Review Article

Planktonic Foraminifera as Oceanographic Proxies: Comparison of Biogeographic Classifications Using Some Southwest Pacific Core-Top Faunas

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Received 29 April 2013; Accepted 17 June 2013

Academic Editors: M. Elskens and M. T. Maldonado

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The distribution of planktonic foraminifera, as free-floating protists, is largely controlled by hydrography. Their death assemblages in surficial sediments provide proxy data on upper water mass properties for paleoceanography. Techniques for mapping faunal distributions for this purpose are compared in a study of 35 core-top samples that span the Subtropical Front in the Southwest Pacific. Faunas are analyzed by taxon composition, order of dominant taxa, and abundance. Taxon composition (presence-absence data) and dominant taxa (ordinal data) recognize groups of sites that approximate major water mass distributions (cool subtropical water, subantarctic water) and clearly define the location of the Subtropical Front. Quantitative data (relative abundances) more closely reflect the success of taxa in upper water mass niches. This information resolves groups of sites that reflect differences in intrawater mass hydrography. Comparisons suggest that abundance data should provide much better oceanographic resolution globally than the widely used ordinal biogeographic classification that identifies only Tropical, Subtropical Transitional, Subpolar and Polar provinces. As the data are strongly structured by variance in the abundance of *Globigerina bulloides*, *Globorotalia inflata*, *Neogloboquadrina incompta*, and *Neogloboquadrina pachyderma*, comparable classifications result from most clustering strategies. Principal coordinates analysis best represents the configuration of sites in two dimensions.

1. Introduction

Although the diversity of the Holocene planktonic foraminiferal fauna is modest, many taxa are distributed through the world ocean [1] and are exemplars for the interpretation of Cenozoic oceans [2]. For paleoceanography, a primary goal is to classify Holocene faunas on the basis of their distributions and to relate them to the hydrography. The biogeography of a single taxon can be simply mapped. The organization of sites according to their faunal content in a manner that is informative for paleoceanography is a more complex task that can be approached at several levels of analysis. Seminal works in this field are those by Imbrie and Kipp [3] and Bé [4]. Although they are widely applied and are similarly focused on the distribution of dominant taxa, little attention has been given to their quite different methods and to their suitability for resolving faunal biogeographies [5].

In developing a regression-based methodology for estimating sea surface temperatures (SST) from abundances of

planktonic foraminifera, Imbrie and Kipp [3] used Q-mode factor analysis (QFA; [6]) to reduce the dimensionality of *n*-taxon core-top faunal counts to a small number of factor assemblages. Each is a statistically distinct linear combination of the *n*-taxa. This simplifies the regression equation and aids its interpretation. The ecological relevance of each factor assemblage was assessed by plotting the geographical distribution of its contribution to each core-top fauna to show its relation to hydrography. While this provides a perspective on faunal biogeography, QFA does not identify discrete geographic/areal units based on faunal similarity. Rather, the underlying concept is a mixture model wherein a small number of notional source assemblages contribute to each core-top fauna.

Much simpler methods were used by Bé and Tolderlund [7] and Bé [4]. From large databases of census data from surface tows and sediment samples, they mapped distributions of the major species and found regions where

they occurred most abundantly. These data were integrated into a classification of five biogeographic provinces in the world ocean, principally defined by dominant taxa. The provinces correspond broadly to major global hydrographic regions [8] and are bi-hemispheric. Although methodology was not detailed, it transforms counts (quantitative data) to ranks (ordinal data). This simplifies the analysis of complex abundance data. Ranks appear to have been determined by careful inspection of data rather than by an algorithm. As with QFA, dominant taxa are of primary importance, but, in a conventional approach to biogeography, taxon distributions are used to define discrete areal units. Unlike QFA, taphocoenses are interpreted as unitary faunas.

An important issue for planktonic foraminiferal biogeography raised by the QFA method is whether it is realistically portrayed with a mixture model. A question raised by the ordinal approach is whether there is significant loss of information when taxon abundances are reduced to ranks. These, and related topics, are addressed via the analysis of core-top faunal data in the work of Weaver et al. [9] from a sector of the Southwest Pacific east and south of New Zealand (36–61°S). The hydrography includes Subtropical Water (STW), the Subtropical Front (STF), Australasian Subantarctic Water (ASW), and the northern front of the Antarctic Circumpolar Current (ACC). It provides a good basis for comparing faunal regions with oceanography.

1.1. Oceanographic Outline. Core-top samples come from a region of diverse bottom topography and complex oceanography spanning the transition from Subtropical to Subantarctic water masses (Figure 1). There are two principal submerged continental blocks. Chatham Rise trends east for c.1300 km off central South Island. Depths at its crest are often <500 m. Southeast of South Island is the vast triangular Campbell Plateau, mostly submerged between 500–1000 m. Between these blocks is Bounty Trough, a failed rift. Bollons Seamount rises over 2000 m above the abyssal Southwest Pacific basin off Campbell Plateau. Chatham Rise deepens northward into Hikurangi Plateau, bordered on the west by the New Zealand plate boundary. For comparison with faunal data, core sites are grouped into North Chatham, Bounty Trough, and Campbell Plateau bathymetric regions. Site #35 (61°S) is from the Southern Ocean.

The Subtropical Front (STF) lies over Chatham Rise. It is defined by surface temperature gradients of 4°C/200 km and strong along-rise currents [11–13]. Primary production in the frontal zone is high [14]. Flow from the north of warm, highly saline, nutrient-depleted Subtropical Surface Water (STW) extends south into the STF at ~43°S. South of the STF is cold, less saline, nutrient-replete, Australasian Subantarctic Water (ASW) covering Bounty Trough and Campbell Plateau. The southern boundary of this water mass is marked at the leading edge of the Antarctic Circumpolar Current by the swift flowing (27–39 cm s⁻¹) Subantarctic Front (SAF). The Southland Front, a local feature of the STF, separates a narrow band of STW on the southeastern South Island shelf from ASW [15].

Local oceanic circulation tends to dominate the oceanic environment east of New Zealand. Subtropical water flows around the tip of North Cape and forms the south-eastward flowing East Auckland Current [16]. This current extends as far as East Cape before forming the southward-flowing East Cape Current [11, 17], which is deflected eastward by Chatham Rise. In this northern region, upper ocean circulation is also strongly influenced by three variable, semipermanent, anticyclonic eddies. In the south the Southland Current, about 90% ASW [15] flows around southern New Zealand and swings northward along the east coast of the South Island. Part of this flow turns eastward along the southern flank of Chatham Rise, while a component continues north through Mernoo Saddle. Campbell Plateau is characterized by weak mean flows but cyclonic flow is well developed around western Bounty Trough [18].

1.2. Previous Work. Kustanovich [19] recognized five biogeographic regions (Figure 2(a)) between 18–54°S, based on species composition and dominance. Apart from the STF, no relation between the hydrography and regional boundaries was noted. Eade [20] found that distributions of faunas in plankton tows between 18–36°S were related to the principal water masses. Several boundaries correspond closely to those of Kustanovich [19]. Cluster analysis of faunal abundances in 234 surface sediment samples from the South Pacific by Parker and Berger [21] placed all from the New Zealand region in one group which spanned the STF (Figure 2(b)). This result may be related to the method used to calculate faunal similarity.

Although the scale of Bé [4, Figure 7] prevents close assessment, sites #1–2 of Weaver et al. [9] are in his Subtropical Province. Remaining sites north of the STF and those in Bounty Trough are in the Transitional Province. The Polar Province includes sites on Campbell Plateau. More details are shown in Figure 1 which treats line weights for taxa in Bé [4, Figure 8] as rank indices and applies them to Weaver et al. [9, Table 3]. On this basis, seven of the eight faunas north of Chatham Rise (Figure 1(a)) are identified as Transitional because *Globorotalia inflata* is the highest ranked species; *Neogloboquadrina pachyderma* and *Globigerina bulloides* are in second rank at several sites. Ten faunas in Bounty Trough are allocated to the Subantarctic Province because *Globigerina bulloides* is dominant. *Neogloboquadrina pachyderma* is in second rank in nine faunas. Six Campbell Plateau faunas in which *Globigerina bulloides* is in first rank are classed as Subantarctic. The remaining eight, with *Neogloboquadrina pachyderma* in first rank, are identified as Polar.

Hayward [23] provided a taxonomic review of the fauna living in the New Zealand region and showed the distribution of taxa relative to Bé's [4] provinces. Martinez [22] recognized three QFA assemblages in Tasman Sea core-tops. Principal taxa in the factor 2 assemblage, which extended to the vicinity of site #1 of this study (Figure 2(c)), are *Globigerina quinqueloba* and *Globigerinita glutinata*. Although the assemblage was identified with the Transitional Province,

FIGURE 1: (a) Core locations, bathymetry, circulation, and classification of core-top faunas in Weaver et al. [9] following criteria in Bé [4]. To harmonize with the latter, *Neogloboquadrina pachyderma* coiling variants are combined with the p/d intergrade and *Globigerina bulloides* with *Globigerina falconensis*. (b)–(d) Dominance maps for factor assemblages in the FA-20 model [10] applied to the same data (redrawn from [9, Figure 3]). Contours enclose areas in which factor loadings exceed the stated value. Loadings specify the percent variance in site faunas accounted for by each factor assemblage.

Globorotalia inflata is only a minor component. Weaver et al. [9] applied the QFA model FA20 of Molino et al. [10] to the present data (Figures 1(b)–1(d)). Although the model was developed from Atlantic core-top faunas, the explained variance (communality) indicates that it is also applicable to the Southwest Pacific faunas. Regions of highest dominance of the polar, subpolar, transitional, and upwelling assemblages approximated the principal oceanographic features.

2. Data and Methods

I use data in Weaver et al. [9, Table 3]. They counted between 241–552 specimens from the $\geq 150 \mu\text{m}$ fraction in each sample. Taxonomic categories are those of Imbrie and Kipp [3]. Core-top locations are shown in Figure 1. Analyses seek to reveal the structure of the data (exploratory data mining). In the absence of prior knowledge of data structure, the study

FIGURE 2: (a) Faunal regions using the distribution and abundance of species in surface samples. Redrawn from Kustanovich [19, Figure 7]. (b) Cluster analysis of relative abundances of taxa in South Pacific surface sediments: distribution of Cluster I in the vicinity of New Zealand. Redrawn from Parker and Berger [21, Figure 7b]. (c) Dominance map of Factor 2 assemblage in a Q-mode analysis of core-top faunas principally north and west of New Zealand. Redrawn from Martinez [22, Figure 6b]; compare with Figure 1(b).

uses unsupervised learning tools—cluster analyses and low-dimension projections. Each tool is referenced in its figure caption. Kaufman and Rousseeuw [24] provide a readily accessible introduction to cluster analysis.

Faunas are analyzed at three levels of complexity. At the primary level are species lists. Species ranked by their abundance (ordinal data) provide a second level of faunal representation. Bé [4, Tables 3, 5–7; Figure 8] variously listed species in rank order, identified dominant and cooccurring taxa, and used line weights to show species importance in his faunal provinces. This suggests that his is an ordinal classification. At a third level of analysis taxon counts are treated as continuous variables (quantitative data), as in Imbrie and Kipp [3].

3. Results

3.1. Taxon Composition, Presence-Absence Classification. Taxon presence-absence data form two high-level clusters (Figure 3(a)) that are partitioned about the STF. The exception to this bathymetric/water mass separation is Site #17 (Bounty Trough) which is placed with North Chatham sites. A weaker boundary in the southern cluster partitions most Bounty Trough sites from most Campbell Plateau sites. *Globigerina bulloides*, *Neogloboquadrina incompta*, and *Globorotalia inflata* occur in all faunas (Figure 8). Only slightly less persistent are *Globigerinita glutinata* and *Globorotalia truncatulinoides* (s). Of remaining taxa, most decrease in persistence from north to south. Northernmost site #1 has the most diverse fauna (21 taxa) and Southern Ocean site #35 has the least diverse (5 taxa).

3.2. Ordinal Data, Classification by Rank. Taxon abundances at each site are transformed to their rank order. Bé's [4, Figure 8] classification focused on major taxa. For comparison, Figure 3(b) shows a classification using the five highest ranks. The classification is similar to that using presence-absence data. North Chatham sites, excluding #1, form a well-defined group with *Globorotalia inflata* in first rank. Sites in western Bounty Trough form a low-level cluster; others join with sites scattered across Campbell Plateau. All have *Globigerina bulloides* in first rank and most have *Neogloboquadrina incompta*, *Neogloboquadrina pachyderma*, *Globorotalia inflata* in ranks 2–3. Sites on the southern margin of Campbell Plateau are distinguished. All have *Neogloboquadrina pachyderma* in first rank. Southern Ocean site #35 is identified as an outlier, principally because *Globorotalia inflata* is in second rank.

3.3. Quantitative Data: Projections and Classification by Abundance

3.3.1. Projections. By rotating the data matrix onto its principal axes, eigenvector methods provide two-dimensional views of the multivariate relative abundance data that often account for most of the variance. Singular value decomposition (SVD, [27]) resolves the structure of the data by finding vector matrices that allow both objects (sites) and variates (taxa) to be projected onto the principal axes. The biplot (Figure 4(a)) identifies species that are major sources of inter-site variation. The vector for *Neogloboquadrina pachyderma* is associated with Campbell Plateau sites. Vectors for *Neogloboquadrina incompta* and *Globigerina bulloides* enclose Bounty Trough sites and the vector for *Globorotalia inflata* is in

FIGURE 3: (a) Agglomerative classification of sites (Figure 1) using presence-absence data with function `agnes()`. Euclidean metric, Ward cluster strategy. Agglomerative coefficient = 0.83. (b) Agglomerative classification of sites (Figure 1) using ordinal data. Taxa ranked with function `daisy()`. Sites clustered using five highest ranked taxa using function `agnes()`. Euclidean metric, Ward cluster strategy. Agglomerative coefficient = 0.86. Functions are in R package `cluster` available from <http://cran.r-project.org/web/packages/cluster/>.

the direction of North Chatham sites. Distances between sites projected onto the principal axes in the principal coordinates analysis (Figure 4(b)) approximate those in the similarity matrix [28]. Nonmetric multidimensional scaling (Figure 4(c); [29]) operates on the rank order of similarities between sites; these are reflected in the two-dimensional plot. All projections show Southern Ocean site #35 as an outlier. Sites #1 and #17 lie between the major groups.

3.3.2. Classification. Although projections indicate that sites are clustered, some are poorly delimited, as is their number. Cluster validation (Figure 5(a)) indicates that clusters resolved by several strategies are maximally compact (silhouette index, [24]) when there are 3–5 groups. The 4-group fuzzy classification (Figure 5(b)) shows that Bounty Trough and Campbell Plateau sites form the most compact groups. Measured by their silhouette widths, sites #1 and #17, already identified as intermediates in some projections (Figures 3(a) and 3(b)), are poor fits as are southern Campbell Plateau sites #25, #26, and #30. The hierarchical agglomerative classification (Figure 5(c)) produces three high-level groups that correspond to the North Chatham, Bounty Trough, and Campbell Plateau bathymetric regions. Site #1 is mapped as an outlier in the North Chatham region. Western Bounty Trough sites are tightly clustered and distinguished from sites #18 and #22 at its eastern margin. Site #17, a poor fit in Figure 5(b), is allocated to its source bathymetric region. Southern sites form a low-level group within the Campbell Plateau cluster.

3.4. Regional Biogeography. The regional biogeography (Figure 6) considers results from all views of the data but is based primarily on classifications with quantitative data. It recognizes 3 biotopes, several with subbiotopes. Units are based on faunal similarity, with the constraint that sites within the same unit are adjacent.

3.4.1. Hikurangi Biotope (HB). Included are sites #2–8 from the North Chatham bathymetric region. In all views of the data, the southern boundary coincides with the STF. Faunas have between 12–17 species. In all faunas *Globorotalia inflata* is commonest taxon, followed either by *Globigerina bulloides* or *Neogloboquadrina incompta*. Only at site #6 does *Globorotalia truncatulinoides* (s) move as high as third rank. It is a first rank taxon in the Transitional Province of Bé [4]. Although rankings of leading taxa are relatively stable, the abundance of *Globorotalia inflata* varies greatly (39–80%). This affects the configuration of HB sites in Figure 4(a), contributes to a low average silhouette width in the fuzzy classification (Figure 5(a)), and to high-level linkages of subgroups in the consensus classification (Figure 5(d)).

HB1. Sites #2, #5, and #8. These are located between 36–43°S at slope depths near North Island. They are in the vicinity of the East Cape Current. Although *Globorotalia inflata* and *Globigerina bulloides* maintain their rank positions, the abundance of the latter (19–22%) is higher than elsewhere in the region.

HB2. Sites #3, #4. *Globorotalia inflata* is strongly dominant (65–80%) at these deep sites (3654 m, 3003 m) on Hikurangi Plateau. No other species exceeds 11%; faunas are the least equitable in the biotope. The sites are outliers in projections (Figure 4).

HB3. Sites #6, #7. Although site #7 is higher on the northern flank of Chatham Rise than is site #6, they form a low-level cluster in dendrograms (Figure 5). *Neogloboquadrina incompta* (25–31%) is much more abundant than in other subregions.

Outlier. Site #1 has the most species-rich fauna (21 taxa). In composition, it is grouped with other North Chatham sites but with ordinal data it is linked to Bounty Basin sites

FIGURE 4: Projections of sites onto principal axes for two largest eigenvalues. (a) Singular value decomposition (SVD), vectors are projections of major taxa; 87% variance shown. (b) Principal coordinates analysis; 53% variance shown. (c) Nonmetric multidimensional scaling, Euclidean distances. All computed with PAST v1.11 (<http://folk.uio.no/ohammer/past/>) Site identifiers [9, Table 1] are grouped by bathymetric regions.

(Figure 3). Important contributors to its distance from other North Chatham faunas using quantitative data are the reduced abundance of *Globorotalia inflata* (17%, third-ranked) and strong representations of *Globigerina bulloides* (20%) and *Globigerina falconensis*.

3.4.2. Bounty Biotope (BB). Sites #9–16, #18–19, and #22 form a compact group in all projections and classifications. Of Bounty Trough sites, only #17 is excluded. Diversity (8–16) is

commonly lower than in HB faunas. Minor species in the latter that are not recorded here are *Globigerinella aequilateralis*, *Globigerinoides sacculifer*, *Neogloboquadrina dutertrei*, and *Pulleniatina obliquiloculata*. No fauna is strongly dominated by one species and species distributions are more equitable than in HB.

BB1. Sites #9–16, #19. These sites are under a local gyre in ASW and have closely similar faunas. They form a tight cluster in

FIGURE 5: Classifications using relative abundance data. (a) Optimal number of clusters for five strategies in R package *clValid*; see <http://cran.r-project.org/web/packages/clValid/vignettes/clValid.pdf> for details. Silhouette width (Kaufman and Rousseeuw [24]) measures the difference between the distance of the site to the nearest-neighbor group and its distance from others in the same group. The higher the index is on the -1 to +1 scale the better is the site classified. (b) Silhouette plot of fuzzy classification using function *fanny()*; four groups specified, euclidean metric. Agglomerative classification with function *agnes()*. Euclidean metric, Ward cluster strategy. Agglomerative coefficient = 0.92. (d) Consensus hierarchical classification that synthesizes dendrograms produced by Ward, single, complete, average, mcquitty, median, and centroid cluster methods; see <http://cran.r-project.org/web/packages/clue/vignettes/clue.pdf> for detail.

quantitative classifications (Figure 5). In all, *Globigerina bulloides* is dominant (32–40%) and *Neogloboquadrina incompta* (12–25%) and *Globorotalia inflata* (11–18%) are second or third ranked.

BB2. Sites #18, #22. Site #22 is adjacent to Bollons Seamount and, like site #18, is a deep site at the margin of the Southwest Pacific Basin. Both are differentiated from other BB sites by greater abundance of *Globigerina bulloides* (47–49%).

Outlier. The composition of the site #17 fauna is similar to that at some HB sites (Figure 3(a)). Another similarity is the abundance of *Globorotalia inflata* (33%). Griggs et al. (1983) [30] found evidence of dissolution in this core (Q217).

Weaver et al. [9] considered that site #17 might not represent true core-top material.

3.4.3. Campbell Biotope (CB). Species diversity (7–10) in Campbell Plateau faunas is commonly lower than in Bounty Trough faunas. There are no records of *Globigerina calida*, *Globigerina digitata*, *Globigerinoides tenellus*, *Globorotalia crassula*, and *Globorotalia hirsuta*. Sites are rather homogeneous in faunal composition.

CB1. Sites #20–21, #23–24, #27–29, and #32 form a compact group (Figure 5(b)). As in BB, *Globigerina bulloides* (34–44%) is the first-ranked taxon but *Neogloboquadrina pachyderma* (23–35%) displaces *Neogloboquadrina incompta* (3–10%) in

FIGURE 6: (a) Regional biogeography constructed from data in Figures 3–5. Site #35 is identified as an outlier but would likely classify as polar in a more inclusive higher southern latitude survey. Similarly, site #1 may represent the Northern Fauna of Kustanovich [19]. (b)–(e) Abundance plots for *Globorotalia inflata*, *Neogloboquadrina incompta*, *Globigerina bulloides*, and *Neogloboquadrina pachyderma*. Approximate position of the STF and SAF after Northcote and Neil [26, Figure 1].

second rank. Very similar faunas occur at widely separated sites across the plateau.

CB2. Sites #30–31, #33–34 at the southern margin of Campbell Plateau are separated from other CB faunas in the projection (Figure 4(a)) and unified in quantitative classifications (Figures 5(c) and 5(d)) primarily by increased abundance of *Neogloboquadrina pachyderma* (50–52%). Faunas in southern interior plateau sites #25–26 have lesser representations of *Neogloboquadrina pachyderma*. They link with this group in

the consensus classification (Figure 5(d)), although the fuzzy classification (Figure 5(b)) indicates that the relation is weak.

Outlier. Southern Ocean site #35 has the least diverse fauna (5 taxa), but its composition is similar to some southern CB sites (Figure 3(a)). The position of *Globorotalia inflata* in second rank distinguishes the fauna from those in CB2 (Figure 3(b)). But it is the dominance of *Neogloboquadrina pachyderma* (86%) that distances the fauna from others in projections and classifications (Figures 4 and 5).

4. Discussion

4.1. The Subtropical Front as a Species Boundary: Taxon Distributions. Taxon composition is the primary carrier of faunal information. Although many planktonic foraminiferal taxa have wide meridional distributions [1] and the STF appears to be a “leaky” boundary between STW and ASW [12], presence-absence data define its location very clearly. Comparison of taxon distributions (Figure 8) with the hierarchical classification (Figure 3(a)) shows that its location is better defined by a mapping that considers all taxa than by any pairwise comparison of taxon ranges.

The persistence of taxa reveals some aspects of the STF as a faunal boundary. Taxa that are present at all STW sites (persistence = 100%) are highly persistent (>80%) in ASW south of the front. Excepting *Globigerina digitata*, taxa present in at least one of the three southernmost sites under STW (#6–#8) are present in ASW. *Globigerinella aequilateralis*, *Globigerinoides sacculifer*, and *Globigerinoides tenellus* occur only at northern STW sites (#1–#5). *Globigerina quinqueloba* and *Neoglobobulimina pachyderma* are highly persistent in ASW, but their persistence in STW declines to 37–50%. While these observations are dependent on sample size (taxa whose population abundance is <2% are unlikely to be represented in the smallest sample counted ($n = 241$)), they suggest that the faunal composition boundary between STW and ASW faunas is much broader than the STF as defined by physical hydrography [31]. Particularly, some subtropical taxa become very impersistent or disappear from the core-top record about 40°S. If species abundances are also considered, the STF acts like a high-pass filter that removes taxa with small populations.

4.2. Ordinal Classification and Taphonomy. Transformation of abundances to ordinal data reduces variance and, therefore, information. Here, classification of sites by ordinal data only marginally improves the resolution of groups (agglomerative coefficient = 0.86) over the presence-absence analysis (0.83). Neither level of analysis performs as well as quantitative data. This suggests that, for classification, there is little value in transforming abundance data to ordinal. From an analysis of Imbrie and Kipp’s [3] data transformed to ranks, Sancetta [32] found that they identified assemblages almost identical with those produced with quantitative data. However, her ranks do not represent strictly ordinal data. They were constructed by assigning ranks to binned percentages rather than ordering abundances by <, =, > relationships.

Ordinal data are also of interest because Kidwell [33] found that fossil mollusc faunas commonly preserve the species rank signal of their source living faunas and may mitigate the effects of taphonomy and time averaging on quantitative data [5, 34]. A few local data are relevant. Table 1 lists Pearson r , a measure of linear relationship in quantitative data, and Kendall tau, a measure of monotonic association in ranked data, between faunas from sediment traps and nearby core-tops. Of interest is whether ranked data indicate association between living and core-top faunas when quantitative data do not.

TABLE 1: Relationships between faunas in sediment traps and nearby core-top samples. NCR and SCR data are from King and Howard [25]. Trap 1-2, TAN0307, and SO136 data are from Northcote and Neil [26]. Pearson r measures linear relationship in quantitative data; Kendall tau measures monotonic relationship in ranked data. Taxa that did not occur in either sample were excluded from the data.

	Kendall tau	Prob. tau = 0	Pearson r	Prob. $r = 0$
NCR300:NCR1000	0.67	$3.65E - 04$	0.99	$5.03E - 13$
NCR1000:Site #8	0.28	0.144	0.98	$1.23E - 11$
NCR1000:Site #7	0.36	0.068	0.91	$1.17E - 06$
SCR300:SCR1000	0.66	0.004	0.87	$1.97E - 04$
SCR300:Site #12	0.55	0.037	0.63	0.052
SCR1000:Site #12	0.82	$4.65E - 04$	0.91	$5.18E - 05$
Trap 1:Trap 2	0.64	0.001	0.55	0.034
Trap 1:Site #21	0.56	0.023	0.35	0.287
Trap 1:Site #24	0.46	0.051	0.43	0.158
Trap 1:Site #25	0.41	0.098	0.42	0.201
Trap 1:Site #27	0.34	0.181	0.28	0.412
Trap 1:TAN0307	0.37	0.173	0.11	0.761
Trap 2:SO136	0.37	0.045	0.06	0.804
Trap 2:Site #24	0.65	0.002	0.26	0.346

Sites #7 and #8 are in the vicinity of sediment trap NCR [25] just north of the STF. In these core-top faunas, respectively, at 1408 m and 850 m, abundances of major taxa that may have accumulated over as much 1850 years [9] are comparable with those recorded over 11 months at NCR (null hypothesis rejected using Pearson r). This suggests that annual variance in abundance has been dominant and stable, relative to interannual variance [35], and taphonomic effects are minimal. Trap SCR is near the southern margin of the STF in Bounty Trough [25]. The fauna trapped over 8 months at 1000 m is similar to that at site #12. In quantitative and ranked comparisons, the null hypothesis is strongly rejected. Again, no significant degradation of the living signal is detected in the fossil core-top fauna. There are no data on the age of core-top faunas in this region. Northcote and Neil [26] reported on faunas collected over 14 months in their sediment Trap 1, sited in the thermally isolated, relatively quiet water of the interior of Campbell Plateau and in Trap 2 on its current-swept eastern margin (Figure 1). Faunas at both sites differed significantly from those in nearby core-tops. This is confirmed for quantitative data; the null hypothesis is not rejected at the 5% level in any of the five comparisons. Correlation coefficients are higher for ranked data; for sites #21 and #24 the null hypothesis is rejected at the 5% level. Radiocarbon dates (yr BP, data from Christine Prior, GNS) for *Globigerina bulloides* (5524), *Globorotalia inflata* (4582), and *Globorotalia truncatulinoides* (3919) from site #21 suggest that, for this middle Holocene fauna, ranked data better preserve the Trap 1 faunal signal than do quantitative data.

4.3. Quantitative Classifications and QFA. Organization of sites is substantially raised (agglomerative coefficient = 0.92)

FIGURE 7: (a) Taxon scores in factor 2 assemblage from Q-mode factor analysis of Weaver et al. [9, Table 3] using Paleo ToolBox <http://www.pangaea.de/software/files/Windows/PaleoTools/>. (b) Relative abundance of taxa at site #3 (Figure 1); this fauna is an outlier in projections (Figure 4). (c) Relative abundance of taxa in average HB fauna (Figure 6).

when relative abundances of taxa are analyzed. These data are a much more sensitive measure of species success in near-surface niches than are species ranks. Like water mass differentiation, groups of sites within water masses are identified that may indicate local contrasts in hydrography. Some are related to bathymetry, as with Bounty Trough and Campbell Plateau faunas. These second order features are not resolved in QFA dominance maps (Figures 1(b)–1(d)).

The provincial approach to biogeography of Bé [4] and QFA models based on Imbrie and Kipp [3] are clearly distinguished by their levels of data analysis. The former is ordinal; the latter is quantitative. Perhaps more importantly,

the provincial approach is holistic and treats faunas as units whereas QFA decomposes faunas into nominal source assemblages. This identifies it as a method for analyzing mixtures [36] rather than for mapping the areal distribution of faunas. Each factor assemblage represents a statistically independent notional source fauna. All site faunas are modelled as mixtures of these source faunas. Core-top faunas are taphocoenoses. Although some specimens may be advected in zonal jets and eddies, shell sinking velocities of ~500 m/day [37, 38] imply that most core-top faunas are from populations living near the site. Therefore, studies that apply QFA to core-top faunas seek to resolve statistically independent faunas in

FIGURE 8: Taxon distribution. Nomenclature as in [9].

the overlying water column. Principal scenarios are vertical stratification and seasonal replacement [3, page 83]. For oceanography, unmixing of core-top faunas to identify their source populations in the water column is valuable but should be distinguished from primary-level biogeographic mappings that accept core-top faunas as unitary entities.

Varimax rotation [39] is a critical component in Imbrie and Kipp's [3] method. It rotates the principal axes of the data matrix to positions close to vectors for the most divergent faunas. Such faunas include the most atypical. Some are highly inequitable with one strongly dominant taxon. They identify pelagic environments with few resources for most taxa. Some may be in water masses distant from the core-top faunas being unmixed. Often, names which are attached to the factor assemblages (e.g., Molfino et al. [10] are related to the provincial nomenclature of Bé [4]). So named, dominance maps may suggest substantial advection and misleading hydrographic scenarios.

Although varimax rotation simplifies data interpretation [3, 10], the realignment of principal axes towards divergent faunas may generate factor scores that significantly misrepresent faunas in a water mass. *Globorotalia inflata* strongly

dominates a factor assemblage (Figure 7(a)) resolved by QFA of the Weaver et al. [9] data. It corresponds to the Transitional assemblages of Bé and Hutson [40] and Molfino et al. [10]. The distribution of factor scores compares well with relative abundances of taxa at site #3 (Figure 7(b)) which is a divergent fauna (Figure 4). Although *Globorotalia inflata* is dominant, the average HB fauna (Figure 7(c)) is more diverse and equitable. The dominance map for this factor assemblage effectively shows the distribution of a single species. The value of this approach for resolution of vertical stratification and/or seasonal mixing faunas in core-top faunas is equivocal. In view of the source of core-top faunas, it seems logical that the training sets for mixture analysis should be data on living faunas collected at various depths/seasons in the same water mass.

4.4. Taxa as Hydrographic Proxies. Related to their food sources, planktonic foraminiferal species tend to preferentially occupy particular niches in the upper ocean [41] so have the potential to provide proxy data on near-surface hydrography. Data on taxa contributing largely to variance in abundance data (Figure 4) are noted. Their distributions

are more directly interpretable as hydrographic proxies than are the corresponding factor assemblage dominance maps (cf. Figures 1(b)–1(d) and Figures 6(b)–6(e)).

Globigerina bulloides lacks symbiont algae and is primarily a herbivore although it is also a zooplankton predator [42]. It is abundant in near-surface water when biomass is high, as in upwelling pulses [43]. Kincaid et al. [44] found that its abundance is correlated with phytoplankton blooms. Vertically stratified plankton tows in the Southern Ocean between 41–53°S [45] show its abundance covaries closely with fluorescence maxima, a biomass proxy, in near-surface water. Schiebel et al. [46] found that its abundance is closely related to entrainment of nutrient-rich water. The primary domain of *Globigerina bulloides* is in ASW (Figures 1 and 6(d)). Rather uniform abundances in BB and CB indicate similar resource availability in the macronutrient-rich low-chlorophyll mixed layer over Bounty Trough and Campbell Plateau [26]. Larger populations at deep water sites east of Bounty Trough (BB2) and around the margin of Campbell Plateau may reflect turbulent entrainment of nutrients into the mixed layer. Although its abundance is often related to algal biomass, the taxon shows no response to elevated chlorophyll-a levels associated with the STF [47]. This may relate to the composition of the flora. Small-celled species, particularly nanoflagellates, predominate in ASW whereas floras about the STF are dominated by diatoms [48]. At sites under STW, the taxon is most abundant nearest North Island (HB1), possibly responding to high nutrient levels near the shelf break, and at site #1. It is notably rare in HB2, near a region with high chlorophyll-a concentrations [49].

From three Northern Hemisphere trap studies, Sautter and Thunell [43] found that *Neogloboquadrina incompta* was primarily located within or below the thermocline and was responsive to heightened fertility. Pak and Kennett [50] showed that it calcifies near the thermocline. Reynolds and Thunell [51] and Sautter and Sancetta [52] noted that populations increased when near-surface water was weakly stratified. Its abundance at 1000 m at trap SCR in Bounty Trough [25] compares with those in nearby core-tops (~20%–25%) but drops to 2% at 300 m. Unlike *Globigerina bulloides*, the taxon is most abundant about the STF where it may reflect fertility in the vicinity of the thermocline. It is common in all Bounty Trough sites but is more populous adjacent to the margin of the STF (sites #11, #12) than at the southern margin of the trough (sites #16, #19). Although its abundance map (Figure 6(c)) identifies the location of the STF, large populations particularly characterize the northern margin (HB3). As in the Benguela region [53] this may relate to the distribution of a specific diatom food resource [54] that flourishes at the margin of highly productive water.

Globorotalia inflata is a deep-dwelling omnivore that lives on diatoms, dinoflagellates, and animal tissue [40, 41]. The largest population in stratified traps at 41°S (Atlantic Ocean, [45]) was between 200–300 m, well below the fluorescence maximum at ~50 m. With stable isotope data for trapped specimens from STW through to Antarctic Surface Water, King and Howard [55] inferred calcification depths between 0–100 m. Its record in Traps NCR and SCR [25] (Figure 1) is consistent with the HB data. Its relative abundance is

much greater in STW than in ASW. The STF marks a sharp decline in its abundance (Figure 6(b)). It is strongly dominant in HB2 which is in the vicinity of the STF region [49] and features relatively high chlorophyll-a concentrations and winter deepening of the mixed layer. Although its abundance at site #3 in HB2 may be enhanced by dissolution [9, Figure 2]), the biotope possibly captures a strong trophic signal. *Globorotalia inflata* maintains quite uniform abundances (10–20%) in most Bounty Trough and Campbell Plateau faunas. Only at the southwest margin of the latter are they <10%. These data, which are consistent with those collected from traps between 47–54°S near Tasmania [56], contrast with its 62% abundance in Trap 1 at Pukaki Rise (Figure 1). This is higher than its average in HB (49%). In BB and CP core-top faunas it is most abundant at site #17 (33%) which similarly has *Globigerina bulloides* in second rank. Although quantitative data strongly differentiate the Trap 1 fauna, several core-top faunas are comparable in rank tests (Table 1). *Globorotalia inflata* is widely distributed through ASW and is the third-ranked taxon in several CB faunas. Trap 1 data [26] show that larger populations seasonally occupy Campbell Plateau but knowledge of their size, age-structure, and taphonomy over longer intervals is required to understand this response.

Neogloboquadrina pachyderma was trapped mainly between 0–100 m at Southern Ocean sites (50°S, 53°S), near the polar front zone [45], but was principally present between 75–200 m, below the fluorescence maxima at some northern sites (41–47°S). Kohfeld et al. [57] showed that shells calcified at surface water temperatures in the Southern Ocean. Food sources include diatoms [58]. This taxon dominates Southern Ocean faunas, of which site #35 is representative. It is less dominant (~50%) in CB2 faunas at sites around the southern margin of Campbell Plateau. These locations are at the leading edge of the ACC where the SAF meets Campbell Plateau [18] and the taxon's abundance may reflect mixing with ASW. Over Campbell Plateau, it contributes between 20–40% of most faunas but sharply declines to ≤10% at its northern margin. This clearly defined bathymetric relation indicates that population size is not directly linked to SST, as is commonly suggested. It is a minor contributor to Bounty Trough faunas and drops below sample resolution at site #12, as it does in most HB faunas. Indeed if, as Darling et al. [59] found, as much as 1.5% of *Neogloboquadrina incompta* coil sinistrally, *Neogloboquadrina pachyderma* may not be present in HB faunas.

5. Conclusions

Bé's [4] provincial biogeography of planktonic foraminifera is viewed as an ordinal classification that treats faunas holistically. QFA operates on quantitative data and seeks to resolve faunas into source assemblages. The two methods are distinct in their level of analysis and in their objective. Their outputs are not directly comparable.

QFA is a tool for mixture analysis rather than for mapping regional biogeographies. It treats all core-top faunas as composites of nominal assemblages. These are modelled on

the most divergent faunas in a core-top dataset. It is questionable whether there is a valid ecological rationale for their use as prototypes in preference to the statistics of living faunas.

Analyses of core-top faunal distributions from 35–61°S in the Southwest Pacific show that presence-absence and ordinal data detect the STF but are much less effective than quantitative data for identifying lesser hydrographic features. This suggests that Bé's [4] ordinal classification does not realize the potential value of planktonic foraminifera as paleoceanographic proxies. However, ordinal data may be less susceptible than quantitative to taphonomic modification. There is scope for review and better definition of the global provinces. Their distribution may not be as simple as presently envisaged [5].

Biotopes in the transect reflect variation in the abundance of four dominant taxa which relate to the distribution and structure of water masses. Deep-dwelling *Globorotalia inflata* characterizes the STW biotope. Two biotopes are recognized in ASW south of Chatham Rise. In both, a nutrient-rich mixed layer is indicated by similar abundances of *Globigerina bulloides*, but they are differentiated by changes in the relative abundances of deeper-dwelling species (*Neogloboquadrina incompta* and *Globorotalia inflata*). These biotopes identify the bathymetric contrast between Bounty Trough and Campbell Plateau. Although most are insufficiently sampled, subbiotopes resolve lesser contrasts within water masses.

Acknowledgments

The author thanks Helen Neil (NIWA) for assistance with Section 1.1, Christine Prior (GNS Science) for access to unpublished radiocarbon dates, and Hugh Grenfell (Geomarine Research) for comments on a draft manuscript.

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