

Testing the effects of tropical temperature, productivity, and mixed-layer depth on foraminiferal transfer functions

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Abstract. Statistical transfer functions relate living planktonic foraminiferal species of the central equatorial Pacific to measured sea surface temperature, integrated primary productivity, and mixed-layer depth. The faunal estimates successfully reconstruct latitudinal patterns observed in both warm (El Niño, February-March 1992) and cool (La Niña, August-September 1992) seasonal settings. Predictions of mixed-layer depth appear to be unbiased by temperature or productivity in our data set but tend to underestimate deep mixed layers. Interactions between productivity and temperature, perhaps through their common influence on respiration and growth rates, bias foraminiferal transfer functions for both properties. Paleocceanographic estimates may be improved by accounting for such biological processes that translate the environment into a faunal response preserved in the geologic record.

1. Introduction

How well do planktonic foraminifera species track changes in tropical oceanography near the sea surface? Can temperature responses [*Climate: Long-Range Investigation, Mapping, and Prediction (CLIMAP)* 1981] be isolated from other possible responses, such as those associated with productivity [Mix, 1989] or water column structure [Andreasen and Ravelo, 1997]? Could the faunal estimates be wrong because two or more of these variables interact in complex ways? Could intercorrelation of variables in the calibration data sets make it impossible to constrain independent equations?

On a global scale, sea surface temperature and primary productivity are essentially uncorrelated. This offers hope that statistical transfer-function estimates of these variables, calibrated using a broad geographic array of core tops, may be independent [Mix, 1989]. Within the tropics, map patterns of primary productivity are generally correlated to mixed-layer or pycnocline depth [Berger *et al.*, 1988; Levitus, 1982]. This makes it difficult to calibrate independent equations to predict these two properties using core tops. Thus it is unclear whether paleocceanographic transfer functions can really isolate these different properties of the upper ocean or whether these three likely influences on faunal composition could be confused in the geologic record.

Here we test such faunal transfer functions by using living planktonic foraminifera to estimate two seasonal regimes in a transect across the central equatorial Pacific upwelling system from 12°S to 9°N. The test we make with the living fauna is important because the key environmental parameters, here primary productivity and upper water column temperature and structure, were measured in detail at the same time the foraminifera were sampled. This removes some of the ambiguity inherent in calibrating equations with atlas data

and undated core tops, which average over different spatial scales and timescales. The comparison of two seasons is important for two reasons. First, the contrast of upper ocean properties between our sampling in February-March and August-September of 1992 (roughly peak El Niño and La Niña events) yields a large range of environments and faunas. Second, the relationships between the environmental properties differ radically within the two seasons. These seasonal differences provide a measure of independence between properties, which helps us assess whether all the transfer functions are reliable.

2. Methods

Populations of living planktonic foraminifera >64 µm in size were sampled in plankton tows, using the Multiple Opening and Closing Net Environmental Sampling System (MOCNESS). Samples were taken along the U.S. Joint Global Ocean Flux Study (JGOFS) equatorial Pacific transect (9°N-12°S, near 140°W) at 11 stations in February-March and 12 stations in August-September, both in 1992. Live (protoplasm full) foraminiferal species were counted at shell sizes >150 µm.

For the purposes of this paper, species percentages at each station were calculated from standing stocks integrated from 0 to 100 m. This integration approximated the average composition of the living fauna throughout the euphotic zone that would eventually sink to build the geologic record. At depths >100 m, standing stocks of foraminifera dropped sharply. Most specimens at these depths lacked protoplasm, and by inference, were dead.

On the day of each plankton tow, temperatures were measured during routine conductivity-temperature-depth (CTD) casts [Murray *et al.*, 1995]. Primary productivity was measured by 12-hour in situ ¹⁴C incubation at each site [Barber *et al.*, 1996]. These values were integrated from the surface to the putative 0.1% light level depth (~120 m) to yield an estimate of integrated primary productivity (mmol C m⁻² d⁻¹). Mixed-layer depth (meters) was estimated from CTD profiles using the Levitus [1982] definition, i.e., the

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shallowest depth at which density was 0.125 density units higher, or at which temperature was 0.5°C lower, than at the sea surface.

Prior to data analysis the species percentages were logarithmically transformed to improve normality. A *Q*-mode, varimax-rotated factor model then simplified the combined data set into orthonormal faunal assemblages appropriate for use in transfer functions. Faunal transfer functions were calibrated using stepwise multiple regression of the assemblage factor loadings (including squared terms and interactions [CLIMAP, 1981]) onto each environmental variable using data from both seasons. Terms were included in an equation only if they were significant at the 95% level. Statistical tests for significance of regression relationships follow Dixon and Massey [1969].

3. Results

3.1. Environmental Properties

El Niño conditions in February-March led to warm surface water temperatures (~28°C) and deep mixed layers (70-100 m)

across the entire transect (Figure 1a). Equatorial upwelling influenced temperature little at the sea surface because the thermocline was deep and the upwelled water was warm. Productivity was high on the equator, >1 mmol C m⁻³ d⁻¹ (Figure 1c) or >80 mmol C m⁻² d⁻¹ integrated through the euphotic zone, because upwelled water was enriched in nutrients [Barber *et al.*, 1996]. This provides an important test of the response of the foraminiferal species to productivity and food supply in the absence of large temperature or mixed-layer depth gradients.

During the La Niña conditions of August-September, strong upwelling from a shallow thermocline cooled the equatorial band to <25°C and compressed the mixed layer to <20 m depth near 2°N (Figure 1b). Upwelled nutrients fueled high productivity near the equator (Figure 1d), with maxima >2.5 mmol C m⁻³ d⁻¹ (or >130 mmol C m⁻² d⁻¹ integrated through the euphotic zone) at convergences near 2°N and 2°S. Subtropical waters with relatively deep mixed layers and warm temperatures occurred south of 5°S and north of 3°N. August-September had a larger range of sea surface temperatures, productivity, and mixed-layer depth than

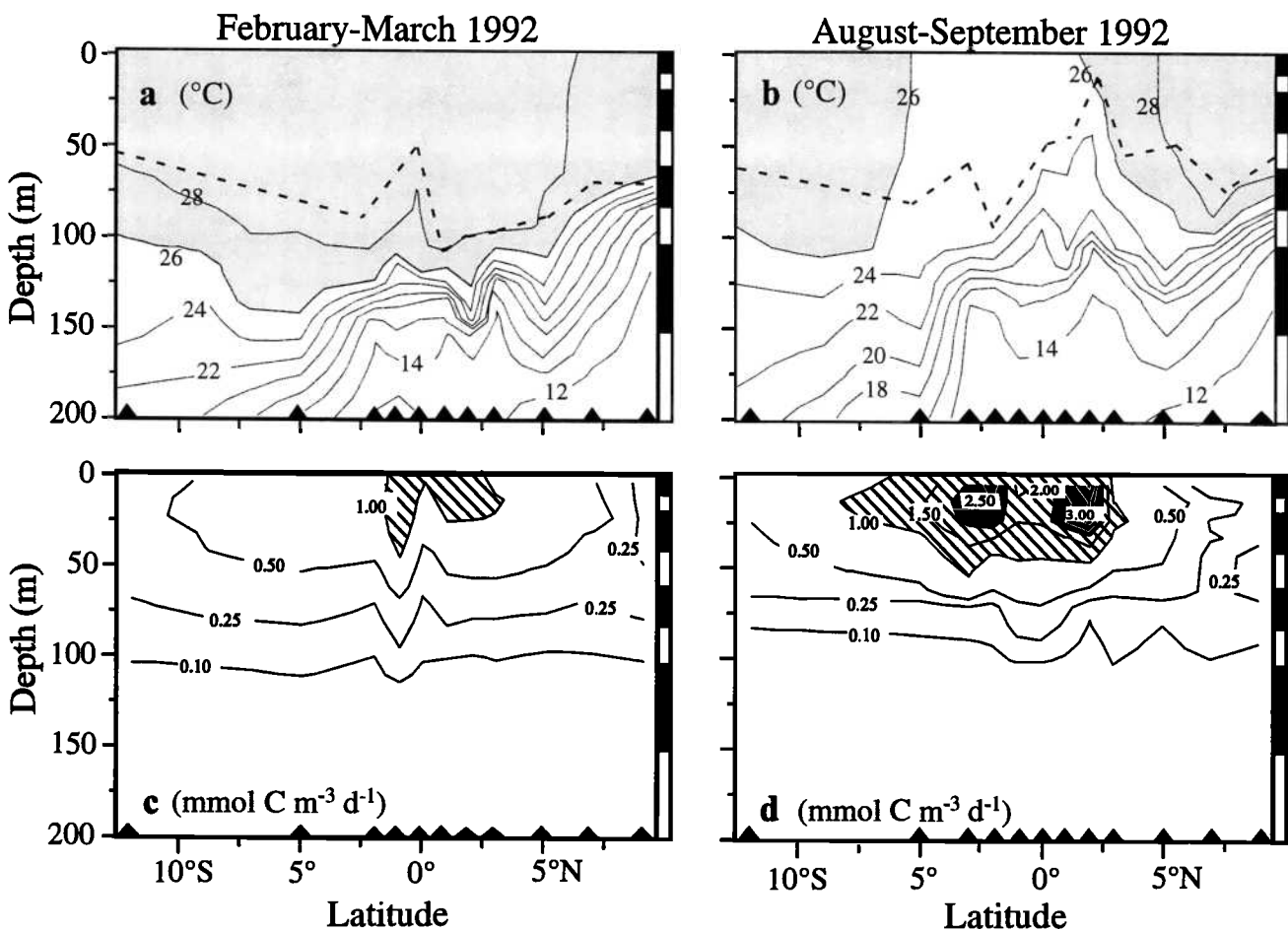


Figure 1. Latitudinal sections of ocean properties in the central tropical Pacific, along the U.S. Joint Global Ocean Flux Study (JGOFS) transect at 140°W [Murray *et al.*, 1995; Barber *et al.*, 1996]: (a) temperature (°C) during February-March 1992 (El Niño conditions), (b) temperature (°C) during August-September 1992 (La Niña conditions), (c) in situ primary productivity (mmol C m⁻³ d⁻¹) during February-March 1992, and (d) In situ primary productivity (mmol C m⁻³ d⁻¹) during August-September 1992. The dashed line represents the depth of the mixed layer. Solid triangles along the bottom of each field mark the location of a Multiple Opening and Closing Net Environmental Sampling System (MOCNESS) plankton tow station. Bands along the right side of each field outline the net tow intervals at each station.

Table 1. Correlations (r) Between Environmental Properties

Item	Number of Observations	SST versus PROD	SST versus MLD	PROD versus MLD
Tows, Feb.-March 1992 (El Niño)	11	<u>0.60</u>	0.23	0.50
Tows, Aug.-Sept. 1992 (La Niña)	12	<u>-0.92</u>	0.17	-0.22
Tows, seasons combined	23	<u>-0.70</u>	<u>0.40</u>	-0.16
Global core tops, 40°N-40°S	906	<u>-0.10</u>	<u>-0.21</u>	<u>-0.46</u>
Pacific core tops, 24°N-24°S	171	<u>-0.55</u>	<u>0.73</u> ^a	<u>-0.84</u> ^a

Values underlined are significantly different from zero (95% confidence). SST is the sea surface temperature; PROD is the 0-100 m integrated primary productivity; MLD is the mixed-layer depth.
^aFor this data set only, MLD is the depth to 18°C isotherm (following *Andreassen and Ravelo* [1997]).

February-March and thus provided a large dynamic range of all variables to test the response of the foraminiferal fauna.

Relationships between these three environmental variables differed during the two seasons (Table 1). Productivity was significantly (>95% level) positively correlated to surface temperature ($r = 0.60$) during February-March because nutrient-rich water that upwelled was warm. In contrast, productivity was negatively correlated to surface temperature ($r = -0.92$) in August-September, when cool water upwelled. Correlations between mixed-layer depth and either sea surface temperature or productivity were not significantly different from zero in either season.

The transfer functions were calibrated with data combined from both seasons. In this combined data set, temperature and productivity were significantly negatively correlated ($r = -0.70$), and mixed-layer depth was significantly positively correlated with temperature ($r = 0.40$). There was not a significant correlation between mixed-layer depth and productivity.

3.2. Foraminiferal Fauna

This paper limits the discussion to the depth integrated species percentages, factor assemblages, and transfer functions for temperature, productivity, and mixed-layer depth. Detailed evaluation of other properties and documentation of raw species standing stocks at each depth in the water column occur elsewhere [*Watkins et al.*, 1996, 1997]. Raw data are available from the U.S. JGOFS database via internet (<http://www1.who.edu/jg/dir/jgofs/eqpac/>). The foraminiferal species abundances, integrated over the upper 100 m of the water column, appear here in Table 2.

A Q -mode factor model of the foraminiferal abundance data (0-100 m) resolved three significant orthogonal faunal assemblages that explained 94% of the data set (Table 3). A fourth factor would explain <2% of the data, which is not significant in this small data set. Seasonal and spatial weightings of these assemblages were expressed as the loadings of the three faunal factors (Table 4).

Factor 1, dominated by *Globorotalia tumida* and *Globoquadrina conglomerata*, was most important at and north of the equator in February-March but shifted south of the equator in August-September (Figure 2). A similar assemblage has been associated previously with warm equatorial waters of the central and western Pacific in both

plankton tows and core top sediments [*Bradshaw*, 1959; *Coulbourn et al.*, 1980].

Factor 2, which included several herbivorous species such as *Globorotalia menardii*, *Globigerinita glutinata*, and *Globigerina bulloides*, had the highest loadings at 2°S in February-March and 0-3°N in August-September. These species are common in core top sediments of the eastern equatorial Pacific and in the tropics are often associated with cool, highly productive waters [*Bradshaw*, 1959; *Parker and Berger*, 1971]. The widespread species *Pulleniatina obliquiloculata* and *Neogloboquadrina dutertrei* were present in both factors 1 and 2 about equally.

Factor 3, a typical subtropical assemblage containing the species *Globigerinoides sacculifer* and *Globigerinoides ruber*, was most prominent away from the equator in both seasons. These species obtain some of their nutrition from symbiotic algae [*Caron et al.*, 1981; *Gastrich and Bartha*, 1988] and thus are well suited for survival in the ocean's oligotrophic subtropical regions.

3.3. Statistical Transfer Functions

The multiple regressions of faunal factor loadings on environmental variables explain 52% of the variance in temperature and productivity ($r = 0.72$) and 62% in mixed-layer depth ($r = 0.79$) for the combined data sets from February-March and August-September (Table 5). Given the small data sets, 95% confidence limits on these correlations preclude saying one equation is better than another. Standard RMS errors of the estimates were $\pm 1.1^\circ\text{C}$ for sea surface temperature, $\pm 23 \text{ mmol C m}^{-2} \text{ d}^{-1}$ for integrated primary productivity, and $\pm 15 \text{ m}$ for mixed-layer depth.

Within these equations, factor 2 was associated with cooler surface temperatures, higher productivity, and shallow mixed layers. Factor 3 was associated with lower productivity and deeper mixed layers. Factor 1 was weakly related to cooler temperatures but strongly associated with deeper mixed layers. Factor 1 did not appear in the productivity transfer function, which means its inclusion would not have significantly improved estimates of productivity. These associations are all consistent with the geographic ranges of the species known for core top and plankton tow studies.

When the predictions of the three transfer functions were considered on a seasonal basis (Figure 3), all the estimates

Table 2. Total Standing Stock of Foraminifera (Living Shells m⁻³) and Species Percentages Integrated From 0-100 m at Each Sample Latitude in the U.S. Joint Global Ocean Flux Study (JGOFS) Transect Near 140°W

Latitude	Total Standing Stock	conglb, %	ruber, %	sacc, %	aequi, %	calida, %	bull, %	dut, %	cnglm, %	obliq, %	menard, %	tumida, %	glut, %	Other %
<i>February-March 1992</i>														
9°N	12.8	2.1	1.0	53.0	1.0	0.9	0.0	3.2	6.5	1.6	0.0	17.5	0.0	1.7
7°N	18.7	8.3	17.1	15.0	2.7	1.2	0.0	8.5	10.6	7.3	0.4	21.0	3.7	0.8
5°N	41.4	2.2	2.5	6.0	7.7	1.0	0.0	5.6	29.9	9.1	0.3	29.6	3.3	1.2
3°N	134.7	1.8	4.8	8.0	2.7	2.6	0.0	8.7	21.0	15.5	0.0	20.4	7.8	9.0
2°N	62.4	2.9	5.8	9.4	2.6	1.5	0.1	6.2	17.3	21.9	0.3	15.3	11.2	3.4
1°N	53.0	2.3	3.2	9.0	6.8	1.3	0.0	12.3	16.7	29.6	0.9	7.9	6.8	1.7
0°	28.8	0.5	2.4	7.0	7.2	5.0	0.0	8.3	29.9	27.8	3.9	1.5	4.7	0.5
1°S	12.4	1.3	1.0	6.1	12.0	2.0	0.0	4.1	38.3	12.7	6.7	3.9	6.2	0.7
2°S	16.0	2.1	10.4	12.3	13.5	0.7	0.0	4.8	2.0	13.3	8.2	0.0	15.4	2.8
5°S	30.6	3.2	13.5	40.2	9.9	3.0	0.0	3.0	0.1	3.5	2.5	0.0	11.8	2.8
12°S	17.8	1.6	11.4	58.0	3.2	2.0	0.0	0.3	1.2	0.0	0.0	0.0	14.1	1.5
<i>August-September 1992</i>														
9°N	4.0	4.3	14.8	66.0	2.2	2.2	0.0	2.1	2.1	0.0	0.0	0.0	0.0	0.2
7°N	10.8	7.5	25.0	47.5	5.3	0.8	0.0	4.9	0.4	0.0	0.0	0.0	2.7	0.6
5°N	20.5	6.0	15.3	8.5	7.2	1.6	1.0	10.5	8.3	12.2	3.9	1.1	22.1	0.5
3°N	57.8	2.9	9.5	10.9	4.3	2.5	0.7	12.3	0.8	11.1	18.1	0.0	21.6	3.1
2°N	400.0	1.9	10.4	6.1	3.2	2.2	20.1	8.4	0.2	12.2	12.2	0.1	14.2	35.2
1°N	108.3	0.7	12.4	8.3	6.4	2.8	16.1	10.6	0.1	9.5	5.2	0.0	18.8	9.9
0°	25.6	0.3	12.7	12.9	3.2	2.0	4.8	9.6	5.2	17.0	13.8	0.0	16.0	0.6
1°S	109.5	2.3	14.0	13.4	4.2	0.8	7.6	7.0	10.5	11.1	2.4	8.9	14.1	4.1
2°S	72.5	2.0	12.1	15.4	7.9	1.8	5.1	9.0	11.3	10.8	4.0	8.5	9.1	2.2
3°S	107.8	1.7	14.6	12.2	7.4	0.4	13.6	7.4	10.0	8.5	1.5	7.8	12.4	2.7
5°S	52.0	3.9	8.3	26.5	5.8	1.7	0.5	7.6	18.5	7.0	0.6	13.8	3.1	1.4
12°S	19.2	10.6	18.0	23.2	1.7	0.0	0.0	0.0	33.5	0.0	0.0	0.3	6.2	1.2

Here, conglb is *Globigerinoides conglobatus*, ruber is *Globigerinoides ruber*, sacc is *Globigerinoides sacculifer*, aequi is *Globigerinella aequilateralis*, calida is *Globigerinella calida*, bull is *Globigerina bulloides*, dut is *Neogloboquadrina dutertrei*, cnglm is *Globoquadrina conglomerata*, obliq is *Pulleniatina obliquiloculata*, menard is *Globorotalia menardii*, tumida is *Globorotalia tumida*, and glut is *Globigerinita glutinata*.

except that of mixed-layer depth in February-March were statistically significant. Considering the confidence limits of the regression analyses, we can say that in August-September the estimates of mixed-layer depth were significantly better ($r = 0.84 \pm 0.03$) than those of sea surface temperature ($r = 0.68 \pm 0.06$), but essentially of the same quality as the estimates of productivity ($r = 0.77 \pm 0.05$). In February-March the estimates of sea surface temperature ($r = 0.72 \pm 0.05$) were as good as those of productivity ($r = 0.71 \pm 0.06$).

Table 3. Factor Scores Describe Orthonormal Assemblages

Species	Factor 1	Factor 2	Factor 3
<i>Globoquadrina conglomerata</i>	0.611	-0.145	0.036
<i>Globorotalia tumida</i>	0.607	-0.247	-0.063
<i>Pulleniatina obliquiloculata</i>	0.390	0.366	-0.286
<i>Neogloboquadrina dutertrei</i>	0.232	0.274	-0.012
<i>Globorotalia menardii</i>	-0.031	0.467	-0.177
<i>Globigerinita glutinata</i>	0.064	0.466	0.054
<i>Globigerina bulloides</i>	-0.062	0.354	-0.125
<i>Globigerinella aequilateralis</i>	0.141	0.236	0.119
<i>Globigerinella calida</i>	0.060	0.134	0.073
<i>Globigerinoides sacculifer</i>	0.107	0.058	0.714
<i>Globigerinoides ruber</i>	-0.027	0.268	0.469
<i>Globigerinoides conglobatus</i>	0.087	-0.016	0.337
Percentage of data explained	38%	33%	24%

As a sensitivity test (not shown), we repeated the above experiments using the fauna integrated from 0-40 m, rather than 0-100 m. Faunal factors and their loadings from this smaller data set were very similar to those above. Transfer functions were calibrated using these factor loadings, including both February-March and August-September samples. The results were significant predictions of primary productivity and mixed-layer depth (which contained the same dominant terms as the 0-100 m equations). Unlike the 0-100 m equations, however, the predictions of sea surface temperature were not significant.

A second sensitivity test, which calibrated equations with the fauna from 0-100 m using only the August-September samples (the more spatially variable La Niña conditions), yielded statistically significant equations for all three variables, with results for sea surface temperature significantly better ($r = 0.86 \pm 0.03$ at 95% confidence) than for mixed-layer depth ($r = 0.66 \pm 0.06$ at 95% confidence).

Thus all three transfer functions produced significant results, with the exceptions that estimates of sea surface temperatures were not successful in one sensitivity test and that predictions of mixed-layer depths were not significant in a test from one season. The predictions of integrated primary productivity were the only ones to pass all tests of significance. We infer from these experiments that all of the variables considered, primary productivity, sea surface

Table 4. Factor Loadings and Ocean Property Data Used to Calibrate Transfer Functions

Latitude	COMM	Factor 1	Factor 2	Factor 3	SST	PROD	MLD
<i>February-March 1992</i>							
9°N	0.88	0.75	0.07	0.56	26.5	27	70
7°N	0.95	0.76	0.35	0.50	27.9	38	70
5°N	0.99	0.91	0.27	0.28	28.4	54	90
3°N	0.97	0.86	0.36	0.31	28.4	63	100
2°N	0.97	0.83	0.42	0.33	28.3	64	100
1°N	0.98	0.82	0.48	0.28	28.5	65	110
0°	0.91	0.75	0.56	0.21	28.3	46	50
1°S	0.91	0.79	0.50	0.15	28.5	83	70
2°S	0.93	0.44	0.76	0.40	28.6	49	90
5°S	0.95	0.30	0.67	0.65	28.7	60	80
12°S	0.92	0.24	0.44	0.81	28.5	34	54
<i>August-September 1992</i>							
9°N	0.94	0.30	0.27	0.88	28.3	24	55
7°N	0.96	0.24	0.43	0.84	28.3	22	77
5°N	0.97	0.58	0.69	0.41	28.1	42	50
3°N	0.95	0.37	0.83	0.35	27.0	57	55
2°N	0.95	0.30	0.90	0.24	24.2	135	10
1°N	0.96	0.30	0.89	0.30	24.7	no data	45
0°	0.97	0.45	0.82	0.29	24.9	94	50
1°S	0.95	0.67	0.61	0.36	25.3	93	75
2°S	0.98	0.68	0.61	0.37	25.3	112	100
3°S	0.92	0.64	0.61	0.36	25.3	115	60
5°S	0.99	0.78	0.37	0.49	25.9	67	85
12°S	0.82	0.47	0.23	0.74	26.4	34	65

COMM is Communality, the fraction of pooled population variance explained by a linear combination of the three factors. SST is the sea surface temperature in °C. PROD is primary productivity integrated over the euphotic zone in $\text{mmol C m}^{-2} \text{d}^{-1}$. MLD is the mixed-layer depth in meters using the definition of *Levitus* [1982].

temperature, and mixed-layer depth could influence the foraminiferal fauna.

4. Discussion

4.1. Spatial Patterns and Correlations Between Variables

To further explore the significance of the faunal transfer functions, we examined the spatial patterns of the predictions of temperature, productivity, and mixed-layer depth in the two seasons. The temperature transfer function was reasonably successful in reconstructing the measured latitudinal patterns of sea surface temperature in both seasons (Figures 4a and 4b). It reproduced both the observed decrease in sea surface temperature to the north in February-March and the sharp temperature minimum at 2°N observed in August-September. The productivity equation simulated the broad equatorial maximum of primary productivity apparent during both seasons (Figures 4c and 4d). The mixed-layer depth equation successfully predicted the shallow mixed layer at 2°N in August-September (Figures 4e and 4f).

The transfer functions derived from the combined data set also preserved the different relationships between temperature and productivity in the two seasons. Temperature and productivity estimates were essentially uncorrelated ($r = 0.19$) in the February-March samples and were strongly inversely correlated ($r = -0.80$) in the August-September samples, roughly similar to the different seasonal

patterns of observed values ($r = 0.60$ for February-March and $r = -0.92$ for August-September). Transfer functions correctly reproduced the different sign of correlations between temperature and productivity in February-March and August-September even though the equations were calibrated with the combined data sets in which the two variables were significantly negatively correlated (Table 1). This success of the equations in reproducing the different latitudinal patterns and seasonal relationships of the environmental properties, rather than just mimicking the correlation structure in the calibration data set, is encouraging for the use of preserved fauna to reconstruct past values of multiple variables.

4.2. Analysis of Residuals and Biological Processes

The transfer functions were not perfect, of course. It is important to assess whether these imperfections were randomly distributed, such as might happen with noise in counting the species, or whether they were systematic, implying an inappropriate statistical model. To explore these possibilities, we plotted residual errors of each estimate (i.e., estimated minus observed values) versus the observed values of the three environmental variables (Figure 5). Some important relationships emerged.

Positive temperature residuals (indicating transfer function temperature estimates that were too warm) occurred when productivity was high, and negative temperature residuals occurred when productivity was low (Figure 5b).

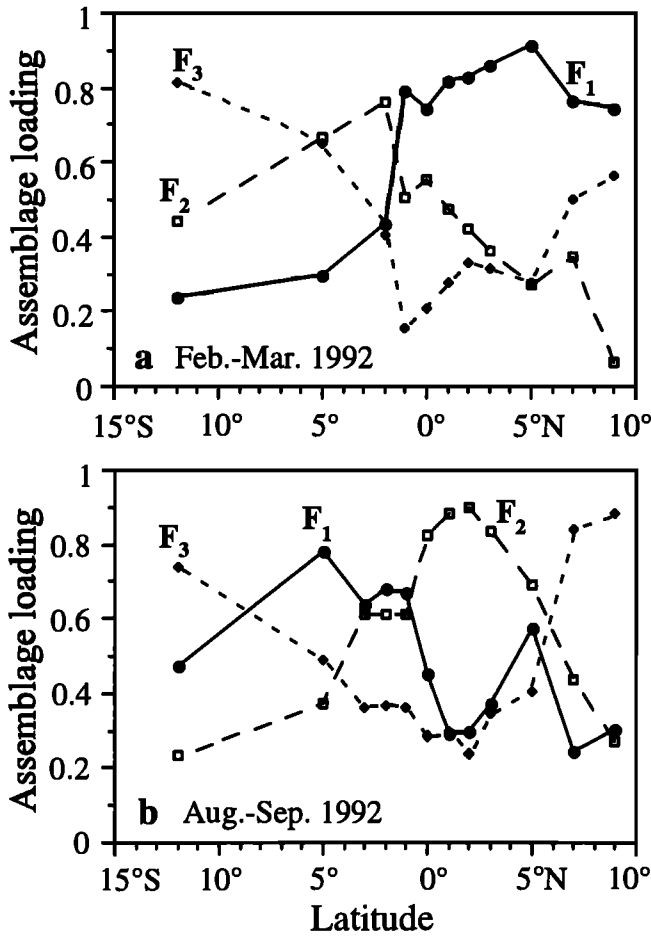


Figure 2. Latitudinal patterns of foraminiferal factor assemblage loadings record the relative abundance of each assemblage at each sampling station: (a) February-March 1992 and (b) August-September 1992. See Table 3 for assemblage compositions.

Similarly, productivity estimates were too high (residuals positive) when temperatures were warmer and too low when temperatures were cooler (Figure 5d). This implies a possible interaction between these environmental variables in the faunal response.

We suggest that the link between variables in the response of foraminiferal species is respiration rate, which is driven by both temperature and food supply. This combines a so-called "Q₁₀ Effect," in which respiration rate increases exponentially with temperature [Gauld and Raymond, 1953],

Table 5. Transfer Function Equations Calibrated With Central Tropical Pacific Plankton Tows

	r ²	RMS Error
Sea surface temperature	0.52	±1.1°C
Integrated primary productivity	0.52	±23 mmol C m ⁻² d ⁻¹
Mixed layer depth	0.62	±15 meters

Sea surface temperature is $31.6 - 10.0 (F_2)^2 - 11.9 (F_1 F_3) + 11.3 (F_2 F_3) - 3.7 (F_3)^2$; integrated primary productivity is $62.5 - 66.2 (F_3) + 57.9 (F_2)$; and mixed layer depth is $0.9 + 109.0 (F_1)^2 + 216.1 (F_2 F_3) - 35.0 (F_2)$.

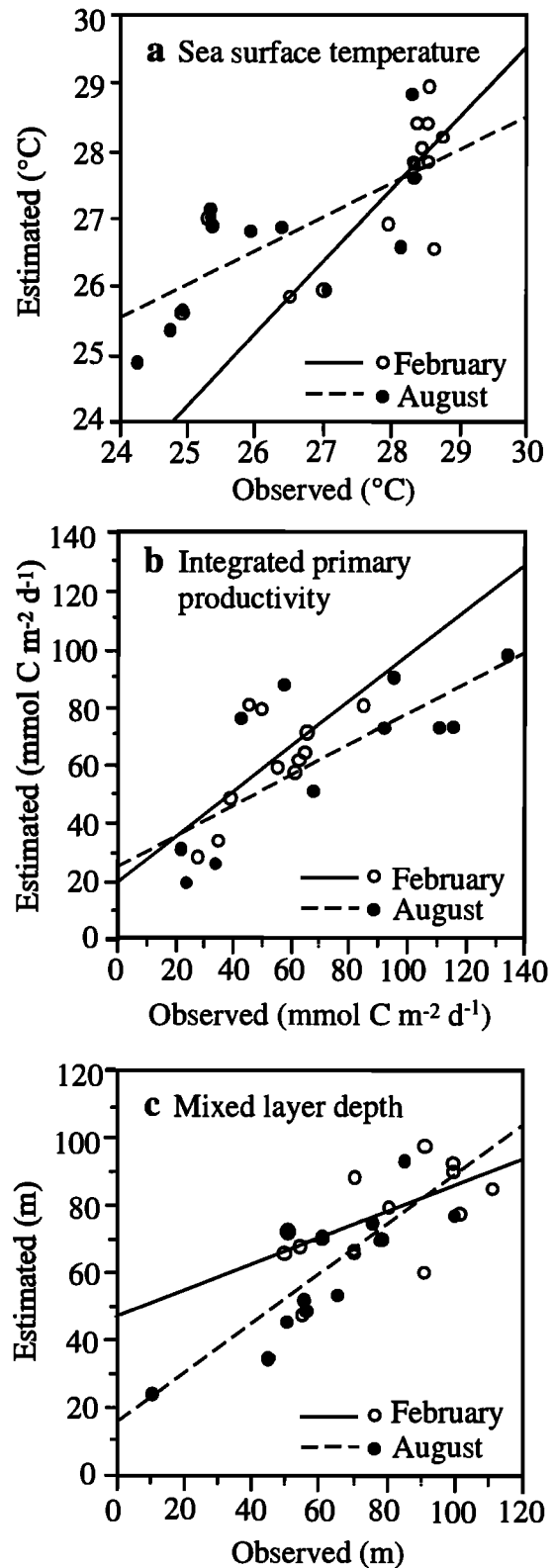


Figure 3. Model estimate plotted versus observed values for three environmental properties: (a) sea surface temperature (°C), (b) integrated primary productivity (mmol C m⁻² d⁻¹), and (c) mixed-layer depth (meters). Models were derived from 0-100 m integrated fauna data combined from both seasons. Open circles and solid regression lines are samples from February-March 1992. Solid circles and dashed regression lines are samples from August-September 1992.

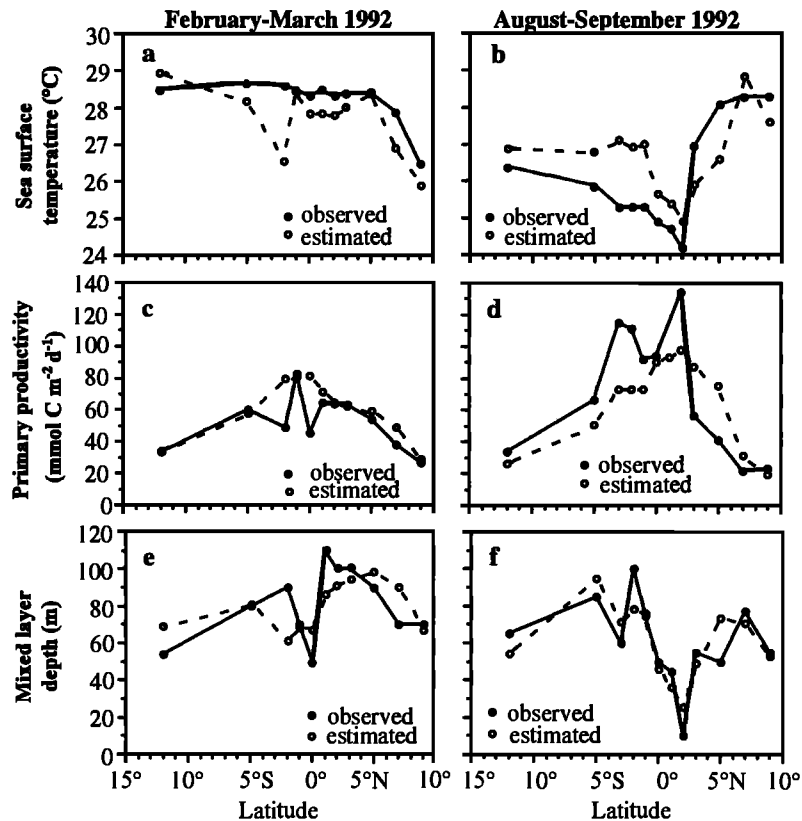


Figure 4. Latitudinal patterns of observed (solid circles and solid lines) and estimated (open circles and dashed lines) ocean properties: (a) sea surface temperature ($^{\circ}\text{C}$) in February-March 1992, (b) sea surface temperature ($^{\circ}\text{C}$) in August-September 1992, (c) integrated primary productivity ($\text{mmol C m}^{-2} \text{d}^{-1}$) in February-March 1992, (d) integrated primary productivity ($\text{mmol C m}^{-2} \text{d}^{-1}$) in August-September 1992, (e) mixed layer depth (meters) in February-March 1992, and (f) mixed layer depth (meters) in August-September 1992.

with an "Ivlev Effect," in which growth rate (and the respiration associated with this growth) increases logarithmically with food stocks [Ivlev, 1961; Vidal, 1980]. Thus a high food supply associated with productive regions may yield overestimates in transfer-function temperatures because the foraminiferal species abundances actually reflect the characteristic growth and respiration rates driven by both variables.

The residuals of mixed-layer depth appear to be randomly distributed relative to temperature and productivity (Figures 5g and 5h). Thus the estimates of mixed-layer depth were not biased by the other variables examined here. If our inference about the biological cause of interactions between temperature and productivity is correct, this is not surprising. Respiration rate is probably not related to mixed-layer depth. There was a tendency for estimates of mixed-layer depth to be too large when the mixed layer was shallow and too small when the mixed layer was deep (Figure 5i). This means that the transfer function did not adequately capture the full sensitivity of the variations in mixed-layer depth.

4.3. Implications for the Geologic Record

Our study of the living fauna offers hope that foraminifera in the geologic record may be used to reconstruct more than one property of the upper ocean. It also suggests caution and

yields some insights into processes that may bias geologic transfer functions.

There are some limitations in this relatively small data set. We examined three variables (temperature, productivity, and mixed-layer depth) that are likely candidates for primary control of species assemblage, but certainly other influences may exist as well. Although we examined a relatively large range of faunas in this dynamic equatorial system by studying the extreme events of El Niño and La Niña, we sampled a relatively small region. This, no doubt, caused us to miss taxa important in other regions and in the geologic record. Different life spans and preservation change the relative weighting of species in sedimentary assemblages relative to plankton tows. Thus the equations calibrated here with plankton tow data should not be applied directly to geologic data.

Estimates of all three variables we considered were viable. The estimates of productivity were the only ones to pass all statistical tests of significance for seasonal and annual estimates and for several sensitivity tests involving subsets of the data. This suggests that estimates of paleoproductivity in the geologic record will be useful.

The combined influences of productivity and temperature on foraminiferal populations may bias both estimates. Productivity estimates appear to be too high at warm temperatures, and temperature estimates appear to be too warm

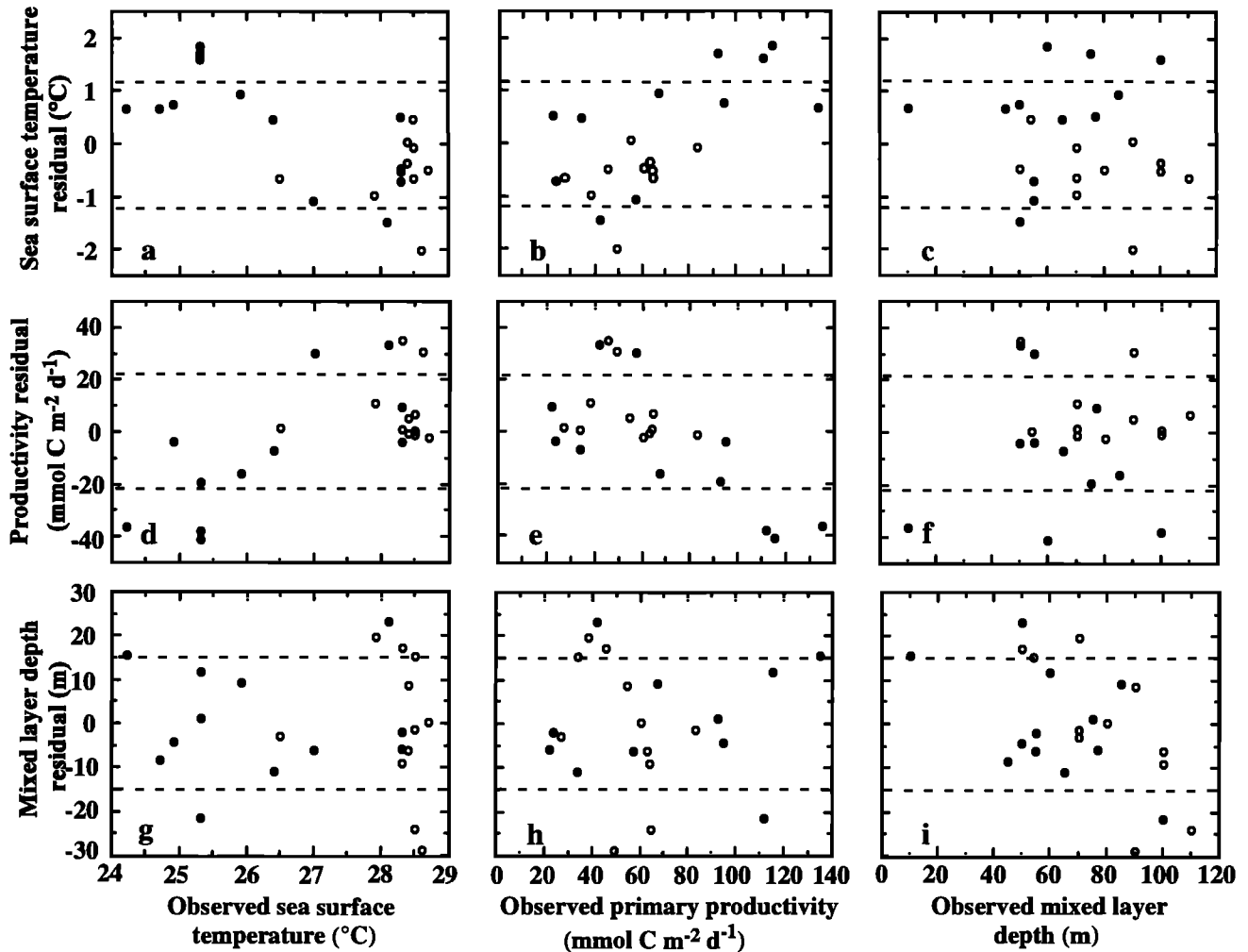


Figure 5. Model residual errors of ocean properties (estimated minus observed) plotted versus observed properties assess bias or interaction of properties in the transfer-function estimates: (a) temperature residuals versus observed sea-surface temperatures, (b) temperature residuals versus observed primary productivity, (c) temperature residuals versus observed mixed layer depth, (d) productivity residuals versus observed sea surface temperatures, (e) productivity residuals versus observed mixed layer depth, (f) productivity residuals versus observed mixed layer depth, (g) mixed layer depth residuals versus observed sea surface temperatures, (h) mixed-layer depth residuals versus observed primary productivity, and (i) mixed layer depth residuals versus observed mixed layer depth. Dashed horizontal lines mark the average $\pm 1\sigma$ RMS errors of regression. Open circles are samples from February-March 1992; solid circles are samples from August-September 1992.

at high productivity values. This relationship suggests some biological process that combines these effects. We speculate that the link is through respiration rate, which is known to be influenced by both temperature and feeding rate in most organisms. If this type of bias exists in geologic transfer functions, it could perhaps account for some of the mismatches between transfer function and geochemical temperature estimates of the last glacial maximum [CLIMAP, 1981; Guilderson *et al.*, 1994].

To detect and remove this bias from geologic estimates of temperature and productivity may be difficult, but a key fact leads us to think it may be possible. In the set of all core tops in which foraminifera have been counted between 40°N and 40°S [Prell, 1985] the correlation between mean annual sea surface temperature [Levitus, 1982] and primary productivity (data from Berger *et al.* [1988]) is nearly zero (Table 1). This

statistical independence of properties in the water column means that we may be able to detect interactions and biases in the core top calibrations and, by including the relevant processes in predictive models, to correct for them in the geologic record. Of course, analysts must be careful in assembling their core top calibration data sets to maintain this statistical independence.

Some have used the geologic record of foraminifera species to assess changes in mixed-layer (or pycnocline) depth [Andreasen and Ravelo, 1997]. Our finding that an apparently unbiased relationship may exist between the living fauna and mixed-layer depth indicates that such attempts are reasonable. Here too, however, we suggest caution. In the modern ocean, mixed-layer depth (or pycnocline depth) and primary productivity are highly correlated with each other, especially in the tropics (Table 1).

Productivity and food supplies tend to be higher where the pycnocline is shallow because of the higher availability of nutrients. Indeed, some biologists have used water column structure to predict modern primary productivity [Herbland and Voituriez, 1979]. Thus, in a core top calibration of faunal transfer functions it would be very difficult to distinguish between these two properties.

Our observation of a consistent relationship of the living fauna to primary productivity present in two very different seasonal settings suggests that the fauna responds to primary productivity as well as mixed-layer depth, at least in the central Pacific setting we studied. If the relationship of food supply to pycnocline structure stayed constant through time, then it is very likely that transfer-function estimates of mixed-layer depth would be successful. But if the relationship between these properties changes, for example, because of regional changes in subsurface nutrients or in eolian fluxes of nutrients without corresponding changes in water column structure, then changing productivity could drive erroneous transfer-function estimates of mixed-layer depth.

5. Conclusions

By using the living fauna and in situ measures of environmental properties (sea surface temperature, integrated primary productivity, and mixed-layer depth) we evaluated potential interactions between these properties as they influence foraminiferal populations. Key elements of our transfer function test were a large dynamic range provided by the seasonal contrast between El Niño and La Niña events in 1992 and different relationships between the environmental properties in the two seasons that provided statistical independence.

Three orthogonal faunal assemblages accounted for 94% of the living fauna of the central equatorial Pacific. Transfer function equations reconstructed about half the observed variance of temperature, productivity, and mixed-layer depth when both seasons were included in the calibration. The estimates of primary productivity were statistically significant in both seasons and robust in all sensitivity tests. This suggests that estimates of paleo-productivity in the geologic record will be useful. Estimates of temperature and mixed-layer depth passed most of the statistical tests we applied and successfully reconstructed the spatial and seasonal patterns across the equatorial Pacific upwelling system. This offers hope that more than one environmental

property can be extracted from population data in the fossil record.

Transfer function estimates of temperature were warmer than observations when productivity was high and cooler than observations when productivity was low. Similarly, productivity estimates were too high when temperatures were warm and too low when temperatures were cool. Thus the combined influences of productivity and temperature on foraminiferal populations may bias both estimates. We suggest that the biases come from biological respiration rate, which is known to be influenced by both temperature and feeding rate. This type of bias in geologic transfer functions could perhaps account for some of the mismatches between faunal and chemical temperature estimates of the last glacial maximum.

Caution is warranted in using transfer functions to predict multiple properties of ancient oceans. Many of the properties (for example productivity and mixed-layer depth) are correlated in the modern ocean. This means that geologic transfer functions calibrated with core tops may confuse one ocean property for another, and if the relationships between properties change through time, the transfer function estimates could be erroneous. The problem is worse in regional calibrations than in global arrays.

Progress will come from two approaches. Studies of the living fauna, both in the field and in cultures, will lead to a better understanding of the physical, chemical, and biologic processes that influence populations of shell-forming plankton. More attention to optimizing the design of core top data sets will improve statistical independence of key properties of the calibrations. By combining insights into biological response mechanisms that may bias transfer functions from studies of the living fauna, with a new generation of high-quality core top calibrations an opportunity now exists to improve transfer functions and our understanding of changes in multiple properties of past oceans.

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