Origin and maintenance of a high nitrate condition in the equatorial Pacific

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(Received 24 January 1995; in revised form 26 January 1996; accepted 4 February 1996)

Abstract—The physical and biological causes for the equatorial nutrient anomaly were investigated using an ecosystem model embedded within an ocean general circulation model to determine the nitrate budget for the equatorial Pacific Ocean. In the 140°W region the effects of mixing on nitrate concentration were small compared to the effects of advection; upwelling and zonal transport to the east in the Equatorial Undercurrent were the major processes in the nitrate budget. At 140°W on the equator annual $J_{\text{NO}_3}$, the total net physical supply of nitrate to the euphotic layer, was 3.76 mmol m$^{-2}$ day$^{-1}$; the vertical integrated (0–120 m) new production calculated from the ecosystem model was 3.36 mmol m$^{-2}$ day$^{-1}$ or, in carbon units, 22.26 mmol C m$^{-2}$ day$^{-1}$. The vertical supply of nitrate ($-\omega \text{NO}_3/\partial z$) due to the upwelling is controlled by two factors, the vertical velocity and vertical gradient of nitrate concentration. The vertical velocity reaches the maximum during climatological fall, but the vertical gradient of nitrate is weaker in the fall. Therefore, the vertical supply of nitrate is smaller than in spring.

To investigate the role of physiological limitation of phytoplankton photosynthesis and specific growth rate on the maintenance of the high nutrient–low chlorophyll (HNLC) condition, a model experiment was performed that included, unchanged from previous model runs, the physical conditions and density-dependent grazing function, but greatly reduced physiological limitations by increasing $\alpha$ (initial slope of $P-I$ curve) and $P_{\text{max}}$ (maximum specific growth rate) values. When this was done, vertical integrated primary production at 140°W on the equator doubled (from 83 to 166 mmol C m$^{-2}$ day$^{-1}$), but the zooplankton grazing on the phytoplankton also doubled (from 75 to 150 mmol C m$^{-2}$ day$^{-1}$). Zooplankton biomass doubled, but there was only a slight increase in phytoplankton biomass; no phytoplankton bloom formed in this model experiment. With potential physiological limitations of phytoplankton rates greatly reduced, the characteristic equatorial plume of unused surface layer nitrate still persisted; but the nitrate-rich plume was smaller in horizontal extent and the maximum concentration was reduced by half from observed concentrations. While the reduction in the extent of the nitrate-rich plume indicates that physiological limitation plays a significant role in the maintenance of the nutrient anomaly, its persistence demonstrates that physical processes and grazing also are involved. Copyright © 1996 Elsevier Science Ltd

1. INTRODUCTION

Equatorial waters of the central and eastern Pacific ocean are unusually cool and nutrient-rich relative to tropical waters just north and south of the equatorial zone. That this tropical anomaly is set up by equatorial upwelling was recognized by early studies in the region (Graham, 1941; Cromwell, 1953; Montgomery, 1954; Sette, 1955). After the basic physical and chemical coupling was explained, a second anomalous characteristic of the equatorial

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system became apparent: the persistence of unused inorganic plant nutrients despite abundant light and the absence of deep mixing. The mixed layer is always an order of magnitude less than the critical depth as defined by Sverdrup (1953). The persistence of anomalous high-nutrient concentrations and low concentrations of phytoplankton biomass comprise the equatorial enigma, a puzzle that attracted the attention of a second generation of equatorial oceanographers (Barber and Ryther, 1969; Thomas, 1972; Walsh, 1976). Efforts to explain the equatorial enigma were based on sparse data and, for the most part, were not very convincing. Recently, three aspects of equatorial studies have advanced: (1) work in the region has collected a wealth of physical, chemical and biological observations (Murray et al., 1994, 1995); (2) successful modeling of equatorial physics has been developed (Philander et al., 1987; Philander and Seigel, 1985); and (3) ecosystem models embedded within ocean general circulation models have been developed (Sarmiento et al., 1993; Chai, 1995; Toggweiler and Carson, 1995). These advances set the stage for a new effort to understand the origin and maintenance of the persistently high-nutrient conditions of the equatorial Pacific Ocean. This paper reports an effort to describe and understand equatorial nutrient conditions using a relatively simple ecosystem model embedded within a complex ocean general circulation model.

2. MODEL DESCRIPTION

2.1. Physical model

This analysis used the Modular Ocean Model (MOM) (Pacanowski et al., 1991), which is a current version of the Geophysical Fluid Dynamics Laboratory (GFDL) Ocean General Circulation Model (OGCM) developed by Bryan (1969) and Cox (1984). The MOM was modified to focus on the tropical Pacific Ocean in a manner similar to that implemented by Philander et al. (1987); the model spatial domain was from 50°N to 40°S and from 80°W to 130°E. Meridional resolution was 1/3° between 10°N and 10°S, and the grid spacing increased gradually poleward out of this region; longitudinal resolution was 1° over the entire domain. There were 27 levels in the vertical with 17 levels in the upper 300 m, providing a resolution of 10 m within the upper 120 m. Realistic topography was interpolated to the nearest model level. The inertial-gravity waves are eliminated by a semi-implicit scheme of the Coriolis force, where the Coriolis force is evaluated at the future time step. The time step in the model is 1 h. The explicit horizontal eddy diffusivity coefficient was 10^7 cm^2 s^{-1}. Above the background value of 0.01 cm^2 s^{-1}, the vertical eddy diffusivity coefficient was Richardson number-dependent according to the format described by Pacanowski and Philander (1981).

The model was initialized with January climatological temperature and salinity (Levitus, 1982) at zero current velocities. To study seasonal variation, we forced the model with the Comprehensive Ocean Atmosphere Data Set (COADS) monthly wind and air temperature (Slutz et al., 1985; Oort et al., 1987). The climatological monthly mean wind velocities and air temperature were averaged over the period of 1950–1979. The drag coefficient was assigned a value of 1.4 x 10^{-3} in the surface wind-stress calculation. The heat flux calculation was similar to that used by Philander et al. (1987). The surface salinity in the model was restored to the observed climatological monthly mean salinity (Levitus, 1982). The boundaries at 40°S and 50°N were closed walls, and water was forced to flow along, not through them. A decay term $\kappa (T^* - T)$ was added to the temperature equation [$\kappa (S^* - S)$ for the salinity equation], which restored it to the observed temperature $T^*$ (salinity $S^*$) field at
the two closed walls. The value $\kappa$ varies smoothly from 0.5 day$^{-1}$ at the walls to zero at 5° away them. After several years of integration, or "spin-up", the model achieved a quasi-equilibrium state in the upper ocean. The five ecosystem balance equations, given in Section 2.2, were solved simultaneously with the physical model.

2.2. Biological model

The biological model consisted of five compartments describing phytoplankton (P), zooplankton (Z), non-living particulate organic nitrogen (D), and two forms of dissolved inorganic nitrogen: nitrate (NO$_3$) and ammonium (NH$_4$). Figure 1 depicts the inter-compartment flows of the ecosystem, and five equations describing each flow all take the form:

$$\frac{\partial C_i}{\partial t} = \text{PHYSICAL} (C_i) + \text{BIOLOGY} (C_i); \ i = 1, ..., 5.$$  \hspace{1cm} (1)

(For example, $C_1 = \text{NO}_3$, $C_2 = \text{NH}_4$, and so on.) The term PHYSICAL ($C_i$) represents the concentration change due to physical processes, including advection and diffusion:

$$\text{PHYSICAL} (C_i) \equiv -u \frac{\partial C_i}{\partial x} - v \frac{\partial C_i}{\partial y} - w \frac{\partial C_i}{\partial z} + \frac{\partial}{\partial x} \left( K_h \frac{\partial C_i}{\partial x} \right) + \frac{\partial}{\partial y} \left( K_h \frac{\partial C_i}{\partial y} \right) + \frac{\partial}{\partial z} \left( K_v \frac{\partial C_i}{\partial z} \right)$$ \hspace{1cm} (2)

The $u$, $v$ and $w$ here are the velocity field. The $K_h$ and $K_v$ are the horizontal and vertical diffusion coefficients. The value of $\delta p = 1$ except when the convection adjustment occurs in which $\delta p = 0$. The term BIOLOGY ($C_i$) represents biological sources and sinks for the concentration field. In the euphotic zone (the upper 120 m), the biological terms, BIOLOGY ($C_i$), are:

![Diagram of the upper-ocean ecosystem model. See text of Section 2.2 for a description of terms, and Table 1 for values of the parameters.](image-url)

Fig. 1. A diagram of the upper-ocean ecosystem model. See text of Section 2.2 for a description of terms, and Table 1 for values of the parameters.
\[ \text{BIOLOGY (NO}_3\text{)} = - \frac{\text{NP}}{\text{new production}} \]

\[ \text{BIOLOGY (NH}_4\text{)} = - \frac{\text{RP}}{\text{reg. production}} + \frac{\mu Z}{\text{NH}_4 \text{ regeneration}} \]

\[ \text{BIOLOGY (P)} = + \left( \frac{\text{NP} + \text{RP}}{\text{total production}} - \frac{G_1}{\text{grazing}} - \frac{\partial}{\partial z}(w_1 P) - \frac{m_1 P}{\text{mortality}} \right) \]

\[ \text{BIOLOGY (Z)} = + \gamma \left( \frac{G_1 + G_2}{\text{net grazing}} - \frac{\mu Z}{\text{NH}_4 \text{ regeneration}} - \frac{\partial}{\partial z}(w_2 Z) - \frac{m_2 Z}{\text{mortality}} \right) \]

\[ \text{BIOLOGY (D)} = + \left( 1 - \gamma \right) \left( \frac{G_1 + G_2}{\text{unassimilated grazing}} - \frac{G_2}{\text{grazing}} - \frac{\partial}{\partial z}(w_3 D) + \frac{m_1 P}{\text{mortality}} \right) \]

The dimensionless parameter \( \gamma \) is assimilation efficiency, zooplankton excretion rate to ammonium \( \mu \) (day\(^{-1}\)), sinking velocities \( w_1 \) (m day\(^{-1}\)), \( w_2 \) (m day\(^{-1}\)), \( w_3 \) (m day\(^{-1}\)), and mortality rate \( m_1 \) (day\(^{-1}\)), \( m_2 \) (day\(^{-1}\)) are specified in Table 1.

Growth functions were written as follows:

\[ \text{new production : NP} = P_{\text{max}} \frac{\text{NO}_3}{K_{\text{NO}_3} + \text{NO}_3} e^{-\psi \text{NH}_4} \frac{1 - e^{-\alpha P}}{\text{light regulation}} \]

\[ \text{reg. production : RP} = P_{\text{max}} \frac{\text{NH}_4}{K_{\text{NH}_4} + \text{NH}_4} \frac{1 - e^{-\alpha P}}{\text{light regulation}} \]

The parameter \( P_{\text{max}} \) represents the maximum specific growth rate when nitrogen and light are saturated for growth. Conceptually, \( P_{\text{max}} \) may be regulated by other factors not included explicitly in the model (light, nitrate and ammonia). We can explore the potential effects of these implicit limiting agents by changing \( P_{\text{max}} \) directly. It must be kept in mind that the \( P_{\text{max}} \) and \( \alpha \) terms in the model are not equivalent to the \( P_{\text{max}} \) and \( \alpha \) parameters used to describe the chlorophyll-normalized light response curve because changes in the N:chlorophyll ratio affect chlorophyll-normalized and N-normalized parameters differently.

Grazing functions were written as follows:

\[ G_1 = G_{\text{max}} \frac{\xi_1 P}{K_{\text{gr}} + \xi_1 P + \xi_2 D} \frac{P}{\text{Pave}} Z \]

\[ G_2 = G_{\text{max}} \frac{\xi_2 D}{K_{\text{gr}} + \xi_1 P + \xi_2 D} \frac{D}{\text{Dave}} Z \]
Table 1. Biological model parameters

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Symbol</th>
<th>Value</th>
<th>Unit</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum specific growth rate</td>
<td>$P_{\text{max}}$</td>
<td>2.0</td>
<td>day$^{-1}$</td>
<td>Barber and Chavez (1991); Lindley, personal communication</td>
</tr>
<tr>
<td>Initial slope of $P-I$ curve</td>
<td>$\alpha$</td>
<td>0.1</td>
<td>day$^{-1}$ (W m$^{-2}$)$^{-1}$</td>
<td>Evans and Parslow (1985); Lindley, personal communication</td>
</tr>
<tr>
<td>Ammonium inhibition parameter</td>
<td>$\psi$</td>
<td>6.0</td>
<td>(mmol m$^{-3}$)$^{-1}$</td>
<td>Hoffmann and Ambler (1988)</td>
</tr>
<tr>
<td>Light attenuation due to water</td>
<td>$k_1$</td>
<td>0.046</td>
<td>m$^{-1}$</td>
<td>Evans and Parslow (1985); Fasham et al. (1990)</td>
</tr>
<tr>
<td>Light attenuation by phytoplankton</td>
<td>$k_2$</td>
<td>0.03</td>
<td>m$^{-1}$ (mmol m$^{-3}$)$^{-1}$</td>
<td>Evans and Parslow (1985); Fasham et al. (1990)</td>
</tr>
<tr>
<td>Phytoplankton specific mortality rate</td>
<td>$m_1$</td>
<td>0.05</td>
<td>day$^{-1}$</td>
<td>Fasham (1995)</td>
</tr>
<tr>
<td>Phytoplankton sinking speed</td>
<td>$w_1$</td>
<td>1.0</td>
<td>m day$^{-1}$</td>
<td>Jamart et al. (1977, 1979)</td>
</tr>
<tr>
<td>Half-saturation for nitrate uptake</td>
<td>$K_{\text{NO}_3}$</td>
<td>0.25</td>
<td>mmol m$^{-3}$</td>
<td>Eppl ey et al. (1969)</td>
</tr>
<tr>
<td>Half-saturation for ammonium uptake</td>
<td>$K_{\text{NH}_4}$</td>
<td>0.05</td>
<td>mmol m$^{-3}$</td>
<td>Fasham (1995)</td>
</tr>
<tr>
<td>Averaged surface noonlight irradiance</td>
<td>$I_{0,\text{soonn}}$</td>
<td>350</td>
<td>W m$^{-2}$</td>
<td>Foley (personal communication)</td>
</tr>
<tr>
<td>Zooplankton maximum growth rate</td>
<td>$G_{\text{max}}$</td>
<td>1.0</td>
<td>day$^{-1}$</td>
<td>Paffenhofer and Harris (1976); Landry et al. (1995)</td>
</tr>
<tr>
<td>Assimilation efficiency</td>
<td>$\gamma$</td>
<td>0.75</td>
<td></td>
<td>Fasham (1995)</td>
</tr>
<tr>
<td>Zooplankton excretion rate to ammonium</td>
<td>$\mu$</td>
<td>0.3</td>
<td>day$^{-1}$</td>
<td>Fasham (1995)</td>
</tr>
<tr>
<td>Zooplankton sinking speed</td>
<td>$w_2$</td>
<td>1.0</td>
<td>m day$^{-1}$</td>
<td>Jamart et al. (1977, 1979)</td>
</tr>
<tr>
<td>Zooplankton specific mortality rate</td>
<td>$m_2$</td>
<td>0.05</td>
<td>day$^{-1}$</td>
<td>Fasham (1995)</td>
</tr>
<tr>
<td>Half-saturation for zooplankton ingestion</td>
<td>$K_{gr}$</td>
<td>0.25</td>
<td>mmol m$^{-3}$</td>
<td>Sarmiento et al. (1993)</td>
</tr>
<tr>
<td>Grazing preference for phytoplankton</td>
<td>$\rho_1$</td>
<td>0.75</td>
<td></td>
<td>Fasham et al. (1990)</td>
</tr>
<tr>
<td>Grazing preference for detritus</td>
<td>$\rho_2$</td>
<td>0.25</td>
<td></td>
<td>Fasham et al. (1990)</td>
</tr>
<tr>
<td>Detritus sinking speed</td>
<td>$w_3$</td>
<td>10.0</td>
<td>m day$^{-1}$</td>
<td>Sarmiento et al. (1993)</td>
</tr>
<tr>
<td>Aphotic zone ammonium regeneration rate</td>
<td>$\beta$</td>
<td>0.25</td>
<td>day$^{-1}$</td>
<td>Sarmiento et al. (1993)</td>
</tr>
<tr>
<td>Aphotic zone detritus flux decay exponent</td>
<td>$\delta$</td>
<td>0.858</td>
<td></td>
<td>Martin et al. (1987)</td>
</tr>
</tbody>
</table>

Note: in most cases, a wide range of parameter values is reported in the literature. We have used an apparently reasonable value from within the range.

where $\zeta_1$ and $\zeta_2$ are preferences for a given food type, and defined as following:

$$\zeta_1 = \frac{\rho_1 P}{\rho_1 P + \rho_2 D}$$

$$\zeta_2 = \frac{\rho_2 P}{\rho_1 P + \rho_2 D}.$$  \(11\)

The values for $\rho_1$ and $\rho_2$ are given in Table 1.  $P_{\text{ave}}$ and $D_{\text{ave}}$ are depth-averaged (within the euphotic zone) phytoplankton and detritus concentration, which are defined as:

$$P_{\text{ave}} = \frac{1}{z'} \int_{-z'}^{0} P \, dz$$

$$D_{\text{ave}} = \frac{1}{z'} \int_{-z'}^{0} D \, dz.$$  \(12\)
By modifying the grazing functions with terms \( P/P_{ave} \) and \( D/D_{ave} \), we found that the predator–prey oscillation could be reduced significantly in the model. The second-order grazing function also was suggested by Steele and Henderson (1992). The \( z' \) is the depth of the euphotic zone, and is set to 120 m in the model. \( I \) is the irradiance, and is given by:

\[
I(z, t) = I_0(t) e^{-k_1 z - k_2 \int_0^z P \, dz},
\]

where \( k_1 \) is the attenuation coefficient due to water, and \( k_2 \) is the self-shading parameter due to the phytoplankton. Values for \( k_1 \) and \( k_2 \) are given in Table 1. \( I_0(t) \) is the surface irradiance, and has the form during a 24-h period:

\[
I_0(t) = I_{noon} \sin \left( \frac{t - 6}{12} \pi \right) \quad \text{during day (6 a.m. – 6 p.m.)}
\]

\[
= 0 \quad \text{during night (6 p.m. – 6 a.m.).}
\]

\( I_{noon} \) is the annual mean noontime averaged surface irradiance for the equatorial Pacific, and the value is given in Table 1.

Below the euphotic zone, the biological terms are:

\[
\text{BIOLOGY (NO}_3\text{)} = + \frac{\beta \text{NH}_4}{\text{NO}_3 \text{ regeneration}}
\]

\[
\text{BIOLOGY (NH}_4\text{)} = + \beta (P + Z) \left( - \frac{\partial F(z)}{\partial z} \right) - \frac{\beta \text{NH}_4}{\text{NH}_4 \text{ regeneration}}
\]

\[
\text{BIOLOGY (P)} = - \frac{\beta P}{\text{NH}_4 \text{ regeneration}}
\]

\[
\text{BIOLOGY (Z)} = - \frac{\beta Z}{\text{NH}_4 \text{ regeneration}}
\]

\[
\text{BIOLOGY (D)} = 0 \quad \text{no biological processes}
\]

\( F(z) \) is the downward flux of particulate nitrogen in the form of the sum of sinking phytoplankton (P), zooplankton (Z) and detritus (D). Below the euphotic zone, particulate nitrogen between two layers in the model was converted to increase ammonium concentration. \( F(z) \) is an empirical function determined from Pacific Ocean sediment trap observations by Martin et al. (1987):

\[
F(z) = F(z') \left( \frac{z}{z'} \right)^{-\delta}
\]

\( F(z') \) \((z' = 120 \text{ m})\) is the downward flux of the particulate material at the base of the euphotic zone, and it includes sinking P, Z and D, as well as zooplankton mortality loss in the euphotic zone.

\[
F(z') = w_1 P(z') + w_2 Z(z') + w_3 D(z') + \int_{z'}^{0} m_2 Z \, dz.
\]
Parameter values used in the standard experiment are given in Table 1.

Selection of the parameters was based upon three major sources: (1) papers by Fasham et al. (1990), Sarmiento et al. (1993) and Toggweiler and Carson (1995); (2) observational data (Dugdale and Goering, 1967; Dugdale et al., 1992; Barber and Chavez, 1991; Minas et al., 1986; Peña et al., 1990); and (3) data from 1992 EqPac cruises (Barber et al., 1996; Lindley et al., 1995; Landry et al., 1995; Murray et al., 1995). The five ecosystem balance equations were solved simultaneously with the physical model. There were 12 layers in the euphotic zone, the upper 120 m, with 10 m vertical resolution. Below the euphotic zone, there were 15 layers through the water column. There were no mass fluxes across the air–sea boundary or at the ocean floor. For most of the model domain the water depth is several thousand meters, so fluxes to the ocean floor were not evaluated. Also no mass fluxes across the lateral boundaries were permitted. The model initial condition for the nitrate field was the climatological nitrate field specified by Levitus et al. (1993). The initial values for P, Z, D and NH4 were 0.25 mmol m\(^{-3}\) at the surface, decreasing exponentially with a scale length of 120 m. Chai (1995) has shown that the initial conditions in the euphotic zone for the ecosystem did not alter the final results, because the ecosystem reaches the equilibrium faster than the equatorial physics does.

2.3. Model spin-up and its convergence

The model spin-up must deal with three different adjustments from initial conditions: temperature and salinity (density); dynamic (momentum) and ecosystem components. Beside interactions between the compartments in the ecosystem, the first two influence the ecosystem adjustments through mixing and advection. With surface forcing (air temperature and wind stress) varying with the season, the model achieves a quasi-equilibrium state of annual cycle within a few years, which is the time scale for Rossby waves to cross the Pacific basin. A time-series of nitrate and temperature averaged in the upper 120 m over the entire model domain during an 11-year simulation is shown in Fig. 2. During the initial integration there is a decreasing trend in annual averaged nitrate and an increasing trend in annual averaged temperature, but after 5 years the annual rates of change are less than 0.02 mmol m\(^{-3}\) year\(^{-1}\) and 0.02°C year\(^{-1}\) for nitrate and temperature, respectively.

The adjustment of the remaining components of the ecosystem model is shown in Fig. 3. The quasi-equilibrium state of the annual cycle is achieved very rapidly, unlike nitrate and temperature, and decreasing or increasing trends are less pronounced for phytoplankton, zooplankton, ammonium and detritus during the spin-up stage. To illustrate how the dynamics adjust in the model, a time-series of the velocity field at 140°W on the equator is shown in Fig. 4. After 2 years of model integration, all three components of the velocity field have reached a quasi-equilibrium state such that the annual cycle repeats itself from one year to the next without any trend of decreasing or increasing. Based upon time-series analyses of all model components, we elected to analyze results in the sixth year of the model simulation.

3. RESULTS AND DISCUSSION

Results and discussion are arranged in the following order: the first section presents a comparison between the modeled and observed nitrate and temperature in the equatorial
Pacific; the second discusses the nitrate budget; the third discusses seasonal variation of the nitrate supply due to upwelling; and the fourth addresses maintenance of the high-nutrient condition in the equatorial Pacific by physiological constraints other than light or nitrogen such as iron limitation.

3.1. Comparison between modeled and observed temperature and nitrate

Comparison of modeled vs observed temperature serves as an indicator of the model’s dynamical and thermodynamical performance, and comparison of modeled vs observed nitrate serves as an indicator of both the physical and the ecosystem model performance. The importance of the former is to establish confidence in the simulated circulation patterns that drive the ecosystem model. Modeled temperature is compared with climatological data by Levitus (1982) in Fig. 5. Both the modeled and the observed temperature demonstrate the characteristic pattern with isotherms sloping upward from the west near 180° to the east.
High nitrate condition in the equatorial Pacific

Fig. 3. Weekly mean (a) phytoplankton, (b) zooplankton, (c) ammonium and (d) detritus concentration in the upper 120 m of the whole model domain (40°S–50°N, 130°E–80°W) over an 11-year simulation. Phytoplankton, zooplankton and detritus adjust to the regular seasonal cycle from their initial value faster than ammonium does.

around 100°W. The top of the thermocline (25°C) has a depth of about 150 m in the western Pacific, and it intersects the surface in the eastern region (Halpern, 1980). Modeled temperature at the surface is about 1°C higher than observed in the west, and the position of the modeled 28°C isotherm is close to the position of the observed 29°C isotherm. The longitudes at which various isotherms outcrop in the east are simulated well in the model. The modeled thermoline is slightly more diffuse, indicating that vertical mixing is slightly over estimated in the model. The position of the modeled 20°C isotherm (the core of the thermoline) matches observations rather well [Fig. 5(b)].

Modeled nitrate is compared with National Oceanographic Data Center (NODC) station data processed by Levitus et al. (1993), and with an independent set of observations from Barber and Chavez (1991) in Fig. 6. Like the temperature field (Fig. 5), the modeled and observed isopleths of nitrate concentration slope upward from the west to the east. In the western Pacific where nitrate concentration is low (i.e. close to, or below, the half-saturation concentration), both the data of Barber and Chavez (1991) and the NODC data processed by Levitus et al. (1993) are somewhat higher than the modeled concentrations. In the central and eastern Pacific, where the nitrate concentration is relatively high (i.e. several times the
Fig. 4. Weekly mean velocities at 140°W on the equator over an 11-year simulation. (a) Zonal velocity at the surface; (b) zonal velocity at a depth of 120 m; (c) meridional velocity at the surface; and (d) vertical velocity at 50 m. A 90-day running average filter has been applied to all the velocity components. The velocity on the equator at 140°W adjusts to the regular seasonal cycle of less than 2 years.

half-saturation concentration), modeled nitrate agrees well with both sets of observed concentrations. The positions of the nitrate isopleth outcrops in the central and eastern Pacific between the modeled and observed are quite similar. It is difficult to identify a nitracline (the region of the maximum vertical gradient of nitrate concentration) because it is relatively diffuse in the physically dynamic equatorial region. Following the approach used for temperature [Fig. 5(b)], we compare the positions of the 12 mmol m\(^{-3}\) isopleth in Fig. 6(d). Unlike the 20°C isotherm comparison in Fig. 5(b), differences among the three nitrate datasets are obvious. The differences between the two observed datasets could be attributed to collection in different periods, and also to the difference in data density. Data in the NODC station set were collected mainly in the 1960s and all before 1976, whereas Barber and Chavez station data were collected during the 1980s. Analytical techniques for determining nitrate have been changed somewhat, but another cause may be the different station and bottle spacing and interpolation. The Barber and Chavez (1991) stations were concentrated on the equator and sampled the upper layer very intensively; NODC stations are evenly spaced horizontally, but have much greater vertical spacing. Both observed
nitrate distributions show more synoptical scale variation than the modeled distribution, probably because both observed datasets are composites averaging existing data, which are unevenly distributed in space and time whereas the model results are annual means of a dense and even time-series.

In the equatorial "cold tongue", surface nitrate is well simulated in terms of magnitude (Fig. 7); for example, surface nitrate concentration is 5–6 mmol m$^{-3}$ at 140°W on the equator. Compared to the observations, the model also captures the position of the 4 mmol m$^{-3}$ isopleth reasonably well, especially north of the equator and in the western Pacific. The modeled "tongue" of elevated nitrate is more confined to the equator than is the observed "tongue." The pattern of modeled surface nitrate is symmetrical about the equator, whereas in the observed pattern highest nitrate values are found slightly south of the equator. The asymmetry of nitrate distribution about the equator is discussed in Section 3.4. In the observed data there is variability on the synoptical scale that is not seen in the model results; the source of this difference is probably that the observations were made unevenly both in space and time as discussed above.

Figure 7(b) and (d) compare the satellite-observed sea-surface temperature (Reynolds, 1988) with the modeled SST; this comparison is an independent validation of model performance because the model does not start with nor adjust to the satellite-derived SST. The model simulates the SST very well, in both pattern and absolute value, in the equatorial "cold tongue" region (Philander et al., 1987). In the western Pacific, the modeled SST tends
Fig. 6. Comparisons between the modeled annual mean nitrate concentration and observations along the equator. (a) Modeled data; (b) NODC station data (Levitus et al., 1993); (c) Barber and Chavez (1991) station data. The contour interval is 2.0 mmol m$^{-3}$. Shaded areas are the nitrate concentration between 11 and 13 mmol m$^{-3}$. (d) shows the positions of the 12 mmol m$^{-3}$ isopleths of nitrate concentration, the thick solid line is the modeled data; the thin solid line is the Barber and Chavez (1991) station data; and the dashed line is NODC station data processed by Levitus et al. (1993).

to be 1°C higher than the satellite SST. The likely reason for the difference is that the current version of this model does not include cloud effects in the surface heat flux calculation. Experiments from other modeling groups (Stockdale et al., 1993) have shown that model performance in the western Pacific can be improved by including cloud effects.

The similarity of spatial distributions of nitrate and temperature in the equatorial Pacific seen in Figs 5–7 can be statistically described by the relationship shown in Fig. 8(a), which is generated by three conditions. First, the dominant process controlling the surface temperature and nitrate concentration is vertical advection (Kamykowski and Zentara, 1986) in the form of equatorial upwelling. Secondly, the heat flux across the air–sea interface (which changes surface temperature but not nitrate) is a small contributor to the determination of surface temperature compared to the vertical advection of cooler water. The feature we are discussing is called the "cold tongue" because upwelling prevents it from reaching thermal equilibrium with the atmosphere. The third condition is that the biological uptake of nitrate (which changes nitrate concentration without changing surface temperature) is a small flux relative to the vertical advective supply of nitrate. The modeled temperature vs nitrate concentration from the year 6 model simulation in the region 5°S–5°N, 90°–180°W [Fig. 8(b)] reproduces well the observed temperature and
Fig. 7. Comparisons between observed and the modeled annual mean nitrate concentration and water temperature at the surface. (a) The modeled nitrate concentration; (b) the modeled temperature; (c) observed nitrate concentration (Levitus et al., 1993); (d) annual mean satellite-derived SST (Reynolds, 1988). The contour interval is 1.0 mmol m$^{-3}$ and 1.0°C for nitrate and temperature, respectively.

The modeled phytoplankton concentration, in nitrogen units, was converted to chlorophyll using a nominal grams of chlorophyll to moles of nitrogen ratio of 1.59, which corresponds to a chlorophyll to carbon mass ratio of 1:50 and a C:N mole ratio of 6.625. The comparison between the modeled and the climatological chlorophyll (Barber and Chavez, 1991) is showed in Fig. 9. In-situ chlorophyll measurements showed the chlorophyll maximum was at 50 m, whereas the modeled chlorophyll had the maximum near the surface. The disagreement between model and observations can be due to the variation of the ratio of chlorophyll to carbon with depth. We used a constant value to convert the phytoplankton concentration to chlorophyll because of the paucity of observations available to form a depth-dependent function. Eppley et al. (1991) reported that depth distribution of particulate organic carbon (POC) was uniform over the euphotic zone throughout the region of elevated nitrate and lacked pronounced subsurface maxima in the eastern equatorial Pacific, whereas the chlorophyll had the maximum at about 50 m with a two-fold increase from the surface (Barber and Chavez, 1991; Chavez et al., 1991; Stegmann et al., 1991). Such observations suggest, but do not prove, an increase with depth in the ratio of chlorophyll to phytoplankton carbon. A detailed vertical profile of the chlorophyll to phytoplankton carbon ratio will enable us to recreate, in future versions of the model, the subsurface chlorophyll maximum in the eastern equatorial Pacific where nitrate is replete.
3.2. Nitrate transport and budget in the equatorial Pacific

The predominantly westward surface wind in the equatorial Pacific drives a poleward Ekman transport in both hemispheres. To replace the surface waters that advect to both the south and the north, cool and nutrient-rich waters upwell from below the mixed layer. The westward surface wind also moves the surface water from the east to the west; the surface water therefore tends to accumulate in the western Pacific and an eastward pressure gradient force is generated. Near the surface this pressure gradient force is mainly balanced by the surface wind stress (Gargett, 1991). At greater depth, where the stress diminishes, the pressure gradient force is out of balance, thus forming the eastward Equatorial
Fig. 9. Comparison between the modeled annual mean (dashed line) and the observed climatological (solid line) chlorophyll (Barber and Chavez, 1991) at 140°W on the equator. The difference between model and observations could be due to the ratio of chlorophyll to carbon varying with depth.

Fig. 10. Annual mean velocities along the equator. (a) Zonal velocity, the shaded areas are westward flow, the contour interval is 10.0 cm s⁻¹; (b) meridional velocity, shaded areas are southward flow, the contour interval is 5.0 cm s⁻¹; and (c) vertical velocity, the contour interval is 50.0 cm day⁻¹.
Fig. 11. Annual mean velocities along 140°W. (a) Zonal velocity, the shaded areas are westward flow, the contour interval is 10.0 cm s\(^{-1}\); (b) meridional velocity, the shaded areas are southward flow, the contour interval is 5.0 cm s\(^{-1}\); and (c) vertical velocity, the shaded areas are downwellings, the contour interval is 50.0 cm day\(^{-1}\).

Fig. 12. Comparison between the modeled annual mean and the observed zonal velocity at 140°W on the equator. The solid line is the modeled data, and the dashed line is the observed data averaged over 11 years of mooring measurements from NOAA/PMEL.
Undercurrent. The modeled annual mean ocean circulation along the equator and along the 140°W meridian reproduces well the observed intensity and depth of the undercurrent core (Knauss, 1963) [Figs 10(a) and 11(a)] and the magnitude of equatorial upwelling [Figs 10(c) and 11(c)] (Halpern and Freitag, 1987; Bryden and Brady, 1985). The model also simulates the Equatorial Undercurrent very well in terms of the magnitude and the depth of the undercurrent core at 140°W on the equator (Fig. 12).

Based upon modeled velocity field and nitrate concentration gradients, we have calculated the terms $-u(\partial NO_3/\partial x)$, $-v(\partial NO_3/\partial y)$ and $-w(\partial NO_3/\partial z)$, which are the time rate of change of nitrate concentration due to advection in three different directions. The annual mean $-u(\partial NO_3/\partial z)$, $-v(\partial NO_3/\partial y)$ and $-w(\partial NO_3/\partial z)$ along the equator are shown in Fig. 13. The effects of zonal advection on nitrate [term $-u(\partial NO_3/\partial z)$ in equation (2)] are the supply of nitrate at the surface and removal of nitrate at greater depth where the Equatorial Undercurrent is a dominant process. For example, in the central Pacific at 140°W the Equatorial Undercurrent brings in water of low nitrate concentration from the west; therefore, the nitrate at 140°W is moved zonally to the east by the Equatorial Undercurrent. This suggests that the Equatorial Undercurrent moves nitrate along its path from the western Pacific to the eastern boundary of the tropical Pacific basin. The effects of

Fig. 13. Annual mean effects of advection on nitrate along the equator. (a) $-u(\partial NO_3/\partial x)$, the westward current at the surface supplies nitrate to the east, and the undercurrent removes nitrate to the east; (b) $-v(\partial NO_3/\partial y)$, the northward flow crosses the equator at the surface supplies the nitrate, and the returning flow below 50 m removes the nitrate; and (c) $-w(\partial NO_3/\partial z)$, the equatorial upwelling supplies the nitrate along the most part of the equator. The shaded areas are negative which indicates the removal of nitrate. The contour interval is 0.05 mmol N m$^{-3}$ day$^{-1}$. 
vertical advection on nitrate [term \(-w(\partial \text{NO}_3/\partial z)\) in equation (2)] supply nitrate to the surface layer over most of the central and equatorial Pacific. In the central Pacific, the maximum vertical flux of nitrate by upwelling is between 75 and 125 m, but the maximum upwelling velocity is around 50 m. This is because \(-w(\partial \text{NO}_3/\partial z)\) is controlled not only by the vertical velocity but also by the vertical gradient of nitrate concentration; this point is illustrated in more detail in Section 3.3.

Along 140°W, the time rate of change of concentration due to advection \([-u(\partial \text{NO}_3/\partial x), v(\partial \text{NO}_3/\partial y)\) and \(-w(\partial \text{NO}_3/\partial z)\)] is shown in Fig. 14. Removal of nitrate at greater depth by the Equatorial Undercurrent is well defined between 2°S and 2°N where water is transported eastward. This zonal removal of nitrate is mainly balanced by the vertical supply of upwelled nitrate. Two degrees to either side of the equator the effects of meridional advection become the major supply of nitrate [Fig. 14(b)] to the surface layer. Nitrate transport patterns along a meridian are explained by the equatorial circulation cell along that meridian. First, equatorial divergence upwells water through the upper water column and brings up nitrate-rich water. During this upward movement, part of the nutrient-rich water is carried to the east by the Equatorial Undercurrent, and part is carried poleward by the northward and southward Ekman transport. At greater depth, about 75 m for example, the meridional return flow carries some nutrient-depleted water back to the equator. This

Fig. 14. Annual mean effects of advection on nitrate along 140°W. (a) \(-u(\partial \text{NO}_3/\partial x)\), the removal of nitrate by the undercurrent is defined within 3°S and 3°N; (b) \(-v(\partial \text{NO}_3/\partial y)\), the maximum of nitrate supply by the equatorial divergent occurs at both 3°S and 3°N and (c) \(-w(\partial \text{NO}_3/\partial z)\), the nitrate supply by the equatorial upwelling is confined within 3°S and 3°N.
returning nutrient-poor water joins the nutrient-rich water upwelled from the deeper layer and makes another pass through the meridional cell.

In addition to advection, mixing also affects nitrate concentration. Thus, some parcels of water gain nitrate while others lose nitrate due to mixing. The model results indicate that in the equatorial Pacific the effects of mixing on nitrate are small compared to the effects due to advection.

We have integrated the nitrate conservation equation [equation (2)] from the surface down to 120 m at 140°W on the equator. The contributions from each physical process, the summed net physical supply of nitrate and the modeled new production (a sink for nitrate) are shown in Fig. 15. As discussed above, upwelling and the Equatorial Undercurrent are the two most important terms among the physical processes. The ratio between zonal and vertical transport of nitrate is about 0.5, which suggests that at 140°W on the equator about 50% of the upwelled nitrate is moved to the east by the undercurrent. Mixing effects on nitrate are small compared to the effects due to advection; the ratio between mixing and advection effects on nitrate is about 0.1. New production estimated by the ecosystem model is very close to the sum of physical supply (3.36 mmol N m\(^{-2}\) day\(^{-1}\) new production vs 3.76 mmol N m\(^{-2}\) day\(^{-1}\) physical supply). If converted to the carbon unit, using a C:N ratio of 6.625, in the upper 120 m at 140°W on the equator the vertically integrated new production is 22.26 mmol C m\(^{-2}\) day\(^{-1}\).

The vertically integrated \(-u(\partial \text{NO}_3/\partial x), -v(\partial \text{NO}_3/\partial y)\) and \(-w(\partial \text{NO}_3/\partial z)\) from 15°S to 15°N along 140°W (Fig. 16) demonstrate the dramatic change away from the equator in all three terms. Once again, the maximum supply of nitrate by equatorial upwelling occurs right on the equator [Fig. 16(c)] where the removal of nitrate by the undercurrent also is greatest [Fig. 16(a)]. The effects of meridional transport of nitrate are less clear in Fig. 16(b) because of the vertical integration from 0 to 120 m.

![Graph showing nitrate concentrations](image)

Fig. 15. Annual mean vertically integrated (0–120 m) term balance of nitrate conservation equation at 140°W on the equator. The biological uptake is annual mean new production from the ecosystem calculation [equation (8)]. The difference between the sum of physical supply and new production could be partly due to the time scale of the averaging.
Fig. 16. The vertically integrated (0–120 m) effects of advection on nitrate along 140°W. (a) \(-u(\partial NO_3/\partial x)\); (b) \(-v(\partial NO_3/\partial y)\); and (c) \(-w(\partial NO_3/\partial z)\). A negative value indicates the removal of nitrate.

In order to demonstrate the effect of vertical integration on all three terms \((-u(\partial NO_3/\partial x), v(\partial NO_3/\partial y)\) and \(-w(\partial NO_3/\partial z)\), we show the three vertically integrated advection effects on nitrate over two different depth ranges, 0–50 and 50–120 m, in Fig. 17. Zonal currents are a minor supply of nitrate near the surface where the water is coming from the east, and a removal below the surface where the Equatorial Undercurrent from the west dominates [Fig. 17(a)]. Overall, the vertically integrated effects of zonal advection indicate a net removal of nitrate between 2°S and 2°N, and a net supply of nitrate north of 2°N and south of 2°S. At the surface, meridional flows carry high nitrate concentration water to the south and north from the equator, and meridional advection becomes the major physical supply for nitrate in the area south of 2°S and north of 2°N. The vertically integrated effect of
meridional advection peak at 3°S and 3°N [Fig. 17(b)]. Below 50 m, return flow carries nitrate-depleted water back to the equator, and meridional advection thus becomes a nitrate removal between 50 and 120 m. The vertically integrated effects of vertical advection are positive between 2°S and 2°N, indicating nitrate injection from below. A negative integrated term $-w(\partial\text{NO}_3/\partial z)$ south of 3°S and north of 3°N indicates nitrate is removed from the surface by the circulation. The complexity of the vertical structure of currents in the equatorial Pacific determines the complexity of nitrate transport, and the effects of advection in different directions over the depth ranges must be assessed to investigate the role each physical process plays in the nitrate budget.
Measurements of new production in open oceans are rare: thus, there is a strong interest in estimating the physical supply of nitrate to provide an independent estimate of potential new production and to relate that estimate to other biological and chemical processes, especially the downward particulate organic fluxes (Chavez and Barber, 1987; Lewis et al., 1986; Jenkins, 1988; Murray et al., 1989).

Chavez and Barber (1987) estimated new production in the equatorial "cold tongue" region by two indirect methods: based on a simple physical model; and derived from primary production measurements. In the first approach, they used the upwelling estimate by Wyrtki (1981), $1.58 \times 10^{15} \text{ m}^3 \text{ year}^{-1}$ (or about 50 Sv), in the equatorial "cold tongue" area ($5^\circ \text{S} - 5^\circ \text{N}, 180^\circ - 90^\circ \text{W}$). Assuming that water upwells from 100 m with an average nitrate concentration of 15 mmol m$^{-3}$, and that the upwelled nitrate is completely taken up by phytoplankton, then the potential new production is $0.157 \times 10^{15} \text{ mol C year}^{-1}$. In the second approach, Chavez and Barber (1987) used their climatological primary production observations and an $f$ ratio (the ratio of new production to primary production) of 0.44 from Eppley and Peterson (1979) to estimate new production of $0.071 \times 10^{15} \text{ mol C year}^{-1}$ for the equatorial region. The total net physical supply due to advection and mixing in the equatorial "cold tongue" area from this paper, expressed in C units, provides an estimate of potential new production of $0.060 \times 10^{15} \text{ mol C year}^{-1}$. For the same area, the ecosystem model of this paper yields an estimate of new production by biological uptake of $0.065 \times 10^{15} \text{ mol C year}^{-1}$. Compare the two terms on the right of Fig. 15 to see the similarity of the supply term and the uptake term.

In Table 2 estimates of new production by Chavez and Barber (1987) are compared with the model estimates from this work. The model estimates of new production and potential new production are close to the Chavez and Barber (1987) estimate based on climatological primary production data. However, their calculation using a simple physical model with Wyrtki's upwelling rate yields an estimate of potential new production that is higher by a

<table>
<thead>
<tr>
<th>Source</th>
<th>New production in the &quot;cold tongue&quot; region</th>
<th>The regional-averaged new production</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chavez and Barber (1987) using Wyrtki's upwelling rate of 50 Sv</td>
<td>$0.157 \times 10^{15} \text{ mol C year}^{-1}$</td>
<td>39.50 mmol C m$^{-2}$ day$^{-1}$</td>
</tr>
<tr>
<td>Chavez and Barber (1987) using primary production and an $f$ ratio of 0.44</td>
<td>$0.071 \times 10^{15} \text{ mol C year}^{-1}$</td>
<td>17.86 mmol C m$^{-2}$ day$^{-1}$</td>
</tr>
<tr>
<td>This paper estimating the net annual mean physical flux of nitrate in the upper 120 m</td>
<td>$0.060 \times 10^{15} \text{ mol C year}^{-1}$</td>
<td>15.09 mmol C m$^{-2}$ day$^{-1}$</td>
</tr>
<tr>
<td>This paper calculating new production directly from the ecosystem in the upper 120 m</td>
<td>$0.065 \times 10^{15} \text{ mol C year}^{-1}$</td>
<td>16.35 mmol C m$^{-2}$ day$^{-1}$</td>
</tr>
<tr>
<td>Ku et al. (1995) using the $^{228}\text{Ra}$ budget in the euphotic zone (EqPac)</td>
<td>$0.067 \times 10^{15} \text{ mol C year}^{-1}$</td>
<td>16.78 mmol C m$^{-2}$ day$^{-1}$</td>
</tr>
<tr>
<td>U.S. JGOPS EqPac (McCarthy et al., 1996; P. Wheeler, personal communication)</td>
<td>$0.066 \times 10^{15} \text{ mol C year}^{-1}$</td>
<td>13.25-19.88 mmol C m$^{-2}$ day$^{-1}$</td>
</tr>
<tr>
<td>Toggweiler and Carson (1995) using the model (Fasham et al., 1990) and an Ocean General Circulation Model (OGCM)</td>
<td>$0.087 \times 10^{15} \text{ mol C year}^{-1}$</td>
<td>21.86 mmol C m$^{-2}$ day$^{-1}$</td>
</tr>
</tbody>
</table>
factor of 2.5. The reason for this erroneous high estimate is that nitrate upwelled in the 5°N–5°S, 90°W–180° box clearly is not all taken up by phytoplankton; within that spatial domain considerable nitrate is advected to the south beyond 5°S. Another reason is that Chavez and Barber (1987) considered only the vertical component of the physical supply of nitrate and ignored the zonal or meridional physical loss of nitrate. As shown earlier, both zonal and meridional currents transport some of the upwelled nitrate out of the “cold tongue” area. Table 2 also lists two new production estimates in the “cold tongue” region based on recent U.S. JGOFS EqPac observations (Ku et al., 1995; McCarthy et al., 1996; P. Wheeler, personal communication) and the modeling results of Toggweiler and Carson (1995), which are the only other model estimates for this region. The “cold tongue” (5°N–5°S, 90°W–180°) annual average new production estimate reported in this paper agrees well with both recent U.S. JGOFS EqPac new production measurements. The model results of Toggweiler and Carson (1995) are similar in value to those of this paper, but not as close as the three estimates based on observations (Chavez and Barber, 1987; Ku et al., 1995; McCarthy et al., 1996; P. Wheeler, personal communication).

3.3. Seasonal variability of nitrate supply

The effects of vertical advection on nitrate \((-w\partial\text{NO}_3/\partial z)\) are controlled by two factors, vertical velocity and the vertical gradient of nitrate concentration. As shown in Figs 10(c) and 13(c), a stronger vertical velocity does not necessarily result in a larger term \(-w\partial\text{NO}_3/\partial z\). In those examples maximum vertical velocity occurs at 50 m, but the largest vertical advective flux is found at 125 m, the approximate depth of the strongest gradient in nitrate concentration.

Another example of the two factors at work involves the seasonal variation of vertical velocity. The effects of vertical advection on nitrate supply \((-w\partial\text{NO}_3/\partial z)\) during climatological spring (March–May) are larger than in fall (September–November).
(Fig. 18). The reason for the difference is not vertical velocity itself, which is lower in spring, but seasonal change in strength of the vertical gradient of nitrate concentration. Figure 19 shows vertical velocity and vertical profiles of nitrate concentration during climatological spring and climatological fall. During spring the southeast trade winds are the weakest and the vertical velocity therefore also reaches a minimum; the vertical gradient of nitrate concentration, on the other hand, is slightly stronger in spring than in fall. During fall, the southeast trade is the strongest and the vertical velocity reaches a maximum, but nitrate concentration is more uniform in the upper 75 m. Vertical velocity clearly is determined by the local wind, while the strength of the vertical gradient of nitrate is remotely determined by the basin-scale zonal advection of nitrate. Interannual studies of the basin-wide nitraline during the 1982–1983 El Niño (Barber and Chavez, 1983) showed that remote advective processes dominate local effects such as mixing and upwelling. In a parallel manner for
determining the seasonal cycle of nitrate supply, remote effects on the nitrate gradient are more important than local wind-driven variability of vertical velocity.

3.4. Maintenance of the high nitrate condition in the equatorial Pacific

Surface nitrate concentration in the equatorial Pacific is persistently well above the half-saturation concentration ($K_{NO_3}$) for nitrate uptake (Fig. 7). The factors responsible for maintaining such relatively high surface nitrate conditions in the equatorial Pacific remain controversial. When the surface nitrate concentration is several factors above the half-saturation concentration and the phytoplankton uptake of nitrate is saturated, any extra physical supply of nitrate will increase the nitrate concentration. The central and eastern equatorial Pacific Ocean is also characterized by a lower than expected phytoplankton biomass (Barber, 1992). It has been proposed that zooplankton grazing keeps the phytoplankton biomass so low that the phytoplankton do not deplete nitrate at a rate equal to or higher than the rate of physical supply (Frost, 1987, 1991; Frost and Franzen, 1992; Cullen et al., 1992; Landry et al., 1995). A different view is that iron insufficiency or some other micronutrient deficiency limits phytoplankton-specific photosynthetic and growth rates such that "normal" concentration-dependent specific uptake rates of nitrate are not realized. In this view the causal mechanism that prevents nitrate depletion is a physiological limitation to biomass reasons (Martin, 1990; Martin et al., 1991; Donaghay et al., 1991; Duce, 1986). In both views the proximal cause for the failure to delete the abundant euphotic zone nitrate is the failure to accumulate significant levels of phytoplankton biomass, that is, the failure of a "bloom" to form in nitrate-rich waters. In one view the failure is ascribed to the loss term; in the other, it is ascribed to the gain term.

The addition of iron to a 64 km$^2$ area of HNLCC waters in the eastern equatorial Pacific Ocean resulted in a doubling of primary production and a doubling of phytoplankton biomass; the chlorophyll increase, however, was modest (from about 0.3 to about 0.6 mg m$^{-2}$). Importantly, the phytoplankton biomass, after the second day, did not continue to accumulate into a significant bloom and nitrate was not significantly depleted (Martin et al., 1994). This result makes it clear that iron limitation does regulate the physiological photosynthetic and growth rates and, to a lesser degree, the biomass of ambient equatorial phytoplankton. The grazing control on the rate of phytoplankton biomass loss and the iron limitation of specific rates of phytoplankton increase both regulate biomass accumulation and are, of course, complementary (Price et al., 1994; Lindley et al., 1995).

To what degree does iron limitation of physiological rates, by itself, account for the persistently high surface nitrate concentrations of equatorial waters? To address this question we performed several model experiments. The complementary question regarding the role of zooplankton grazing, which keeps the phytoplankton biomass so low that phytoplankton cannot deplete nitrate at such high rates of physical supply, also was investigated by Chai (1995), but is not reported here. In this paper, we present results from an experiment that focused on how physiological constraints on phytoplankton photosynthetic performance and specific growth rate affect surface nitrate concentrations in the equatorial Pacific. The design of this model experiment was based upon observations made in the iron enrichment experiment (IronEx) (Martin et al., 1994; Lindley and Barber, submitted).

The photosynthetic performance of phytoplankton is described with two parameters:
light-limited photosynthesis is described by $\alpha$, the slope of the photosynthetic rate over irradiance at low irradiance; and $I_k$ gives a measure of the irradiance at light saturation. According to the IronEx results (Lindley and Barber, submitted), $\alpha$ doubled inside the iron-enriched patch relative to outside the patch where it remained unchanged (Lindley, 1994; Lindley et al., 1995), while $I_k$ was the same inside and outside the patch. To simulate the enhanced photosynthetic performance with additional iron, we doubled $\alpha$ [0.1 to 0.2 day$^{-1}$ (W m$^{-2}$)$^{-1}$] and kept $I_k$ the same in the model. As a consequence of doubling $\alpha$ and holding $I_k$ constant, $P_{\text{max}}$ doubled from 2.0 to 4.0 day$^{-1}$, since $P_{\text{max}}$ is equal to $\alpha \times I_k$. Is 4.0 day$^{-1}$ a realistic, or observed, maximum specific growth rate at equatorial temperatures? The answer is no. About 3.0 day$^{-1}$ is the observed maximum specific growth rate at these temperatures according to Eppley (1972). A $P_{\text{max}}$ of 4.0 is above the observed specific growth rate, so using this value is equivalent to setting growth limitations due to micronutrients such as iron at an extremely high, but not unrealistic, value. In effect, we removed or greatly reduced all physiological limitations. By keeping all other model parameters the same, including the grazing formulation, the effect of removing a physiological constraint on photosynthetic performance or growth can be distinguished from effects of physical processes and grazing.

With the higher $\alpha$ and $P_{\text{max}}$ values, the model again reached a steady state after 5 years of integration; the annual mean during the sixth year is presented in comparison with the

Fig. 20. The surface nitrate concentration comparison between (a) normal simulation [$\alpha=0.1$ day$^{-1}$ (W m$^{-2}$)$^{-1}$, and $P_{\text{max}}=2.0$ day$^{-1}$] and (b) doubled rate simulation [$\alpha=0.2$ day$^{-1}$ (W m$^{-2}$)$^{-1}$, and $P_{\text{max}}=4.0$ day$^{-1}$]. The contour interval is 1 mmol m$^{-3}$. With a higher physiological performance of phytoplankton, the pool of the unused surface nitrate is reduced as well as the concentration.
results from the simulation using $z$ and $P_{\text{max}}$ based on observed equatorial rates. Comparison of surface nitrate concentrations between the observed and doubled $z$ and $P_{\text{max}}$ simulations (Fig. 20) shows that, with the higher $z$ and $P_{\text{max}}$, the size of the high nitrate pool was reduced. The positions of the 1 mmol m$^{-2}$ contours are closer to the equator and farther to the east. However, a large equatorial region of relatively high nitrate (concentrations above $K_{\text{NO}_3}$) persisted east of 150°W between 5°S and 5°N when the physiological rates were set at rates that are extremely high.

The result from the normal simulation shows that from the equator northward along 140°W the concentration of modeled surface nitrate is the same as the observed nitrate concentration (Fig. 21), but the modeled nitrate is lower than observed south of the equator. This disagreement between the model and observations provides additional insight on physiological regulation that can be related to the observed pattern of iron supply in the real ocean. The model uses the same maximum inherent growth rate north and south of the equator based primarily upon the Barber and Chavez (1991) data from stations located right on the equator. Recently, Lindley et al. (1995) and Gordon et al. (in press) hypothesized that upwelling from the Equatorial Undercurrent is the major source of iron to the euphotic zone at the equator. On the other hand, a few degrees poleward from the equator, both to the north and to the south, eolian iron becomes increasingly important as a source of new iron. There is a decreasing trend in the observed eolian iron flux pattern (Duce and Tindale, 1991; Rea et al., 1994) from north of the equator to the south. Based upon the hypothesis of Lindley et al. (1995) and Gordon et al. (in press), and the iron flux observations of Duce and Tindale (1991), if 2.0 day$^{-1}$ is the maximum specific growth rate on the equator, the maximum specific growth rate should be smaller in the Southern Hemisphere because eolian iron flux is an order of magnitude lower there. With a higher maximum specific growth rate in the model than in the real world, phytoplankton in the model consume more nitrate, producing modeled nitrate concentrations south of the equator that are lower than those observed. The explanation is that in the real ocean the gradient in eolian iron flux produces a gradient in photosynthetic performance and specific growth rate, nitrate uptake and, ultimately, nitrate concentration. We speculate that in the central equatorial Pacific the

![Graph](image-url)

Fig. 21. The surface nitrate concentration comparison along 140°W. Both normal and doubled simulations show that the modeled surface nitrate distribution is symmetrical across the equator, whereas the observed distribution is asymmetrical.
asymmetric biological uptake of nitrate about the equator is responsible for increased surface nitrate concentration in the Southern Hemisphere. With a lower \( \alpha \) and \( P_{\text{max}} \) simulation in the south of the equator, the modeled surface nitrate concentration in the south increased and comparison between the model results and observations was improved (Chai, 1995).

By doubling \( \alpha \) and \( P_{\text{max}} \) in the model experiment, we simulated an equatorial environment in which the physiological limitation of maximum specific photosynthetic and growth rates are greatly reduced. Equatorial primary production doubled, but the surface nitrate concentration at 140°W on the equator was only reduced to 2 mmol m\(^{-3}\) from 5 mmol m\(^{-3}\). This model result suggests that failure to accumulate phytoplankton biomass, despite high rates of specific activity, plays a role in determining the modeled surface nitrate levels.

Comparison of the surface phytoplankton concentration between the normal and the doubled \( \alpha \) and \( P_{\text{max}} \) simulation is shown in Fig. 22(a). The phytoplankton concentration

![Graph showing phytoplankton concentrations](image)

**Fig. 22.** Time-series of weekly mean surface of (a) phytoplankton and (b) zooplankton at 140°W on the equator between the enhanced biological uptake and the standard experiment. The surface phytoplankton concentrations are at the same level between the enhanced growth and normal growth, but the zooplankton concentration was doubled in the enhanced growth. It seems that the effects of iron benefit zooplankton more than phytoplankton.
increased only slightly (from 0.21 to 0.25 mmol m\(^{-3}\)) after \(\alpha\) and \(P_{\text{max}}\) were doubled. This accounts for why surface nitrate remained at 2 mmol m\(^{-3}\) instead of going to total depletion. Not enough phytoplankton biomass accumulated in the model experiment to deplete surface nitrate, even though the phytoplankton present grow at very fast rates.

On the other hand, the surface zooplankton biomass doubled (from 0.5 to 1.0 mmol m\(^{-3}\)) after the \(\alpha\) and \(P_{\text{max}}\) were doubled [Fig. 22(b)]. The increase of grazers kept phytoplankton biomass at relatively low levels even though the phytoplankton grew faster. This can be seen clearly from Fig. 23, which compares vertically integrated primary production and zooplankton grazing on phytoplankton (secondary production) in the normal simulation and doubled \(\alpha\) and \(P_{\text{max}}\) simulation. The primary production doubled (from 83 to 166 mmol C m\(^{-2}\) day\(^{-1}\)) after \(\alpha\) and \(P_{\text{max}}\) were doubled, but the zooplankton grazing on the phytoplankton also doubled (from 75 to 150 mmol C m\(^{-2}\) day\(^{-1}\)). In IronEx (Martin et al., 1994) the primary production was increased by a factor of 2 for 9 days inside the patch, but after the second day biomass remained constant. The model results suggest that a doubling
of zooplankton grazing must have occurred during IronEx in the iron-enriched patch.

Enhanced physiological performance of phytoplankton doubled the primary production in the model experiment; however, increased zooplankton grazing that accompanied enhanced phytoplankton growth in the model prevented the development of a phytoplankton bloom with enough biomass to deplete surface nitrate. The model results suggest that when phytoplankton growth and zooplankton grazing are tightly coupled, enhancement of physiological rates such as the elimination of iron limitation will not eliminate the equatorial high nutrient–low chlorophyll (HNLC) anomaly.

There is no size structure of phytoplankton in our current model; therefore, the grazer assemblage had equal grazing access to all of the enhanced phytoplankton growth in the model. Incorporating size-related vulnerability of phytoplankton to grazing and a size-related zooplankton reproductive rate into our current ecosystem model is needed to further investigate the Iron Hypothesis from a modeling point of view.

4. SUMMARY

We developed and embedded a five-component ecosystem into an ocean general circulation model for the equatorial Pacific. The physical–biological model was validated by its ability to reproduce the observed nitrate concentration and the characteristic equatorial nitrate–temperature relationship. The results from the physical–biological model are as follows.

1. The equatorial undercurrent transports the nitrate along its path from west to east, resulting in a net accumulation of nitrate in the central and eastern part of the basin, where equatorial upwelling brings nitrate to the surface. The effect of mixing on nitrate concentration is small compared to the effects due to advection. The total net physical supply (due to the advection and mixing) in the equatorial “cold tongue” area, expressed in carbon units, is equivalent to a new production rate of $0.06 \times 10^{15}$ mol C year$^{-1}$, or averaged over the “cold tongue” area is 15.09 mmol C m$^{-2}$ day$^{-1}$.

2. Vertical supply of nitrate ($-w\partial NO_3/\partial z$) due to the upwelling is controlled by two factors, the vertical velocity and vertical gradient of nitrate concentration. During climatological fall, the vertical velocity reaches the maximum but the vertical supply of nitrate during fall is smaller than in spring because the vertical gradient of nitrate is weaker.

3. A combination of physical processes, physiological limitation and zooplankton grazing is responsible for determining the size and absolute value of surface nitrate concentration. Even with extremely high physiological rates (doubled $\alpha$ and $P_{\text{max}}$), a persistent pool of unused surface nitrate remained, but its size and concentration were reduced. This model result suggests that if the equatorial Pacific ocean were micronutrient replete such that there were no physiological limitations, the maximum nitrate concentration would be reduced by half from its present concentration, but the equatorial nutrient anomaly would persist.

4. Vertically integrated primary production was doubled by doubling $\alpha$ and $P_{\text{max}}$, but the phytoplankton biomass remained at a similar level and nitrate was not significantly depleted in the model experiment. Zooplankton grazing on phytoplankton also was doubled by doubling $\alpha$ and $P_{\text{max}}$, which resulted in a doubling of zooplankton biomass.

5. The model results suggest that the physiological state of phytoplankton ($\alpha$ and $P_{\text{max}}$) are not constant for the whole equatorial Pacific, but follow the eolian iron flux pattern, with a better performance (higher $\alpha$ and $P_{\text{max}}$) in the Northern Hemisphere and decreasing rates in the Southern Hemisphere. In the real ocean, the north to south gradient in eolian iron flux
(and \( z \)) apparently drives an asymmetric biological uptake of nitrate which is responsible for higher surface nitrate concentrations in the Southern Hemisphere.

Acknowledgements—This research was supported by NASA Grant NAGW-3655, and a Cray Research Fellowship awarded to F. C. by the North Carolina Supercomputing Center. Work at sea was supported by NSF Grant OCE-9024373. J. R. Toggweiler of GFDL/NOAA generously provided advice and guidance throughout the course of this work. S. Carson, J. W. Murray and an anonymous reviewer made comments that improved the final version of the manuscript. We would like to thank Dr. McPhaden of TOGA–TAO Project Office for providing mooring velocity data at 140°W on the equator. This publication is U.S. JGOFS contribution number 211.

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