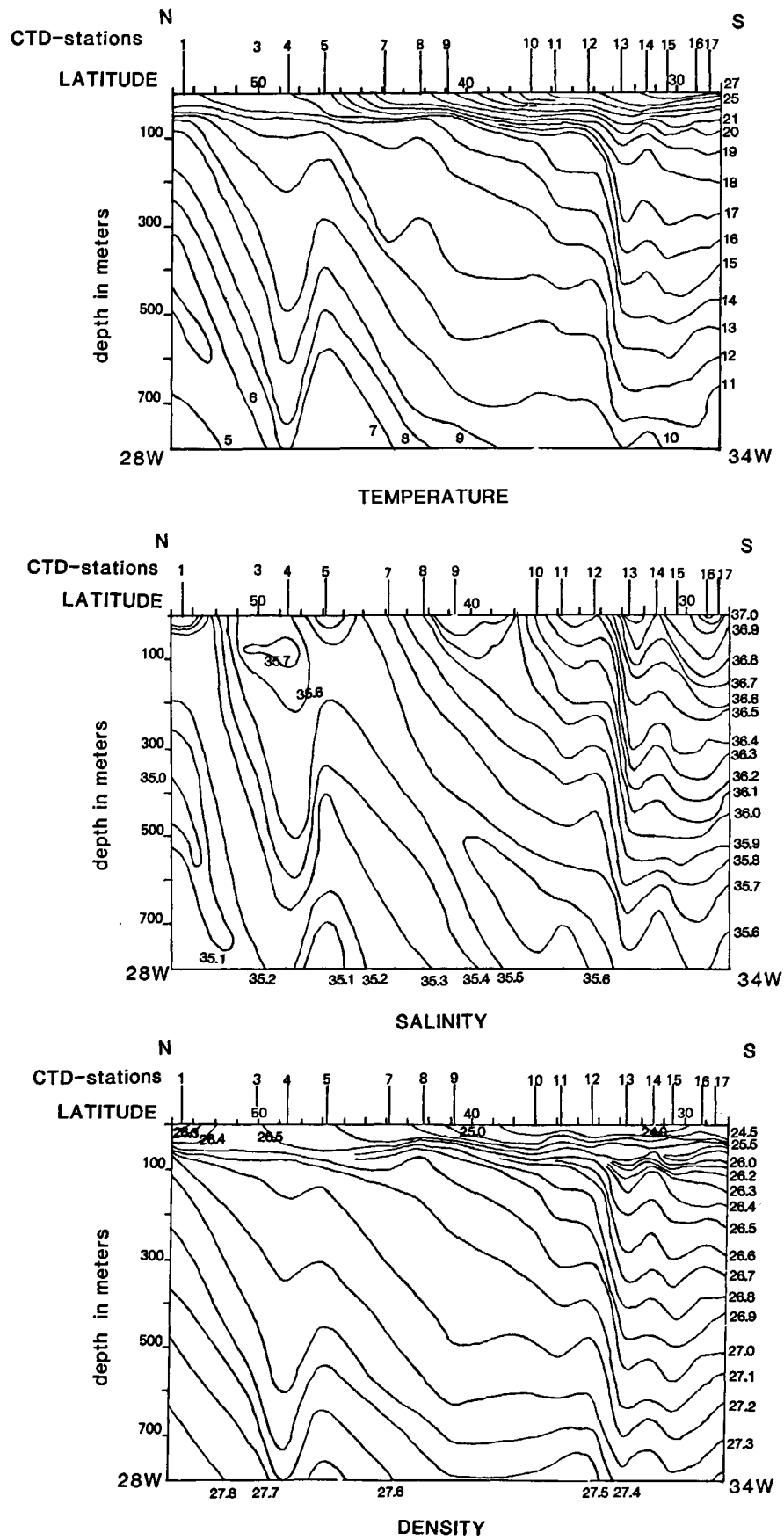


Figure 4

Isoline sections of:
 a temperature in °C;
 b salinity in practical units ‰;
 c density in σ_t (after Ganssen et al., 1986).
 For station locations see Figure 1 a.

isohalines at the surface do not give such a strong signal, but the isohaline meridional section (Fig. 4 b) does show a clear signal in the shape of a relatively fresh water lens. In the isopycnal section (Fig. 4 c), this feature is less evident, but still apparent. Because of its presence in the surface waters and the water column, we conclude this feature to be associated with a frontal zone, rather than a local eddy. At 34° N the isotherms show a second increase in density as well as a northwest deflection. The surface isohalines reflect the same feature, in a somewhat weaker form. Examination of the CTD N-S sections of temperature, salinity and density (Fig. 4) reveals a sharp downward bend in the isolines, indicating a frontal zone. This frontal zone coincides

with the Subtropical Front, also referred to as the AFZ (Siedler *et al.*, 1985), associated with the AC. The observed deflection at the surface may indicate meandering or may be an effect of the 8-day time lag between our measurements. At about 51°N the isotherms have a low gradient in map view but only the CTD sections show a sudden dip of the isolines, which is interpreted as the boundary between the SW and the NAC. The observed features are in general less evident in the upper 25 m of water, because of superimposed seasonal surface warming or mixing. Our observations are summarized in a hydrographic interpretation chart for this area, showing the position of the most evident water masses during APNAP I (Fig. 5).

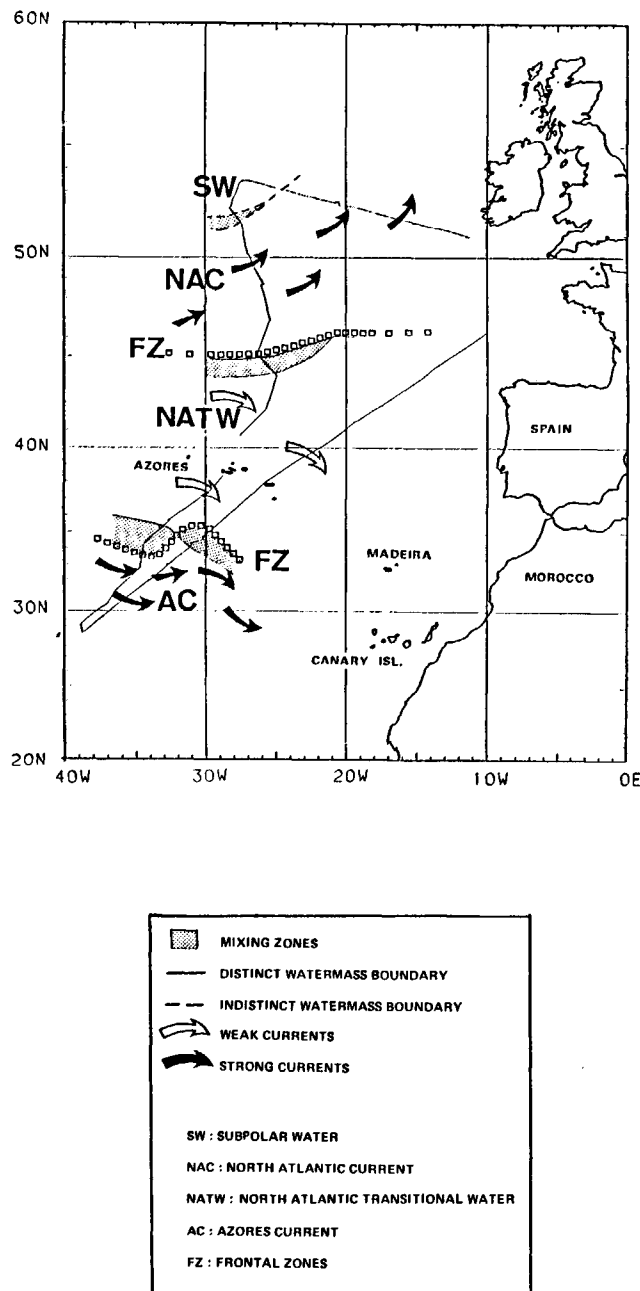


Figure 5

Hydrographic interpretation of the studied area for August and September 1986, based on both surface water and CTD data. Approximate current velocities are for NATW after Krauss (1986) and for the NAC and AC after Krauss (1986) and Käse and Siedler (1982).

Planktic foraminiferal assemblages

Weighted pair group cluster analyses on samples (fraction 125-250 μm , Fig. 6 a and b) and curves of relative species frequencies (Fig. 7 a and b) are intended to describe the possible relationship between distributional patterns of foraminifera and water masses. We excluded species with a lower frequency than 2 % from all analyses. Water masses recorded in the studied area are not restricted to a certain latitude, but also

extend longitudinally. Therefore analyses were executed on two sets of data. Samples collected along the meridional section will give sharper boundaries (Fig. 1 b) and an improved correlation at subcluster level (Fig. 6 b). This is because the meridional section crosses most of the water masses obliquely and water mass boundaries tend to fade out towards the east (Krauss and Käse, 1984). The total number of samples shows possible longitudinal shifts of the faunal boundaries towards the east. The four conspicuous sample groupings, shown by

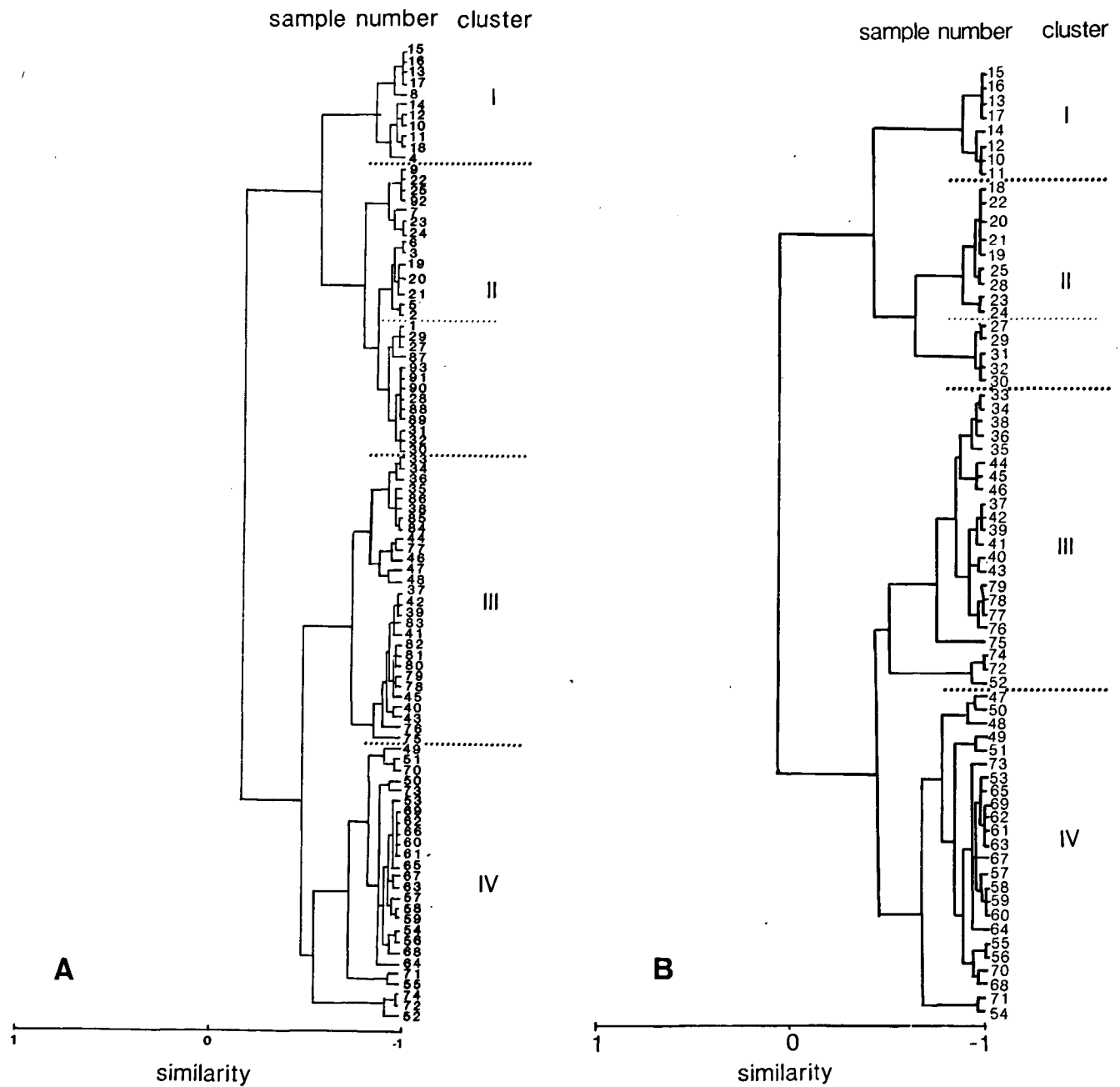


Figure 6

Weighted pair group cluster analysis on counted planktic foraminiferal samples, based on a correlation matrix of relative frequencies, excluding species with a relative abundance lower than 2 %.
 a) 125-250 μm sieve fraction including all samples counted ; b) 125-250 μm sieve fraction including the meridional section (Fig. 1 b).
 Both sample sets show at least four clusters; in cluster II both sample sets give a coincident subdivision.

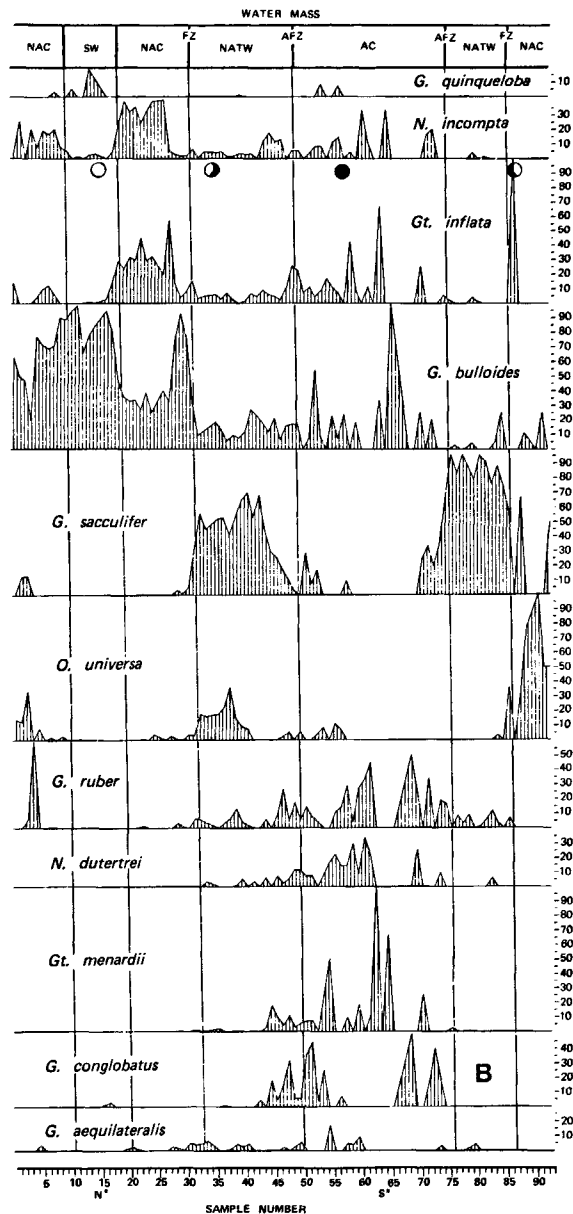
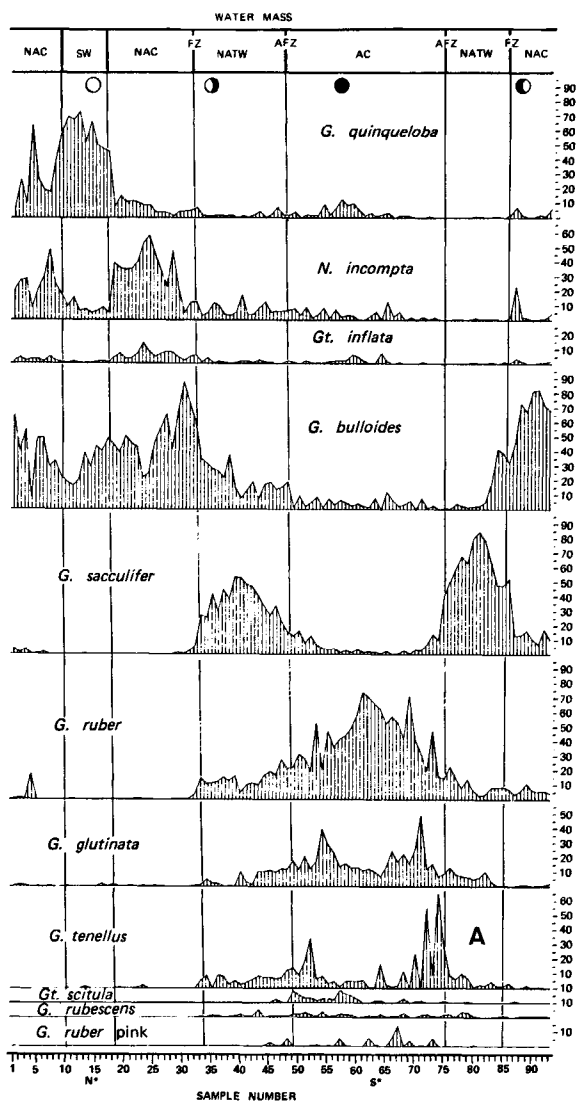


Figure 7

Relative frequencies of planktic foraminifera from surface water along the sample track (see also Fig. 1 b). a) 125-250 µm sieve fraction ; b) 250-500 µm sieve fraction. *G. ruber*=*G. ruber* white. AFZ = Azores Frontal Zone. For further explanations of the water mass abbreviations see Figure 5. N* and S* indicate respectively the northernmost and southernmost samples. Full, half and new moon are indicated at the top of the figures.

cluster analysis of the two data sets (assemblage I-IV; Fig. 6 a and b) almost coincide, when plotted on the map, although a shift of two samples is present at some boundaries (Fig. 8). Cluster analysis on species with a higher relative frequency than 5 % (Fig. 9) was carried out on both size fractions. The coarse fraction gives lower correlations than the fine fraction due to the occasionally low frequencies in the former one and the use of relative frequencies. The fine fraction (Fig. 9 a) clusters in four assemblages, which correspond to the four groupings in the dendrogram of the coarse fraction, but contain different species (Fig. 9 b). Some artificial subclusters also occur, such as a subcluster comprising *Globigerina bulloides* d'Orbigny and *G. quinqueloba* Natland together with a subcluster of *Globigerinoides ruber* (d'Orbigny) pink variety and *Globorotalia truncatulinoides* (d'Orbigny) sinistral. If the curves of the relative frequencies are examined, it becomes apparent

that the species confining these subclusters are, from an ecological point of view, in no way closely related (Bé, 1977). The only two samples containing the latter two have very low absolute frequencies causing artificial relative frequencies and subsequently subclustering. To relate species clusters to sample clusters, curves of the relative frequencies along the sample track (Fig. 7), are examined. This results in specific planktic foraminiferal assemblages (Tab. 3).

Watermasses

SPECIES DISTRIBUTION AND HYDROGRAPHY

The four major faunal assemblages correspond to, but do not always completely coincide with, the water masses defined hydrographically in terms of temperature and

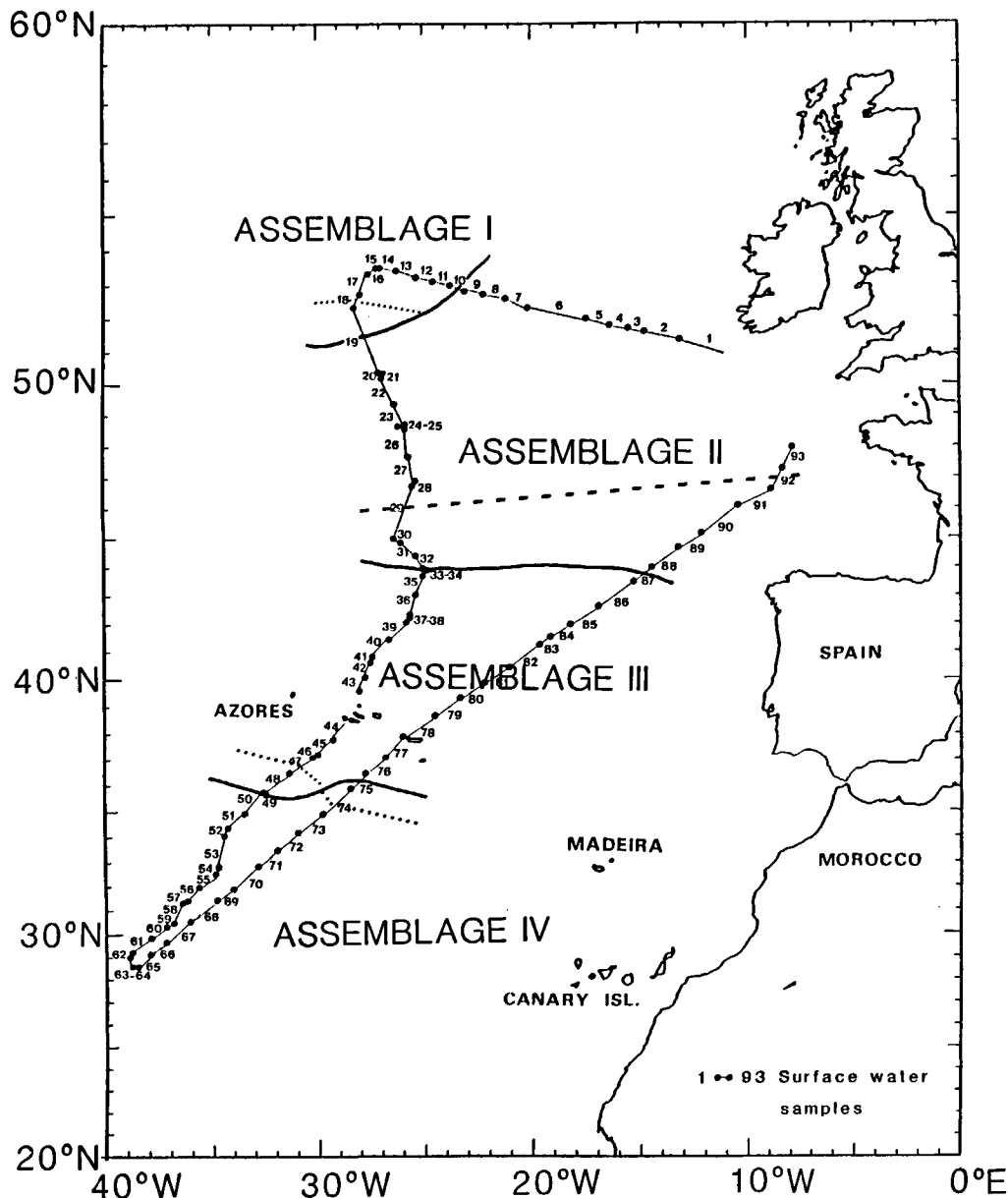


Figure 8

Faunal boundaries, based on cluster analyses of the samples. The two cluster analyses (see also Fig. 6) do not always give coincident sample assemblages; at the boundary a shift of two samples is sometimes present. Solid lines indicate boundaries based on all samples; dotted lines indicate boundaries on the meridional sections; dashed line is based on a subcluster present in both sample sets. For further explanation of assemblages 1-4 see Table 3.

		species clusters	sample clusters		
(64°N)	HYDROGRAPHIC UNITS used in this paper	125-250 µm SIEVE FRACTION	250-500 µm SIEVE FRACTION	ASSEMBLAGE	(64°N)
	SUBPOLAR	<i>G. quinqueloba</i>	<i>G. bulloides</i> <i>G. quinqueloba</i>	I	
52°N	NORTH ATLANTIC CURRENT	<i>G. bulloides</i> <i>Gt. inflata</i> <i>N. incompta</i>	<i>N. incompta</i> <i>Gt. inflata</i>	II	52°N
44°N	NORTH ATLANTIC TRANSITIONAL WATER	<i>G. sacculifer</i> <i>G. aequilateralis</i>	<i>G. sacculifer</i> <i>O. universa</i>	III	44°N
34°N	AZORES CURRENT (subtropical)	<i>G. ruber</i> <i>G. glutinata</i> <i>G. tenellus</i> <i>Gt. scitula</i> <i>G. rubescens</i> <i>N. dutertrei</i>	<i>G. ruber</i> <i>N. dutertrei</i> <i>Gt. menardii</i> <i>G. aequilateralis</i> <i>G. conglobatus</i> <i>P. obliquelocelata</i>	IV	34°N
(15°N)					(15°N)

Table 3

Relation of specific planktic foraminiferal assemblages I-IV, derived from sample clusters, with species clusters and described water masses for August and September 1986. No polar water is encountered during APNAP I cruise (latitudes at boundaries are only valid along the eastern track).

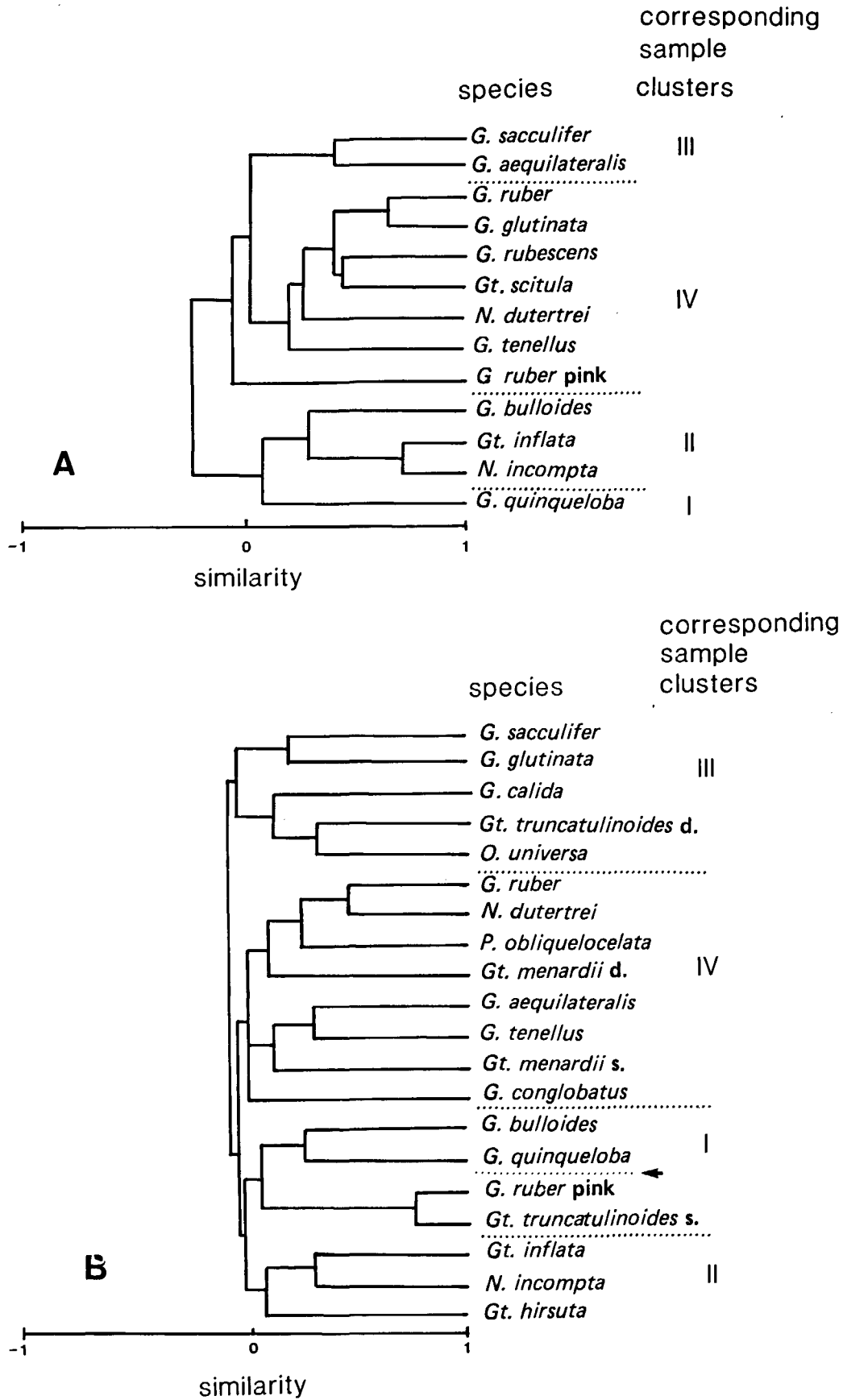


Figure 9

Weighted pair group cluster analysis on species, based on a correlation matrix of relative frequencies. Species with a lower relative abundance than 5% are excluded.

a) dendrogram of the 125-250 μm fraction; b) dendrogram of the 250-500 μm fraction. Both sieve fractions show four clusters, although the coarse fraction shows artificial subclustering (see text).

salinity (Wüst, 1935; Williams *et al.*, 1968 *b*; compare Fig. 5 and 8).

For example, the sharp faunal boundary between assemblage I and II at 52° N corresponds largely to the turnover of Subpolar Water and the North Atlantic Current (NAC) at about 51° N. North of this boundary the foraminifers *Globigerina quinqueloba* and only large *G. bulloides* are the frequent species; south of this the species *Neogloboquadrina incompta* (Cifelli), *Globorotalia inflata* (d'Orbigny) and *G. bulloides* are most abundant (Tab. 3). At 47° N a weak boundary can also be seen, considering the clustered samples, although this boundary has no clearly defined hydrographical counterpart. This feature, which cannot be traced in clusters based on species, possibly corresponds to the northern part of the frontal zone observed at the same latitude. A more evident faunal boundary is shown at 44°N along with the transition between the NAC and the North Atlantic Transitional Water (NATW, at about 45°N), forming also the southern part of the frontal zone. The NATW is characterized by an assemblage of the species *Globigerinoides sacculifer* (Brady), *Globigerinella aequilateralis* (Brady) and to a lesser extent *Orbulina universa* (d'Orbigny). Around 34°N a distinct faunal boundary is present, coinciding with a strong frontal zone (34-36°N), which confines the Azores Current (AC) to the North. The AC is characterized by a high number of species, with *Globigerinoides ruber*, *Globigerinita glutinata* (Egger), *Globigerinoides tenellus* Parker, *Globigerina rubescens* Hofker, and *Globorotalia scitula* (Brady) as dominant species in the fine fraction .

In the coarse fraction the AC contains the species *G. ruber*, *Neogloboquadrina dutertrei* (d'Orbigny) and to a lesser extent *G. aequilateralis*, *Globorotalia menardii* (Parker, Jones and Brady), *Globigerinoides conglobatus* (Brady) and *Pulleniatina obliquiloculata* (Parker and Jones).

Information indices and hydrography

Information indices add valuable water mass characteristics to those already defined on foraminiferal assemblages and physico-chemical environmental properties. As expected (Shih, 1979; Pianka, 1966; Pielou, 1975; 1979; van Soest, 1979) the contoured Shannon-Wiener index (Fig. 10 *a* and *b*) shows that in general the diversity increases southward and westward (*see also* the diversity curves of Fig. 12). The coarse fraction (250-500 µm, Fig. 10 *b*) has more variation in diversity than the fine fraction (125-250 µm, Fig 10 *a*), because the Shannon-Wiener index takes both the number of species and the relative abundance of each species into consideration. Since the coarse fraction has very variable frequencies, although the number of species remains equal, this results in artificially variable diversities. The Subpolar Water contains a low diverse planktic fauna. In the NAC the diversity increases only slightly southward especially in the coarser fraction. This low diversity can be related to seasonal variability of the environment and periodic high nutrient supplies (*see* McArthur, 1965; Hallock, 1987). The NATW shows a

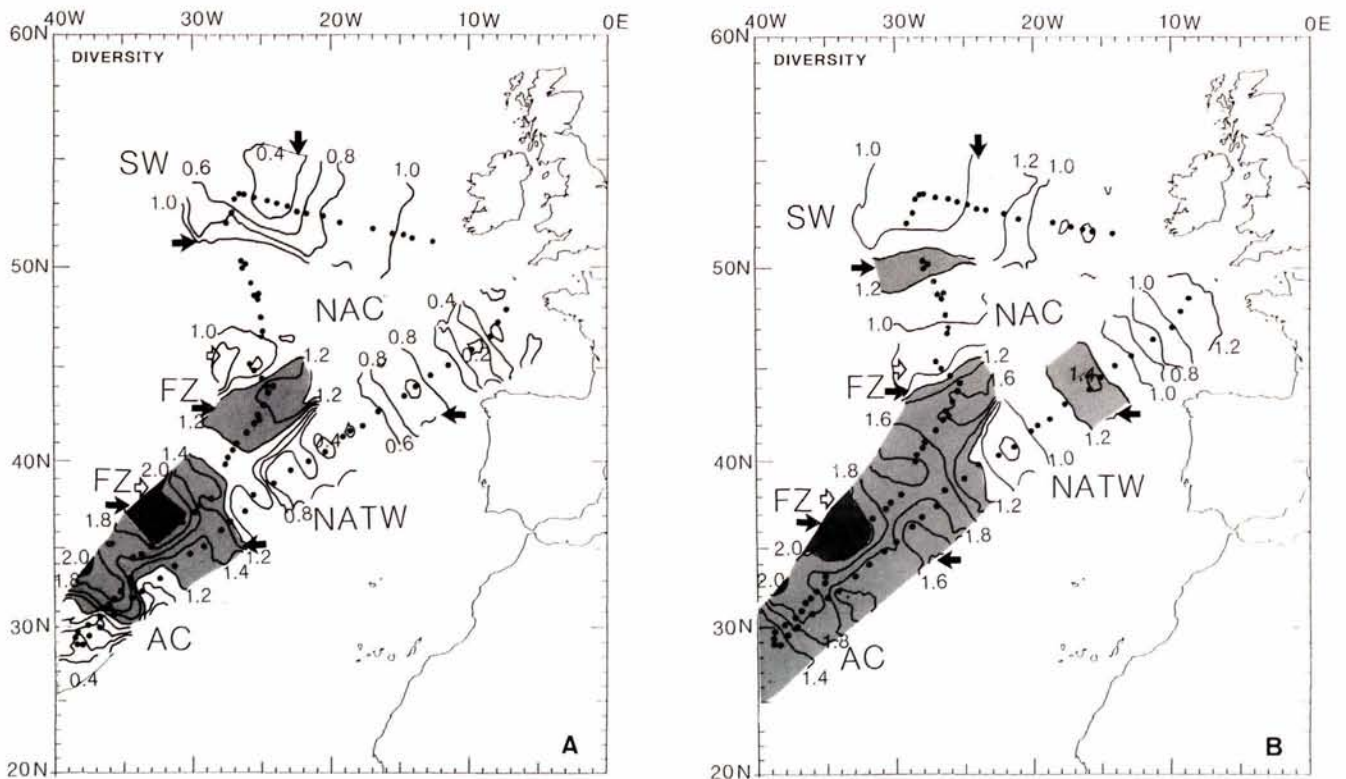


Figure 10

August-September 1986 planktic foraminiferal diversities (Shannon-Wiener index) contoured at a 0.2 interval.

a) 125-250 µm sieve fraction ; b) 250-500 µm sieve fraction.

Also shown are sample track and water mass boundaries ; main boundaries are indicated by solid arrows, open arrows indicate boundaries only present in the meridional samples (for legend see Fig. 5). Note the maximum diversity at the FZ north of the AC.

relatively high diversity in the west, decreasing rapidly eastward and being highest towards its boundaries, pointing to broad mixing zones between the water masses. Diversity in the AC is very high although it decreases south of 31°N and strongly towards the east. Equitability contours after the Buzas-Gibson index (Fig. 11) have a more complex pattern (see also the equitability values plotted along the sample track, Fig. 12). Equitability in the Subpolar Water varies from intermediate to high towards the boundaries. No dominant species are present. The NAC has an intermediate to high equitability, especially along the boundaries, decreasing eastward. The NATW has an intermediate to low equitability. The AC shows an intermediate equitability strongly decreasing southward. When the diversity and equitability curves are compared (Fig. 12), all show in their eastern part (sample numbers 65-93) scattered values. This can be attributed to the divergence of current systems towards the eastern boundary of the Northeast Atlantic basin (Krauss, 1986) with mixed faunas of the different water masses as a result.

DISCUSSION

It is shown that water masses can be characterized on the basis of the relative frequencies of planktic foraminifera established by cluster analyses and information indices related to measured hydrographical parameters. Differences within faunal water masses still appear to be considerable in comparison with the differences between the water masses. Samples are relatively easy to cluster; however the species do not cluster mutually to any great extent. This is especially accentuated in the southern watermasses with their low absolute frequencies and their high number of species, which may be attributed in part to the result of dense sampling in which small scale temporal variations will also be recorded.

In addition, the southern currents are more irregular than their northern counterparts, causing less distinct water masses (Weyl, 1978) and are therefore more difficult to characterize. Vertical migration will further alter the

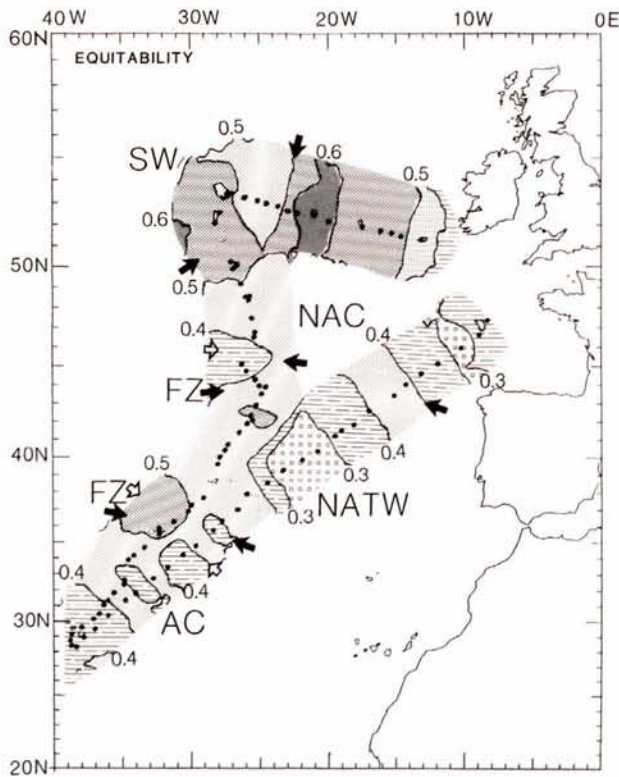


Figure 11 August-September 1986 planktic foraminiferal equitabilities (Buzas-Gibson index) contoured at a 0.1 interval for the 125-250 µm sieve fraction only. Also shown are sample track and water mass boundaries (see also Fig. 12).

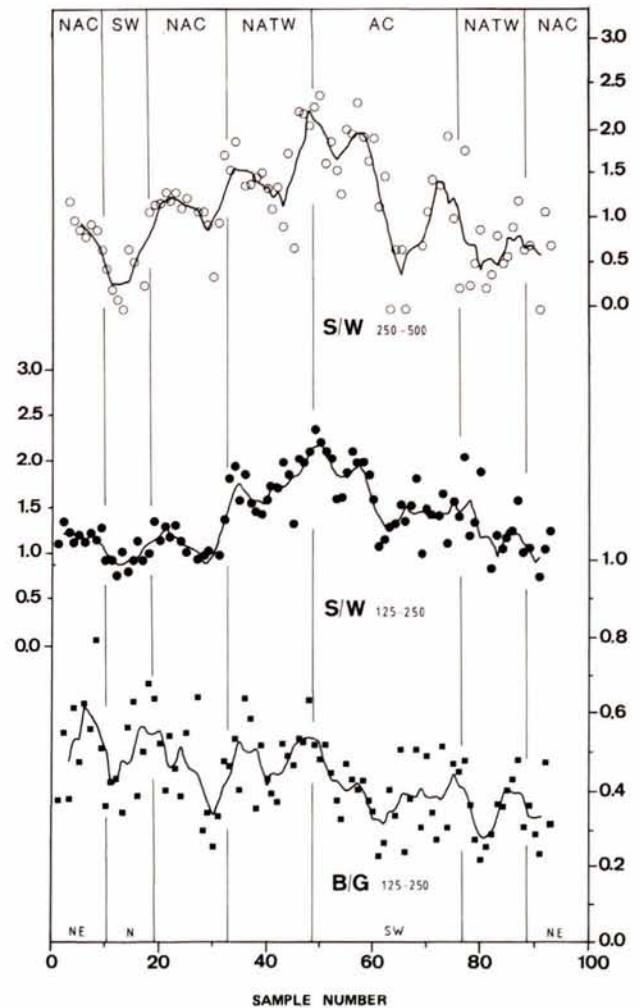


Figure 12 Diversity (S/W:125-250 µm and 250-500 µm) and equitability (B/G:125-250 µm) plotted along the sample track (see also Fig. 1 b). Dots (diversity) and squares (equitability) refer to actual measurements; the solid line, a running average, shows the general trend. Breaks in the direction of the sample track are indicated by NE, N, and SW at the basis of the figure (for the abbreviations of water masses see Fig. 2). Note the high diversity at the NATW-AC boundary and its relatively low equitability.

planktic patterns, because we sampled only the upper 5 m of the surface water at different times.

Broad mixing zones along water masses and especially along frontal zones are reflected in the diversity gradients. These frontal zones are hydrographically distinct water mass boundaries, where species of the adjacent water masses are mixed by converging surface waters, giving rise to a high diversity. But, since mixing also leads to "artificially" strong dominance of those species that occur in both water masses, other than normal (Lloyd and Ghelardi, 1964) this high diversity is associated with a low to intermediate equitability. Mixing also enhances primary productivity, increased turnover rates (Fournier, 1978; Tranter *et al.*, 1983; Angel, 1989) and mortality within displaced foraminiferal populations (Berger, 1971) resulting in a high sediment output, which can characterize frontal zones in the sediments. The high diversity of NATW and the AC probably has its origins in the Northern Sargasso Water (Cifelli and Smith, 1974) and is carried eastward in the AC. When environmental stress becomes too high, part of the coexisting species will disappear. The Sargasso Sea has stable, oligotrophic waters, which are more transparent than eutrophic waters. This results in a broad photic zone with,

seasonally, almost uniform conditions with permit a higher degree of specialization (Hallock, 1987) and therefore a higher diversity. The very low diversity in the northeast might be the result of high nutrient fluxes from the nearby European shelf waters.

The planktic foraminiferal assemblages presented in this paper, characterizing hydrographically defined water masses, suggest that an adjustment of the biogeographic assemblages for zooplankton of CLIMAP, 1981 (Tab. 4), which are supposed to "closely follow the current systems and surface water masses", is called for. CLIMAP's subpolar and transitional/subtropical assemblages coincide with our SW, NAC and NATW. Their eastern tropical assemblage is partially represented in our AC, although we consider these waters to be of subtropical origin. Equitability, being part of the general diversity index, has been related to resource limitations (Pulliam *et al.*, 1967) and tentatively to water mass properties and seasonal movements of foraminiferal populations (Balsam *et al.*, 1980). Further, mixing of populations can be traced by a lower equitability than one would expect, given the high diversity of the sample and following examination of the surrounding environments (Gibson and Buzas, 1973). Our observations confirm this. The NATW is such an example of a water mass comprising mixed populations (*i.e.* of NAC and AC), shown by its low equitability coupled to a high diversity. Frontal zones can also be recognized by mixed populations. Equitability should, however, not be interpreted without diversity and vice versa. The discussed information indices also show potential for interpreting sediments, such as the recognition of paleo-frontal zones. Such interpretations should also take account of the fact that taphonomic processes and time averaging will alter the original information of living populations.

	CLIMAP 1981 biogeographic zooplanktic assemblages	HYDROGRAPHIC UNITS used in this paper	
64°N	POLAR	POLAR* 7	64°N
	SUBPOLAR	SUBPOLAR 1	52°N
46°N		NORTH ATLANTIC CURRENT 1,2,3	44°N
	TRANSITIONAL/ SUBTROPICAL	NORTH ATLANTIC 3 TRANSITIONAL WATER	34°N
34°N		2,4,5,6 AZORES CURRENT (subtropical)	15°N
	EASTERN TROPICAL	TROPICAL* 7,8	

* not encountered during APNAP

- 1: Krauss & Kase, 1984
- 2: Kase *et al.*, 1986
- 3: Krauss, 1986
- 4: Siedler *et al.*, 1985
- 5: Kase & Zenk, 1987
- 6: McCartney & Talley, 1982
- 7: Dietrich *et al.*, 1975
- 8: Tchernia, 1980

Table 4

Climap assemblages related to APNAP I hydrographic units and assemblages. See also Table 3.

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REFERENCES

- Angel M.V. (1979). Vertical profiles of pelagic communities in the vicinity of the Azores Front and their implications to deep ocean ecology. *Prog. Oceanogr.*, **22**, 1-46.
- Balsam W.L., K.W. Flessa, N.G. Kipp and L.G. Du Bois (1980). Planktonic foraminiferal diversity in the interglacial and glacial North Atlantic: a test of diversity gradients as a paleoceanographic technique. *Geology*, **8**, 582-585.
- Bé A.W.H., D.S. Tolderlund (1971). Distribution and ecology of living planktonic foraminifera in surface waters of the Atlantic and Indian Oceans. In: *Micropaleontology of Oceans*, B.M. Funell and W.R. Riedel, editors, Cambridge University Press, London.
- Bé A.W.H. (1977). An Ecological, Zoogeographic and Taxonomic Review of Recent Planktonic Foraminifera. In: *Oceanic Micropaleontology*, A.T.S. Ramsay, editor, Academic Press, London, 1-100.
- Berger W.H. (1974). Planktonic foraminifera: sediment production in an oceanic front. *J. foram. Res.*, **1**, 3, 95-118.
- Brummer G.J.A. and D. Kroon (1988). Planktonic Foraminifera as Tracers of Ocean-Climate History, *Double Ph. D. Thesis, Free University Press, Amsterdam*, 346 pp.
- Cifelli R. and R.K. Smith (1974). Distributional patterns of planktonic foraminifera in the Western North Atlantic. *J. foram. Res.*, **4**, 3, 112-125.
- Cifelli R. and C.S. Benier (1976). Planktonic foraminifera from near the West African coast and a consideration of faunal parcelling in the North Atlantic. *J. foram. Res.*, **6**, 258-273.
- CLIMAP (Climap Project Members) (1976). The surface of the ice-age earth. *Science*, **191**, 1131-1137.
- CLIMAP (Climap Project Members) (1981). Seasonal reconstruction of the earth's surface at the last glacial maximum. In: *GSA Map and Chart Series*, **36** (Text, Map and Microfiche) (leader: A. McIntyre) Geological Society of America.
- Dietrich G., K. Kalle, W. Krauss and G. Siedler (1975). *Allgemeine Meereskunde*; Gebrüder Borntraeger, Berlin.
- Fournier R.O. (1978). Biological aspects of the Nova Scotian Shelf-Break Fronts. In: *Oceanic Fronts in Coastal Processes*. M.J. Bowman and W.E. Esaias, editors, Springer-Verlag, Berlin.
- Ganssen G. (1983). Dokumentation von küstennahem Auftrieb anhand stabiler Isotope in rezenten Foraminiferen vor Nordwest Afrika. *Meteor Forschungs Ergebnisse*, **C**, **37**, 1-46; Gebrüder Borntraeger, Berlin-Stuttgart.
- Ganssen G. and the Shipboard Party (1986). *Shipboard Report APNAP I*; Open File Report, Free University, Amsterdam.
- Gibson T.G. and M.A. Buzas, (1973). Species Diversity: Patterns in Modern and Miocene Foraminifera of the Eastern Margin of North America. *Geol. Soc. Am. Bull.*, **84**, 217-238.
- Hallock P. (1987). Fluctuations in the Trophic Resource Continuum : a factor in global diversity cycles? *Paleoceanography*, **2**, 5, 457-471.
- Käse R.H. and G. Siedler (1982). Meandering of the subtropical front southeast of the Azores. *Nature*, **300**, 245-246.
- Käse, R.H., W. Zenk, T.B. Sanford and W. Hiller (1985). Currents, Fronts and Eddy Fluxes in the Canary Basin. *Prog. Oceanogr.*, **14**, 231-257.
- Käse R.H., J.F. Price, P.L. Richardson and W. Zenk (1986). A Quasi-Synoptic Survey of the Thermocline Circulation and Water Mass Distribution within the Canary Basin. *J. geophys. Res.*, **91**, C8, 9739-9748.
- Käse R.H. and W. Zenk (1987). Reconstructed Mediterranean Salt Lens Trajectories. *J. phys. Oceanogr.*, **17**, 1, 158-163.
- Krauss W. and R.H. Käse (1984). Mean Circulation and Eddy Kinetic Energy in the Eastern North Atlantic. *J. geophys. Res.*, **89**, C3, 3407-3415.
- Krauss W. (1986). The North Atlantic Current. *J. geophys. Res.*, **91**, C4, 5061-5074.
- Lipps J.H., W.H. Berger, M.A. Buzas, R.G. Douglas and C.A. Ross (1979). Foraminiferal Ecology and Paleoecology, *SEPM short course*, **6**, Houston.
- Lloyd M. and R.J. Ghelardi (1964). A table for calculating the "equitability" component of species diversity. *J. Anim. Ecol.*, **33**, 2, 217-225.
- McArthur R.H. (1965). Patterns of species diversity. *Biol. Rev.* **40**, 510-533.
- McCartney M.S. and L.D. Talley (1982). The Subpolar Mode Water of the North Atlantic Ocean. *J. phys. Oceanogr.*, **12**, 1169-1188.
- Pianka E.R. (1966). Latitudinal gradients in species diversity: a review of concepts. *Am. Naturalist*, **100**, 910, 33-46.
- Pielou E.C. (1975). *Ecological Diversity*. John Wiley and Sons, 165 pp.
- Pielou E.C. (1979). *Biogeography*. John Wiley and Sons, 351 pp.
- Pujol C., J. Duprat and A. Pujos-Lamy (1976). Résultats préliminaires de l'étude effectuée par l'Institut de Géologie du Bassin d'Aquitaine concernant la Mission Midlante A (22 mai-19 juin, 1974) dans l'Atlantique orientale entre 15° et 35°N. *Institut Géologie Bassin Aquitaine*, **19**, 3-32.
- Pulliam H.R., E.P. Odum and G.W. Barret, (1967). Equitability and resource limitation. *Ecology*, **49**, 4, 772-774.
- Robinson M.K., M.A. Bauer and E.H. Schroeder (1979). Atlas of North Atlantic-Indian Ocean monthly mean temperatures and mean salinities of the surface layer. *Naval Oceanographic Office Reference Publication*, **18**, Department of the Navy, Washington DC 20373, 7USA.
- Sheldon A.L. (1969). Equitability indices: dependence on the species count. *Ecology*, **50**, 3, 466-467.
- Shih C.T. (1979). East-West diversity. In: *zoogeography and diversity of plankton*. S. V. D. Spoel and A.C. Pierrot-Bults, editors, Bunge Scinetific Publishers, Utrecht.
- Siedler G., W. Zenk and W.J. Emery (1985). Strong Current Events Related to a Subtropical Front in the Northeast Atlantic. *J. phys. Oceanogr.* **15**, 885-897.
- Stootweg A.P. (1978). Computer Contouring with a digital filter. *Mar. geophys. Res.*, **3**, 401-405.
- Soest (van) R.W.M. (1979). North-South diversity. In: *Zoogeography and diversity of plankton*. S.V.D. Spoel and A.C. Pierrot-Bults, editors, Bunge Scientific Publishers, Utrecht.
- Sy A. (1988). Investigation of large scale circulation patterns in the Central North Atlantic: The North Atlantic Current, the Azores Current and the Mediterranean water plume in the area of the Mid Atlantic Ridge. *Deep-Sea Res.*, **35**, 3, 383-413.
- Tchernia P. (1980). *Descriptive Regional Oceanography*. Pergamon Marine Series, **3**.
- Tranter D.J., G.S. Leach and D. Airey (1983). Edge enrichment in an ocean eddy. *Aust. J. mar. Freshwat. Res.* **134**, 665-689.
- Vincent E. and W.H. Berger (1981). Planktonic foraminifera and their use in paleoceanography. In: *The oceanic lithosphere, the sea*, **7**, C. Emiliani, editor, John Wiley and Sons, 1138 pp.
- Weyl P.K. (1978). Micropaleontology and ocean surface climate- the interpretation of planktonic microfossils requires a drifting reference frame. *Science*, **202**, 4367, 475-481.
- Williams J., J.J. Higginson and J.D. Rohrbough (1968 a). Oceanic Surface Currents. In: *Oceanography, contemporary readings in ocean sciences*. Oxford University Press, 1977, New York, 424 pp.
- Williams J., J.J. Higginson and J.D. Rohrbough (1968 b). Oceanic Water Masses and Their Circulation. In: *Oceanography, contemporary readings in ocean sciences*. Oxford University Press, 1977, New York, 424 pp.
- Worthington C.V. (1976). On the North Atlantic circulation. *Johns Hopkins oceanogr. Stud.*, **6**, 110.
- Wüst G. (1935). Schichtung und Zirkulation des Atlantischen Ozeans. Das Bodenwasser und die Stratosphäre. *Wiss. Ergebn. Dt. Atlant. Exped. Meteor*, 1925-27, **6**, 1-288.