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Estimation of new production in the tropical Pacific

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Abstract. A synthesis of field data from nine cruises and 121 stations in the tropical Pacific (15°N–16°S by 135°W–167°E) was used to develop a statistical model relating areal new production rates (based on $^{15}NO_3$ uptake incubations) to other measured biological and chemical water properties. The large dynamic range of *f* ratios (new to primary production) measured in the region (0.01–0.46, with a mean of 0.16 ± 0.08) could not be described by any simple function of any of the more than three dozen measured variables tested. Thus the commonly used approach of extrapolating new production using mean *f* ratios is likely to lead to large uncertainties when used in the tropical Pacific. An alternative approach is examined in which new production is estimated directly by multiple linear regression (MLR) of measured properties. Nearly 80% of variability in new production could be explained with a MLR of four variables together (rates of primary production (or chlorophyll inventories), inventories of ammonium and nitrate, and temperature) better than any single variable alone or any other combination of variables. Each of these variables exhibited effective linearity with respect to new production for this data set, and the robustness of this MLR method to predict new production for other data sets was confirmed by cross validation. These results thus provide a robust, simple tool to extend new production estimates to locations and times where it is not measured directly, using ship-based measurements and potentially remotely sensed data from moorings and satellites.

1. Introduction

Processes controlling the uptake of newly available nutrients and carbon dioxide by phytoplankton in the world's oceans modulate exchange between the largest active carbon reservoirs and the atmosphere [*Falkowski et al.*, 1998] by directly driving the biological pump of organic carbon export to the deep ocean [*Eppley and Peterson*, 1979]. Therefore understanding what controls the magnitude and variability of this new production [*Dugdale and Goering* , 1967] is of great importance to oceanographers and global carbon modelers alike. As such, considerable effort has been made in the last decade to measure and estimate new production within various oceanographic regimes, with special emphasis placed on the vast high-nitrate, low-chlorophyll (HNLC) regions, where incomplete or delayed utilization of new nutrients leave surface CO_2 partial pressures elevated with respect to the atmosphere [*Chavez and Barber*, 1987; *Dugdale et al.*, 1992; *Kurz and Maier-Reimer*, 1993]. These efforts have resulted in the equatorial Pacific upwelling zone being one of the most well studied regions on the globe with respect to these processes [*Murray et al.*, 1994; *Barber et al.*, 1996; *Feely et al.*, 1997].

Despite relatively stable chlorophyll concentrations [*Barber and Chavez*, 1991; *Chavez et al.*, 1996; *Le Borgne et al.*, 1999] the various modes of physical forcing in tropical Pacific surface waters are highly variable with periods as short as days [*Kessler and McPhaden*, 1995]. Geographic position within this region likewise determines a wide range of physical and biological conditions [*Barber and Kogelshatz*, 1990]. The euphotic zone expresses this variability through nutrient inventories that change over 2 orders of magnitude, rates of primary production (PP) ranging from 5 to 180 mmol C m^{-2} d^{-1}, and rates of new production (NP) from 0.03 to 6.3 mmol N m^{-2} d^{-1}. Such large variability of biological fluxes in seemingly stable HNLC regions presents to the oceanographic community a double challenge: (1) to understand how physical, biological, and biogeochemical processes combine to control new production fluxes and (2) to realistically extrapolate measured new production to more meaningful and broader spatial and temporal scales. Attaining each of these interrelated goals is critical to future global modeling efforts that attempt to monitor and predict feedback between the carbon cycle and climate.

Searching for the controls on new production, process studies of the last decade have identified a number of factors that relate directly to nitrate uptake rates representing measured new production. In general, chlorophyll concentrations seem to be positively correlated with nitrate uptake [*Peña et al.*, 1992; *McCarthy et al.*, 1996], which is largely driven by correlations between chlorophyll and primary production [*Barber and Chavez*, 1991]. Most studies show increases in nitrate uptake with increasing nitrate concentrations, especially above threshold concentrations near 3–6 μM [*McCarthy and Nevins*, 1986; *Dugdale and Wilkerson*, 1991; *Wilkerson and Dugdale*, 1992; *Peña et al.*, 1992; *McCarthy et al.*, 1996]. The preferential utilization of regenerated nitrogen, especially ammonium, over nitrate is well documented [*McCarthy*, 1972; *McCarthy et al.*, 1977; *Glibert et al.*, 1982; *Dortch*, 1990], and negative correlations from the inhibitory effect of elevated ammonium concentrations on nitrate uptake rates have been widely observed [*Harrison et al.*, 1987; *Murray et al.*, 1989; *Wheeler and Kokkinakis*, 1990; *Price et al.*, 1994]. New production was also strongly related to diatom abundance and silicate concentration during the most dynamic conditions surveyed in the equatorial Pacific [*Landry et al.*, 1997; *Dugdale and Wilkerson*, 1998; *Dunne et al.*, 1999; R. R. Bidigare et al., unpublished data, 1996], but

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silicate and diatoms did not appear to control new production at more typical nitrate concentrations (<7.5 μ *M*) [*Dunne et al.*, 1999]. Last, iron is now widely acknowledged as the limiting nutrient in HNLC regions, and the supply rate of iron has been proposed as the ultimate control on new production in the equatorial Pacific [*Landry et al.*, 1997; *Gordon et al.*, 1997]. Not only do these combined findings form the basis from which variation in new production can be assessed, but they also illustrate the potential for multivariate statistical estimation of new production from more commonly and easily measured biological and chemical water properties.

In the effort to extrapolate new production to larger spatial and temporal scales, investigators have employed a variety of methods and approaches. By far, the most common method is to multiply estimates of PP by average ratios of new to total production, known as the *f* ratio [*Eppley and Peterson*, 1979; *Chavez and Barber*, 1987; *Sathyendranath et al.*, 1991]. Other approaches calculate nitrate flux balances from estimated nitrate distributions and various physical models [*Chavez and Barber*, 1987; *Fiedler et al.*, 1991; *Peña et al.*, 1994; *Chavez and Toggweiler*, 1995], from satellite marine transparency fields [*Lewis et al.*, 1988] and heat flux balances [*Lewis*, 1992], and from inverse models of the seasonal cycles of temperature, argon, helium, and oxygen [*Spitzer and Jenkins* , 1989]. Several coupled ecosystem-circulation models have explored how past records of physical forcing might control variability in new production [*Chai et al.*, 1996; *Stoens et al.*, 1999; *Leonard et al.*, 1999]. Efforts to monitor or predict new production over changing real conditions with satellites using remotely sensed sea surface temperature and chlorophyll have used nitrate to *f* ratio relationships [*Sathyendranath et al.*, 1991], a "shift-up" nitrate utilization model [*Zimmerman et al.*, 1987; *Dugdale et al.*, 1989; *Dugdale et al.*, 1990], and *f* ratios estimated from a temperature-driven pelagic food web model [*Laws et al.*, 2000].

Many of these methods are limited in their ability to usefully extrapolate, monitor, and predict new production variability from measured ocean properties in the important HNLC environments. Approaches relying on *f* ratios can lead to considerable error in new production estimates owing to the large errors in determining *f* ratios as a simple function of total primary production or nitrate concentrations [*Eppley and Peterson*, 1979; *Harrison et al.*, 1987; *Murray et al.*, 1989; *Dugdale et al.*, 1992]. In addition, the *f* ratio approaches and many nitrate upwelling flux balances are further limited in their usefulness by ignoring variability crucial to annually integrated values [*Platt and Harrison*, 1985] or by ignoring the dynamics of delayed nitrate and CO_2 uptake [*Dugdale et al.*, 1992]. Other methods are simply not applicable to all environments. For example, the shift-up nitrate utilization model consistently overpredicts nitrate uptake rates by several orders of magnitude in all HNLC regions, including the equatorial Pacific [*Dugdale and Wilkerson*, 1991], and the temperature-driven pelagic food web model fails to adequately account for the full range of observed *f* ratios in the tropical Pacific [*Laws et al.*, 2000]. Whereas recent biophysical ecosystem models have demonstrated substantial success at probing physical and biological controls on new production, a strong need still exists for a simple method of estimating new production fluxes at high temporal resolution from more easily obtainable ocean properties.

The goal of this study was to examine existing new production data measured in the tropical Pacific, all based on similar methods of $^{15}NO_3$ uptake, in order to develop a multivariate statistical model of areal new production with respect to other biological and chemical ocean properties. The three main objectives were (1) to test whether measured *f* ratios were directly related to other properties in this region, (2) to determine if other predictive relationships exist in order to extend new production estimates to broader spatial and temporal scales, and (3) to examine such relationships for insight regarding biogeochemical controls on new production. Multiple linear regression (MLR) is particularly suited to these tasks of examining relationships between properties that vary simultaneously. MLR systematically determines which subset of independent variables combine linearly to best explain variability of the chosen dependent variable, taking into account covariance within the independent set [*Neter et al.*, 1996]. Of all multivariate statistical techniques, MLR is the simplest and most analogous to the bivariate techniques in common use and thus provides the most readily interpretable results.

2. Data

Statistical analyses were performed on the combined data sets from nine cruises to the equatorial Pacific (Figure 1 and Table 1). The WEC88 cruise sampled from 15°N to 15°S at 150°W in February–March of 1988, during a rather typical non-El Niño period. WEC8803-B followed a parallel transect to the east (15°N–15°S at 135°W) 1 month later. U.S. Joint Global Ocean Flux Study (JGOFS) EqPac Surveys occupied stations from 12°N to 12°S at 140°W during El Niño reduced upwelling conditions in February–March 1992 (TTN007) and during the dynamic upwelling of August–September 1992 (TTN011). EqPac Time Series repeatedly sampled the equator at 140°W over 3 week periods in March–April 1992 (TTN008) and October 1992 (TTN012). The France JGOFS Flupac cruise occupied stations along the equator from 167°E to 150°W, including a week-long time series at each extreme, in October 1994 during moderate El Niño conditions. Days later, the France JGOFS Olipac cruise followed a meridional transect from 16°S to 1°N at 150°W in November 1994. The Zonal Flux cruise (TTN060) sampled the equator from 165°E to 150°W during a mild La Niña enhanced upwelling in April 1996. The 121 reviewed stations sampled a wide range of conditions that included oligotrophic to HNLC regimes and El Niño to La Niña climates. This synthesis thus looks at every major published study that has measured new production in the tropical Pacific.

The data considered in this synthesis were all used as published by the original investigators, with no correction for differences in experimental methodology or calculation procedure (with the exception of WEC8803-B, whose hourly nitrate uptake rates were multiplied by 12 instead of 24 hours as originally published, for consistency with other studies). All new production measurements were based on similar methods of $^{15}NO_3$ uptake [*Dugdale and Goering*, 1967] during 4–12 hour incubations. Thus the data synthesized here form the most consistent data set of new or export production in the tropical Pacific. The often-cited problem of nutrient perturbation by $^{15}NO_3$ addition is minimized in much of this region because of its HNLC status and because of the use of nanomolar methods for many of the stations with low nitrate concentrations [*McCarthy et al.*, 1996; *Raimbault et al.*, 1999]. Furthermore, export production measurements based on sediment traps and/or dissolved organic carbon (DOC) export are difficult to compare between studies owing to diverse sampling methods and differing corrections for advective components.

Profiles of uptake rates, biomass estimates, and dissolved and particulate chemical concentrations were integrated to various depths. These included mixed layer depths (based on both Δ0.03 and Δ0.125 density units relative to surface values) and euphotic zone depths corresponding to both 1.0 and 0.1% surface irradiance E_0 of photosynthetically active radiation (PAR). These light level depths were either determined by bio-optical profile measurements or estimated with an optical model [*Morel*, 1988] as per the original published studies. Weighted euphotic zone temperature averages were calculated as the ratio of the depth integral to the

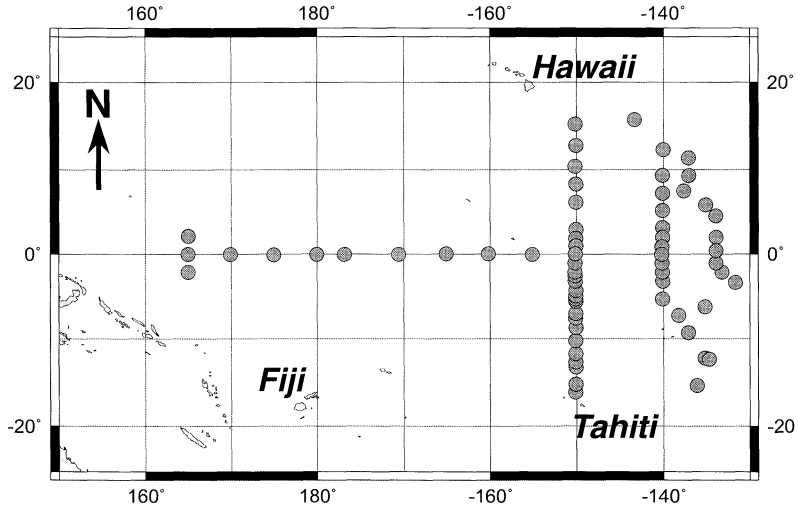

Figure 1. Locations of the 121 stations considered in this text, from the nine following cruises: WEC88, WEC8803-B, EqPac Time Series I and II, EqPac Surveys I and II, Flupac, Olipac, and Zonal Flux. This synthesis and statistical analysis considers every major published study that has measured new production (NP) in the tropical Pacific using ^{15}N-based nitrate uptake methods. Statistical analyses were performed on subsets of these stations (>100) that included data for all considered variables. Underlying map created with GMT software (http://www.aquarius.geomar.de/omc).

depth of integration. All f ratios presented or considered in Section 5 were calculated as the ratio of areal new production rates to primary production rates, both integrated to 1.0% E_0, multiplied by the commonly assumed Redfield carbon-to-nitrogen ratio of 6.6 (mol mol^{-1}).

3. Statistical Methods

Simple, bivariate relationships between all variables were initially explored by calculating the very commonly used Pearson's product-moment correlation coefficient r for each variable pair. The coefficient of determination r^2 gives the fraction of the variability in one variable that can be explained by the other. Scatterplots were used to examine all significant relationships for curvature, normality, and outliers.

MLR is the multivariate extension of simple, bivariate linear regression. MLR fits a hyperplane to multidimensional data by minimizing the sum of squared residuals in a way analogous to simple linear regression [*Neter et al.*, 1996]. The resulting regression equation takes the form:

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_n X_n,$$

where β_0 represents the intercept, β_1 represents the slope with respect to the independent variable X_1 and so on, and n represents the total number of independent variables [*Neter et al.*, 1996]. A multiple coefficient of determination R^2 describes the fit and is equivalent to both the r^2 and slope of a simple linear regression of predicted values as a function of those measured. Therefore the goodness of a MLR fit directly determines the degree to which high values are underpredicted [*Neter et al.*, 1996]. Also, MLR

Table 1. Cruises and Stations Surveyed That Measured $^{15}NO_3$-based New Production in the Tropical Pacific

Cruise	Stations	Dates	Latitude	Longitude	SOI[a]	References
WEC88	21	Feb. 22 to Mar. 15, 1988	15°N–15°S	150°W	−0.8 to −0.1	*Dugdale et al.* [1992], *Wilkerson and Dugdale* [1992]
WEC8803-B	13	Mar. 31 to Apr. 23, 1988	15°N–15°S	133°W–143°W	−0.1 to +0.1	*Peña et al.* [1992]
EqPac Survey I	12	Feb. 3 to Mar. 7, 1992	12°N–12°S	135°W–140°W	−2.5 to −1.4	*McCarthy et al.* [1996]
EqPac Time Series I	8	Mar. 26 to Apr. 9, 1992	0°	140°W	−2.6 to −1.8	P. A. Wheeler[b]
EqPac Survey II	15	Aug. 9 to Sept. 12, 1992	12°N–12°S	135°W–140°W	−0.1 to 0.0	*McCarthy et al.* [1996]
EqPac Time Series II	10	Oct. 2–20, 1992	0°	140°W	−1.9 to −1.1	P. A. Wheeler[b]
Flupac	8	Oct. 2–25, 1994	0°	167°W and 150°W	−1.7 to −1.2	*Rodier and LeBorgne* [1997], *Navarette* [1998]
Olipac	19	Nov. 6–29, 1994	1°N–16°S	150°W	−1.0 to −0.7	*Raimbault et al.* [1999]
Zonal Flux	12	Apr. 20 to May 10, 1996	2°N–2°S	165°W–150°W	+0.3 to +0.6	Aufdenkampe et al. (submitted manuscript, 2000)

[a] Southern Oscillation Index (SOI) values are interpolated from standardized monthly means available from the National Oceanic and Atmospheric Administration (NOAA) Climate Prediction Center (http://www.cpc. ncep.noaa.gov/data/indices/).

[b] See the U. S. Joint Global Oceans Flux Study home page at http://www1.whoi.edu/jgofs.html.

treatments work best when covariance between independent variables is minimal but an adjusted coefficient of determination R^{2*} can be calculated that takes covariance into account. Whereas R^2 will always increase with the addition of a new variable, the adjustment to R^{2*} will drive it toward zero as covariance within the independent set increases. Subset MLR algorithms were fixed to choose the set of independent variables that maximized the adjusted multiple coefficient of determination R^{2*}.

To evaluate the importance of each independent variable within a MLR, partial correlation coefficients, such as $r_{Y3.12}$, were calculated, where the square, $r_{Y3.12}{}^2$, measures the proportionate reduction in the residual sum of squares of Y after X_3 is added to a regression already including X_1 and X_2 [*Neter et al.*, 1996]. The value of the partial correlation coefficient for a variable is independent of the sequence that the variables are included in the MLR. Partial correlation coefficients are analogous to the simple correlation coefficients given in this paper, with the important exception that partial correlation coefficients take into account covariation between all independent variables within the MLR [*Sokal and Rohlf*, 1995].

Implicit in MLR is the assumption that all the independent variables are effectively linear with respect to the dependant variable. This can be tested by inspection of curvature in plots of the MLR standard residuals as a function of each independent variable [*Neter et al.*, 1996]. Thus MLR can often be used to model relationships that are functionally nonlinear if the data set in question satisfies the above requirement of effective linearity, as is often the case when observing a limited range of the full functional relationship. Last, even when data are not effectively linear, they can still be included in MLR analysis by first transforming the data to approximate linearity with a simple function (i.e., log, arcsin, etc.).

Statistical relationships were tested for over three dozen variables using no a priori assumptions. These variables included temperature, salinity, and density; mixed layer depths; daily surface irradiance and irradiance penetration depths; NO_3, NO_2, NH_4, PO_4, SiO_4, and Si/N disappearance ratios; primary production; chlorophyll-specific production; chlorophyll; HPLC pigment data and calculated diatom-associated chlorophyll; bacteria and zooplankton abundance; biogenic silica; suspended particulate organic carbon (POC), particulate organic nitrogen (PON), particulate organic phosphorus (POP), and particulate C/N; trap fluxes of POC, PON, silica, C/N, and Si/N; ^{234}Th export fluxes; latitude; longitude; Southern Oscillation Index (SOI); and others. Most water properties were tested both as integrated values to various depths and also as surface values.

4. Results

For the nine cruises to the tropical Pacific region surveyed here, measured f ratios were not related to any other property or combination of properties. The 114 measured areal f ratios ranged from 0.01 to 0.46 and have a mean of 0.16 ± 0.08 (±50%). Plots of f ratios (Figure 2) show neither a hyperbolic relationship with respect to either total primary production or nitrate inventory as proposed by *Eppley and Peterson* [1979] and *Platt and Harrison* [1985], respectively, for other regions of the world nor a linear relationship with respect to temperature, as suggested by *Laws et al.* [2000] . In addition, f ratios measured during El Niño conditions (mean of 0.16 ± 0.06 with a range of 0.05–0.30, n = 43) were

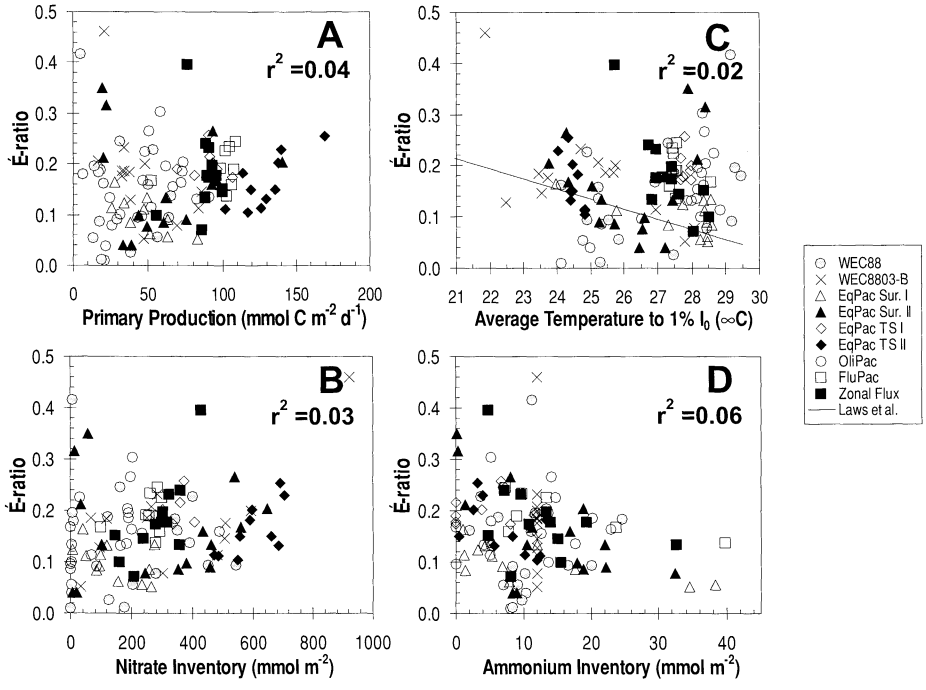

Figure 2. Scatterplots showing measured areal f ratios in the tropical Pacific as a function of (a) measured primary production rates, (b) nitrate inventories, (c) average euphotic zone temperature, and (d) ammonium inventories. The global temperature-NP relationship presented by *Laws et al.* [2000] is shown for comparison with data in Figure 2c; the residual sum of squares for this relationship is nearly twice that of the null hypothesis that the slope is zero and intercept is equal to the mean f ratio. All f ratios presented in this paper are calculated as the ratio of measured areal new production rates to primary production rates, both integrated to 1.0% E_0, multiplied by a molar C/N of 6.6.

Table 2. Simple Correlation Coefficients r for Variable Pairs That Are Most Significant to Multiple Linear Regression (MLR) Results[a]

	n	f Ratio	New Production	Primary Production	Chlorophyll	Ammonia	Nitrate	Temperature	Irradiance	Diatom Chlorophyll
f ratio	101	1.00								
New Production	105	0.55[b]	1.00							
Primary Production	103	0.19	0.86[b]	1.00						
Chlorophyll inventory	107	0.17	0.74[b]	0.81[b]	1.00					
Ammonia inventory	108	−0.24[c]	−0.08	0.08	0.09	1.00				
Nitrate inventory	108	0.17	0.69[b]	0.76[b]	0.80[b]	0.16	1.00			
Temperature average	108	0.13	−0.29[d]	−0.31[d]	−0.35[b]	0.11	−0.57[b]	1.00		
Daily surface irradiance	39	0.41[c]	0.56[b]	0.61[b]	0.27	0.14	0.31	0.05	1.00	
Diatom chlorophyll	46	0.32	0.79[b]	0.74[b]	0.82[b]	0.04	0.76[b]	−0.76[b]	0.35	1.00

[a] The square of presented values r^2 gives the fraction of the variability in one variable that can be explained by the other. Data from WEC8803-B are omitted from the calculation of these values for direct comparison to MLR partial correlation coefficients in Table 3.

[b] Here $p < 0.0005$.

[c] Here $p < 0.05$.

[d] Here $p < 0.005$.

Table 3. Multiple Linear Regression Equations and Statistics for New Production (NP) as a Function of Primary Production (PP) or Chlorophyll Inventory (Chl), Ammonium Inventory A, Nitrate Inventory N, and Temperature T[a]

MLR Equation	R^2	R^2*	SE	n	$\beta_0 \pm$ SE	$\beta_1 \pm$ SE, mmol C m^{-2} d^{-1} or mg Chl m^{-2}	$r_{Y1.234}$	$\beta_2 \pm$ SE, mmol m^{-2}	$r_{Y2.134}$	$\beta_3 \pm$ SE, mmol m^{-2}	$r_{Y3.124}$	$\beta_4 \pm$ SE, °C	$r_{Y4.123}$
$NP = \beta_0 + \beta_1 PP + \beta_2 A + \beta_3 N + \beta_4 T$	0.790	0.781	0.58	100	−1.6 ± 1.4	0.026 ± 0.003[b]	0.72	−0.027 ± 0.007[b]	−0.36	0.0012 ± 0.0006[c]	0.21	0.050 ± 0.049	0.10
$NP = \beta_0 + \beta_1 Chl + \beta_2 A + \beta_3 N + \beta_4 T$	0.625	0.610	0.75	104	−3.8 ± 1.7[b]	0.096 ± 0.022[b]	0.40	−0.028 ± 0.009[d]	−0.29	0.0029 ± 0.0008[b]	0.34	0.117 ± 0.062[c]	0.18

[a] Units of NP are in mmol N m^{-2} d^{-1}. All inventories are integrated to 1.0% E_0 depths, except PP, which is to 0.1% E_0 depths. T is averaged to 1.0% E_0 depths. SE is the standard error of new production estimate and of regression coefficients β. Here $r_{Y1.234}$, $r_{Y2.134}$, $r_{Y3.124}$, and $r_{Y4.123}$ denote partial correlation coefficients.

[b] Here $p < 0.0005$.

[c] Here $p < 0.05$.

[d] Here $p < 0.005$.

indistinguishable from those measured during periods of normal or enhanced upwelling (mean of 0.16 ± 0.09, n = 71) (Figure 2). In fact, f ratios were not strongly related, linearly or otherwise, to any of the parameters examined (other than those involving new production itself) (Table 2). Likewise, MLR analysis showed that no combination of variables could explain variability in f ratios found during the nine cruises surveyed here. No obvious, simple function of observed properties can be used to describe measured f ratios in the tropical Pacific.

New production (NP) itself was highly correlated with a large number of other biogeochemical and biological water properties (Table 2). Not surprisingly, primary production (PP) topped the list (r^2 = 0.74), followed by diatom-associated chlorophyll inventory (Chl_{dia}) (r^2 = 0.62, n = 46 only measured during EqPac), total chlorophyll inventory (r^2 = 0.55), nitrate inventory (r^2 = 0.48), POC inventory (r^2 = 0.39), degrees latitude (r^2 = 0.34), phosphate inventory (r^2 = 0.22), and silicate inventory (r^2 = 0.20). Interpretations for most of these simple, bivariate correlations are severely complicated by the high covariance between them (Table 2), such as that observed between PP and chlorophyll (r^2 = 0.66), PP and nitrate (r^2 = 0.58), PP and POC (r^2 = 0.58), PP and latitude (r^2 = 0.50), Chl and nitrate (r^2 = 0.64), Chl and Chl_{dia} (r^2 = 0.67), Chl_{dia} and temperature (r^2 = 0.57), nitrate and phosphate (r^2 = 0.42), nitrate and silicate (r^2 = 0.35), nitrate and temperature (r^2 = 0.33), etc. One way to aid interpretation of cross-correlated variables, which is common in uncontrolled systems where many parameters vary simultaneously, is to employ multivariate statistical methods.

Multiple linear regressions for new production were constructed from all possible combinations of measured parameters and were ranked according to their adjusted coefficients of determination R^{2*}. For the complete data set of 100 or more stations, depth-integrated PP, euphotic zone inventories of ammonium and nitrate, and depth-averaged euphotic zone temperature formed the most significant combination of independent variables from more than three dozen tested (Table 3). (WEC8803-B was excluded from this MLR because ammonium data were not available.) The multiple coefficient of determination R^2 indicated that 79% of variability in new production could be explained by changes in these four variables alone. Total PP gives the largest contribution to the regression fit, followed by ammonium inventory, nitrate, and finally, temperature, as evidenced from their partial correlation coefficients (i.e., $r_{Y1.234}$). Chlorophyll inventory offered a reasonable substitute for PP (Table 3) with the resulting MLR (R^2 = 0.63) receiving similar contributions from nitrate, chlorophyll, and ammonium. All other variables, such as latitude, POC, phosphate, silicate, and silicate-to-nitrate disappearance ratios, degraded the MLR fit (i.e., R^{2*} decreased) when added to either set of four variables, mostly due to too much covariance with one of the other primary variables. Likewise, for the entire data set, no other variable could explain enough of the remaining variance in NP on its own to replace any of the first four parameters in either of the two MLRs of Table 3.

The square of the partial correlation coefficient for a MLR variable, such as $r_{Y1.234}^2$ for PP, represents, for example, the fraction of the residual that is explained by adding PP to an MLR already including ammonium, nitrate, and temperature. The term $r_{Y1.234}^2$ can only be high if the variability in PP explains some of the variability in NP that has not been explained by ammonium, nitrate, and temperature. Thus comparison of MLR partial correlation coefficients (Table 3) with simple correlation coefficients (Table 2) can highlight previously hidden relationships between MLR variables and new production that were obscured by covariance. For example, the temperature-NP correlation reverses sign in the MLR because the inclusion of nitrate already accounts for upwelling-stimulated effects on NP. Similarly, the strong ammonium-NP relationship results from ammonium explaining much of what PP cannot, yet from a bivariate perspective this relationship is completely hidden in the noise of more dominant variables.

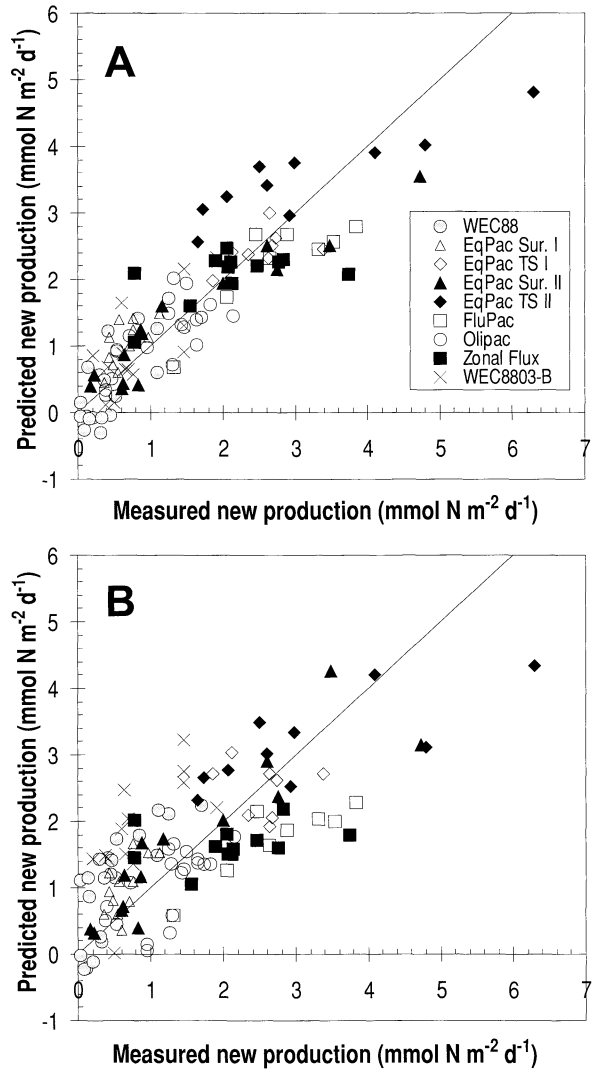

Figure 3. New production predicted from multiple linear regressions (MLR) of (a) primary production, ammonia and nitrate inventories, and temperature or (b) chlorophyll, ammonia and nitrate inventories, and temperature plotted versus measured new production for eight cruises in the equatorial Pacific. The line represents a perfect 1:1 fit. A ninth cruise, WEC8803-B, was not used in the MLR because ammonia data were not available but was plotted using MLR equations by assuming a constant 12 mmol NH_4 m^{-2}. Open symbols represent cruises during El Niño conditions.

Plots of measured new production versus values predicted by the regression equations allowed inspection of the statistical fit in two dimensions (Figure 3). All individual cruises exhibited both overprediction and underprediction of measured values, and MLR residuals closely followed a normal distribution ($p < 0.005$). Much of the underprediction of highest values is a direct statistical consequence of MLR in the absence of a perfect fit (i.e., R^2 = slope of fit <1.0), and for NP > 4 mmol N m^{-2} d^{-1}, >50% of the residual can be accounted for by this. No stations measured during

these eight cruises that had complete data were excluded from the MLRs, yet no gross outliers were observed as defined by >3 standard residual units [*Neter et al.*, 1996]. The basic assumption of linearity inherent in MLR was also validated by this data set. Specifically, plots of standard residuals of the overall MLR as a function of each independent variable showed no curvature (Figure 4), indicating that primary production, chlorophyll, ammonium, nitrate, and temperature are all effectively linear with

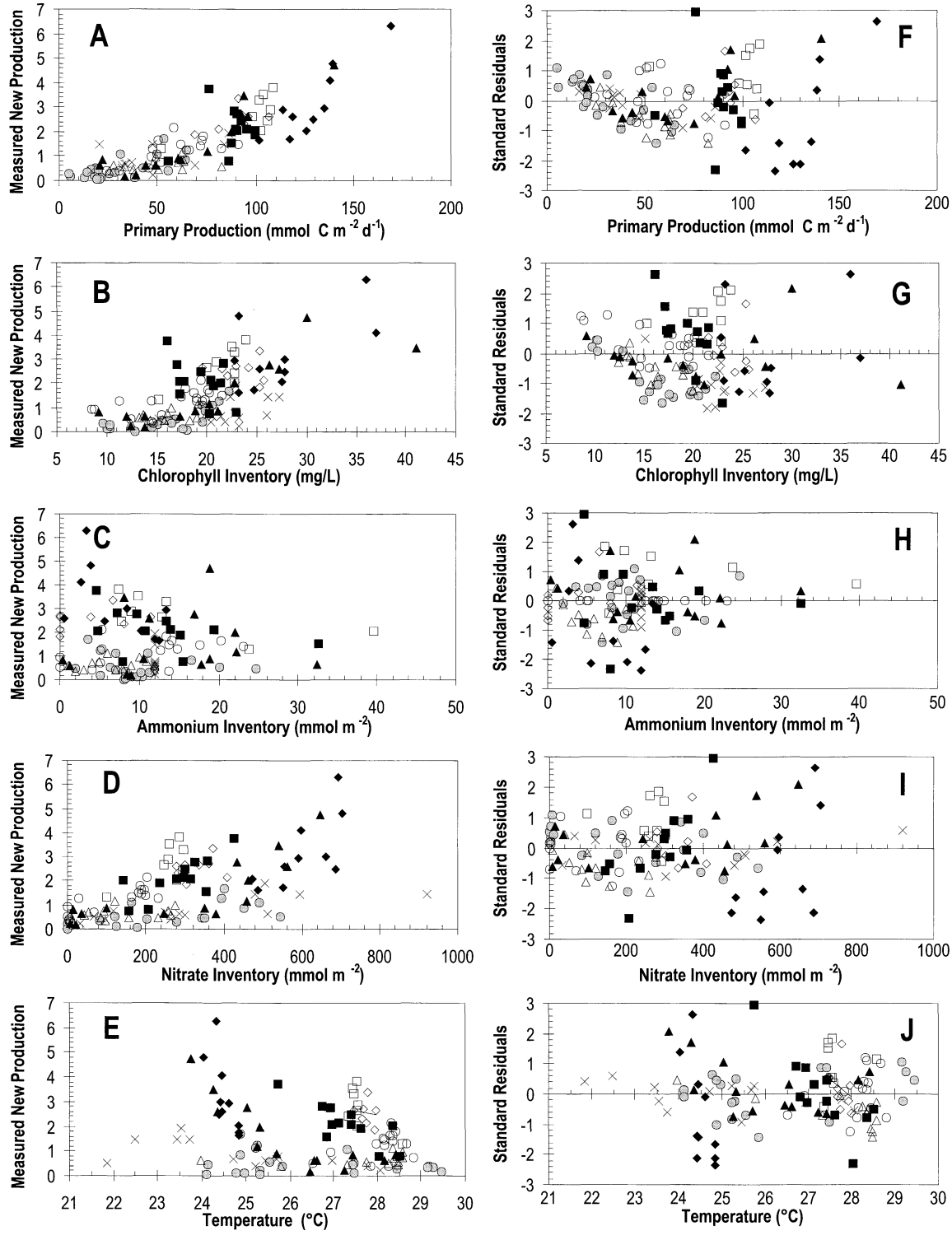

Figure 4. Scatterplots showing measured new production values for each cruise versus (a) measured primary production, (b) chlorophyll, (c) ammonia, (d) nitrate, and (e) temperature and (f–j) standard residuals of the MLR-predicted new production versus the same water properties. Standard residuals for all subplots except Figures 4b and 4g are those calculated from the first MLR in Table 3, whereas those for Figures 4b and 4g are from the second MLR. New production is given in units of mmol N m^{-2} d^{-1}.

respect to new production in this system and do not require transformation [*Neter et al.*, 1996]. Thus, while the fundamental responses of many biological functions are nonlinear, the observed response of new production to the MLR variables is best captured by linear functions. For the statistical analysis presented here, there is no justification to use anything but a linear relationship.

The final integration depths chosen for each variable in Tables 2 and 3 were those conferring the greatest partial correlation coefficients. Inventories of chlorophyll and diatom-chlorophyll integrated to 1% E_0 exhibited substantially higher significance than inventories integrated to 0.1% E_0, whereas the choice of integration or averaging depth made only slight and inconsistent differences for nitrate, ammonium, PP, and temperature. Surface and mixed layer values for these properties, despite sometimes having higher simple correlations to new production, actually degraded MLR fits. Last, water property profiles taken from hydrocasts nearest in time to the collection cast for new production (and thus most closely representing conditions within incubations) consistently gave better fits than station-averaged values.

The ability of this MLR method to predict new production for other data sets was demonstrated by cross validation, in which new production from each cruise was predicted from the MLR of the remaining seven. This procedure did not significantly degrade the fit, indicating that no single cruise was responsible for determining regression coefficients. MLR analysis for individual cruises confirmed that PP (or chlorophyll), ammonium and nitrate inventories, and temperature were consistently the most important variables for all cruises, although individual cruises often did not have enough stations or variability between stations to establish statistical significance for all four variables (A. K. Aufdenkampe et al., Biogeochemical and physical controls on new production in the tropical Pacific, submitted to *Deep-Sea Research, Part II*, 2000) (hereinafter referred to as Aufdenkampe et al., submitted manuscript, 2000). Equally encouraging was that the range given by the MLR slopes of the individual cruises and their associated standard errors (Aufdenkampe et al., submitted manuscript, 2000) generally overlapped the slopes of the overall regressions (Table 3). However, close inspection of these partial slopes along with scatterplots of each property versus standard residuals of the overall MLR (Figure 4) suggests that of the dominant variables, the slopes of nitrate with respect to NP exhibited the largest variability between cruises, followed by PP and then ammonium. These differences, which may be due to variability in unmeasured parameters or more complex processes, may explain some of the remaining MLR residual and cause some of the systematic prediction errors observed for certain cruises (i.e., EqPac Time Series II and Zonal Flux).

MLR analysis for subsets of stations allowed tests of larger sets of independent variables that were not measured at all stations or during all cruises. Daily incident surface irradiance was the one variable that when added to chlorophyll, ammonium, nitrate, and temperature, improved the MLR fit substantially for the 38 stations (EqPac Surveys I and II and Zonal Flux) with irradiance data (R^2 = 0.84 versus R^2 = 0.73). Special attention was paid to relationships involving silicate because of several recent studies suggesting the important role of silicate and diatoms in controlling new production [*Landry et al.*, 1997; *Dugdale and Wilkerson*, 1998]. MLR analyses of the subsets of stations having data for sediment trap silica fluxes and sediment trap silica-to-nitrogen flux ratios and biogenic silica inventories (Table 4) showed that none of these parameters exhibited stronger partial correlations to new production than did nitrate. This is consistent with findings for silicate inventories and silicate-to-nitrate disappearance ratios ($(SiO_4/NO_3)_{dis}$) within the full data set (Table 4). Thus silicate itself does not appear to exert a strong direct control on new production during typical conditions.

Table 4. Comparison of Partial Correlation Coefficients for Equivalent MLRs in Which Nitrate is Replaced by a Silicate Variable

Si variable	n	With Nitrate Partial r	With Si-Variable Partial r
SiO_4 inventory	85	0.172	0.059
$(SiO_4/NO_3)_{dis}$	85	0.172	0.089
Trap Si flux	30	0.307	0.192
Trap Si/N ratio	29	0.308	0.005
Biogenic Si inventory	22	0.285	0.267

To test the importance of diatoms directly, it is possible to calculate the chlorophyll contribution by diatoms from the detailed HPLC pigment data set collected only during the four EqPac cruises [*Bidigare and Ondrusek*, 1996]. For two of the four cruises, Survey II and Time Series II (which each sampled upwelling fronts associated with tropical instability waves), diatom-associated chlorophyll inventory was highly correlated with NP (r^2 = 0.93 and r^2 = 0.56, respectively, $p < 0.01$). Of all the variables, Chl_{dia} gave the highest simple correlation to NP observed during Survey II (for PP and Chl r^2 = 0.76 and r^2 = 0.67 with NP, respectively) but not during any of the other three cruises, where PP and other parameters showed stronger simple correlations to NP. However, because covariance among these three parameters was high during all cruises (Table 2), MLR analysis was again required to sort out which variables were the most important. For the entire EqPac data set (n = 45), addition of diatom chlorophyll as a fifth independent variable did improve the fit of the MLR relationship (R^{2*} = 0.84 versus R^{2*} = 0.79). Partial correlations coefficients were 0.54, 0.53, 0.46, 0.31, and 0.18 for ammonium, Chl_{dia}, PP, temperature, and nitrate, respectively, yet if either nitrate or temperature were removed from the MLR, primary production again dominated. Removal from the analysis of the five stations with new production exceeding 3.5 mmol N m^{-2} d^{-1} reduced diatom chlorophyll to a nonsignificant parameter, demonstrating that the importance of Chl_{dia} within the MLR is highly leveraged by the few stations that sampled upwelling fronts.

5. Discussion

This synthesis of $^{15}NO_3$-based new production data for the tropical Pacific demonstrates that f ratios in this region cannot be predicted as a simple function of observed water properties as has been suggested for other regions of the world [*Eppley and Peterson*, 1979; *Platt and Harrison*, 1985; *Laws et al.*, 2000]. Because of the very large dynamic range of depth-integrated f ratios observed in the tropical Pacific (Figure 2), using the mean f ratio to extrapolate new production will result in estimates having a standard error of ±50% with the possibility for underestimation or overestimation by more than a factor of 3. Clearly, for this region, another simple approach is needed to extend new production flux estimates to where and when it was not measured directly. Multiple linear regression analysis of published new production data seems to have provided just that tool.

A MLR of observed primary production, ammonium, nitrate, and temperature can predict measured new production values with a R^2 of 0.79 in a region exhibiting high variability for all these properties. This fit for such a broad set of data is especially impressive considering that six teams collected the data with little coordination of methods or intercalibration. This

finding demonstrates that these MLR results (the equations given in Table 3) have the potential to serve as a robust, objective tool to extrapolate new production to larger spatial and temporal scales within the tropical Pacific region. Estimates based on these MLR equations, with a standard error of 0.58 mmol N m^{-2} d^{-1} (Table 3), would have uncertainties ranging from ~10 to 50% at all but the lowest new production fluxes. In addition to reducing estimate errors (especially those of outliers), the MLR approach is more robust and adaptable to a wider range of conditions by explicitly accounting for the effects of several variables, many of which may be proxies for more complex processes. Discussion supporting this robustness of the MLR model follows.

MLR results in many ways support the intuitive concept behind the f ratio. The MLR partial slope with respect to primary production (Table 3), when multiplied by the Redfield C/N of 6.6, gives what is close to the mean f ratio (0.17) for the data set. Mathematically, this slope represents the asymptotic value of the ratio of new to primary production when the other three variables (ammonium, nitrate, and temperature) are held constant at their mean values. This can be seen by rearranging the first MLR equation from Table 3 into the form:

$$f\text{ratio} = 6.6\frac{\text{NP}}{\text{PP}} = 6.6\left(\beta_{\text{PP}} + \frac{\beta_A A + \beta_N N + \beta_T T + \beta_0}{\text{PP}}\right)$$

$$= \left(0.17 + \frac{-0.19A + 0.008N + 0.33T - 11}{\text{PP}}\right)$$

where A, N, and T represent ammonium, nitrate, and temperature and β_0 is the MLR intercept as in Table 3. Interestingly enough, the multiple linear regression equation actually results in the f ratio being a hyperbolic function of primary production (Figure 5a) similar to that proposed by *Eppley and Peterson* [1979]. The MLR equation goes a step further, however, by providing a means to evaluate how the ratio of new to primary production will change as water properties deviate from their mean values. As can be seen in Figure 5b, the range of possible f ratios that can be calculated from the rearranged MLR equation is quite large at low values of primary production (<50 mmol C m^{-2} d^{-1}), yet f ratios converge toward mean values as primary production increases. This modeled distribution is consistent with observations (Figure 2a), where the range of measured f ratios decreases as primary production increases. Thus, for the tropical Pacific the MLR approach offers a more viable alternative to f ratios as a simple means of estimating new production, and MLR results also confirm that f ratios are a complicated, nonlinear function of primary production and other variables during conditions typical of most oligotrophic and mesotropic environments.

The ability of these simple multiple linear equations to predict new production, which results from complex biological community interactions, is not as surprising as one might initially think. The fact that nitrate, ammonium, PP, or chlorophyll and temperature, without any a priori assumptions, were found to be the most significant field measurements explaining new production fits well with past findings. Positive relationships of new production to both chlorophyll and nitrate concentrations have been commonly observed [*Platt and Harrison*, 1985; *Wilkerson and Dugdale*, 1992; *Peña et al.*, 1992; *McCarthy et al.*, 1996], and elevated ammonium has been found sometimes to depress rates of new production [*Murray et al.*, 1989; *Harrison et al.*, 1987; *Dortch*, 1990; *Wheeler and Kokkinakis*, 1990]. However, these previous studies all found highly variable slopes between these properties and new production that previously could not be explained; neither PP, chlorophyll, ammonium, nor nitrate alone is sufficient to predict new production reliably. Our results demonstrate that the individual relationships of these variables with new production in the equatorial Pacific are, in fact, surprisingly consistent, once effects of the other variables are taken into account (Table 3).

The small but positive partial slope of temperature with respect to NP (+0.05 mmol N m^{-2} d^{-1} per °C) is perhaps the least intuitive of all the MLR results because of temperature's negative simple correlation to nitrate (Table 2). However, MLR removes the effects of this correlation to yield a NP-to-temperature partial slope that is certainly positive despite large uncertainty in its magnitude (Table 3). Temperature's effect on biochemical rates [*Eppley*, 1972; *White et al.*, 1991] is well known; however, the subsequent temperature effect on new production fluxes is due to complex interactions within the community. The pelagic food web model of *Laws et al.* [2000] explores these various effects by assuming a Q_{10} of 1.9 for autotrophic phytoplankton and heterotrophic bacteria and a Q_{10} of 2.7 for zooplankton. Their results suggest that at low rates of primary production similar to those found throughout the tropical Pacific, export production should increase slightly with increasing temperature, which is consistent with MLR results. However, in their model, f ratio exhibits a strongly negative relationship to temperature at higher primary production that is typical of coastal upwelling regions.

The success of MLR raises the question, Why should the relationship of NP to these sets of four variables be effectively linear and with a constant slope throughout the tropical Pacific? Biological processes generally exhibit nonlinear functionality with respect to controlling variables. For instance, nutrient and substrate uptake rates typically follow hyperbolic Michaelis-Menton saturation kinetics, and temperature's effect on biochemical rates is exponential. However, over a limited range these functions can often be reasonably approximated as linear, especially when considering errors found in real data. The sum of all these underlying nonlinear effects in a complex system can result in effectively linear relationships between variables. The relationship between f ratio and temperature that results from the pelagic food web model of *Laws et al.* [2000] is a case in point. Within the range of 10–30°C and 10–100 mg N m^{-3} d^{-1} primary production, their modeled relationship is effectively linear. Last and most importantly, the success of the MLR may be largely due to the principle variables acting as proxies for nonlinear or more complex processes. Ammonium is known to recycle in the upper water column

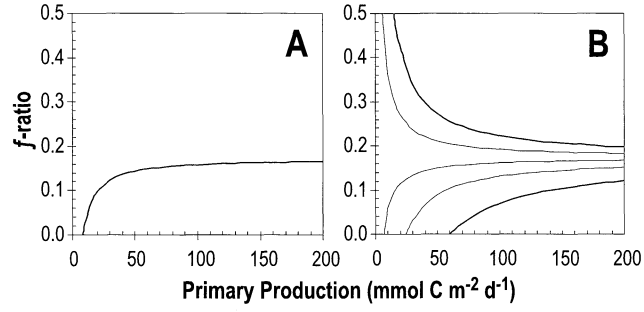

Figure 5. Plots of modeled f ratio as a function of total primary production, using the first MLR-derived equation from Table 3. Mean values of ammonium, nitrate, and temperature (10.8 mmol m^{-2}, 260 mmol m^{-2}, and 26.9°C, respectively) are used in Figure 5a. The full range of possible curves are shown in Figure 5b, where the top line is calculated from the minimum observed ammonium inventory (0 mmol m^{-2}) and maximum values of nitrate and temperature (705 mmol m^{-2} and 29.5°C), the bottom line is calculated from the maximum ammonium (39.6 mmol m^{-2}) and minimum nitrate and temperature (0 mmol m^{-2} and 21.9°C), and intermediate lines are calculated from intermediate values.

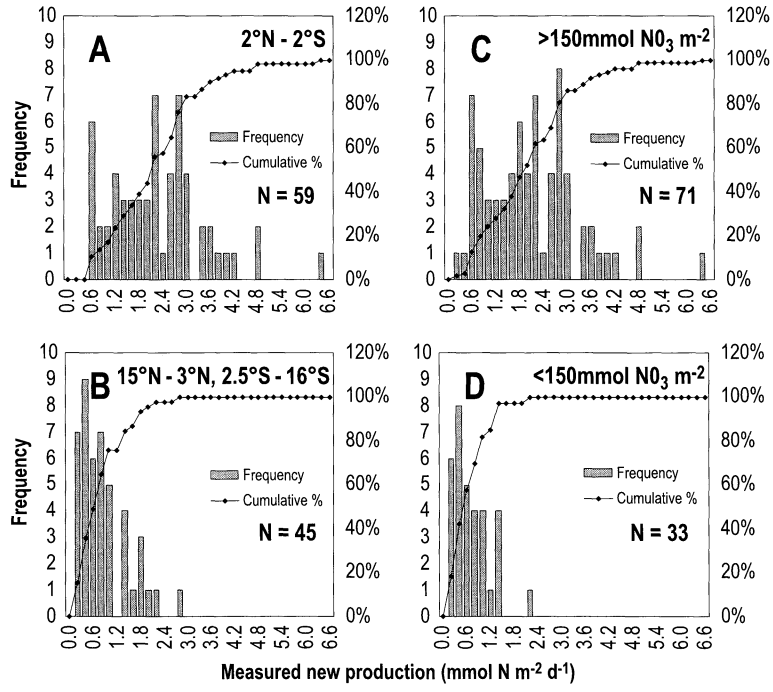

Figure 6. Histograms of new production measured (a) in equatorial upwelling regions defined by 2°N–2°S, (b) in off-equator regions from 15° to 3°N and 2.5° to 16°S, (c) during high-nutrient low-chlorophyll (HNLC) conditions defined by nitrate inventories >150 mmol N m^{-2} , and (d) during oligotrophic conditions where nitrate is <150 mmol N m^{-2} (corresponding to a mean 1.8 μ *M* nitrate over the average 1.0% E_0 depth of 82 m). Histograms of new production as sorted by the Southern Oscillation Index (SOI) for either the entire data set or only equatorial stations (2°N–2°S) exhibited NP distributions with even larger overlap than those shown here. The median SOI for stations in data set is −0.7.

with rates very similar to those of iron, and the principle source of new iron in the equatorial Pacific, water upwelled from the Equatorial Undercurrent, is also the principle source of nitrate to the system.

Another biogeochemical insight of this statistical analysis is that silicate was less of a control on NP than nitrate under the majority of conditions. Diatom-associated chlorophyll did indeed seem to be important, but only a few stations during uncommonly high NP dictated much of the NP-Chl_{dia} relationship. These findings are consistent with the conclusion of *Dunne et al.* [1999] that diatoms regulate new production fluxes only during highly dynamic, nonsteady state conditions, such as the passage of tropical instability waves, but that diatoms do not dominate new production during more common and less dynamic conditions. Knowledge of diatom abundance would certainly help improve MLR-based estimations of new production at its highest values. However, as stated previously, most of the underprediction of these high values is directly attributable to statistical consequences that all MLRs exhibit in the absence of a perfect fit. Therefore the lack of actual diatom abundance data for most studies is not critical to future efforts to estimate new production from MLR.

This synthesis and statistical analysis also demonstrates that the processes that control new production in the tropical Pacific are much more continuous and less discrete than generally acknowledged. In other words, the terms commonly used to describe the state of the Pacific Ocean (El Niño versus La Niña, oligotrophic versus mesotrophic, or subtropical gyre versus equatorial upwelling zone) seem to be inadequate at clearly delineating one state of new production processes from another. These binary, descriptive groupings simply exhibit too much overlap in their measured rates of new production (Figures 3 and 6) to be useful in explaining or predicting NP. For example, prior efforts to reconcile EqPac Time Series I new production of 1.9–3.4 mmol N m^{-2} d^{-1} (P. A. Wheeler, U.S. JGOFS home page at http://www1.whoi.edu/jgofs.html) with a single value of 0.5 mmol N m^{-2} d^{-1} measured only a few weeks earlier at the same location during EqPac Survey I [*McCarthy et al.*, 1996] were difficult at best using only descriptive, categorical explanations. This MLR analysis, however, explains such differences quite well by using a continuous, quantitative, multivariate representation of the state of the ocean with respect to potential new production.

The fact that even within time series much of the NP data can be explained by MLR suggests that the large variability in $^{15}NO_3$ uptake data for the tropical Pacific reflects the variability of the state of the ocean and not of the measurement methods. Thus it is no wonder that the very spatially and temporally localized estimates of new production derived from $^{15}NO_3$ measurements rarely match export production estimates, given the much longer and wider scales over which sediment traps [*Siegel and Deuser*, 1997] and ^{234}Th deficiency methods (24.1 day half life) integrate. Future work might focus on reconciling differences between new and export production estimates by tracking the properties of the water mass that is sampled by a trap or by sinking ^{234}Th and integrating daily new production estimated from MLR equations over the integration time of those other methods.

The most important finding of this study is that MLR results supply a tool with which new production can be more accurately integrated over larger temporal and spatial scales using measured, modeled, or remotely sensed biogeochemical data. Because the method is so fast and simple, the MLR equations could be used to estimate new production for most cruises and stations where it was not measured. These equations make use of data that can all be

analyzed within a few hours on a ship; thus this method could even help direct planning of station positioning in quasi-real time during a cruise. The second equation in Table 3 allows for direct estimation of NP with chlorophyll where PP data are not available, thus extending substantially the usefulness of this MLR method to stations where the *f* ratio approach first requires modeling primary productivity. To extend the MLR method a step further using remotely sensed data, one could potentially employ an approach similar to that of *Sathyendranath et al.* [1991], who translated satellite-derived sea surface temperature into estimates of nitrate and sea color into chlorophyll and primary productivity. Such algorithms exist for many regions of the world [*Garside and Garside*, 1995; *Morel et al.*, 1996]; however, new production would then be estimated using MLR equations instead of the highly uncertain nitrate to *f* ratio relationship as done by *Sathyendranath et al.* [1991]. There are obstacles to an MLR-based approach using remotely acquired data, but solutions may not be far off. Whereas satellite methods are limited to describing the mixed layer, ocean mooring networks currently monitor vertical temperature, salinity, irradiance, chlorophyll, and nitrate structure [*Kessler and McPhaden*, 1995; *Chavez et al.*, 1997]. Ammonia remains the one important parameter requiring ship-based sampling, and this paper serves as a call for development of mooring-based ammonia analyses. Once accomplished, real-time monitoring of new production in the world's oceans using MLR-based estimations from merged satellite, mooring and ship data, could become a straightforward procedure.

6. Conclusions

The ability to estimate new production in the tropical Pacific with a single MLR of a few commonly measured properties highlights a certain uniformity of controlling processes despite the immense heterogeneity of inventories and fluxes in the upper ocean of this region. While only giving purely statistical results with no explicit cause-and-effect relationships, the MLR approach removes many of the typical spurious correlations that obscure more important underlying relationships. MLR results agree well with findings from process studies (i.e., inhibition by ammonium) and yield clues as to the relative importance of biogeochemical properties (i.e., nitrate over silicate) in controlling new production. The power of multivariate statistics to sort out relationships from observational data with many simultaneously varying variables has been a largely underused tool in chemical and biological oceanography. Yet despite these insights this MLR analysis does not directly address fluxes of nutrients into the euphotic zone, which are the ultimate biogeochemical controls on new production.

Perhaps most importantly, the results from this study provide a robust, fast, and useful statistical method of estimating new production fluxes from more commonly measured water column properties. Accurately estimating new and export production in the tropical Pacific over highly variable conditions remains of especial importance to future efforts to monitor and manage the global carbon cycle precisely because of its HNLC status. In HNLC regions the extent to which uptake of upwelled nutrients is delayed directly determines the degree to which sea-to-air carbon dioxide fluxes are enhanced [*Dugdale et al.*, 1992; *Kurz and Maier-Reimer*, 1993]. Routine application of MLR-based models to merged ship, mooring, and satellite data has potential to offer real-time monitoring of new production in the world's oceans.

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