10-1996

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Original Publication Citation

Moisan, J.R., & Hofmann, E.E. (1996). Modeling nutrient and plankton processes in the California coastal transition zone: 1. A time- and depth-dependent model. *Journal of Geophysical Research*, 101(C10), 22647-22676. doi: 10.1029/96jc01718

Modeling nutrient and plankton processes in the California coastal transition zone

1. A time- and depth-dependent model

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Abstract. A time- and depth-dependent, physical-bio-optical model was developed for the California coastal transition zone (CTZ) with the overall objective of understanding and quantifying the processes that contribute to the vertical and temporal development of nutrient and plankton distributions in the CTZ. The model food web components included silicate, nitrate, ammonium, two phytoplankton size fractions, copepods, doliolids, euphausiids, and a detritus pool. The wavelength-dependent subsurface irradiance field was attenuated by seawater and phytoplankton pigments. The one-dimensional (1-D) model adequately simulated the development and maintenance of a subsurface chlorophyll maximum in different regions within the CTZ. An analysis of the individual terms in the model governing equations revealed that phytoplankton in situ growth was primarily responsible for the creation and maintenance of the subsurface chlorophyll maximum at both coastal and oceanic regions in the CTZ. The depth to which the maximum in situ growth occurred was controlled by the combined effect of light and nutrient limitation. Also, the simulated bio-optical fields demonstrated the effect of nonlinear couplings between food web components and the subsurface irradiance field on vertical biological distributions. In particular, the *e*-folding scale of the subsurface photosynthetically available radiation (PAR) was influenced by the level of zooplankton grazing.

1. Introduction

Prior to the introduction of satellites as tools for gathering synoptic surface data on the oceans, the California Current system (CCS) was generally thought to be a broad, shallow, slow eastern boundary current with a steady, southward drift [Hickey, 1979; Mooers and Robinson, 1984]. However, on the basis of coastal zone color scanner (CZCS) and advanced very high resolution radiometer (AVHRR) measurements and recent field studies, it is now recognized that a subregion of the CCS, the coastal transition zone (CTZ), is characterized by cold, nutrient- and pigment-rich filaments that originate near the coast and extend offshore as much as 300 km [Flament *et al.*, 1985; Abbott and Zion, 1987; Strub *et al.*, 1991]. Transports and maximum horizontal velocities associated with these filaments are 2–6 Sv and 50 cm s⁻¹, respectively [Strub *et al.*, 1991]. Because of this, these narrow (50 km wide) filaments may provide an important mechanism for the across-shelf

transport of heat, nutrients, biota and pollutants [Mooers and Robinson, 1984].

The circulation dynamics underlying these mesoscale features [Haidvogel *et al.*, 1991a; Walstad *et al.*, 1991] and their effects on plankton processes [Abbott and Barksdale, 1991; Mackas *et al.*, 1991; Chavez *et al.*, 1991; Bucklin, 1991; Hofmann *et al.*, 1991; Smith and Lane, 1991] have only recently been investigated. These filaments develop and decay over a period of a few weeks [Flament *et al.*, 1985] and occur most frequently during the spring and summer [Peláez and McGowan, 1986].

Observations from the 1987 and 1988 CTZ field surveys (Figure 1) provided a basis to describe the plankton dynamics associated with these filaments [Chavez *et al.*, 1991; Hood *et al.*, 1990, 1991]. In general, inshore plankton assemblages appear to be separated from offshore plankton assemblages by the presence of a strong density front created by a strong equatorward flowing baroclinic coastal jet. Meanders in this alongshore jet cause the entrained neritic plankton assemblages to become advected rapidly offshore. Downwelling in regions within the core of the meandering jet subducts the phytoplankton assemblages to depths greater than 70 m [Strub *et al.*, 1991]. Due to subduction, deep chlorophyll maxima are observed that are deeper and composed of different species than those normally found in the deep chlorophyll maxima in this region [Chavez *et al.*, 1991]. Evidence for this subduction process is also observed

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Figure 1. Location of the coastal (A1, shaded circle) and oceanic (E2, open circle) stations from which data were obtained to initialize the model. The lines indicate the standardized grid that was used for the 1988 CTZ field survey. The solid squares indicate station locations. Figure adapted from Huyer *et al.* [1991].

in ^{222}Rn , nutrients, oxygen, temperature, and salinity distributions [Kadko *et al.*, 1991].

The distribution of zooplankton assemblages within the CTZ show a trend in their distribution relative to the position of the filaments [Mackas *et al.*, 1991]. High concentrations of the doliolid *Doliolita gegenbauri* were observed south and east of filaments. Along the warm side of the jet and extending into nonfilament waters to the west and north, the zooplankton assemblage was composed primarily of high concentrations of *Doliolita* sp. along with a mixture of smaller copepods, pteropod larvae and chaetognaths. The euphausiid *Euphausia pacifica* was found throughout the filament, but was primarily concentrated along the southern margin of the filament. High concentrations of the copepod *Eucalanus californicus* were found within the cold core of the filament and along the northern and western margins [Mackas *et al.*, 1991].

Quantification of the effect of the physical and biological processes on the distribution, development and fate of the plankton in the CTZ is difficult to do on the basis of field studies alone because of the time-dependent nature of this region. This paper is the first of a series of three studies that were conducted using a set of increasingly complex and sophisticated physical-bio-optical models [Moisan *et al.*, this issue; Moisan and Hofmann, this issue]. This first paper presents the results from a time- and depth-dependent, physical-bio-optical model. The model is a nine-component food

web model which has been coupled to a wavelength-dependent subsurface irradiance model. The physical processes which have been included are vertical advection and diffusion. This model has been developed for the CTZ region with the overall objective of understanding and quantifying the vertical and temporal development of nutrient and plankton distributions at two different locations (coastal and oceanic) within the CTZ. The results from this model are compared with actual data collected during the CTZ field surveys.

This paper has two primary objectives. The first is to simulate the spatial and temporal development of the subsurface chlorophyll maximum and to assess the relative importance of the physical and biological processes which contributed to its development. This model also provides a test on the formulations used to simulate the bio-optical processes which are also used in the three-dimensional (3-D) physical-bio-optical model, presented by Moisan *et al.* [this issue]. The second objective is to determine the sensitivity of the simulated distributions to the parameters and processes included in the model. The results from the sensitivity analysis are also useful in gaining insight on the interactions between the bio-optical and food-web dynamics.

The second section presents the model equations and parameterizations used for the physical, food web, and bio-optical portions of the model. The results from the sensitivity analysis and the simulations from the two different locations within the CTZ are presented in sec-

tion 3. Finally, section 4 discusses the results obtained from the simulations of two extreme regions in the CTZ (coastal and oceanic) and compares these to observations collected from the CTZ field surveys (Figure 1).

2. Methods

2.1. Model Equations

A one-dimensional (z) time-dependent physical-bio-optical model was used. The physical portion included the effects of vertical velocity (biological and advective) and vertical diffusion. The biological portion consisted of a nine-component food web that included silicate, nitrate, ammonium, two phytoplankton size fractions, three zooplankton categories and a detritus pool. Transfers within the food web occurred through nutrient uptake by phytoplankton, differential grazing by zooplankton, and nutrient recycling (Figure 2). Coupled to the food web model was a modified version of the subsurface spectral irradiance model of *Sathyendranath and Platt [1988]*.

The model therefore was a system of nine coupled partial differential equations that governed the vertical and time distribution of a nonconservative quantity and was of the form

$$\frac{\partial B}{\partial t} = \frac{\partial}{\partial z} \left(K_z \frac{\partial B}{\partial z} \right) - (w + w_{\text{biology}}) \frac{\partial B}{\partial z} + S + r_{\text{nudge}}(B_{\text{clim}} - B), \quad (1)$$

where B was a non-conservative quantity (one of the nine components in the biological model), w was the vertical advective velocity, w_{biology} was the vertical sinking or migration rate of the biological component, K_z was a vertical diffusion coefficient, S was the source or sink term for B , and r_{nudge} was the rate at which the biological component was restored back to B_{clim} , the climatological mean of the biological component.

Detrital sinking rates are difficult to estimate due to the size and dependence on the trophic origin associated with the sinking rates of detrital material [*Michaels and Silver, 1988*]. Hence the model retained only those portions of detrital material which have observed sinking rates slow enough to be retained in the upper ocean for longer than the observed detrital recycling time of 10 days. Specifically, zooplankton fecal material was not allowed to enter into the detrital pool but was assumed to sink rapidly out through the bottom of the model domain. The remainder of the detrital material, which consisted only of dead plankton, had a sinking rate of 1 m d^{-1} . The vertical sinking rates for the large (1 m d^{-1}) and small (0.1 m d^{-1}) phytoplankton size fractions were based on laboratory measurements given by *Smayda [1970]*, *Bienfang and Szyper [1982]*, and *Smetacek [1985]*. Because no vertical migration was observed to occur in the CTZ, the zooplankton portion of the model was not given any vertical migration behavior [*Huntley et al., 1995*]. The source and sink terms, S , for the biological processes of the model were adapted for the CTZ from the time-dependent biological model of *Hofmann and Ambler [1988]*. Detailed descriptions of these are presented in later sections.

The model described by equation (1) was implemented in a 100-m-deep domain. Simulations were extended for 60 days to assure that a steady state was reached.

2.2. Vertical Velocity and Diffusion

The range of vertical advective velocities used in the model simulations were obtained from simulated velocity fields generated by a regional primitive equation circulation model that simulated the circulation conditions in the CTZ [*Haidvogel et al., 1991a, b*]. The upper 100-m depth-dependent vertical velocities from this model were nearly linear, with maximal absolute velocities at 100 m and zero velocity at the surface.

A linear fit of these simulated vertical velocities obtained a correlation coefficient of 0.93. The structure of the vertical velocity field in the upper ocean due to long wavelike processes is close to linear and decays to zero at the sea surface. Because of these simulations and observations, the vertical velocity field in the model simulations was set to zero at the surface and increased or decreased linearly with depth to a maximum absolute value at 100 m. The range of possible vertical velocities at 100 m, the bottom of the domain, was obtained from the simulated circulation distributions described by *Haidvogel et al. [1991a]*. The linear increase (decrease) in vertical advection with depth was balanced by a constant horizontal convergence (divergence) throughout the upper 100 m.

Figure 2. Schematic of the nitrogen pathways to and from the model biological components incorporated into the time- and depth-dependent physical-bio-optical model. For simplicity, the loss pathways due to sinking are not shown.

While both upwelling and downwelling are observed in the CTZ, the vertical velocity in the model simulations was set to zero unless otherwise specified. This allowed investigation of the interactions among biological and optical properties independent of the circulation effects. We also did not investigate the net effect of a varying upwelling and downwelling velocity field on the food web. The focus of the simulations in each region was on biological processes and food web interactions. Also, for most of the offshore regions of the CTZ, vertical velocities are reduced and have a minor effect on the biological processes. The specific effects of circulation are investigated in the accompanying papers [Moisan *et al.*, this issue; Moisan and Hofmann, this issue].

The vertical diffusion parameter, K_z , was set at a constant value of $1 \text{ cm}^2 \text{ s}^{-1}$. This value is lower than the range of values used in the 3-D circulation model, 5 to $25 \text{ cm}^2 \text{ s}^{-1}$ [Hardvogel *et al.*, 1991a; Moisan *et al.*, this issue]; however, it is within the range of values used to model other upwelling regions such as off the coast of Oregon [Wroblewski, 1977, 1983]. This value of $1 \text{ cm}^2 \text{ s}^{-1}$ is also the observed mean value off the Oregon Coast, a coastal upwelling region not unlike that of the California coast [Halpern, 1974].

2.3. Climatological Nudging

The biological components in the model were forced back to a specified background climatology, B_{clim} over a time rate, r_{nudge} , of 100 days. The background climatologies for both the nitrate and silicate concentrations were set to the initial conditions. All other biological component background climatologies were set to zero. By setting the background climatologies of the biological fields to zero, the resulting biological fields are then a result of the biological forcing and not a result of the climatological forcing.

The climatological nudging term was introduced for two reasons. First, the climatological nudging term was introduced to account for those physical and biological processes which the 1-D model was unable to resolve. One specific process which the 1-D model was unable to resolve was the horizontal advection and diffusion of nutrients. Second, a climatological nudging term was included in the 3-D circulation model [Hardvogel *et al.*, 1991a], for which the 1-D model was being developed [Moisan *et al.*, this issue]. The inclusion of the climatological nudging term in the 1-D model made the 1-D model's system of equations consistent with those in the 3-D model. Finally, because the climatological nudging had a long timescale (100 days), its effect on the time rate of change of the model simulations was insignificant.

2.4. Biological Processes

2.4.1. Phytoplankton. The model includes two groups of phytoplankton. The large ($> 5 \mu\text{m}$) phytoplankton size fraction represents a typical silicate- and nitrate-dependent neritic-type diatom that grows best under high nutrient and light conditions. In contrast, the small ($< 5 \mu\text{m}$) phytoplankton size fraction represents a typical, nonsilicate-, nitrate-dependent, oceanic-

type flagellate that grows best under low nutrient and low light conditions. These phytoplankton size fractions represent the dominant taxa observed in the CTZ [Hood *et al.*, 1990, 1991; Chavez *et al.*, 1991]. The concentration and relative abundance of these two size fractions changed in response to differences in growth and loss processes:

$$S = \text{Growth} - \text{Respiration} - \text{Death} - \text{Grazing}, \quad (2)$$

where the first two processes represent net production. Phytoplankton net production is obtained from estimated carbon uptake rates ($\text{mg C (mg chlorophyll } a)^{-1} \text{ s}^{-1}$). The phytoplankton net production rates were then used to estimate a nitrogen uptake rate by assuming a constant C:N Redfield ratio of 6. Carbon uptake rates were obtained in the CTZ by Hood *et al.* [1991].

Net primary production rates were calculated using a relationship modified from Platt *et al.* [1980] which allows for nutrient limitation, diurnal variation and photoinhibition. This relationship is of the form

$$PP(z, t) = L(z, t)N(z, t)P_s^B(t) \left[1 - \exp\left(\frac{-\alpha(t)\text{PAR}(z, t)}{P_s^B(t)}\right) \right] \exp\left(\frac{-\beta(t)\text{PAR}(z, t)}{P_s^B(t)}\right). \quad (3)$$

The terms on the right side of equation (3) represent nutrient limitation (L), the time- and depth-dependent phytoplankton concentrations (N), and the biomass normalized nitrogen uptake rate,

$$P_s^B(t) = \frac{P_{\text{max}}(t) \left[(\alpha(t) + \beta(t))/\alpha(t) \right]}{\left[\beta(t)/(\alpha(t) + \beta(t)) \right]^{(\beta(t)/\alpha(t))}}, \quad (4)$$

where the P_{max} is the maximum realized photosynthetic rate normalized to biomass ($\text{mg N (mg N)}^{-1} \text{ s}^{-1}$), α is the initial slope of the P/I curve ($\text{mg N (mg N)}^{-1} (\text{E m}^{-1} \text{ s}^{-1})^{-1}$), and β is the photoinhibition ($\text{mg N (mg N)}^{-1} (\text{E m}^{-1} \text{ s}^{-1})^{-1}$). The final term in equation (3) is modified by the underwater photosynthetically available radiation ($\text{PAR}(z, t)$).

The formulations used for estimating primary production were based on standard photosynthesis versus irradiance models which give a relationship between the rate of photosynthesis and irradiance. For this study, photosynthesis versus light measurements obtained for the CTZ [Hood *et al.*, 1991] were used to parameterize the model. These parameters also contain a diel periodicity which was modeled using the empirical equation given by MacCaull and Platt [1977]. This diel periodicity is consistent with the CTZ observations. The form of this equation is

$$v(t) = v_{\text{max}} \left[b_m + b_a 2^{-n} \left(1 + \cos\left[\frac{2\pi}{24}(t - b_p)\right] \right)^n \right] \quad (5)$$

and the values for each of the parameters are given in Table 1.

Table 1. Values of the Parameters Used For the Large and Small Phytoplankton Diurnal Photosynthetic Relationships

$v(t)$	Units	$v_{\max}$	b_m	b_a	b_p, hours	n
$P_{\max \text{LPP}}$	s^{-1}	1.042×10^{-4}	0.25	0.75	12	1
$P_{\max \text{SPP}}$	s^{-1}	2.430×10^{-5}	0.90	0.10	12	1
α_{LPP}	$(\text{E m}^{-1} \text{s}^{-1})^{-1}$	6.944×10^{-1}	0.90	0.10	12	2
α_{SPP}	$(\text{E m}^{-1} \text{s}^{-1})^{-1}$	1.736×10^{-1}	0.90	0.10	12	2
β_{LPP}^a	$(\text{E m}^{-1} \text{s}^{-1})^{-1}$	5.555×10^{-3}	1.00	0.00	12	1
β_{SPP}^a	$(\text{E m}^{-1} \text{s}^{-1})^{-1}$	8.333×10^{-3}	1.00	0.00	12	1

Subscripts are LPP, large phytoplankton, and SPP, small phytoplankton

^aThe parameters β_{LPP} and β_{SPP} did not show time variability.

Phytoplankton nutrient dependence was assumed to follow Michaelis-Menten kinetics for both size fractions [Davis *et al.*, 1978; Dugdale *et al.*, 1981]. Because the model contained three nutrients (nitrate, silicate and ammonium), a multiple nutrient limitation model with a “threshold” (i.e., Liebig’s “law of the minimum”) relation [DeGroot, 1983] was used. Thus the nutrient limitation term in equation (3) is obtained from

$$L(z, t) = \text{MIN} \left[\frac{[\text{SiO}_4] - SC}{KS + [\text{SiO}_4] - 2SC}; \frac{f[\text{NO}_3^-]\sigma}{[\text{NO}_3^-] + KN} + \frac{(1-f)[\text{NH}_4^+]}{[\text{NH}_4^+] + KA} \right], \quad (6)$$

where $[\text{SiO}_4]$, $[\text{NO}_3^-]$ and $[\text{NH}_4^+]$ are the concentrations (mg m^{-3}) of silicate, nitrate, and ammonium, respectively, at a given depth and time, and SC is the critical concentration of silicate for the specific phytoplankton size fraction, below which no growth will occur. The existence of a critical silicate concentration for phytoplankton growth in the CTZ is suggested by the lack of silicate values below approximately $1 \mu\text{mol SiO}_4^-$ [Moisan, 1993]. The lack of a critical silicate concentration for phytoplankton growth would allow the phytoplankton to use silicate at lower concentrations, and therefore the silicate values in the CTZ would be lower than that observed. The remaining coefficients in the Michaelis-Menten expressions in equation (6) are defined in Table 2.

The coefficient σ in equation (6) is the fraction of the total nitrogen used by the specific phytoplankton size class relative to the concentration of ammonium and

is specified using the “flip switch” relationship of McCarthy [1981]. As ammonium concentrations increase, more of the required nitrogen needed to support phytoplankton growth comes from the ammonium portion of the total available nitrogen pool.

The final part of the nutrient limitation term, f , is the depth-dependent f ratio [Harrison *et al.*, 1987]. This term indicates the relative effect of nitrate- versus ammonium-based primary production and is given by

$$f = \frac{\frac{[\text{NO}_3^-]\sigma}{[\text{NO}_3^-] + KN}}{\frac{[\text{NO}_3^-]\sigma}{[\text{NO}_3^-] + KN} + \frac{[\text{NH}_4^+]}{[\text{NH}_4^+] + KA}}, \quad (7)$$

where the terms and coefficients have been defined previously. The f term is used to partition the primary production rates of the large and small phytoplankton into regenerated (ammonium derived) and new (nitrate derived) production.

The final processes included in the phytoplankton equation represent losses due to cell death and zooplankton grazing. Cell death consists of processes such as cell autolysis or disease (e.g., viral infections). Measurements from the CTZ that can be used to parameterize these processes are not available. Thus phytoplankton loss was assumed to have a linear dependence on phytoplankton concentration. The rate of cell death was further assumed to be 10% per day for both phytoplankton size fractions. This rate is consistent with that used in other biological models [e.g., Hofmann and Ambler, 1988]. Losses due to zooplankton grazing were obtained as described in the following section.

Table 2. Definition, Value, Units and Source For the Coefficients in Michaelis-Menten Relationships Used in the Phytoplankton Nutrient Limitation Terms

Name	Definition	LLP Value ^a	SPP Value ^a	Units
SC	critical SiO_4^+ concentration	18.62 ^b	00.00 ^e	$\text{mg SiO}_4^- \text{m}^{-3}$
KS	SiO_4^+ half-saturation constant	47.18 ^b	00.00 ^e	$\text{mg SiO}_4^- \text{m}^{-3}$
KN	NO_3^- half-saturation constant	42.00 ^c	26.60 ^c	$\text{mg NO}_3^- \text{m}^{-3}$
KA	NH_4^+ half-saturation constant	32.62 ^d	8.12 ^d	$\text{mg NH}_4^+ \text{m}^{-3}$

^aLPP, large phytoplankton; SPP, small phytoplankton

^bPaasche [1973a, b]

^cMacIsaac and Dugdale [1969]

^dEppley *et al.* [1969]

^eNo silicate limitation for the small phytoplankton.

2.4.2. Zooplankton. The zooplankton distributions obtained during the CTZ field studies [Mackas *et al.*, 1991; Smith and Lane, 1991] indicated that three taxa accounted for a large portion ($\approx 75\%$) of the zooplankton biomass: the herbivorous copepod *Eucalanus californicus*, the omnivorous euphausiid *Euphausia pacifica*, and the gelatinous doliolid *Doliolletta gegenbauri*. These three species provided the basis for the three zooplankton grazers that are included in the biological model. The concentration and relative abundance of these species changes in response to several processes:

$$S = \text{Growth} - \text{Predation Mortality} - \text{Natural Mortality}. \quad (8)$$

Growth results from the sum of the assimilated ingestion and total metabolic losses and may be negative. Predation represents losses from the three zooplankton species through transfers to higher trophic levels. Natural mortality includes processes such as disease. The formulations that were used to describe the processes on the right side of equation (8) for each of the three species are described in the following sections.

2.4.2.1. Copepods: *Eucalanus californicus* is a large copepod, $0.004\text{--}0.6$ mg C animal⁻¹, whose genus can selectively graze prey that are greater than $5\ \mu\text{m}$ [Price and Paffenhöfer, 1983, 1984; Mackas *et al.*, 1991]. Therefore in this model, *E. californicus* ingests only the largest phytoplankton size fraction. Ingestion rates as a function of prey concentration measured specifically for *E. californicus* are not available. Therefore ingestion rates for this animal were obtained using values measured for *Calanus pacificus*, a copepod of similar size

and trophic state. The grazing rates for *C. pacificus* [Frost, 1972, 1975, 1980, 1985, 1988; Smith and Lane, 1988; Vidal and Smith, 1985; Downing and Rigler, 1984] were used with an Ivlev-type model to obtain the time- and depth-dependent ingestion rate,

$$I(z, t) = N(z, t)I_{\max} [1 - \exp[-\delta(\text{FOOD}(z, t) - \text{Th}^I)]] \quad (9)$$

where $N(z, t)$ represents the concentration of copepods. The definition and values used for the parameters that define the Ivlev grazing curve are given in Table 3. The effect of the available prey on the grazing rate was included through $\text{FOOD}(z, t)$ which represented the ambient concentration of large phytoplankton at a given depth and time. For values of $\text{FOOD}(z, t)$ less than the grazing threshold, the ingestion rate is zero. The ingestion rate was further constrained with a mass balance requirement, such that the amount of food ingested in a time step cannot exceed the available food.

The efficiency with which the copepod assimilates food was assumed to vary with ingestion rate and hence food concentration. The formulation, suggested from the data presented by Landry *et al.* [1984], assumed that the assimilation efficiency, $AE(z, t)$, varied between a minimum and maximum value as

$$AE(z, t) = (AE_{\max} - AE_{\min})\exp[-\tau I(z, t)] + AE_{\min}, \quad (10)$$

where $AE_{\max}$ and $AE_{\min}$ are the maximum and minimum assimilation efficiencies, respectively. The assimilation efficiency decreases or increases exponentially between these bounds with an e-folding scale, τ , that is

Table 3. Values, Units and Definitions For the Parameters Used In the Equations to Calculate Growth, Ingestion, Egestion, Predation, Death, Molting and Reproduction Rates For the Copepod *Eucalanus californicus*, the Euphausiid *Euphausia pacifica*, and the Doliolid *Doliolletta gegenbauri*

Parameter	Definition	Copepod	Euphausiid	Doliolid	Unit
M	nitrogen mass per animal	0.1167	0.375	0.01953	mg N (animal) ⁻¹
DW	dry weight per animal	1.6091	3.205	0.1953	mg dry wt (animal) ⁻¹
C:N	carbon to nitrogen ratio	3.9	3.9	4.2	mmol C (mmol N) ⁻¹
$F_{\max}$	maximum filtration rate	NA	NA	3.4×10^{-4}	m ³ (animal) ⁻¹ d ⁻¹
$I_{\max}$	maximum ingestion rate	0.2	0.12	NA	d ⁻¹
δ	ingestion e-folding scale	0.105	0.105	NA	(mg N) ⁻¹ m ³
Th_I	ingestion threshold	0.1228	0	NA	mg N m ⁻³
$AE_{\max}$	maximum assimilation efficiency	0.925	0.95	0.95	dimensionless
$AE_{\min}$	minimum assimilation efficiency	0.733	0.70	0.70	dimensionless
τ	assimilation efficiency e-folding scale	7.33×10^6	1.369×10^6	1.466×10^7	(mg N) ⁻¹ m ³
RQ	respiratory quotient	0.97	0.97	0.97	dimensionless
$G_{\max}$	maximum growth rate	0.05	0.036	0.165	d ⁻¹
ζ	growth e-folding scale	0.105	0.105	0.105	(mg N) ⁻¹ m ³
Q_{10}^{molt}	Q_{10} term for molting	NA	1.86	NA	dimensionless
MT_0	maximum molting rate	NA	NA	NA	mg N (animal) ⁻¹ s ⁻¹
$D_{\text{rate}}^{\text{pred}}$	predation mortality rate	0.005	0.0025	0.015	d ⁻¹
ϵ	predation e-folding scale	0.1	0.1	0.1	(mg N) ⁻¹ m ³
Th^P	predation threshold	0.02	0.02	0.07	mg N m ⁻³
$D_{\text{rate}}^{\text{nat}}$	natural mortality rate	0.005	0.0025	0.015	d ⁻¹

^aNA, not applicable.

modified by the ingestion rate, $I(z, t)$. As the ingestion rate increased in response to higher food concentrations, the assimilation efficiency approached its lower bound. The values for the parameters in equation (10) are given in Table 3, and the relationship between assimilation efficiency and food concentration is shown in Figure 3a. The assimilated ingestion was calculated as the product of the assimilation efficiency and ingestion rates. The fraction of ingested food that was not assimilated represents egestion, i.e. fecal pellet formation. The relationship between ingestion, assimilated ingestion, and egestion over a range of food concentrations is shown in Figure 3d.

Metabolic losses were assumed to be the result of excretion, molting, and reproduction. The excretion rate of nitrogenous waste by respiration was obtained using a general relationship suggested by *Omori and Ikeda* [1984] that relates respiration rate, animal body weight, and temperature as

$$Ex(z, t) = \left(\frac{N(z, t)}{M} \right) \left(\frac{DW a (DW)^b RQ 14}{22.4(C:N)} \right), \quad (11)$$

where, DW is the mean animal dry weight, RQ is the respiratory quotient and $(C:N)$ is the carbon to nitrogen ratio. The values $22.4 \text{ (L O}_2 \text{ mol}^{-1})$ and $14 \text{ (mg N mol}^{-1})$ convert the respiration rate into the appropriate units. The definition and values of the parameters used in equation (11) are given in Table 3. The effect of the ambient temperature on the respiration rate is included through the coefficients that modify the effect of the animal dry weight, DW , where

$$\begin{aligned} a &= 10^{0.02438 \text{ TEM}(z, t) - 0.1838} \\ b &= -0.01090 \text{ TEM}(z, t) - .1082, \end{aligned}$$

where $\text{TEM}(z, t)$ is the ambient temperature at a given depth and time. The formulations for a and b are obtained from the general relationship suggested by *Omori and Ikeda* [1984], and the values obtained from this equation for *Eucalanus californicus* compare well with other derived general respiration curves specific to copepods [Dagg et al., 1982; Vidal and Whitledge, 1982; Vidal, 1980a].

The loss of nitrogen due to molting was estimated from a growth- and temperature-dependent relationship that is obtained for *Calanus pacificus* [Vidal, 1980b] and is of the form

$$MT(z, t) = \begin{cases} \frac{N(z, t)}{M} (a + bGM) & G > 0 \\ \frac{N(z, t)}{M} aM & G \leq 0 \end{cases}, \quad (12)$$

where the effect of temperature is introduced through the empirical coefficients

$$\begin{aligned} a &= -0.371 + 0.586 \log(\text{TEM}(z, t)) \\ b &= 0.02192 + 0.001278 \text{ TEM}(z, t). \end{aligned}$$

Relationship (12) depends on the animal growth rate, G , which is the assimilated nitrogen remaining after respiration losses. For times when the respiration rate exceeded the assimilation rate, the term was negative; i.e. starvation occurred. As a consistency check, the optimal growth rate at a given food concentration was obtained from an Ivlev-type growth relationship which was empirically derived from the growth relationship given by Vidal [1980a, b, c, d] as

$$G^{\text{opt}} = N(z, t) G_{\text{max}} [1 - \exp[-\zeta(\text{FOOD}(z, t) - \text{Th}^1)]]. \quad (13)$$

Figure 3. Relationship between the processes included in the zooplankton portion of the model at 10°C for a range of food concentrations. Assimilation efficiency for (a) copepods, (b) doliolids, and (c) euphausiids. Ingestion, assimilated ingestion, growth, reproduction, egestion, reproduction, and molting rates for (d) copepods, (e) doliolids, and (f) euphausiids.

The definition and values for the parameters in equations (12) and (13) are given in Table 3. The actual growth rate used to determine the molting rate was specified using the minimum of the optimal and calculated growth rate in order to ensure mass conservation. The dependence of the growth rate and the molting rate on food concentrations at a given temperature (10°C) is shown in Figure 3d.

The nitrogen loss due to reproductive processes was assumed to be the fraction of assimilated ingestion remaining after the demands of respiration, molting and growth were met [Runge, 1985]. Reproduction was allowed only during periods of positive growth. This dependence of reproductive rate on food concentration is shown in Figure 3d.

The mortality due to predation by higher trophic levels and other natural causes was assumed to be dependent on the concentration of the zooplankton *E. californicus* and to increase to a maximal predation rate at some prey concentration. As discussed in the next section, *E. californicus* was grazed by *Euphausia pacifica* as well, because *Euphausia pacifica* feed preferentially on copepods [Price et al., 1988]. Thus predation losses are given by

$$D_{\text{pred}}(z, t) = \text{EuphausiidPredation} + N(z, t) D_{\text{rate}}^{\text{pred}} [1 - \exp[\epsilon(\text{Th}^P - N(z, t))]]. \quad (14)$$

As with the ingestion rate, predation by other predators was assumed to cease below some threshold concentration Th^P of *E. californicus*. The definition and values used for the coefficients in the predation equation are given in Table 3. Natural mortality, the final loss term, was assumed to be a linear function of population concentration such that:

$$D_{\text{nat}}(z, t) = N(z, t) D_{\text{rate}}^{\text{nat}}. \quad (15)$$

E. californicus has an average life span of 60–120 days. Therefore the weight specific natural mortality rate, $D_{\text{rate}}^{\text{nat}}$, was chosen such that in the absence of starvation and predation, the turnover time of the population was within the average life span. The actual value is given in Table 3.

2.4.2.2. Euphausiids: Euphausiids are large (0.3–4 mg C animal⁻¹), omnivorous zooplankton that feed over a wide range of particle sizes that includes small net phytoplankton up to large copepods and fish larvae [Price et al., 1988]. *Euphausia pacifica* is the most abundant euphausiid off the California coast [Mackas et al., 1991; Smith and Lane, 1991; Lasker, 1966]. Therefore total ingestion for this animal included the herbivorous copepod and the large phytoplankton fraction. Ingestion rates for *E. pacifica* reported by Lasker [1966] and Ross [1982a, b] were used with an Ivlev-type model to obtain ingestion rates for a range of concentrations of food. The parameters are defined as those in the *E. californicus* ingestion equation (9), and the values are given in Table 3. One difference between the euphausiid ingestion equation and that used for *E. californicus* is the

inclusion of a weighting factor, $HC(z, t)$, that allowed *E. pacifica* to have a relative preference for copepods versus phytoplankton. This factor is based upon measurements given by Ohman [1988] and Price et al. [1988] and is defined as

$$HC(z, t) = \frac{N_{\text{LPP}}(z, t)}{3N_{\text{COP}}(z, t) + N_{\text{LPP}}(z, t)}. \quad (16)$$

As the relative abundance of the *E. californicus* increases, *E. pacifica* will feed more preferentially on the copepod fraction than on the large phytoplankton fraction.

The relationship between ingestion rate and assimilation efficiency for *E. pacifica* [Lasker, 1966] was similar to that used for *E. californicus*. The values for the parameters in the assimilation efficiency relationship were modified using the values for *E. pacifica* given by Lasker [1966] and are given in Table 3. The relationship among these three quantities for a range of food concentrations for *E. pacifica* is shown in Figure 3b.

The partitioning of assimilated ingestion into growth and metabolic losses for *E. pacifica* was assumed to be governed by relationships similar to those used for *E. californicus*. Excretion rates for nitrogenous waste by respiration for *E. pacifica*, obtained from equation (11), compared well with field and laboratory measurements given by Lasker [1966], and Ross [1981, 1982a, b, c] for *E. pacifica*. The parameters in the excretion equation were defined as for those in the *E. californicus* excretion equation, and the values are given in Table 3.

The loss of nitrogen due to molting was estimated from a relationship that is obtained for *E. pacificus* [Ross, 1982a, b] and is of the form

$$MT(z, t) = N(z, t) MT_0 (Q_{10}^{\text{molt}})^{(\text{TEM}(z, t)/10)}, \quad (17)$$

where MT_0 is the extrapolated molting rate at 0°C and Q_{10}^{molt} is the calculated Q_{10} value for the molting process. The values used for the parameters in equation (17) are given in Table 3. Unlike the *E. californicus* molting equation, the above relationship did not depend on animal growth because molting is a continuous process in *E. pacifica*, even during periods of starvation [Ross, 1981].

The growth rate was calculated similar to that of the copepod but relied upon measurements given by Ross [1981, 1982a, b]. The parameters are given in Table 3. The dependence of the molting rate and the growth rate on food concentrations at a given temperature is illustrated in Figure 3e.

The nitrogen loss due to reproductive processes was assumed to be the remaining fraction of assimilated ingestion after respiration, molting, and growth have been removed. Reproduction was allowed only during periods of positive growth. This dependence of reproductive rate on food concentration is shown in Figure 3e.

Both predation and natural mortality losses were calculated in a fashion similar to those of the copepods. *E. pacifica* has an average life span of 210–236 days [Ross, 1982b]. Therefore the natural mortality rate was

chosen such that in the absence of starvation and predation, the turnover time of the population was within the average lifespan. The values of the parameters used to estimate both these mortality terms are given in Table 3.

2.4.2.3. Gelatinous zooplankton: The doliolid *Doliolletta gegenbauri* is a nonselective filter feeder and is capable of ingesting both large (being constrained only by the diameter of its aperture [Deibel, 1982b]), and small phytoplankton ($< 5 \mu\text{m}$) fractions and detritus [Deibel, 1985]. Unlike the copepod and euphausiid animals, the ingestion rate of the doliolid is dependent upon the animal's filtration rate, which is limited by the flux of water through the animal's aperture. Thus the filtration rate of water, $F_{\text{DOL}}(z, t)$, for a doliolid of average size, M_{DOL} , was expressed as

$$F(z, t) = F_{\text{max}} \exp[-0.01 N_{\text{LPP}}(z, t)], \quad (18)$$

where F_{max} is the maximum volume flux through the aperture. The exponential term represents the decrease in flux due to the clogging of the animal's filtration mechanism by the large phytoplankton fraction [Madin, 1974; Deibel, 1982b]. The ingestion of food was obtained as

$$I(z, t) = \frac{N(z, t)}{M} F(z, t) \text{FOOD}(z, t) \quad (19)$$

where $\text{FOOD}(z, t)$ is the depth- and time-dependent concentrations (mg N m^{-3}) of the large and small zooplankton size fractions and the detritus pool. The values of the parameters in the ingestion equations are given in Table 3.

The assimilation efficiency was assumed to follow the same relationship used for *E. californicus*, and the parameters are given in Table 3. The relationships among these three quantities for a range of food concentrations are shown in Figures 3c and 3f.

The partitioning of assimilated ingestion into growth and metabolic losses was assumed to be governed by relationships similar to those used for *E. californicus*. Excretion of nitrogenous waste by respiration was obtained using a general relationship suggested by Omori and Ikeda [1984] that relates respiration rate, animal body weight, and temperature. The parameters in the excretion equation were defined as those in the *E. californicus* excretion equation, and the values are given in Table 3. Doliolids do not molt; therefore nitrogen loss due to molting was not included as a metabolic process for this animal.

The growth rate was the assimilated nitrogen remaining after respiration losses. For times when the respiration rate exceeded the assimilation rate, the growth was negative; i.e., starvation occurred. As a consistency check, the optimal growth rate at a given food concentration was obtained from an Ivlev-type growth relationship which was empirically derived from the growth relationship from the field and laboratory measurements given by Heron [1972a, b], and Deibel [1982a, b, 1985]. The parameters were defined similar to those used in the *E. californicus* optimal growth relationship (equation (12)), and the values are given in Table 3.

The dependence of growth on food concentrations at a given temperature is illustrated in Figure 3f.

The nitrogen loss due to reproductive processes was assumed to be the remaining fraction of assimilated ingestion after respiration and growth have been accounted for. Reproduction was only allowed during periods of positive growth. The dependence of reproductive rate on food concentration is shown in Figure 3f.

Both predation and natural mortality losses were calculated in a fashion similar to those of the copepods. *D. gegenbauri* has an average life span of 21–42 days [Heron 1972a]. Therefore the natural mortality rate was chosen such that in the absence of starvation and predation, the turnover time of the population was within the average life span. The values of the parameters used to estimate the mortality terms are given in Table 3.

2.4.3. Detritus. Detritus was included both as a closure term for the nitrate pool and as a food supply for the doliolids. Sources of detritus were provided by phytoplankton and zooplankton mortality. Detritus was removed by ingestion by *D. gegenbauri* and recycling into ammonium. Greater than 90% of the total detritus pool is recycled within the euphotic zone [Wada and Hattori, 1991]. For this study, we assumed the process to be a linear function of the concentration of detritus such that the mean turnover time of the detritus pool is 10 days. This turnover time is within the range of that observed in the Southern California Bight, where the recycling time of particulate organic matter in the surface layer is fairly uniform at about 11 days [Eppley et al., 1983]. A second detritus turnover timescale of 100 days is also introduced with the inclusion of the climatological nudging term.

2.4.4. Nutrients. Phytoplankton nitrate uptake was the only biological process which affected the concentration of nitrate. The rate of this process was governed by the amount of primary production and the f ratio of the two phytoplankton size. As the f ratio increases, more of the nitrogen that is required to support phytoplankton growth comes from the available nitrate.

Inputs to ammonium pool come from the sum of all the respiratory waste from the three zooplankton in the model and detritus recycling. Removal of ammonium by phytoplankton uptake was governed by the amount of primary production and the f ratio of the two phytoplankton size fractions.

Phytoplankton silicate uptake was the only biological process which affected the silicate concentration. This removal rate was calculated from the rate of nitrate uptake and the slope of the silicate to nitrate relationship in the CTZ region. The change in the slope of this relationship results from changes in species composition within the different water masses. Silicate-dependent diatoms, e.g., *Chaetoceros* sp., are dominant in the nutrient-rich waters along the coast, while nonsilicate-dependent phytoplankton, e.g., *Synechococcus* sp., are dominant in the nutrient-poor waters; therefore the uptake of silicate is higher in the nutrient rich waters. Dissolution of silicate from the detritus fraction was assumed to be unimportant given the short generation time of a filament relative to the timescale associated with the dissolution process.

2.5. Optical Model

The bio-optical portion of the model determined the magnitude of the subsurface irradiance field, which varied with depth, wavelength, and time. Both the direct and diffuse components of spectral irradiance at the sea surface were calculated using a simple, wavelength-dependent, solar model for direct normal and diffuse horizontal irradiance [Bird, 1984]. The wavelength-dependent subsurface irradiance field was calculated using the model of Sathyendranath and Platt [1988]. Light attenuation in this model occurs as a function of three major groups of light-absorbing substances: pure seawater, nonchlorophyllous particles and chlorophyllous particles. Specific to this model, the absorption due to gelbstoff and nonchlorophyllous particles is neglected due to low freshwater runoff from the coast in the CTZ. The absorption spectra for the large and small phytoplankton were reconstructed using the technique outlined by Bidigare *et al.* [1990] and are shown in Figure 4. A more detailed description of the bio-optical model is presented by Moisan [1993].

2.6. Model Implementation

2.6.1. Numerical integration. A spectral collocation method was used to solve the system of equations that define the physical-bio-optical model. This provides consistency with the approach used to obtain so-

lutions to the circulation model [Hardvogel *et al.*, 1991a] that provided input to this model. A sigma coordinate transformation was made for the vertical coordinate. This allowed the vertical dependence of the model components to be represented as an expansion of a modified, finite Chebyshev polynomial basis set. The collocation method explicitly solved for the variables at actual collocation points. The collocation points were chosen to correspond to the location of the extrema of the highest-order polynomial. A more complete description of this spectral technique is given by Hardvogel *et al.* [1991b] and Hedström [1990].

The time integration of the model was started with an initial forward time step using an Euler approximation, after which the model was integrated forward through time using a leapfrog technique. A trapezoidal correction step was taken every 30 time steps to avoid mode splitting. Hedström [1990] presents a complete description of this time-stepping technique.

2.6.2. Boundary conditions. The top boundary of the model domain represented the ocean surface and a free-slip boundary condition was used which did not allow material to cross the boundary but did allow for diffusion to occur below the surface. The boundary condition at the bottom of the model domain was more complicated. For periods of downwelling the model used an upwind differencing scheme to calculate the first derivative. During periods of upwelling or no vertical motion, the model used a false boundary to relax back to a constant observed deep water value. The value of the false boundary was set to the initial condition for the inorganic nutrients but was set to zero for all other model constituents.

2.6.3. Initial conditions and model simulations. The initial temperature, salinity, nitrate, silicate, and chlorophyll *a* profiles used in the simulations were obtained from measured distributions from a coastal and oceanic region in the CTZ (Figure 1). The regions were chosen based upon the water mass source definitions given by Strub *et al.* [1991]. All coastal simulations were initialized with cold ($< 10.3^{\circ}\text{C}$), high nutrient ($> 12 \mu\text{mol NO}_3^-$; $> 20 \mu\text{mol SiO}_4^{2-}$), and high chlorophyll concentration ($> 10 \text{ mg chlorophyll } a \text{ m}^{-3}$) water. All oceanic simulations were initialized with warm ($> 14.3^{\circ}\text{C}$), low nutrient ($< 0.1 \mu\text{mol NO}_3^-$; $< 0.2 \mu\text{mol SiO}_4^{2-}$), and low chlorophyll concentration ($< 0.02 \text{ mg chlorophyll } a \text{ m}^{-3}$) water. Partitioning of the chlorophyll between the large and small phytoplankton size fractions was accomplished using the size fraction to chlorophyll relationship of Chavez *et al.* [1991].

Because no information was available on the specific concentration of zooplankton in each region, the initial concentration of copepods, euphausiids, and doliolids was set to 10% of that of their prey items. Both initial ammonium and detritus concentrations were set to constant low values of 1.4 mg N m^{-3} and 14 mg N m^{-3} , respectively, for the coastal simulations and 0.14 mg N m^{-3} and 1.4 mg N m^{-3} , respectively, for oceanic simulations. For each simulation, the initial distributions were then allowed to evolve in the upper 100 m of the water column for 100 days.

Figure 4. Reconstructed in vivo weight-specific absorption spectra for both the large and small phytoplankton size fractions.

Table 4. Summary of the Sensitivity Analysis Results Showing the Range of Values Obtained for the Euphotic Zone (EZ) Depth, Deep Chlorophyll Maximum (DCM) depth (m), and Total Integrated New (NPP) and Regenerated (RPP) Primary Production Rates ($\text{mg C m}^{-2} \text{d}^{-1}$)

Parameter	Parameter Range ^a	EZ	DCM	NPP	RPP
Vertical advection	-5–5 (0) m d^{-1}	11–51	10–30	66–135	347–1516
Vertical diffusion	1–25 (1) $\text{cm}^2 \text{s}^{-1}$	15–27	0–25	84–141	848–971
Incident PAR	20–200 (100) % incident	26–29	10–30	26–109	196–1208
Sinking rates	0–500 (100) % estimated	27–39	25–40	84–117	862–1144
Phytoplankton mortality	0.1–1 (0.1) day^{-1}	31–>100	25–35	33–91	837–1126
Zooplankton grazing	0–200 (100) % estimated	23–33	25	23–118	851–890
Zooplankton mortality	0–0.2 (≈ 0.003) day^{-1}	24–37	25	15–154	840–924
Detritus recycling	0.1–0.5 (0.1) day^{-1}	13–31	5–25	92–549	220–901

^aValues within parenthesis are those used in the coastal and oceanic simulation.

The simulations run with the model are divided into two parts. In the first part, the model sensitivity to changes in parameters and processes was explored. The processes included in the food web and bio-optical models described earlier are based on formulations that contain approximately 150 parameters. Values for the majority of these parameters were specified using laboratory or field measurements, many of which were from studies within the CTZ. However, some of these processes, such as zooplankton mortality and detrital recycling efficiency, were based upon formulations that include unknown, poorly known, or poorly constrained parameters. Often, these processes are those that control the input or removal of material at the lower and upper end of the food web. Therefore the sensitivity analysis of the food web and bio-optical model focused on those processes that control the rate of flow of nitrogen through the food web: vertical advection, vertical diffusion, incident PAR, phytoplankton cell and detritus sinking rates, phytoplankton mortality, zooplankton grazing, zooplankton mortality and detritus recycling efficiency.

Model sensitivity to each of the processes tested was obtained after 100 days of simulation. The results were quantified by comparing the depth of the euphotic zone (1% PAR), chlorophyll maximum and the total integrated [0 to 100 m] regenerated and new primary production for both phytoplankton size fractions. The exact range of values tested is shown in Table 4. For all sensitivity analysis simulations, the coastal initial conditions were used.

The second part of the 1-D model simulations investigated the physical-bio-optical interactions that occur at specific locations (coastal and oceanic) within the CTZ. Because these are the extreme conditions observed within the CTZ, comparison of the results obtained from these simulations provided insight into the mechanisms controlling the temporal and spatial development of the plankton populations within the CTZ. In this way, the model was also used to validate the parameterizations used to estimate the biological source and sink terms in the CTZ. With this in mind, the model has served as a testing stage in the development of a 3-D, time-dependent physical bio-optical model, the re-

sults of which are presented in *Moisan et al.* [this issue] and *Moisan and Hofmann* [this issue].

3. Results

3.1. Validation of the Bio-Optical Model

Because the biological model was coupled to a bio-optical model, we felt it was necessary to demonstrate the ability of the bio-optical model to simulate the underwater PAR field. Incident PAR values over 24 hours were measured at about 10 m above the sea surface during the 1988 CTZ field surveys [C. O. Davis, personal communication, 1990]. The day to day variations in the magnitude of the measured CTZ PAR values at a specific time of day were primarily due to cloud cover. The model simulated PAR values (not shown) at all times of the day were within the range of the measured values for that time. Depth-dependent PAR measurements were also obtained during the 1988 CTZ field studies [C. O. Davis, personal communication, 1990]. These distributions and the corresponding vertical chlorophyll distributions were obtained at both coastal and oceanic environments. The pigment distribution from a coastal station (Figure 5a) was characterized by low surface values of chlorophyll *a* ($1.2 \text{ mg chlorophyll } a \text{ m}^{-3}$) which increased to a maximum of $9.4 \text{ mg chlorophyll } a \text{ m}^{-3}$ at 15 m. High chlorophyll concentrations resulted in a strong attenuation of the PAR (Figure 5c). The estimated mean light attenuation coefficient at this location was 0.18 m^{-1} , which is within the range of values reported for coastal regions [Jerlov, 1976]. Chlorophyll concentrations at the oceanic stations (Figures 5b) were much lower and showed only a slight increase below 20 m. Vertical light attenuation in these locations was reduced, as evidenced by the lower mean attenuation coefficient of 0.08 m^{-1} .

Both coastal and oceanic chlorophyll distributions were used with the bio-optical model to obtain a simulated depth-dependent PAR field. The simulated PAR fields (Figures 5c and 5d) were similar to the actual observed vertical PAR distributions at each location. At the coastal station, the simulated and observed PAR fields were nearly identical. The differences were greater

Figure 5. The vertical distribution of chlorophyll *a* measured during the 1988 CTZ field studies at (a) coastal and (b) oceanic locations, with corresponding (c) coastal and (d) oceanic vertical distribution of PAR. The simulated vertical PAR distributions (dotted line) obtained using the two chlorophyll profiles is also shown. The measured chlorophyll and PAR distributions were provided courtesy of C. O. Davis.

at the offshore location and arose primarily from sensor noise (e.g., ship motion) and variations in cloud cover. On the basis of these comparisons, it was assumed that the bio-optical model adequately reproduced the observed surface and depth-dependent PAR fields for both coastal and oceanic regions in the CTZ.

3.2. Sensitivity Analysis

Model sensitivity was explored in order to gain insight on the bio-optical and food web dynamics and to determine the extent to which changes in the parameters and processes modified the model results. Several non-linear interactions in the 1-D model were observed, even though the number of links in the food web, which is defined as the number of nonzero elements in the interaction matrix (Table 5), was low. The results presented below are from a noninclusive group of sensitivity analysis cases which focus on those processes that control the rate of flow of nitrogen through the food web and includes: vertical advection, vertical diffusion, incident PAR, phytoplankton cell and detritus sinking, phytoplankton mortality, zooplankton grazing, zooplankton mortality, and detrital recycling. A summary of the sensitivity analyses performed is presented in Table 4.

3.2.1. Vertical advection. Vertical advection is one process which controls the rate at which new nutrients (nitrate and silicate) are made available to the phytoplankton. Within the CTZ, vertical advection can reach maximum upwelling or downwelling velocities of 5 m d^{-1} or more [Kadko *et al.*, 1991]. The effect of vertical velocities over this range (-5 to 5 m d^{-1} ; negative values indicate downwelling) on the model results was tested (Figure 6). Because the model assumed a constant horizontal divergence (convergence) in the water column to calculate the depth-dependent vertical velocities, upwelling (downwelling) also increased (decreased) the vertical gradients of all the model constituents by causing the isopleths to converge (diverge) vertically in the water column. This is shown in Figure 6, where most of the isopleths are more closely spaced in the upwelling simulations.

Nitrate concentrations increased as vertical advection increased from downwelling to upwelling. The nitrate field contained the shallowest and sharpest nutricline at the highest upwelling velocities. Increased nutrient supply at higher vertical velocities allowed the large phytoplankton biomass to increase and caused the euphotic zone to shallow from 51 m to 11 m. The largest change in euphotic zone depth occurred at low absolute ver-

Table 5. Food Web Linkage Matrix

From	To								
	SiO_4^+	NO_3^-	NH_4^+	DET	LPP	SPP	COP	DOL	EUP
SiO_4^+	---	---	---	---	-X-	-X-	---	---	---
NO_3^-	---	---	---	---	-X-	-X-	---	---	---
NH_4^+	---	---	---	---	-X-	-X-	---	---	---
DET	---	---	-X-	---	---	---	---	-X-	---
LPP	---	---	---	-X-	---	---	-X-	-X-	-X-
SPP	---	---	---	-X-	---	---	---	-X-	---
COP	---	---	-X-	-X-	---	---	---	---	-X-
DOL	---	---	-X-	-X-	---	---	---	---	---
EUP	---	---	-X-	-X-	---	---	---	---	---

In the matrix, X denotes a linkage between the food web components. Abbreviations are DET, detritus; LPP, large phytoplankton; SPP, small phytoplankton; COP, copepods; DOL, doliolids; and EUP, euphausiids.

Figure 6. The sensitivity of the model steady-state solution's (a) euphotic zone depth, (b) chlorophyll maximum depth, (c) large and (d) small phytoplankton depth-integrated regenerated (solid line) and new (dashed line) primary production rates, and (e) nitrate, (f) ammonia, (g) detritus, (h) large phytoplankton, (i) small phytoplankton, (j) copepod, (k) doliolid, and (l) euphausiid vertical distributions to changes in vertical advection rates (-5 to 5 m d^{-1}). Contour levels are 2.5 mg N m^{-3} , $0.025 \text{ mg N m}^{-3}$, 5 mg N m^{-3} , $2 \text{ mg chlorophyll } a \text{ m}^{-3}$, $5 \text{ } \mu\text{g chlorophyll } a \text{ m}^{-3}$, 0.5 mg N m^{-3} , 5 mg N m^{-3} , and 0.25 mg N m^{-3} for Figure 6e through 6l, respectively.

tical advection rates. This was the range of vertical velocity values to which the nitrate profile was highly sensitive. It is within this range that the water column changes from one that is primarily nutrient limited (downwelling regions) to one that is primarily light limited (upwelling regions). As a result, it was also the

range of values where the most rapid change in phytoplankton biomass occurred. Small phytoplankton were most concentrated at the downwelling velocities, since they were able to outcompete the large phytoplankton at low nutrient concentrations. However, because of the divergence associated with the downwelling, a

Figure 7. Same as Figure 6, but for changes in vertical diffusion (1 to 25 $\text{cm}^2 \text{s}^{-1}$). Contour levels are 1 mg N m^{-3} , 0.05 mg N m^{-3} , 2.5 mg N m^{-3} , 0.5 $\text{mg chlorophyll a m}^{-3}$, 2 $\mu\text{g chlorophyll a m}^{-3}$, 0.5 mg N m^{-3} , 0.5 mg N m^{-3} , and 0.25 mg N m^{-3} for Figure 7e through 7l, respectively.

deep chlorophyll maximum never formed at the higher rates of downwelling. The divergence also destroyed the sharp nutricline and lowered the rate of upward nutrient flux.

The depth-integrated new primary production rates for both the large and small phytoplankton covaried with the biomass concentrations. This was also observed in the regenerated primary production rates, but to a lesser extent. The increase in primary production in the large phytoplankton was caused by the shallowing of the nutricline. In the small phytoplankton, the

increase was caused by reduced competition for nutrients and decreased grazing pressure.

3.2.2. Vertical eddy diffusion. The sensitivity of the model to changes in vertical eddy diffusion was investigated using vertical eddy diffusion coefficients ranging from 1 to 25 $\text{cm}^2 \text{s}^{-1}$ (Figure 7). This range of values was within the range of estimated ocean vertical eddy diffusion coefficients [Wroblewski, 1977, 1983]. It was also within the range of values observed off the Oregon coast, a coastal upwelling region not unlike that of the California coast [Halpern, 1974].

Vertical eddy diffusion injected nitrate and silicate into the euphotic zone from depth and also smoothed the vertical structure of the biological fields. A sharp, 40 m deep nitracline developed at low diffusivity. At higher diffusivities, the nitrate profiles became linear, and the nitracline disappears. Increased diffusivities caused the large phytoplankton to grow better at the surface, the chlorophyll maximum to shallow from 25 m to the surface, and the euphotic zone to shallow from 27 m to 15 m. No other processes or parameter tested in the sensitivity analysis allowed the chlorophyll maximum to shallow to the surface. At high diffusivities, the phytoplankton were no longer nutrient limited. Also, while photoinhibition did occur at the surface, its effect on the rate of primary production was not enough to keep the chlorophyll maximum from reaching the surface.

3.2.3. Incident PAR. The fraction of incident PAR penetrating the water column also controls the rate of primary production. Decreases and even increases in incident PAR from that observed under clear sky conditions are caused primarily by cloud scattering and absorption. The sensitivity of the model to changes in incident PAR was investigated by varying the incident PAR from 20% to 200% of that measured under clear sky conditions in the CTZ (Figure 8).

The depth of the euphotic zone did not change significantly over the full range of incident PAR values tested. However, the depth of the chlorophyll maximum increased from 10 m to 30 m with increasing PAR values. Increased incident PAR allowed the phytoplankton to grow more rapidly at depth due to increased light at higher nutrient levels. The increase in light also caused the phytoplankton to grow slower at the surface due to the effect of photoinhibition, but this effect on the integrated primary production rates was slight. The increase in growth at depth was significantly higher than the decrease at the surface, and as a result, new primary production rates in both phytoplankton populations increased linearly with increasing PAR values. The increased growth rates resulted in a deeper nitracline, which caused the chlorophyll maximum to also develop at a deeper depth. The phytoplankton and detritus concentrations covaried with changes in PAR. The increase in zooplankton biomass was less than that observed in the phytoplankton because of the low trophic energy transfer efficiencies. In fact, changes in the euphausiid biomass were even smaller because the euphausiids are at an even higher trophic level.

3.2.4. Phytoplankton cell and detritus sinking rates. Model sensitivity to phytoplankton cell and detritus sinking rates was tested over a range of values varying from 0 to 5 times their estimated sinking rates (1, 0.1, and 1 m d⁻¹ for the large and small phytoplankton and detritus, respectively) (Figure 9). Increased sinking rates removed phytoplankton from the upper water column, which resulted in a deeper euphotic zone. Increased sinking rates also moved nutrient-limited phytoplankton into nutrient-rich water. The combination of increased light and nutrient availability allowed the phytoplankton to take up more nitrate.

As the sinking rates increased, the small phytoplankton species dominated over the large phytoplankton, especially within the chlorophyll maximum. Finally, the magnitude of the deep chlorophyll maximum decreased with increasing sinking rates as a result of the decrease in the available light at the depth of the chlorophyll maximum.

3.2.5. Phytoplankton mortality. Algal cell mortality consists of processes such as cell autolysis or disease (e.g., viral infections). Measurements from the CTZ that can be used to parameterize these processes are not available. Model sensitivity was explored over a wide range of phytoplankton mortality rates (0.1–1.0 d⁻¹; Figure 10). The depth of the euphotic zone was very sensitive to the phytoplankton mortality rates. Increased phytoplankton mortality rates caused the euphotic zone to deepen. This was due to the decreased attenuation of light by the phytoplankton biomass.

The zooplankton biomass was inversely related to the phytoplankton mortality rates. At low phytoplankton mortality rates, the zooplankton populations increased and caused the ammonia concentrations to also increase. In the model, ammonia concentrations help control the rate of nitrate uptake. At the low phytoplankton mortality rates, the increased ammonia reduced the nitrate uptake rates. As a result, the nitracline was shallowest at low phytoplankton mortality rates. This reduced modification in nutrient uptake is also observed in the depth-integrated primary production rates.

3.2.6. Zooplankton grazing. The rate of grazing controls the transfer of biomass from the phytoplankton to the zooplankton. Model sensitivity to different levels of grazing pressure was determined by incrementally increasing the grazing pressure on the two phytoplankton from 0% to 200% of their estimated values (Figure 11).

The euphotic zone depth increased with increasing grazing pressure because the zooplankton removed the nutrient-limited, hence slower-growing, phytoplankton from the surface. As a result, the depth-integrated regenerated primary production rates for both phytoplankton also increased due to decreased light attenuation and increased ammonium production. Regenerated primary production increased more than new primary production because of the increased ammonium production. This illustrated one of the nonlinear feedbacks that can occur in marine food webs.

The nonlinear interaction between zooplankton grazing and light attenuation was further illustrated by two sets of simulations that used different vertical velocities and zooplankton grazing rates. In the first set of simulations, no zooplankton grazing was allowed, and the vertical advection was specified at 1 m d⁻¹ upward, 0 m d⁻¹, and 1 m d⁻¹ downward. The simulated depth of the 10% PAR level resulting from these conditions showed little variation over 20 days (Figure 12). However, when grazing was allowed, the 10% PAR level deepened during the 20-day simulation, even for conditions with no vertical advection or upwelling. These results demonstrate that the euphotic zone depth was

Figure 8. Same as Figure 6, but for changes in incident PAR (0 to 200% of the observed incident PAR). Contour levels are 2.5 mg N m^{-3} , 0.05 mg N m^{-3} , 5 mg N m^{-3} , $1 \text{ mg chlorophyll } a \text{ m}^{-3}$, $5 \mu\text{g chlorophyll } a \text{ m}^{-3}$, 0.5 mg N m^{-3} , 0.25 mg N m^{-3} , and 0.25 mg N m^{-3} for 8e through 8l, respectively.

as sensitive to the level of zooplankton grazing as it was to upwelling/downwelling processes.

Changes in the level of zooplankton grazing pressure did not change the depth of the chlorophyll maximum. However, increased grazing pressure did lower the magnitude of the chlorophyll maximum.

3.2.7. Zooplankton mortality. The rate of flow of zooplankton biomass into the detritus pool is controlled by the zooplankton mortality term. Zooplankton mortality results from processes such as starvation,

predation, and disease. Measurements from the CTZ that can be used to parameterize these processes are not available. Model sensitivity to zooplankton mortality was investigated by varying zooplankton mortality rates from 0 to 0.2 day^{-1} (Figure 13).

As in the zooplankton grazing sensitivity analysis case, the depth of the resulting chlorophyll maximum was constant at 25 m for all levels of zooplankton mortality tested. However, unlike the zooplankton mortality cases, the depth of the euphotic zone decreased

Figure 9. Same as Figure 6, but for changes in sinking rates (0 to 500% of the estimated values). Contour levels are 2.5 mg N m⁻³, 0.05 mg N m⁻³, 5 mg N m⁻³, 0.5 mg chlorophyll *a* m⁻³, 5 μg chlorophyll *a* m⁻³, 0.5 mg N m⁻³, 0.1 mg N m⁻³, and 0.25 mg N m⁻³ for 9e through 9l, respectively.

from 37 m to 24 m. This change was caused by the increased zooplankton concentrations at the low zooplankton mortality rates. The increased zooplankton biomass at the low mortality rates grazed down the phytoplankton. However, the increased light, due to decreased phytoplankton, and the increased available nutrients, due to increased light and ammonium, together increased the chlorophyll specific primary production.

3.2.8. Detrital recycling. The recycling of detritus into ammonium provides a nutrient source for the phytoplankton. The rate at which this occurs in the

California region has been observed to be fairly uniform at about 11 days [Eppley *et al.*, 1983]. However, in other regions, such as the southeastern United States, recycling rates have been observed to vary on the order of 3–11 days [Hanson *et al.*, 1990]. Thus the sensitivity of the simulated distributions to changes in the rate (0.1–0.5 day⁻¹) of detrital recycling was explored (Figure 14).

Both the euphotic zone and subsurface chlorophyll maximum shallowed with increased detrital recycling. Variations in recycling rate had the largest effect on

Figure 10. Same as Figure 6, but for changes in phytoplankton mortality (0 to 100 days⁻¹). Contour levels are 2.5 mg N m⁻³, 0.05 mg N m⁻³, 5 mg N m⁻³, 0.5 mg chlorophyll *a* m⁻³, 5 μ g chlorophyll *a* m⁻³, 0.5 mg N m⁻³, 0.1 mg N m⁻³, and 0.5 mg N m⁻³ for 10e through 10l, respectively.

the depth-integrated primary production rates for both phytoplankton. The depth-integrated regenerated primary production rates for the small phytoplankton increased rapidly to a maximum at a detrital recycling rate of 0.3 day⁻¹ and decreased slowly at higher recycling rates. The large phytoplankton, while not as sensitive, showed increasing depth-integrated regenerated primary production rates with increasing detrital recycling rates. The slight decrease in depth-integrated re-

generated primary production for the small phytoplankton at high detritus recycling rates was caused by the shallowing of the large phytoplankton chlorophyll maximum which shaded the deeper small phytoplankton.

The rate of detrital recycling had an opposite effect on the depth-integrated new production. The depth-integrated new production rates for the small phytoplankton decreased with increased recycling rates. This trend was expected because the "flip switch" relation-

Figure 11. Same as Figure 6, but for changes in zooplankton grazing (0 to 200% of the estimated values). Contour levels are 2.5 mg N m^{-3} , $0.025 \text{ mg N m}^{-3}$, 5 mg N m^{-3} , $1 \text{ mg chlorophyll } a \text{ m}^{-3}$, $5 \mu\text{g chlorophyll } a \text{ m}^{-3}$, 0.5 mg N m^{-3} , 0.5 mg N m^{-3} , and 0.25 mg N m^{-3} for 11e through 11l, respectively.

ship between ammonium and nitrate uptake [McCarthy, 1981] is specified in the model. With this relationship, nitrate uptake is very sensitive to small increases in ammonium concentrations.

3.3. CTZ Simulations

The simulations presented in the previous sections illustrated the response of the model to variations in parameters and environmental conditions. The next ap-

plication of the 1-D model used observations from the CTZ. Specifically, the model was initialized using nutrient and chlorophyll vertical distributions that were measured at a coastal and oceanic region in the CTZ (see Figure 1). This allowed us to investigate the interactions among biological and optical properties independent of circulation effects. The CTZ is a transition region between the coastal region and the oceanic region. It is our belief that by adequately simulating both extreme regions the model was then also capable

Figure 12. Simulated time evolution of the depth of the 10% PAR level obtained using variable vertical velocities and grazing rates. The upper set of three curves represents the depth of the 10% PAR level for the conditions of no grazing with vertical velocities of 1 m d^{-1} (upper dashed line; an upwelling simulation), 0 m d^{-1} (central solid line), and -1 m d^{-1} (lower dashed line; a downwelling simulation). The lower set of three curves represents the depth of the 10% PAR level when grazing is allowed with vertical velocities of 1 m d^{-1} (upper dashed line; an upwelling simulation), 0 m d^{-1} (central solid line), and -1 m d^{-1} (lower dashed line; a downwelling simulation).

of simulating the transition region which divides them. Rather than presenting results from a series of simulations forced by the background nutrient conditions at different distances across shelf, we present the results from two extreme locations of the CTZ and focus on the biological processes which control the structure of the food web at these locations. Both simulations were run for 100 days, a time well beyond that required for transient adjustments to occur and for biological processes to come into equilibrium. Because of the inclusion of the climatological adjustment scale, there is a much longer timescale required for the steady state. However, the two solutions do not differ greatly. The results shown focus on the first 60 days of these 100-day simulations. All results shown are daily averaged to remove the diurnal signals.

3.3.1. Coastal region simulation. The results from the coastal simulation are shown in Figures 15 and 16. A shallow nitracline persisted throughout the simulation and deepened from only 20 to 40 m over the first 60 days. Because the model assumed a depth-independent vertical eddy diffusivity coefficient, the depth at which nutrient diffusion was largest was also

the depth where the change in the gradient of the nutrient profile was largest. This depth was located just above the nitracline. It was at this depth that the phytoplankton nitrate uptake was highest. The nitracline deepened because the phytoplankton nitrate uptake was greater than upward vertical diffusion of nitrate, and conversely, the deepening of the nitracline caused the chlorophyll maximum to also deepen over the course of the simulation. The depth of the euphotic zone and the depth and magnitude of the chlorophyll maximum were controlled by the large phytoplankton. Also, the magnitude of the chlorophyll maximum decreased with depth as a result of decreased PAR. The mean downward displacement of the chlorophyll maximum was about 0.13 m d^{-1} .

All three zooplankton components were confined to the upper 50 m of the water column, where the available food was located. Copepod and euphausiid concentrations were highest at the start of the simulation and decreased to maximum steady state concentrations of about 4 and 2 mg N m^{-3} , respectively. Their decrease followed the decrease in the large phytoplankton concentrations, which was the primary food source for these two zooplankton. A bloom in the doliolids on day 20 resulted from a peak in the detritus pool on day 10. The peak in the detritus pool was caused by the initial bloom in the large phytoplankton.

The transient adjustments to the initial conditions did not greatly alter the model solution. The largest variability in depth-averaged biomass was observed in the phytoplankton. Much of this variability was caused by decreasing biomass due to the decrease in nitrate and silicate concentrations.

Both the copepod and euphausiid depth-averaged biomass decreased by about half over the first 60 days. The mean doliolid biomass increased from about 1.5 to 4 mg N m^{-3} on day 25, after which it decreased slowly to 1.6 mg N m^{-3} , which was close to its initial value. Total zooplankton biomass overall declined by half.

The formation and maintenance of the chlorophyll maximum was controlled by various processes. The vertical distribution of these contributing processes (Figure 16) showed that processes such as grazing played a role in the initial formation of the subsurface chlorophyll maximum. However, the chlorophyll maximum was maintained primarily through in situ primary production. The depth to which the chlorophyll maximum reached a steady state was controlled by the inverse relationship that exists with depth between nutrient and PAR. In the model, maximum net growth occurred when the combined effects of light and nutrient limitation were minimal.

3.3.2. Oceanic region simulation. The results from the coastal simulation are shown in Figures 17 and 18. Nitrate concentrations changed little over the course of the simulation. A deep 90-m nitracline existed throughout the simulation. As in the coastal simulation, the region of highest nitrate diffusion was located just above the nitracline, at a point where the change in the gradient of the nitracline was the greatest. The flux of nutrients at this depth was balanced by the rate of

Figure 13. Same as Figure 6, but for changes in zooplankton mortality (0 to 20 days⁻¹). Contour levels are 2.5 mg N m⁻³, 0.05 mg N m⁻³, 5 mg N m⁻³, 1 mg chlorophyll *a* m⁻³, 5 μ g chlorophyll *a* m⁻³, 0.5 mg N m⁻³, 0.25 mg N m⁻³, and 1 mg N m⁻³ for 13e through 13l, respectively.

depth-integrated new primary production occurring at shallower depths and maintained the deep 83-m chlorophyll maximum.

The steady state phytoplankton concentrations were reversed from those of the initial conditions, which were obtained using the size fraction to chlorophyll concentration relationship of *Chavez et al.* [1991]. Within the first 20 days of simulation, the depth-averaged large

phytoplankton biomass increased from 0.08 mg chlorophyll *a* m⁻³ to 0.32 mg chlorophyll *a* m⁻³, while the depth-averaged small phytoplankton biomass decreased from about 0.25 to 0.05 mg chlorophyll *a* m⁻³. However, the total depth-averaged phytoplankton biomass remained relatively unchanged over the 100 days of simulation and varied between 0.33 mg chlorophyll *a* m⁻³ and 0.37 mg chlorophyll *a* m⁻³. The magnitude of the

Figure 14. Same as Figure 6, but for changes in detrital recycling (0 to 20 days^{-1}). Contour levels are 2.5 mg N m^{-3} , 0.25 mg N m^{-3} , 2.5 mg N m^{-3} , 1 $\text{mg chlorophyll a m}^{-3}$, 5 $\mu\text{g chlorophyll a m}^{-3}$, 1 mg N m^{-3} , 0.25 mg N m^{-3} , and 1 mg N m^{-3} for 14e through 14l, respectively.

resulting depth-averaged phytoplankton biomass was much higher in the coastal simulation, which averaged about 2 $\text{mg chlorophyll a m}^{-3}$.

Unlike the coastal simulation, all three zooplankton were confined to the lower 50 m of the water column. Yet like the coastal simulation, the distribution of the zooplankton followed the distribution of the available food. All the zooplankton concentrations decreased at a rate faster than that observed in the coastal simulation. The oceanic simulation was capable of supporting

a zooplankton population equal to only about 2% of the available total food concentration. The low trophic efficiency was primarily caused by low new primary production rates. As a comparison, the coastal simulation supported a zooplankton population which was about 25% of the available food.

The formation and maintenance of the chlorophyll maximum was controlled by the same processes as that observed in the coastal simulation. The vertical distribution of these contributing processes (Figure 16)

Figure 15. Simulated 60-day time evolution of the (a) euphotic zone depth, (b) chlorophyll maximum depth, (c) depth-averaged large (solid line) and small (dotted line) phytoplankton concentrations, (d) depth-averaged copepod (dotted line), doliolid (short-dashed line), euphausiid (large-dashed line), and total zooplankton (solid line) concentrations, and the depth dependent (e) nitrate, (f) ammonium, (g) detritus, (h) large and (i) small phytoplankton size fractions, (j) copepod, (k) doliolid and (l) euphausiid concentrations for the coastal simulation. Contour levels are 5 mg N m^{-3} , 0.1 mg N m^{-3} , 10 mg N m^{-3} , $2.5 \text{ mg chlorophyll } a \text{ m}^{-3}$, $50 \mu\text{g chlorophyll } a \text{ m}^{-3}$, 2.5 mg N m^{-3} , 2.5 mg N m^{-3} , and 1 mg N m^{-3} for 15e through 15l, respectively.

showed that processes such as grazing played a role in the initial formation of the subsurface chlorophyll maximum. Also, as in the coastal simulation, the chlorophyll maximum was primarily maintained through in situ primary production.

4. Discussion and Conclusions

The CTZ divides the inshore neritic and offshore oligotrophic regions, which differ from each other in temperature, nutrients, and plankton community structure.

Figure 16. The vertical profile of the individual terms in the 1-D model governing equations for (a) day 20 and (b) day 60 of the coastal simulation (integrated over 1 day) which were responsible for the formation and maintenance of the chlorophyll maximum.

The 1-D physical-bio-optical model was developed to simulate these two extreme regions.

The model results showed that the processes which controlled the rate of new nutrient input also controlled the type of ecosystem which developed. A coastal ecosystem developed in the high new nutrient flux regions. This was because increased nutrient fluxes increased the Si:N ratio and allowed the fast growing coastal diatoms to dominate over the smaller non-siliceous phytoplankton. The coastal diatoms were better able to compete for the nitrate and ammonia under silicate-replete conditions. This ability of marine diatoms to dominate over nonsiliceous flagellates has been demonstrated in laboratory experiments [Sommer, 1994].

The transition between phytoplankton assemblages is also observed in the CTZ. High nutrient concentrations along the coast support a high phytoplankton biomass (about $8 \text{ mg chlorophyll } a \text{ m}^{-3}$), which is typically dominated by large silicate-dependent centric diatoms (about $10\text{--}100 \text{ cells mL}^{-1}$) [Hood *et al.*, 1990, 1991; Jones *et al.*, 1991; Chavez *et al.*, 1991]. The high concentrations of nutrients are maintained by a shallow nutricline at about 30 m. A subsurface chlorophyll maximum is not always present, but when it is present it is no deeper than 30 m. Also, the high phytoplankton concentrations reduce the depth of the euphotic zone to about 25 m [Chavez *et al.*, 1991].

The offshore regions of the CTZ lack a consistent nutrient supply mechanism such as upwelling. Waters in this region are warmer and contain lower nutrient and phytoplankton concentrations. The phytoplank-

ton assemblages in this region tend to be dominated by smaller (less than $5 \mu\text{m}$) single-celled nonsiliceous species such as *Synechococcus* sp. and prochlorophytes [Chavez *et al.*, 1991]. Unlike the coastal regions, the nutricline ($> 80 \text{ m}$), subsurface chlorophyll maximum ($> 80 \text{ m}$) and euphotic zone ($> 90 \text{ m}$) are found deeper in the water column [Simpson *et al.*, 1986; Hood *et al.*, 1990, 1991; Jones *et al.*, 1991; Chavez *et al.*, 1991].

In the coastal simulation, under no vertical advection conditions, the depths of the nutricline, subsurface chlorophyll maximum, and euphotic zone were 35, 30, and 28 m, respectively. All of these were close to the maximum extent of that observed in the coastal regions of the CTZ. However, the coastal zone in the CTZ is an upwelling region, and, in the sensitivity analyses, upwelling caused the nitracline, subsurface chlorophyll maximum, and euphotic zone to shallow to 25 m, 10 m, and 11 m, respectively. In the oceanic simulation, the depths of the nutricline, subsurface chlorophyll maximum, and euphotic zone were 95, 85, and 95 m, respectively. As in the CTZ observations [Chavez *et al.*, 1991], the depths of the top of the nutricline, subsurface chlorophyll maximum, and euphotic zone were all at similar depths (about 80–90 m).

The region separating the coastal and offshore areas is largely influenced by offshore advecting filaments. Because of this, the patterns in the pelagic ecosystem within the CTZ are complex. However, in general, water is upwelled along the coast and advected offshore. Initially, the upwelled water is nutrient-rich and cold and contains low plankton biomass. As water is advected offshore, in situ processes alter the envi-

Figure 17. Same as Figure 15, but for the oceanic simulation. Contour levels are 0.5 mg N m^{-3} , $1 \mu\text{g-N m}^{-3}$, 1 mg N m^{-3} , $0.2 \text{ mg chlorophyll } a \text{ m}^{-3}$, $50 \mu\text{g chlorophyll } a \text{ m}^{-3}$, 0.02 mg N m^{-3} , $0.025 \text{ mg N m}^{-3}$, and 0.02 mg N m^{-3} for 17e through 17l, respectively.

ronment from eutrophic to oligotrophic [Abbott *et al.*, 1990]. Silicate-dependent diatoms grow rapidly and deplete the water column of nutrients, after which diatom growth decreases due to silicate limitation. Eventually detrital nitrogen is recycled into ammonium and allows the nonsiliceous oceanic phytoplankton to better compete with the coastal diatoms for the available nutrients.

The large phytoplankton dominated in both coastal and oceanic simulations. However, the smaller phytoplankton population was more significant offshore than

onshore. There was a shift in the simulated phytoplankton assemblage toward the smaller phytoplankton from onshore to offshore. In the coastal simulation, the large phytoplankton biomass was 100 times that of the small phytoplankton, while in the oceanic simulation the large phytoplankton was only 6 times greater, a considerable difference or species shift. In the sensitivity simulations, we observed that the small phytoplankton dominated in the coastal simulation when downwelling occurred and when vertical diffusion was low. It may be that

Figure 18. Same as Figure 16, but for the oceanic simulation.

the background vertical diffusion in the oceanic simulation was too high. In fact, *Jamart et al.* [1977] used a background vertical diffusion coefficient of $0.5 \text{ cm}^2 \text{ m}^{-1}$ to simulate phytoplankton growth and nutrient distribution in the Pacific Ocean, while we used a vertical diffusion coefficient of $1.0 \text{ cm}^2 \text{ m}^{-1}$ to simulate both the coastal and oceanic cases. Unfortunately, all of our sensitivity simulations were carried out using the climatological nutrient profile observed along the coast, a region where we expected to see the large phytoplankton dominate. Had the sensitivity analysis been carried out using the oceanic climatological nutrient profiles, the small phytoplankton would have played a more important role.

In both the CTZ field observations and the 1-D simulations, the total amount of zooplankton biomass decreased from inshore to offshore. The total zooplankton biomass from the CTZ field survey showed highest zooplankton biomass in the inshore waters at about 1 mmol N m^{-3} and lowest offshore at less than $0.2 \text{ mmol N m}^{-3}$ [Mackas et al., 1991]. In the 1-D simulations, the total zooplankton biomass was also highest in the coastal simulation (4 mmol N m^{-3}) and decreased to about $0.08 \text{ mmol N m}^{-3}$ in the oceanic simulations. While the trends are correct, the 1-D model simulations overestimated (underestimated) the total zooplankton biomass in the inshore (offshore) simulation. Comparisons between the observed and modeled distributions of the three zooplankton represented in the model are mixed. In both the coastal simulation and the CTZ observations, all three zooplankton occur. Doliolids continued to prosper in the oceanic simulation but were not observed in the CTZ observations. However, large

amounts of heteropod larvae, which feed on doliolids, were observed in the offshore regions of the CTZ. The absence of this predation pressure in the 1-D model may be one reason for their continued presence in the oceanic simulations. Because of the large spatial (and temporal) variability in the CTZ zooplankton observations and the temporal variability in the 1-D simulated zooplankton biomass, it is difficult to draw conclusions from comparing the observations against the simulation.

The change from silicate- to nitrogen-limited phytoplankton was also suggested by the nonlinear relationship observed in the NO_3^- versus SiO_4^- property plots from the CTZ survey data. High Si:N ratios occur in high-nutrient water, e.g., nutrient-rich coastal and filament regions, where silicate uptake is high as a result of the presence of high concentrations of silicate-dependent phytoplankton. Conversely, lower silicate to nitrate ratios occur in low-nutrient water, e.g., oceanic water, where the nonsilicate-dependent phytoplankton assemblages were more dominant. As the silicate concentrations are depleted, the Si:N ratio decreases because the phytoplankton assemblage changes to a non-siliceous assemblage, and the demand for silicate decreases. Detritus recycling into ammonium, which may account for as much as 54% and 82% of the coastal and open ocean production, respectively, would only serve to increase this effect by helping to maintain higher Si:N ratios in the nutrient-poor oceanic waters, where detrital recycling into ammonium is higher [Eppley and Peterson, 1979].

The spatial scale of the transition from coastal to oceanic ecosystem is about 100 km. It is within that 100-km coastal band that the subsurface chlorophyll

maximum in the CTZ observations sink from about 20 m to about 80 m. This scale is controlled by the spatial scale of the depth of the nutricline. The 1-D simulations were able to simulate the extremes in depths of the coastal and oceanic subsurface chlorophyll maxima. The results from the coastal and oceanic simulations and the observed mean cross-shelf distributions of nitrate can be interpolated in order to predict the general cross-shelf spatial structure of the ecosystem transition. Such results would be closely analogous to results from an N by 1-D model that was forced with a cross-shelf spatially varying nutrient field but did not include the effects of horizontal diffusion and advection. This of course also assumes that the mean field is also a steady state field.

A prominent feature of the CTZ is that phytoplankton assemblages approach maximum concentrations at subsurface levels [Hood *et al.*, 1990, 1991; Chavez *et al.*, 1991; Jones *et al.*, 1991]. These chlorophyll maxima have been observed in several different environments including polar [El-Sayed and Jitts, 1973] and equatorial regions [Venrick *et al.*, 1973; Gould, 1987]. The results of the 1-D simulations showed that the chlorophyll maximum deepened with increasing distance from shore, approximately 25 m onshore to approximately 85 m offshore. This trend is in agreement with the 1988 CTZ field survey observations, where the chlorophyll maximum was found at approximately 20 m onshore and approximately 80 m offshore [Chavez *et al.*, 1991; Washburn *et al.*, 1991].

While the major processes that contribute to the development and maintenance of the chlorophyll maximum are known [Anderson, 1969; Roman *et al.*, 1986; Cullen and Eppley, 1981; Cullen *et al.*, 1982, 1983; Venrick, 1984], little is known about their relative contribution. A disadvantage of field studies is that sampling occurs only on small spatial scales and populations are difficult to track in space and time. An alternative method is to use model simulations to obtain a balanced perspective of the relative contributing processes involved in the development and maintenance of the subsurface chlorophyll maximum.

The model developed by Jamart *et al.* [1977] to investigate vertical chlorophyll distributions off the coast of Oregon shows clearly that the relative contribution of physical and biological processes changes during the development and maintenance of the subsurface chlorophyll maximum. Their model shows that the development and subsequent sinking of the subsurface chlorophyll maximum is caused by both cell sinking associated with nutrient depletion and in situ primary production. Grazing plays a role in determining the rate at which the subsurface chlorophyll maximum develops. However, in situ primary production is primarily responsible for its maintenance [Jamart *et al.*, 1977]. Similar results are also obtained in a physical-biological model developed by Varela *et al.* [1992, 1994]. Their model shows that the depth and magnitude of the chlorophyll maximum is determined mainly by vertical eddy diffusion and light attenuation, suggesting a balance between the amount of available light energy and upward flux of nutrients.

The analysis of the processes included in our 1-D model also showed that in situ growth was primarily responsible for the creation and maintenance of the chlorophyll maximum layer in all regions of the CTZ (see Figures 16 and 18). Maximum in situ growth occurred at depths where the effect of light limitation and nutrient limitation were least. It was the effect of nutrient limitation and light inhibition at the surface and light limitation at depth which was responsible for creating a maximum growth rate at depth, resulting in a chlorophyll maximum. The chlorophyll maximum developed deeper in the offshore region because both the nutricline and the euphotic zone depth were deeper offshore.

The results from the sensitivity analysis were able to quantify the relative effects of different processes on the depth of the subsurface chlorophyll maximum. Several studies postulate that grazing may be an important process in the development of the subsurface chlorophyll maximum [Lorenzen, 1967; Venrick *et al.*, 1973; Fairbanks and Wiebe, 1980; Longhurst and Herman, 1981; Roman *et al.*, 1986; Gould, 1987]. Roman *et al.* [1986] hypothesize that grazing serves to remove phytoplankton biomass in the upper water column and shifts absolute production to depth. While this was observed in the model results, it had no effect on the resulting depth of the subsurface chlorophyll maximum. This was also true for the zooplankton mortality sensitivity results.

The subsurface chlorophyll maximum shallowed with increased vertical diffusion and detrital recycling and deepened with increased incident PAR, sinking rates, and phytoplankton mortality rates. A linear relationship existed between the amount of incident PAR and the depth of the subsurface chlorophyll maximum. This implies that a seasonal variability in the depth of the subsurface chlorophyll maximum should be observed as a result of the seasonal variability of the solar zenith angles.

Because of the diverging isopleths associated with the downwelling velocities, no deep (> 50 m) chlorophyll maximum was observed to form. Upwelling, however, formed sharper subsurface chlorophyll maxima due to the convergence of the isopleths. Water mass subduction has been shown to be an important process associated with the offshore flowing portion of the filament [Washburn *et al.*, 1991]. Downwelling along the northern offshore flowing side of the filament was observed to be as high as $20\text{--}40\text{ m d}^{-1}$ [Kadko *et al.*, 1991; Dewey *et al.*, 1991]. This rapid subduction of water can have a considerable effect on the plankton dynamics. Washburn *et al.* [1991] suggested that the phytoplankton in the water column within the filament may have been downwelled over 100 m as they were advected offshore while entrained within the filament. Also, Abbott *et al.* [1990] favored the explanation that downwelling was in part responsible for the optical and biological properties measured by a fixed-depth drifter as it was advected offshore while entrained within a filament.

The downwelling directly associated with the filaments may have a vertical structure that is different than the linear structure used in the model. Because

this downwelling structure varies with position along the filament, a time-varying velocity structure that simulates that observed while following a water mass as it is advected within the filament may be needed in order to simulate the anomalous deep chlorophyll maxima observed within the filament regions. The results from a series of simulated Lagrangian drifter experiments, designed to elucidate these vertical advection effects on plankton dynamics are presented by Moisan and Hofmann [this issue].

Finally, the results from coupling this food web and bio-optical model to a 3-D ocean circulation model are presented by Moisan *et al.* [this issue]. The 1-D model provided a test on the formulations used to simulate the bio-optical processes which were also used in the 3-D physical-bio-optical model [Moisan *et al.*, this issue]. The results from this 3-D model focus on the across-shore flux and transport of carbon within the filaments.

Acknowledgments. We thank D. B. Haidvogel and K. S. Hedström for helping us understand spectral methods. We thank J. M. Klinck for his help in forging through the many numerical and technical problems encountered while developing a model of such complexity. We thank R. Bidigare, R. Hood, S. Smith, D. Mackas, L. Washburn, B. Jones, C. Davis, F. Chavez, J. Huyer, C. Paulson, and others within the CTZ group for providing us with the wealth of data used to complete this study. This research was supported by the Office of Naval Research under grant N00014-90-J-1930. Computer resources and facilities were provided by the Commonwealth Center for Coastal Physical Oceanography, Naval Research Laboratory, and Stennis Space Center. This support is gratefully acknowledged. This research was performed by J.R.M. in partial fulfillment of the requirements for a Ph.D. degree at Old Dominion University.

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Received September 22, 1995; revised May 9, 1996; accepted May 23, 1996.)