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**BIOLOGICAL CONSEQUENCES OF ENVIRONMENTAL
CHANGES RELATED TO COASTAL UPWELLING:
A SIMULATION STUDY**

STEVEN OLSON HOWE

MASTER

May 1979

**OCEANOGRAPHIC SCIENCES DIVISION
DEPARTMENT OF ENERGY AND ENVIRONMENT**

**BROOKHAVEN NATIONAL LABORATORY
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Abstract

Two simulation models of marine ecosystem dynamics are formulated and applied to field data. The first is a time-dependent model of phytoplankton growth in nutrient-enriched batch cultures where spatial gradients of dependent variables and the effects of higher trophic level processes are not included. Rates of photosynthesis, nutrient uptake, chlorophyll synthesis and cell division for a single phytoplankton functional group are simulated as functions of photosynthetically active solar radiation, dissolved nutrient concentrations and cell quotas of carbon, nitrogen and silica. Comparisons of simulated results with published field data show that the model can represent the effects of light and nutrient limitation important in the control of primary production in a coastal upwelling region.

The second model combines the phytoplankton growth model with a time dependent, two-dimensional model of coastal upwelling off northwest Africa. Herbivores are represented by one type of fish and two size classes of zooplankton. Results from simulation experiments show a flux of nutrient-rich water into the euphotic zone supporting high rates of primary production seaward of a turbid nearshore region. High ammonium concentrations, observed in the nearshore region, are shown to be sensitive to local physical circulation processes and phytoplankton uptake rates. Simulated rates of primary production may exceed the observed rates and the losses attributed to physiological mortality and ingestion by herbivores. An underestimate of the significance of grazing related to the vertical distribution and ingestion rates of the zooplankton is identified as the factor responsible for the difference between observed and simulated results.

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CHAPTER 1

INTRODUCTION

Over most of its surface the ocean is a dilute and impoverished biological broth. Vertical density stratification limits the upward flux of nutrients necessary to support autotrophic growth at the surface where light is abundant. Upwelling, however, brings large quantities of nutrient-rich water to the surface and its effects on biological productivity are dramatic. Whereas primary production may average only $0.14 \text{ g C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ in the open ocean, it may occasionally surpass $10.0 \text{ g C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ in upwelling areas (Ryther, et al. 1971). Furthermore, it has been estimated that about half of the total annual world's fish catch is taken in upwelling regions which occupy a fraction of one percent of the ocean's surface (Ryther 1969).

Systematic investigations of a few of the anomalous regions of the oceans where upwelling occurs began early in this century (Cushing, 1971). More recent studies have shown that similar physical features and biological communities are common to all of the major upwelling systems (Walsh 1972). A comparison of ecosystem yields suggests that differences in meteorology, bottom topography and water mass characteristics may, however, have important consequences for particular systems (Walsh, 1976a).

Simulation models offer an approach towards assessment of the interactions of these types of environmental characteristics and an understanding of the extent to which they influence the productivity of upwelling ecosystems. In this study, two simulation models are formulated at different levels of ecosystem complexity. The first is

a model of phytoplankton growth in the absence of the effects of circulation and higher trophic level processes. Rates of photosynthesis, nutrient uptake, chlorophyll synthesis and cell division for a phytoplankton population are simulated as functions of photosynthetically active solar radiation, dissolved nutrient concentrations and cell quotas of carbon, nitrogen and silica. This model will be referred to as the phytoplankton growth model and is first applied to a field study off California of phytoplankton growth in nutrient-enriched batch cultures where spatial gradients of dependent variables can be ignored. The second model uses the first as a submodel and also includes the effects of physical circulation, nutrient regeneration from the bottom, and grazing and excretion of herbivorous fish and zooplankton in a study of biological responses to upwelling off northwest Africa.

The coastal upwelling region off northwest Africa has recently been studied during a number of expeditions as part of CINECA (Cooperative Investigations of the North East Central Atlantic). One of these expeditions, JOINT-I, took place during the months of February to May, 1974, and was the first major expedition of the Coastal Upwelling Ecosystems Analysis (CUEA) Program. Barber (1977) has introduced the organization of JOINT-I and reviewed its scientific objectives. One of the objectives was to develop a series of simulation models that would provide the basis for a predictive understanding of the response of upwelling ecosystems to natural variation, man-induced perturbation, or different management strategies. The models used in this simulation study represent a contribution to that series and have been formulated in an attempt to account for some of the phytoplankton

responses to time dependent coastal upwelling and changes in the associated nutrient fields.

Some elements of the ecosystem model are considered to be its structural characteristics and have been defined to resemble features of the northwest African upwelling system. Structural characteristics, based on CUEA field observations, include approximations for the shelf topography, boundary conditions, nonchlorophyll components of the submarine light extinction and the biomass of herbivorous fish and zooplankton. Time varying estimates of solar radiation and upwelling circulation, although calculated in theoretical submodels, are also included as structural characteristics of the environment.

Experiments performed with the ecosystem model were designed to investigate the biological responses to the physical process of upwelling. The experiments or simulated cases are related by a common set of boundary conditions and functional relationships among the biological components. The differences among cases are due to the absence or occurrence of simulated upwelling, and differences in the intensity of vertical mixing. Comparisons of JOINT-I observations with results from these simulation experiments show how some biological characteristics of the northwest African upwelling ecosystem may occur as consequences of the interaction of structures and functions represented in the model. The simulation experiments also identify other characteristics which are less well understood. Recognition of these characteristics and their significance in the simulation experiments offers a strategy towards improving future models and, hopefully, their predictive capabilities.

CHAPTER 2
THE PHYTOPLANKTON GROWTH MODEL

2.1 Formulation

An equation describing the distribution of a generalized nonconservative, S , in the sea is

$$\frac{\partial S}{\partial t} = \Delta \cdot K \Delta S - \Delta \cdot v S + R \quad [2.1]$$

where

t = time

$\Delta \cdot K \Delta S$ = the effects of turbulent mixing;

$\Delta \cdot v S$ = the effects of advection, and

R = nonconservative effects. R includes the effects of biological and chemical interactions affecting S .

When spatial gradients of the nonconservative variable can be ignored, the equation [2.1] may be written more simply as

$$\frac{dS}{dt} = R. \quad [2.2]$$

In this model of phytoplankton growth, a set of such equations describes the time dependent responses of variables for cell numbers and particulate silica, nitrogen, carbon and chlorophyll representing a single phytoplankton population. Although several distinct phytoplankton populations could be represented in the model by increasing the number of equations, only one population will be considered in this study. Equations [2.3-2.10] are the eight basic state equations and [2.11-2.24] define the algebraic relationships among the state variables. Michaelis-Menton type functions [2.18-2.21] describe uptake of

nitrate, ammonium and silicate, and a modified form [2.23] of Steele's (1962) equation describes net photosynthetic fixation of carbon as a function of light intensity. Concentrations of ammonium are assumed to reduce the maximal uptake rate of nitrate [2.20] and ammonium and nitrate uptake are combined to represent total nitrogen uptake [2.22]. Chlorophyll synthesis is related to the nitrogen quota status of the cells [2.24] and cell division rate is described as a general form of the function proposed by Droop (1973) [2.15-2.17] to relate growth rate to the cell quota of a limiting nutrient. The effects of temperature and losses due to grazing, sinking or physiological mortality are not included.

In the equations below, numerically subscripted uppercase letters represent state (dependent or dynamic) variables or state variable-dependent specific rates. Numerical subscripts refer to a compound or element according to the following convention:

<u>Numerical Subscript Symbol, n</u>	<u>Compound or Element</u>
1	Silica
2	Nitrate Nitrogen
3	Ammonium Nitrogen
4	Total Nitrogen
5	Carbon
6	Chlorophyll

Although they may appear in only one function, model parameters expressed as lower case letters are also subscripted for clarity according to the convention above. In a few cases the literature convention for alphabetically subscripting some unambiguous forcing functions and constants has been retained. All symbols are defined in Appendix 4 and in the rationale for the derivation of each function following the list of equations. The BIOCEAN simulation system, described in Appendix I, was used to integrate the model equations.

$$\frac{dP_n}{dt} = P_n V_n \quad \text{for } n = 1,4,5,6 \quad [2.3-2.6]$$

$$\frac{dS_1}{dt} = -V_1 P_1 + \alpha_1 \quad [2.7]$$

$$\frac{dS_2}{dt} = -V_2 P_4 + \alpha_2 \quad [2.8]$$

$$\frac{dS_3}{dt} = -V_3 P_4 + \alpha_3 \quad [2.9]$$

$$\frac{dN}{dt} = GN \quad [2.10]$$

$$C_n = \frac{P_n}{N} \quad \text{for } n = 1,4,5,6 \quad [2.11-2.14]$$

$$G = 0, \text{ if } C_n \leq d_n \left. \vphantom{G} \right\} \text{ for } n = 1, 4, 5 \quad [2.15-2.17]$$

$$= \text{minimum of } [g(C_n - d_n)/C_n], \text{ otherwise}$$

$$V_1 = v_1(S_1/(k_1 + S_1)) \text{ if } C_1 < c_1 \text{ and } V_1 < G \quad [2.18]$$

$$= 0, \text{ otherwise}$$

$$V_2 = v_2'(S_2/(k_2 + S_2)) \text{ if } C_4 < c_4 \text{ and } V_4 < G \quad [2.19]$$

$$= 0, \text{ otherwise}$$

$$V_2' = v_2 - a_3 S_3 \quad [2.20]$$

$$V_3 = v_3(S_3/(k_3 + S_3)) \text{ if } C_4 < c_4 \text{ and } V_4 < G \quad [2.21]$$

$$= 0, \text{ otherwise}$$

$$V_4 = V_2 + V_3 \quad [2.22]$$

$$V_5 = (Q_{\max} \cdot I_{\max} \cdot K_c \cdot P_6) \cdot \quad [2.23]$$

$$(\exp [-I_z/I_{\max}] - \exp [-I_o/I_{\max}]) / (K_T \cdot z)) - R_5,$$

$$\text{if } C_5 < c_5 \text{ and } V_5 < G$$

$$= 0, \text{ otherwise}$$

$$P_6 V_6 = P_6 (g(C_4 - d_4)/(C_4)) \text{ if } G \text{ is minimum for } n = 1 \text{ or } \quad [2.24]$$

$$n = 5 \text{ in equations } [2.14-2.16]$$

$$= e_6 V_4 P_4 \text{ if } G \text{ is minimum for } n = 4 \text{ in} \\ \text{equations } [2.14-2.16]$$

$$= 0 \text{ if } C_6 \geq c_6 \text{ and } V_6 \geq G$$

2.2 Rationale

2.2a Photosynthesis. The function for photosynthetic fixation of carbon [2.23] is based on the following form of Steele's (1962) equation expressing photosynthesis rate as a function of light intensity

$$P = P_{\max} (I_0/I_{\max}) (\exp [1 - (I_0/I_{\max})]). \quad [2.25]$$

For a layer of finite optical thickness, z , with a constant total extinction coefficient, K_t , Steele's equation may be analytically integrated (Vollenweider 1965) to give:

$$P(z) = P_{\max} (\exp [1 - (I_z/I_{\max})] - \exp [1 - (I_0/I_{\max})]) / K_t \quad [2.26]$$

where

$P(z)$ = rate of photosynthesis per unit surface area of the layer of thickness, z , meters;

K_t = average total spectral extinction coefficient (m^{-1}) for sea water and all light attenuating components. K_t may be regarded as the sum of several partial extinction coefficients (Lorenzen 1972),

$$K_t = K_w + K_c P_6 + K_d X; \quad [2.27]$$

K_w = average spectral extinction coefficient for seawater = 0.04 m^{-1} (Lorenzen 1972);

K_c = average spectral extinction coefficient per unit phytoplankton concentration, where phytoplankton concentration is expressed as P_6 , the concentration of chlorophyll a , and

$$K_c = 0.016 \text{ m}^2 \cdot \text{mg} \cdot \text{Chl } a^{-1} \text{ (Bannister 1974);}$$

K_d = average spectral extinction coefficient for all other materials of concentration X in the water column;

$I_{\max}$ = the light intensity at which the maximum photosynthesis rate occurs; $I_{\max}$ may vary with phytoplankton class, species, and physiological state; however $I_{\max}$ is assumed constant in this model and equal to $2.07 \text{ einst m}^{-2} \text{ hr}^{-1}$ (approximately 10.8 ly hr^{-1} or 2715 ft-c) (Parsons and Takahashi 1973);

I_0 = light intensity at the surface of a depth interval ($\text{einsteins} \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$);

I_z = light intensity at the bottom of a depth interval;

I_z is calculated as $I_z = I_0 \exp [-K_t z]$.

The integrated mean photosynthetic carbon production rate for a layer of thickness z is given as:

$$\overline{P(Z)} = P(Z)/z \quad [2.28]$$

These and other similarly integrated production equations may be useful for steady state calculations, but are unsatisfactory for dynamic populations. $P_{\max}$, the light saturated or maximal rate of photosynthesis with dimensions of carbon mass fixed per volume and time is not adequately expressed as a single constant, because it is not an explicit function of phytoplankton concentration. For Steele's equation, Bannister (1974) shows that $P_{\max}$ may be defined in more fundamental terms as

$$P_{\max} = Q_{\max} I_{\max} K_c P_0 \exp [-1] \quad [2.29]$$

where

$Q_{\max}$ = the maximum quantum yield; quantum yield is the ratio of the rate of photosynthesis and the rate at which light is absorbed by the phytoplankton; quantum yield becomes maximum at low light intensities and is assumed to be a constant of 60 m moles carbon einstein⁻¹ (Bannister 1974; Platt and Jassby (1976)).

The other parameters are defined following [2.26]. Substitution of [2.29] for $P_{\max}$ in [2.26] and [2.28] gives the expression used in the model to calculate the integrated-mean gross photosynthetic carbon fixation for a layer of thickness z :

$$P(Z) = (Q_{\max} I_{\max} K_c P_6) (\exp[-I_z/I_{\max}] - \exp[-I_0/I_{\max}]) / K_t z \quad [2.30]$$

This function expresses the mean rate of production as a rate of photosynthesis integrated over the light available through a depth interval, divided by the thickness of the interval.

2.b Solar radiation. Incident solar radiation values required for the evaluation of the photosynthesis function are calculated in a submodel adapted from the SOLRAD program of McCullough and Porter (1971). Direct, clear sky radiation fluxes for 111 spectral intervals within the wavelength range of 290 to 4000 nm can be computed with SOLRAD for any time period or geographic position when visibility and precipitable water content of the atmosphere are specified. Total incident radiation is the sum of direct and diffuse radiation and empirical approximations are used in this study to calculate the diffuse component of total radiation.

Diffuse radiation, D , is approximated to within $0.013 \text{ ly min}^{-1}$ by

$$D = 0.54 (s_0 - s_s) \sin h \quad [2.31]$$

where h is the angle of the sun above the horizon, s_0 is the sub-ozone intensity of direct radiation and s_s is the intensity of direct radiation at the sea surface after attenuation due to atmospheric scattering (Sivkov 1971).

Some of the direct and diffuse radiation reflected at the surface is returned by the atmosphere due to secondary scattering. Sea surface albedo, A , is calculated as

$$A = 0.04/(\sin h + 0.04) \quad [2.32]$$

following Portman and Ryznar (1971). The effects of secondary scattering on increasing the total incoming flux are included in a factor, F (Sivkov 1971) where

$$F = 1/(1-0.2 \cdot A) \quad [2.33]$$

Incident radiation, I , is obtained by adding direct and diffuse radiation components integrated over the desired wavelength range and allowing for the effects of secondary scattering

$$I = (D + s_s') \cdot F \quad [2.34]$$

where s_s' is direct radiation at the sea surface after attenuation due to atmospheric scattering and water vapor absorption. Calculations of incident radiation are limited to the sensitivity range of the measuring instrument when comparisons with observations are made. Values of I_0 used in the model are based on a calculation of I for the photosynthetically active spectral interval because the parameters in the function for photosynthesis are expressed in terms of radiation in this wavelength range. The amount of incident photosynthetically active

radiation is then reduced to simulate in situ conditions by the surface albedo factor, A, or by a screening factor equivalent to a specified experimental treatment for the surface of an artificial enclosure.

2.2c Nutrient Uptake and Growth. Caperon (1967) and Dugdale (1967) found the Michaelis-Menton equation, originally applied by Monod (1942) to describe the nutrient-limited growth of bacterial populations, could also express the rate of nutrient uptake by algae as a function of nutrient concentration. The equation has subsequently been widely applied in laboratory (Eppley, et al. 1969; Eppley and Renger 1974; Eppley and Thomas 1969; Carpenter and Guillard 1971), field (MacIssac and Dugdale 1969; Goering, et al. 1973) and modelling studies (O'Brien and Wroblewski 1973; Lehman, et al. 1975; Bierman, et al. 1973). Variability of kinetic parameters has been documented (Eppley, et al. 1969; Falkowski 1975) and Eppley, et al. (1969) have discussed the significance of differences in uptake efficiencies and their potential effect on the outcome of species competition for nutrients.

Several significant characteristics of phytoplankton growth subject to environmental changes are, however, not adequately accounted for by simple Michaelis-Menton kinetics. Growth rate has been observed to be related to the cellular content or quota of a limiting nutrient and not necessarily to its external concentration (Fuhs 1969; Droop 1974). Except in a steady state environment, instantaneous growth rate is a function of the integrated nutrient experience or past history of the population (Caperon 1969; Williams 1971) rather than current environmental conditions. Another problem with the simple Michaelis-Menton

relationship is that nutrient uptake and growth are fundamentally functionally different processes and are not adequately described by the same kinetic expression. Maximum uptake rates may exceed the maximum cell division rate by a factor of 2 to 20 (Droop 1968; Eppley and Thomas 1969; Syrett 1962; Healey 1973) and cell division may occur using internally stored nutrient in the absence of external nutrient supply (Williams 1971).

In the formulation of this model, uptake and growth are thus treated as individual, but related processes. Uptake processes increase cell quotas and the particulate biomass of the population. The status of the cell quotas reflects the past nutrient history of the cells and varies as a function of absolute and relative concentrations of nutrients in the environment. Growth, however, is considered to be cell division. Cell division produces more cells with no change in biomass and consequently reduces cell quotas.

The cell division rate, G , is determined according to the following expression as the minimum of a general function proposed by Droop (1973) to relate growth rate and cell quota

$$G = g (C_n - d_n) / C_n \quad [2.35]$$

where

G = cell division rate (hr^{-1});

g = maximum cell division rate; $g = 0.08 \text{ hr}^{-1}$ is assumed characteristic of upwelling areas (Eppley 1972);

C_n = cell quota of nutrient n (pg atoms cell $^{-1}$);

d_n = minimum cell quota of nutrient n . When $C_n < d_n$, cell division rate is zero. For all quotas, d_n is defined

conservatively (Caperon and Meyer 1972, p. 625) to be $d_n = 0.25 \cdot c_n$, where c_n is a maximum quota which is not exceeded by continued uptake. Maximum carbon quota (c_5) must be specified during initialization and essentially defines the maximum phytoplankton cell size. Maximum nitrogen quota (c_4) is defined as $c_4 = 0.25 \cdot c_5$ and allows a minimum C/N ratio by atoms of 4 (Banse 1974). Maximum silica quota (c_1) is defined on the basis of the mean chemical composition of diatoms grown in continuous culture at high dilution rates (Greater than 0.6 hr^{-1} , (Harrison, et al. 1976)) to be $c_1 = 0.35 \cdot c_4$.

A Michaelis-Menton function

$$V_n = v_n (S_n / (k_n + S_n)), \quad [2.36]$$

where

V_n = specific nutrient uptake rate (hr^{-1});

v_n = maximum specific nutrient uptake rate ($v_n = 0.12 \text{ hr}^{-1}$, a rate twice the maximum attainable growth rate, is assumed);

k_n = half-saturation constant for uptake ($k_n = 1.0 \mu\text{g at l}^{-1}$ is assumed (Eppley, et al. 1969; MacIsaac and Dugdale 1969));

S_n = concentration of nutrient n ($\mu\text{g at l}^{-1}$),

is used to determine the nutrient uptake rate when the cell quota of a particular nutrient is less than maximum. No simulated uptake occurs if the cell quota exceeds the maximum quota and the uptake rate exceeds the cell division rate.

Nitrate uptake, V_2 , and ammonium uptake, V_3 , are considered separately because of the differences in the relative importance of these sources of nitrogen within oligotrophic and eutrophic systems (Dugdale and Goering 1967). When nitrate and ammonium are both present in the environment, ammonium is usually taken up preferentially and nitrate uptake is partially or completely inhibited until the ammonium is exhausted (Syrett and Morris 1963; Caperon and Meyer 1972). Field measurements from the Peru Current (MacIsaac and Dugdale 1969), the subtropical Pacific (Goering, et al. 1970), the California Current (McCarthy 1972), the Saronikos Gulf (MacIsaac and Dugdale 1972) and the Chesapeake Bay (McCarthy, et al. 1977) support the observation that ammonium is the preferred inorganic nitrogen source.

Ammonium may cause partial inhibition at oceanic concentrations (Eppley, et al. 1969) and effectively lower the maximal uptake rate of nitrate. The effect can be approximated by

$$V_2' = v_2 - a_3 S_3$$

where

V_2' = maximum specific uptake rate of nitrate (hr^{-1}) in the presence of an ammonium concentration, S_3 ;

v_2 = maximum specific uptake rate of nitrate (hr^{-1}) in the absence of ammonium;

a_3 = a coefficient with a value of $\sim .01$ (Dugdale and MacIsaac 1971; Conway 1977).

These uptake functions all increase cell quotas and biomass whenever a given quota is less than maximum. Net photosynthesis (gross photosynthesis minus respiration), although not described by a

Michaelis-Menton function, is similarly treated as the uptake process increasing the cell quota and population biomass of carbon. When a cell quota maximum has been reached and the current uptake rate exceeds the cell division rate, uptake is stopped until one or both of these conditions change. This method of relating environmental conditions, internal nutrient status and cell division rate avoids the use of end-product inhibition expressions for uptake and allows growth to be determined by one factor in shortest supply instead of a multiplicative interaction of several submaximal fractional uptake expressions.

2.2d Respiration. Respiration tends to diminish cell quotas of carbon. In the model, respiration rate is considered to be a function of growth rate, as expressed below in the linear relationship (Bannister 1974), based on the data of Myers and Graham (1971)

$$R_5 = f_5 + b_5 G \quad [2.37]$$

where

R_5 = carbon respiration rate (hr^{-1});

f_5 = basal respiration rate ($f = 0.003 \text{ hr}^{-1}$) when growth rate ($G(\text{hr}^{-1})$) is zero;

b_5 = a constant, 0.11.

The range of calculated carbon-specific respiration rates appears reasonable in relationship to the size of the organisms and to the simulated rate of photosynthesis. The simulated respiration rate varies between 0.003 hr^{-1} and 0.010 hr^{-1} as the growth rate varies between minimum and maximum attainable values of 0.00 and 0.06 hr^{-1} . Banse's (1976) review suggests rates of approximately 0.01 hr^{-1} could be expected on the basis of the size of the phytoplankton (if, as in

this application the maximum carbon quota c_5 is 36.6 pg at C cell⁻¹ and d_5 , the minimum carbon quota is 9.2 pg at C cell⁻¹). Observed respiration rates are often reported as 5 to 10 percent of the light-saturated rate of photosynthesis (Ryther 1956; Steeman-Nielsen and Jorgensen 1968) and [2.37] gives a possible range in respiration rates of 4 to 15 percent of the simulated maximum rate of photosynthesis.

2.2e Chlorophyll Synthesis. Chlorophyll a concentration is commonly used as a representation of phytoplankton standing stock, but relatively little is published concerning the functional relationship of environmental conditions and the chlorophyll synthesis rate of marine phytoplankton at the time scale of this model. It is known, however, that chlorophyll a synthesis is very closely associated with nitrogen metabolism (Strickland 1965) and that synthesis of chlorophyll is limited in the absence of dissolved nitrogen. Accordingly, simulated chlorophyll synthesis rate, V_6 , is considered in the model to be a function of the nitrogen quota when nitrogen is not limiting cell division,

$$V_6 = g (C_4 - d_4)/C_4. \quad [2.38]$$

For the alternative condition, when nitrogen is limiting cell division, the synthesis of chlorophyll is considered to be dependent on the uptake of nitrogen. The dependence is based on the amount of nitrogen required for the synthesis of chlorophyll molecules and on a nitrogen/chlorophyll composition ratio observed for nitrogen-limited phytoplankton. Chlorophyll a weighs 893 g mole⁻¹ (Shuman and Lorenzen 1975) and with four nitrogen atoms per molecule, chlorophyll a is 6.27% nitrogen by weight. Under conditions of nitrogen limitation, when the

cell nitrogen to chlorophyll ratio may equal 16/1 (Strickland 1965), chlorophyll contains 0.39% ($0.0627/16 = 0.0039$) of the cell nitrogen. If this condition is to be maintained, 0.39% of net nitrogen uptake must go to chlorophyll synthesis. In other words, for each mole of nitrogen assimilated, chlorophyll increases by 0.875 g.

To summarize, the equations used to define the rate of chlorophyll synthesis are:

$$\begin{aligned}
 P_6 V_6 &= P_6 (g(C_4 - d_4)/C_4) \text{ if cell nitrogen is not limiting} \\
 &\qquad\qquad\qquad \text{cell division;} \\
 &= e_6 V_4 P_4 \qquad\qquad\qquad \text{if cell nitrogen is limiting cell [2.24]} \\
 &\qquad\qquad\qquad \text{division rate;} \\
 &= 0 \qquad\qquad\qquad \text{if } C_6 \geq c_6 \text{ and } V_6 \geq G
 \end{aligned}$$

where

P_6 is chlorophyll ($\mu\text{g} \cdot \text{l}^{-1}$);

V_6 is the specific rate of increases of chlorophyll (hr^{-1}).

The product $P_6 V_6$ is the mass increase in chlorophyll per time ($\mu\text{g chlorophyll} \cdot \text{l}^{-1} \cdot \text{hr}^{-1}$). Similarly, P_4 and V_4 are particulate nitrogen ($\mu\text{g at l}^{-1}$) and the specific uptake rate of nitrogen (hr^{-1}) respectively;

$e_6 = 0.875 \text{ chlorophyll (g atom total nitrogen uptake)}^{-1}$;

e_6 is the factor relating nitrogen uptake and chlorophyll synthesis when nitrogen is limiting cell division.

Chlorophyll synthesis is stopped if the chlorophyll per cell (C_6) exceeds the maximum quota and the chlorophyll synthesis rate exceeds the cell division rate, G . The maximum chlorophyll quota is defined according to the assumption that the minimum nitrogen to chlorophyll

ratio (by weight) is 5 (Strickland 1965) and the minimum carbon to chlorophyll ratio (by weight) is 36.

2.3 Application

One of the ultimate purposes of this simulation study is to relate changes in the physiological characteristics of phytoplankton populations to changes in a realistically complex environment. The growth model is first applied, however, to a field experiment designed to eliminate some in situ sources of natural variability. Eppey, Carlucci, et al. (1971), from 2-15 July, 1970, carried out an intensive study of the growth, physiology and chemical composition of phytoplankton, maintained in 200 liter batch cultures at sea to remove the organisms from the effects of advection and turbulence within the California upwelling ecosystem. A fairly complete set of nutrient, biomass and phytoplankton rate measurements was obtained as the cultures responded to suddenly elevated nutrient concentrations. Nutrient-depleted surface seawater was filtered through 183 μ mesh to remove the larger zooplankton. It was then supplied with trace metals, vitamins, phosphate, silicate and one of three sources of nitrogen; nitrate, ammonium, or urea. In one treatment the batch culture received all nutrient additions except the nitrogen source. Temperature was maintained between 20° and 25°C and solar insolation was reduced to about 20% of natural intensity with a neutral density filter.

Measurements of incident solar radiation are not reported for the experiment, but the timing and intensity of the incident radiation measured off Oregon with an Eppey pyranometer (sensitive to wavelengths

less than 2800 nm) on 11 July, 1973 (Reed and Halpern 1974) is approximated within 5% (Figure 1) by the solar radiation submodel, assuming 25 km visibility and 3 cm precipitable water (Portman and Ryznar 1971). In substantial agreement with previous observations (Strickland 1958), simulated values of photosynthetically active radiation vary between 48% and 50% of the total incident flux, depending on the altitude of the sun. At 32°N (the approximate latitude of San Diego) on 11 July (the approximate time of the batch experiments) the simulated photosynthetically active radiation (Figure 2) is 361 ly d^{-1} or approximately $69.4 \text{ einsteins m}^{-2} \text{ d}^{-1}$, if the average energy of an einstein of visible solar light is 52 Kcal (Bannister 1974). Values used in the model at each iteration are reduced from surface incident values by 80% to represent light conditions inside the partially shaded experimental containers. The mean light path through the batch culture container, depth z in [2.23] and [2.30], is assumed to be 1 meter, and the attenuation of light inside the container due to causes other than water and phytoplankton biomass ($K_d X$ in [2.27]) is assumed to be negligible.

The phytoplankton growth model was run to consider two different treatments of the batch cultures. In the first treatment, the culture received trace metals, vitamins, but no inorganic nitrogen source. In the second treatment, the culture received similar additions, but nitrate was added as the source of inorganic nitrogen. Initial values of each state variable are listed in Table 1 and are based on data reported by Eppley, Carlucci, et al. (1971) and Univ. Calif. Inst. Mar. Resour. (1972). The maximum carbon quota, c_5 , is arbitrarily assumed to be twice the initial carbon quota. Initial quotas which were not

Figure 1. A comparison of measured (—) (Reed and Halper, 1974) and computed (● ●) clear-day solar radiation of wavelengths less than 2800 nm at 45°15.8'N, 124° 7.8'W, 120 Km off the Oregon coast on 11, July 1973.

Figure 2. Simulated photosynthetically active radiation (wave-lengths less than 720 nm) as a function of time at 32°N on 11 July.

Table 1. Initial values of variables used in the simulations of the two nutrient treatments. Initial particulate carbon, P_5 , is defined as the product of the carbon per cell ($18.3 \text{ pg at C cell}^{-1}$, from Table 3 of Eppley, Carlucci, et al. (1971)) and the initial cell numbers, N.

Treatment 1		Treatment 2	
All nutrients added except nitrogen		All nutrients added, nitrate as the nitrogen source	
Variable			
P ₁	0.09 µg at l ⁻¹	P ₁	0.09 µg at l ⁻¹
P ₄	0.26 "	P ₄	0.26 "
P ₅	6.41 "	P ₅	6.41 "
P ₆	0.73 µg l ⁻¹	P ₆	0.73 µg l ⁻¹
S ₁	22.8 µg at l ⁻¹	S ₁	50.0 µg at l ⁻¹
S ₂	0.0 "	S ₂	5.0 "
S ₃	0.33 "	S ₃	0.33 "
N	0.35 x 10 ⁶ cells l ⁻¹	N	0.35 x 10 ⁶ cells l ⁻¹

measured at the beginning of the experiment are set to minimum values to represent the effects of pretreatment low-nutrient conditions.

The two treatments differ with respect to the initial values of nutrients, S_1 , S_2 , S_3 (silicate, nitrate and ammonium, respectively) added at the start of the experiment and the additions of nutrients, made during the course of the experiment. No further additions were made to treatment 1, but an ammonium concentration of approximately $0.33 \mu\text{g at l}^{-1}$ persisted during the period of observation. In the second treatment with nitrate added, the ammonium concentration increased with time. The persistent ammonium concentrations in each treatment could be attributed to nitrate reduction in the dark or to excretion by those microzooplankton not removed by the pretreatment filtering. Zooplankton processes or other possible sources of ammonium are not represented in the equations of this model and the observed ammonium concentrations are therefore treated as a given condition of the experiment. The regression equation (Aird 1972)

$$S_3 = 0.33 \exp [0.17 t]$$

is used to specify the ammonium concentration, S_3 , as a function of time, t , in hours since the beginning of the experiment (Figure 7). This condition unfortunately precludes a mass balance, but it reproduces the nutrient environment for this model of phytoplankton growth and it avoids the introduction of variables and functions for which no data exist.

Concentrations of nitrate and silicate are increased in the simulation according to the schedule used in the actual experiment. The nitrate concentration was increased by $20 \mu\text{g at l}^{-1}$ after 28 hours and

Figure 3. Observed (●) and simulated (—) silicate concentrations in the treatment without an added nitrogen source. In all of the following comparisons of observed and simulated concentrations, time zero is 0600 hours and the darkened areas on the abscissa are night-time periods.

Figure 4. Observed (●) and simulated (—) concentrations of chlorophyll a in the treatment without an added nitrogen source.

Figure 5. Observed (●) and simulated (—) cell numbers in the treatment without an added nitrogen source.

Figure 6. The simulated variation in the carbon to chlorophyll ratio (by weight) in the treatment without an added nitrogen source.

50 μg at 1^{-1} after 77 hours. Also after 77 hours, the concentration of silicate was increased by 67 μg at 1^{-1} .

2.4 Results

A comparison of the observations and calculated results for the treatment lacking an added nitrogen source is made in Figure 3 to 5. Relatively few measurements were made on the culture with no nitrogen added. The nitrate concentration remained essentially undetectable and addition of all the other nutrients had little or no effect on growth, suggesting nitrogen was the factor limiting population growth in this experiment.

It is difficult to understand how an ammonium concentration of approximately 0.33 μg at 1^{-1} could persist during the experimental treatment unless it was sustained by microzooplankton activity or some other regenerative source. In the absence of simulated grazing losses this constant concentration, not depleted by simulated uptake, sustains some simulated phytoplankton growth and causes the mean simulated population growth (0.022 hr^{-1}) to overestimate the slower observed population growth rate (0.012 hr^{-1}) calculated from initial and final diatom cell counts. The effects of nitrogen depletion, however, remain evident in the simulation results. The average atomic C/N ratio is high (17.9) and carbon to chlorophyll ratio (by weight) also high, varies between extremes of 90 and 170 (Figure 6). A comparison of these ratios with the observations is not possible because measurements of particulate carbon, nitrogen and chlorophyll were not made simultaneously during the course of this experiment.

Figure 7. A comparison of the observed ammonium concentration (●) and the graph of the function, $S_3 = .33 \exp [.017t]$, used to specify the ammonium concentration during the course of the treatment with nitrate added as the nitrogen source. Time zero is at 0600 hrs local time and darkened areas on the abscissa are night time periods.

Figure 8. Observed (●) and simulated (—) nitrate concentrations in the treatment with nitrate added as a nitrogen source.

Figure 9. Observed (●) and simulated (—) silicate concentrations in the treatment with nitrate added as a nitrogen source.

Figure 10. Observed (●) and simulated (—) cell numbers in the treatment with nitrate added as a nitrogen source.

Figure 11. Observed (●) and simulated (—) chlorophyll a concentrations in the treatment with nitrate added as a nitrogen source.

Figure 12. Observed (●) and simulated (—) particulate carbon concentrations in the treatment with nitrate added as a nitrogen source. The circled observation at 84 hours may be erroneously high (Banse, 1974).

Figure 13. Observed (●) and simulated (—) particulate nitrogen concentrations in the treatment with nitrate added as a nitrogen source.

Figure 14. Observed (●) and simulated (—) values of the carbon to chlorophyll ratio (by weight) in the treatment with nitrate added as a nitrogen source.

Figure 15. The simulated growth rate (hr^{-1}) during the course of the treatment with nitrate added as a nitrogen source. The mean observed growth rate was 0.039 hr^{-1} .

Figure 16. A comparison of measured and simulated nitrogen assimilation rates as a function of time.

The simulated growth response for treatment 2 contrasts with the previous results. Figure 8 to 14 show that population biomass and, consequently, nutrient uptake are much higher during treatment 2 with an added inorganic nitrogen source. Increases in simulated cell numbers, phytoplankton chlorophyll, carbon and nitrogen and decreases in nitrate and silicate concentrations correspond with measured changes occurring during the first 70 to 80 hours of the 96 hour experimental period of treatment 2. A depletion of vitamin B₁₂ occurred during treatment 2 after 72 hours (Eppley, Carlucci, et al. 1971) and may have been responsible for decreases in some physiological rates, particularly chlorophyll synthesis, after that time. Model growth and uptake equations are not functions of vitamin concentration and do not express rate decreases due to vitamin depletion. A divergence of some of the simulated results and observations after 70 hours may be due to the absence of vitamin sensitive functions in the model and again may also be attributable to the lack of grazing functions in the model equations.

The observed phytoplankton cell division rate was 0.039 hr^{-1} and the mean simulated rate is 0.042 hr^{-1} . Silica was the factor initially limiting simulated cell division rate, but carbon, through light limitation, became the most limiting factor after 13 hours in the simulation. Observed phytoplankton cell division was partially synchronous and most cells divided in the afternoon and early evening. The simulated growth rate also varies periodically (Figure 15) and highest rates occur in the late afternoon. Other examples of diel periodicities occurring in phase within both the experiment and the simulation

are changes in the carbon to chlorophyll ratio (Figure 14) and nitrogen uptake rate (Figure 16). The measured and simulated nitrogen uptake rates are for 6 hour intervals between sampling times and are expressed as the quotient of the nutrient concentration decrease occurring during the 6 hour interval and the mean particulate nitrogen concentration.

2.5 Discussion

A comparison of the available observations with the simulated results suggest that many characteristics of phytoplankton growth are represented in the model. One of the interesting features of both the experiment and the simulation is the occurrence of diel variability in physiological rates and chemical composition. Unlike Walsh's (1975) treatment of multiple nutrient regulation in a phytoplankton growth model, none of the uptake parameters in this model are specified as periodic functions of time. The periodic behavior produced by the model is not due to explicit periodic forcing of the uptake functions, but occurs as a consequence of the relationship between carbon and nutrient cell quotas and the periodic variation of solar radiation directly affecting the carbon quota.

This model remains, however, an extremely simplified paradigm unable to completely account for some growth characteristics. For example, the periodic variation in simulated nitrate uptake rate has been described (Figure 16). The assimilation of nitrogen by phytoplankton populations is known to be light dependent (Grant 1967; Grant and Turner 1969; MacIsaac and Dugdale 1972) and often, as in the culture experiment, shows a diel periodicity with higher rates of assimilation occurring during the day and lower rates occurring during the

night (Eppley, et al. 1970; Eppley, Rogers and McCarthy 1971). The model results indicate, however, that simulated nitrogen uptake is higher than observed during the day and ceases completely for some period at night. Falkowski (1975) showed that nitrate uptake is correlated with the hydrolysis of ATP and suggested that ATP is the rate limiting substrate in the dark at non-limiting nitrate concentrations. The ATP necessary to maintain nitrate uptake could be produced by either photosynthesis in the light or respiration in the dark. Future models with a stronger biochemical basis, perhaps including high energy phosphate fluxes might better resolve the details of this type of physiological periodicity.

An important feature of this model is that cell division and biosynthetic processes such as nutrient assimilation and carbon fixation are separate, but related functions. These functions have been explicitly represented in an attempt to account for the characteristics of each process and to more clearly show how the success of a population could depend on simple process interrelationships and to conditions in the external environment. For example, when cell division occurs at a specific rate, G , at half the maximal rate, then

$$G = (g/2) (1 - (d_n/c_n)) \quad [2.39]$$

In general, the specific rate uptake rate, V_n , is

$$V_n = v_n(S_n/(k_n + S_n)) \quad [2.40]$$

At steady state, growth and uptake rates are equal and

$$(g/2) (1 - (d_n/c_n)) = v_n(S_n/(k_n + S_n)) \quad [2.41]$$

Solving for S_n gives the half-saturation constant for growth, K_g , or the nutrient concentration sustaining half the maximal growth rate

$$K_g = S_n = k_n \frac{\left(\frac{g}{2v_n} \left(1 - \frac{d_n}{c_n} \right) \right)}{\left(1 - \frac{g}{2v_n} \left(1 - \frac{d_n}{c_n} \right) \right)} \quad [2.42]$$

This equation conveniently expresses the half-saturation constant for growth, K_g , as a function of the half-saturation constant, k_n , for uptake. In general, maximal uptake rates, v_n , are greater than maximal growth rates, g (see explanation following equation [2.32]). If the ratio of maximum and minimum quotas (C_n and d_n) is constant, then the half-saturation constant for growth is given as a function of the ratio v_n and g (Figure 17).

The relationship expressed in [2.42] offers an explanation of why observed half-saturation constants for growth may be much lower than the half-saturation constants for uptake (Caperon and Meyer 1972; Droop 1968). An implication of this result is that comparisons of half-saturation constants for uptake to determine competitive advantages among phytoplankton populations at low nutrient concentrations may not necessarily be definitive. Generally, the species with the lower k_n half-saturation constant for uptake is expected to have a competitive advantage over another at low nutrient concentrations (Dugdale 1967). However, if growth and uptake processes of phytoplankton are described by the equations of this model, a species with a higher half-saturation constant and a high maximal uptake rate could out compete, at low

nutrient concentrations, another species with a lower k_n value, but with a maximal uptake rate more nearly equal to its maximum division rate.

This phytoplankton growth model has been formulated to describe the relationships among several of the most important environmental factors affecting the physiology of primary production. It has been applied to the batch culture study to verify that its formulation is internally consistent and that it may realistically represent the effects of light or nutrient limitation important in the control of primary production in an upwelling region. In the following section, this phytoplankton growth model, and solar radiation submodel, are incorporated in a spatially and functionally more complex model of ecosystem processes of the upwelling region off northwest Africa.

Figure 17: The half-saturation constant for growth k_g as a function of the ratio of maximum uptake and cell division rates. k_g is expressed as a fraction of the half-saturation constant for uptake.

CHAPTER 3

THE NORTHWEST AFRICA UPWELLING ECOSYSTEM MODEL

3.1 Formulation

The formulation of the ecosystem model is based on the experimental design of the JOINT-I expedition of the Coastal Upwelling Ecosystems Analysis program. Barber's (1977) description of JOINT-I discusses the considerations which led to the selection of the site for the field study and design for deployment of the current meters. Historical data indicated that the region near Cap Blanc (Figure 18) is characterized by a pattern of relatively consistent upwelling occurring over a shallow continental shelf with a sharp shelf break at at $\sim 100\text{m}$) and a steep continental slope. Hydrographic and air reconnaissance surveys made prior to the cruise and an analysis of JOINT-I data by Mittelstaedt et al. (1975) indicate that the region is also characterized by a high degree of longshore uniformity with little three dimensional structure.

If it is assumed that upwelling in the JOINT-I study area occurs as a two dimensional process then [2.1] can be written as

$$\frac{\partial S}{\partial t} = \frac{\partial K_x (\partial S / \partial x)}{\partial x} + \frac{\partial K_z (\partial S / \partial z)}{\partial z} - \frac{\partial (uS)}{\partial x} - \frac{\partial (wS)}{\partial z} + R \quad [3.1]$$

where

x, z = spatial coordinates with x positive offshore and z positive vertically downwards;
 u, w = velocity components in the x and z directions, respectively;

Figure 18. Location of the JOINT-I study. The circles and triangles indicate the position of moored current meter arrays and meteorological towers. The squares indicate the locations on the 21°40'N transect where productivity and hydrographic stations were repeatedly occupied. From Barber (1977).

K_x, K_z = coefficients of horizontal and vertical eddy diffusivity, respectively.

R = nonconservative effects

A set of similar equations is used to describe changes in the distribution of each variable in this ecosystem model. The first four terms on the right represent the turbulent mixing and advection effects of the circulation and are functionally similar for all variables at a given location. The nonconservative R term, however, represents changes due to biological and chemical interactions and is usually different for each variable at a given location. Therefore, the nonconservative interactions will be discussed separately following a description of the physical circulation system. The spatial segmentation convention, definition of the boundary conditions and the numerical methods used to integrate the equations are discussed in Appendices I and II.

3.1a Physical Circulation. Mittelstaedt et al. (1975) describe the general flow patterns in the northwest African upwelling region. They show that alongshore flow near the coast was characterized by an equatorward surface current with speeds of $10\text{--}20 \text{ cm s}^{-1}$ extending over much of the shelf ($\sim 40 \text{ km}$ wide) and a poleward undercurrent between 200 and 300 m depth along the slope moving northward at a mean speed of 10 cm s^{-1} . The strongest vertical velocities on the order of $10^{-2} \text{ cm s}^{-1}$ occurred near the bottom at the shelf break (between 100 and 150 m). Rising water became a part of the subsurface onshore flow and upwelled into the surface layer on the shelf and near the coast.

In order to formulate and run the ecosystem model it is necessary to quantitatively represent the above largely qualitative description of the circulation. One approach to the problem of rationally quantifying the flow field is to utilize the results from a hydrodynamic model (Wroblewski 1977). When development of this ecosystem model was begun, the model of Hamilton and Rattray (1978) was the only structurally compatible hydrodynamic model to have been applied to the northwest African upwelling region. It was therefore used to generate the flow fields required in the ecosystem model.

The Hamilton and Rattray hydrodynamic model, to be referred to as the physical submodel, solves the equations of continuity, mass and momentum conservation for a continuously stratified coastal region with variable shelf topography, given the wind stress and offshore density profile. The equations of the physical submodel and are listed in Appendix V. For further details of the mathematical formulation and the numerical methods used see Hamilton and Rattray (1978).

Beginning at initial time $t = 0$ in the physical submodel, a wind stress is impulsively applied to a circulation system with level isopycnals. At every iteration ($\Delta t = 30$ minutes) the physical submodel generates a new u , v , w flow field as the system spins-up. Because alongshore gradients are ignored in the ecosystem model only the u and w components of the flow at each iteration are used in the ecosystem model.

The grids of both models are arranged in a vertical plane normal to the coast, but the grid spacing is variable in the ecosystem model

and regular in the circulation submodel. Ecosystem model grid spacing varies from 5 km x 5 m nearshore to 20 km x 20 m offshore below 60 m (Figure 19). The 5 km x 10 m regular grid of the physical submodel maps easily onto the system model grid, and simplified the task of maintaining continuity when the physical submodel results were post processed prior to use in the ecosystem model.

Hamilton and Rattray (1978) indicate that the physical submodel results "are not meant to be a detailed simulation since no attempt has been made to tune the model to the data." However, from a comparison of hydrographic sections and current meter data they conclude that the correspondence between the model and field data are reasonable considering the simplifications made in the model. With a constant equatorward wind stress of 1 dyne cm^{-2} the physical submodel generates a sequence of flow fields similar to the observed upwelling circulation. Examples of the calculated flow fields after 2, 5, and 10 days constant wind stress are shown in Figures 20 to 22. For comparison, Figure 23a is a schematic diagram of the mean upwelling circulation from Mittelstaedt, et al. (1975). Mittelstaedt, et al. (1975) measured a decrease in shoreward transport inside the shelf break and therefore showed upwelling occurring over the entire shelf. In substantial agreement with this observation the physical submodel generates upwelling flow into the base of the euphotic zone over most of the shelf and at the shelf break after a spin-up time of several days. A maximum upwelling velocity of $2.8 \times 10^{-2} \text{ cm s}^{-1}$ near the bottom at the shelf break is of the same order as the maximum suggested by Mittelstaedt

Figure 19. The grid system of the system model. The grid spacing varies from 5 km in the horizontal by 5 m in the vertical nearshore to 20 km by 20 m in the offshore area below 60 m.

Figure 20. Resultant current velocity vectors plotted from horizontal and vertical currents in the circulation submodel after 2 days simulation time.

Figure 21. Resultant current velocity vectors plotted from horizontal and vertical currents in the circulation submodel after 5 days simulation time.

Figure 22. Resultant current velocity vectors plotted from horizontal and vertical currents calculated in the circulation submodel after 10 days simulation time.

Figure 23(a)

Figure 23(b)

Figure 23

A schematic diagram showing the mean cross shelf flow during active upwelling in the JOINT-I study area. From Mittelstaedt, et al. (1975). The letters at the top of the illustration show the location of current meter moorings identified in Figure 18. A comparison of simulated and observed onshore-offshore flows. The dashed line is the u component of the velocity profile generated by the upwelling circulation submodel after 10 days simulation time 30 km offshore. The horizontal bars show the ranges of 24.8 hour mean values of the u component during periods of well developed upwelling circulation obtained from current meter measurements 32 km offshore. The current meter observations are based on Figure 10 in Mittelstaedt, et al. (1975).

et al. (1975). The mean simulated offshore flow over the shelf reaches 10.5 cm s^{-1} in the upper 10 m and is approximately equal to the observed maximum which averaged 10 cm s^{-1} . In Figure 23b, a comparison is made of current meter measurements 32 km from the coast with the u velocity profile at $x = 30 \text{ km}$ in the physical submodel. The comparison shows the computed velocities occur within or near the ranges of measured u velocities. The zero crossing for both measured and computed velocities is at about 30 to 40 m. Although some discrepancies exist in this comparison and in other comparisons discussed by Hamilton and Rattray (1978) the degree of similarity supports the conclusion that the physical submodel provides for the ecosystem model a useful representation of an upwelling circulation which is similar in many respects to the circulation measured during JOINT-I.

One unusual feature of the upwelling circulation observed during JOINT-I, not reproduced in the physical submodel, was the occurrence of a northward flowing surface current at the offshore boundary of the upwelling regime (Mittelstaedt et al. 1975). Its position varied between approximately 100 to 40 km offshore with changes in the strength and direction of the winds. During occasional intervals of weak winds unfavorable to upwelling, the offshore transport diminished and the northward surface current moved shoreward. The northward surface current may arise from far field regional influences rather than the local wind forcing (Mittelstaedt et al. 1975) so it should not be an expected feature in the physical submodel. The physical submodel,

therefore, most plausibly describes the spin up or development of active upwelling with the northward surface current in an offshore position. Future simulation studies designed to reproduce all of the actual sequence of 1974 upwelling events discussed by Barton et al. (1977) will have to consider the variability in the position of this offshore boundary current, or be spatially confined to the shelf region.

Turbulent mixing processes are parameterized in the eddy coefficients K_x and K_z in [3.1] and are specified as constants in space and time. A horizontal mixing coefficient, K_x , of $1.2 \times 10^6 \text{ cm}^2 \text{ s}^{-1}$ is assumed in all simulation cases. The vertical mixing coefficient, K_z , was usually $1 \text{ cm}^2 \text{ s}^{-1}$, and thus equivalent to the values used in previous models of other upwelling systems (Walsh 1975; Wroblewski 1977). In one case K_z was increased to $40 \text{ cm}^2 \text{ s}^{-1}$ to investigate the effect of strong mixing. Preliminary test cases showed that the K_z value used in this strong mixing case is near the upper limit allowing a stable solution given the time and space differencing conventions of the model. Results from other preliminary cases, run with intermediately valued vertical mixing coefficients, were qualitatively similar so only the extreme cases of 1 and $40 \text{ cm}^2 \text{ s}^{-1}$ are presented here. A K_z value of $125 \text{ cm}^2 \text{ s}^{-1}$ has been reported for the upper mixed layer by Halpern (1977), but values this high could be accommodated in the model only after extensive changes to the space differencing or velocity data storage and retrieval schemes used in the model. Use of the higher and perhaps more realistic eddy coefficients for the mixed layer would also

require that values for eddy coefficients in the less turbulent areas also be defined. The data are not available to support such a differentiation and a maximum useable value of $40 \text{ cm}^2 \text{ s}^{-1}$ value is therefore assumed throughout the simulated space.

3.1b Biological Interactions. The nonconservative terms of the state equations are defined below. Equations [3.2] to [3.9] are the phytoplankton-nutrient state equations with the effects of grazing, physiological mortality or nutrient regeneration included. Equations [3.10] to [3.18] supplement the phytoplankton growth equations and define phytoplankton quotas and uptake or synthesis rates. Grazing rates of the zooplankton are defined in [3.19-3.20], and [3.21-3.22] define grazing rates of the fish. The symbol conventions are the same as those used in the phytoplankton growth model. All symbols are defined as a group in Appendix IV and are individually discussed in the rationale following the equations.

$$R(\text{Silicate}) = -V_1 P_1 + r_1 \quad [3.2]$$

$$R(\text{Nitrate}) = -V_2 P_4 + r_2 \quad [3.3]$$

$$R(\text{Ammonium}) = P_4(-V_3 + \beta_3 Z + \gamma_3 F) + r_3 \quad [3.4]$$

$$R_{\text{Silica}}(\text{Phytoplankton}) = P_1(V_1 - Z - F - m) \quad [3.5]$$

$$R_{\text{Nitrogen}}(\text{Phytoplankton}) = P_4(V_4 - Z - F - m) \quad [3.6]$$

$$R_{\left(\begin{smallmatrix} \text{Phytoplankton} \\ \text{Carbon} \end{smallmatrix}\right)} = P_5 (V_5 - Z - F - m) \quad [3.7]$$

$$R_{\left(\begin{smallmatrix} \text{Phytoplankton} \\ \text{Chlorophyll} \end{smallmatrix}\right)} = P_6 (V_6 - Z - F - m) \quad [3.8]$$

$$R_{\left(\begin{smallmatrix} \text{Phytoplankton} \\ \text{Cell Numbers} \end{smallmatrix}\right)} = N (G - Z - F - m) \quad [3.9]$$

$$C_n = P_n / N \quad \text{for } n = 1, 4, 5, 6 \quad [3.10]$$

$$G = 0 \quad \text{if } C_n \leq d_n \quad \text{for } n = 1, 4, 5 \quad [3.11]$$

$$= \text{minimum of } [g (C_n - d_n) / C_n] \quad \text{otherwise}$$

$$V_1 = v_1 (S_1 / (k_1 + S_1)) \quad \text{if } C_1 < c_1 \text{ and } V_1 < G \quad [3.12]$$

$$= 0 \quad \text{otherwise}$$

$$V_2 = v_2' (S_2 / (k_2 + S_2)) \quad \text{if } C_4 < c_4 \text{ and } V_4 < G \quad [3.13]$$

$$= 0 \quad \text{otherwise}$$

$$V_2' = v_2 - a_3 \cdot S_3 \quad [3.14]$$

$$V_3 = v_3 (S_2 / (k_3 + S_3)) \quad \text{if } C_4 < c_4 \text{ and } V_4 < G \quad [3.15]$$

$$V_4 = V_2 + V_3 \quad [3.16]$$

$$V_5 = ((Q_{\max} \cdot I_{\max} \cdot K_c \cdot C_6) \cdot \quad [3.17]$$

$$(\exp[-I_z / I_{\max}] - \exp[-I_o / I_{\max}]) / (K_t \cdot z))$$

$$- (f_5 + b_5 \cdot G) \text{ if } C_5 < c_5 \text{ and } V_5 < G$$

$$= 0 \quad \text{otherwise}$$

$$\begin{aligned}
 P_6 V_6 &= e_6 \cdot V_4 && \text{if } n = 4 \text{ is minimum in [3.11]} && [3.18] \\
 &= P_6 (g(C_4 - d_4)/C_4) && \text{if } n = 1 \text{ or } n = 5 \text{ is minimum in [3.11]} \\
 &= 0 && \text{if } C_6 \geq c_6 \text{ and } V_6 \geq G
 \end{aligned}$$

$$Z = (q_5 L_5 + \lambda j_5 L_5)/P_5 \quad [3.19]$$

$$L_5 = \psi P_5 + \epsilon \quad [3.20]$$

$$F = (w_5 \cdot M_5)/P_5 \quad [3.21]$$

$$M_5 = \theta \cdot P_5 + \tau \quad [3.22]$$

3.2 Rationale

3.2a Incident Solar Radiation and Submarine Light Attenuation.

Estimates of incident solar radiation are calculated with the submodel used in the phytoplankton growth model. Simulated clear-day solar radiation totaling 665 ly d^{-1} , occurring over a 12.4 hour light day, on 9 April, the approximate midpoint of the JOINT-I expedition, is assumed to be representative of the cruise period. The incident radiation measured aboard the ATLANTIS II averaged 610 ly d^{-1} (Barber and Huntsman 1975). The 9% difference between observed and simulated values can be attributed to occasional cloudiness and shading of the pyranometer by the mast of the ship. Simulated subsurface photosynthetically active radiation totals 310 ly d^{-1} (approximately $59.6 \text{ einst m}^{-2} \text{ d}^{-1}$) and is 47% of the subsurface total.

Light penetrating the sea surface is attenuated by seawater, phytoplankton chlorophyll, and other substances. Equation [2.77] expressing the total attenuation as the sum of three partial extinction coefficients is rewritten here

$$K_t = K_w + K_c \cdot P_6 + K_d \cdot X \quad [2.27]$$

The extinction coefficient of seawater, $K_w = 0.04 \text{ m}^{-1}$ is known (Lorenzen 1972), and the attenuation due to chlorophyll $K_c \cdot P_6$ can be approximated if $K_c = 0.016 \text{ m}^2 (\text{mg Chl a})^{-1}$ (Bannister 1974) and the chlorophyll concentration, P_6 , is known. The attenuation due to other substances, $K_d \cdot X$, may be significant (Lorenzen 1972) and must be explicitly defined in the model.

Estimates of $K_d \cdot X$ for the model have been obtained from measurements of light attenuation and chlorophyll made on the ATLANTIS II. Three of the four terms of the equation for total attenuation are known and the fourth, $K_d \cdot X$ is calculated by difference. Horizontally constant mean values of $K_d \cdot X$ for the cruise period (Table 2) are used in the ecosystems model except in the nearshore 5 km region where attenuation is high and $K_d \cdot X$ equals 0.73 m^{-1} and 0.35 m^{-1} for the 0-5 m and 5-10 m depth intervals, respectively. The high turbidity of the nearshore region caused by high levels of resuspended mineralized particles may be a permanent feature of this upwelling region, even when upwelling occurs over the inner shelf (A. Morel, personal communication).

3.2b Phytoplankton. A preliminary analysis of the phytoplankton samples taken during JOINT-I indicates that the phytoplankton community was composed mainly of diatoms and coccolithophorids. Thalassiosira, Chaetoceros, Dactyliosolen, Leptocylindrus, Nitzschia and Rhizosolenia species were the dominant diatoms, and Coccolithus, Syracosphaera and Pontosphaera species were the dominant coccolithophorids (T. Cowles, D. Blasco, personal communication). Although the coccolithophorids were sometimes numerically abundant, phytoplankton rate measurements

Table 2. The vertical distribution of the mean partial extinction coefficient, $K_d X$, attributable to substances other than seawater and chlorophyll. Values listed are averages calculated from JOINT-I chlorophyll and submarine light measurements made along the transect at 21°40'N. Measurements made within 5 km of the coast are not included in these averages.

Depth Interval	$K_d X$
(m)	(m^{-1})
0-5	0.21
5-10	0.13
10-15	0.11
> 15	0.08

made during JOINT-I did not differentiate between diatoms and coccolithophorids. On the basis of literature data (mainly for Coccolithus and Syracosphaera (= Cricosphaera = Hymenomonas) species), diatoms are typically larger (Strathman 1967) and have higher maximum growth rates (Eppley, et al. 1969b; Eppley 1970) and may therefore be the more trophodynamically important of the two phytoplankton groups found during JOINT-I. Because of the significance of diatoms in other upwelling regions and because the physiological rates and higher trophic level interactions of the diatoms and coccolithophorids were not differentiated in the JOINT-I data, only diatoms are represented in the model equations.

The phytoplankton growth and uptake functions used in the north-west African ecosystem model are, with minor changes, the same as those in the previously discussed phytoplankton growth model. Results from preliminary simulations run with some specific sequences of growth limiting conditions not represented in the batch culture experiment showed that the phytoplankton growth equations could yield unrealistically high C/N ratios approaching 100. Banse's (1974) interpretation of available data on the carbon to nitrogen ratio in phytoplankton suggests, however, that a maximum C/N of 17.5 is more realistic, and this value is used as a limiting condition in the ecosystems model. In the equations this condition is included in a redefinition of c_5 , the minimum carbon quota, as

$$c_5 = \text{minimum of } (c_5, 17.5 \cdot c_4)$$

where

c_4 is the phytoplankton nitrogen quota.

Another change is the addition to the phytoplankton growth equations of a term for physiological death. This form of natural mortality may be potentially significant in the aphotic zone (Lehman et al. 1975), but actual rates are not well known. The death rate, $m = 0.0042 \text{ hr}^{-1}$ used by Wroblewski (1976) is also used in this model whenever the cell division rate is less than 0.0001 hr^{-1} . The death rate is otherwise assumed to be zero.

A final difference between the two sets of phytoplankton equations is related to the need to segment space in the ecosystem model. Photosynthetic fixation of carbon is calculated in the second model using the same function [2.30] as in the phytoplankton growth model. For convenience, the function is rewritten here as

$$P(Z) = (Q_{\max} I_{\max} K_c P_6) \cdot$$

$$(\exp [-I_z/I_{\max}] - \exp [-I_0/I_{\max}]) / (K_t z) \quad [2.30]$$

For each spatial segment of the system model, I_0 and I_z , the photosynthetically active light available at the top and bottom, respectively, of each segment, must be defined before a photosynthesis rate is calculated. In the first layer, I_0 is the light penetrating the sea surface. For each spatial segment in the surface layer the light, I_z , at the bottom boundary of each segment is calculated as

$$I_z = I_0 \exp [-(K_w + K_c P_6 + K_d X)z] \quad [3.23]$$

where

K_w , K_c , and K_dX are the partial extinction coefficients previously discussed;

P_6 is the chlorophyll concentration in each spatial segment;

z is the thickness (m) of the depth interval.

I_z may be different in each spatial segment depending on the chlorophyll concentration and the attenuation of light attributable to other substances. I_z values for the bottom boundary of each segment are stored temporarily during the calculation procedure. The model calculations are done layer by layer, beginning at the surface, so the I_z values stored as bottom boundary values for the segments in the first layer become the upper boundary, I_0 , values for the segments immediately beneath. This procedure is repeated for each layer until the bottom layer is reached during each iteration. If coefficients of light attenuation vary horizontally the light profile of each vertically segmented column is unique and the calculations of light intensity must therefore begin at the surface. If calculations were to begin at the bottom layer, as in the AUGUR simulation program (Morishima et al. 1974), light intensities in the subsurface layers can not be correctly calculated because the integrated attenuation due to chlorophyll and other substances in the space above cannot be considered.

3.2c Zooplankton. Blackburn (1975a) has described in some detail the JOINT-I zooplankton sampling procedures. In summary, vertical net hauls were made from 200 m or the bottom, whichever was less, to the

sea surface with a pair of nonclosing Bongo plankton nets. The net mouth diameter was 60 cm and the mesh size was 102 μ . Samples obtained with the nets were combined and filtered through a series of sieves to yield subsamples of zooplankton in four size ranges of approximately 100-200, 200-500, 500-1000, and > 1000 μ . One quarter of each subsample was weighed wet, oven dried at 60°C for 24 hours or longer and then weighed dry. Portions of the dry weight sample were reweighed and then incinerated in a muffle furnace for 24 hours or longer before weighing the ash residue and by difference obtaining the weight of dry organic matter.

Many of the zooplankton samples were contaminated with phytoplankton. Estimates of phytoplankton contamination in the zooplankton net tows are based on fluorometric measurements of chlorophyll extracted from 0.5 ml subsamples of each tow. The weight of chlorophyll in each subsample was converted to an equivalent weight of carbon, assuming a carbon:chlorophyll ratio of 40.5:1 (Lorenzen 1968) and then to an equivalent weight of dry organic matter, assuming that carbon represents 43% of the dry organic matter of phytoplankton (Cushing et al. 1958).

A comparison of the weights of phytoplankton and zooplankton dry organic matter (Tables 3a and 3b) shows that the phytoplankton were a variable and sometimes significant source of contamination in the zooplankton organic matter in the 100-500 and 500 μ size fractions. For the 100-500 μ fraction it averaged 7% of the zooplankton organic matter weight.

Table 3a. Organic weight of zooplankton collected during JOINT-I over the continental shelf. Weights listed are corrected for contamination by phytoplankton. Phytoplankton contamination in each tow is expressed as a ratio of estimated phytoplankton and zooplankton organic matter weights x 100.

Tow No.	Small Size Fraction (100-500 μ) Weight (mg m ⁻²)	Percent Phytoplankton Contamination	Large Size Fraction (> 500 μ) Weight (mg m ⁻²)	Percent Phytoplankton Contamination
41	914	28	603	11
46	1102	25	549	9
47	992	25	805	8
48	1259	6	258	5
49	1119	5	900	11
50	1689	1	254	13
51	1512	2	234	18
52	1277	2	875	2
65	1807	0	591	1
66	957	0	183	3
67	2341	1	858	10
68	1143	3	815	11
73	3692	2	450	0
75	1340	17	671	9
76	1209	15	556	8
78	1241	5	550	0
100	2186	31	532	0
108	1398	53	355	23
109	3146	21	374	0
$\bar{x} = 1596$			$\bar{x} = 548$	

Table 3b. Organic weight of zooplankton collected seaward of the shelf break. Weights listed are corrected for contamination by phytoplankton. Phytoplankton contamination in each tow is expressed as a ratio of estimated phytoplankton to zooplankton organic matter weights x 100.

Tow No.	Small Size Fraction (100-500 μ) Weight (mg·m ⁻²)	Percent Phytoplankton Contamination	Large Size Fraction (> 500 μ) Weight (mg·m ⁻²)	Percent Phytoplankton Contamination
44	1658	11	5842	1
45	846	33	638	29
54	923	0	3967	0
82	785	15	1307	8
101	1010	6	1152	1
102	534	3	1820	1
$\bar{x} = 959$			$\bar{x} = 2455$	

Analyses of variance made by Blackburn (1975a) on the CUEA wet-weight zooplankton data to investigate differences in biomass by time period, area (shelf vs. slope) and size of the zooplankton showed that smaller zooplankton were more abundant on the shelf and larger zooplankton were more abundant on the slope. The analysis also found no evidence of changes in total zooplankton abundance with time during the two-month sampling period. It is assumed that these conclusions apply to distributions of zooplankton dry organic matter expressed on a per volume basis as well.

The zooplankton weights have been converted to zooplankton concentrations by dividing the organic weights by the volume of water filtered by the nets. Mean zooplankton organic-weight concentrations have been converted to zooplankton carbon concentrations, assuming that carbon is 50% of the organic or ash-free weight of the zooplankton (Mullin 1969). On the shelf, mean values of 12.5 mg C m^{-3} and 3.8 mg C m^{-3} are obtained for the $100\text{--}500 \mu$ and $> 500 \mu$ size fractions, respectively. Offshore, the net tows extended beneath the depth range of the model, but all zooplankton biomass is included within the two size classes of zooplankton as if it inhabited the upper 100 meters only. Accordingly, in the offshore region, the $100\text{--}500 \mu$ fraction averaged 4.9 mg C m^{-3} and the $> 500 \mu$ size fraction averaged 12.4 mg C m^{-3} .

The trophic relationships among the zooplankton are not well defined in the available data. Collections made off northwest Africa prior to JOINT-I (H. Weikert, personal communication) showed copepods

to be most abundant with Calanidae, Eucalanidae, Metridiidae and Temoridae the most ecologically important types. Samples taken during JOINT-I contained mainly copepods and euphausiids, which may eat both phytoplankton and zooplankton (Blackburn 1975c). It is assumed in the model, however, that both size classes of zooplankton are phytophagous.

The feeding rate of the large zooplankton is described by the following recilinear ingestion function proposed by Mullin, et al. (1975) based on the data of Frost (1972) for the feeding of Calanus on Thalassiosira fluviatilis:

$$L_5' = \psi'N + \epsilon' \quad [3.24]$$

where

L_5' = ingestion rate per animal (cells·copepod⁻¹·hr⁻¹);

N = food cell concentration (10⁶ cells·l⁻¹);

ψ' = a filtering constant (l⁻¹·copepod⁻¹·hr⁻¹),

if $N < 3.3 \times 10^6$ cells·l⁻¹ $\psi' = 4.07 \times 10^{-3}$ l⁻¹·copepod·hr⁻¹,

if $N \geq 3.3 \times 10^6$ cells·l⁻¹ $\psi' = 1.54 \times 10^4$ l⁻¹·copepod⁻¹·hr⁻¹;

ϵ' = a constant,

if $N < 3.3 \times 10^6$ cells·l⁻¹ $\epsilon' = 622$ cells·copepod⁻¹·hr⁻¹

if $N \geq 3.3 \times 10^6$ cells·l⁻¹ $\epsilon' = 1.31 \times 10^4$ cells·copepod⁻¹·hr⁻¹

This equation can be generalized by expressing copepod individuals as copepod carbon (14.7 µg at C individual⁻¹, Frost 1972) and cell concentration as carbon concentration (7.83 x 10⁶ µg at C cell⁻¹, Frost 1972). Carbon specific ingestion may then be written as

$$L_5 = \psi P_5 + \epsilon \quad [3.20]$$

where

L_5 = carbon specific ingestion rate of large zooplankton

$(\mu\text{g at phytoplankton carbon } (\mu\text{g at zooplankton carbon})^{-1} \text{ hr}^{-1});$

ψ = a filtering constant $(\text{l} \cdot (\mu\text{g at zooplankton carbon})^{-1} \text{ hr}^{-1}),$

if $P_5 < 25.85 \mu\text{g at C} \cdot \text{l}^{-1}, \psi = 72 \times 10^{-5},$

if $P_5 \geq 25.85 \mu\text{g at C} \cdot \text{l}^{-1}, \psi = -27.12 \times 10^{-6},$

if $P_5 < 1.2 \mu\text{g at C} \cdot \text{l}^{-1},$ the grazing threshold, $\psi = 0;$

ϵ = a constant $(\text{hr}^{-1}),$

if $P_5 < 25.85 \mu\text{g at C} \cdot \text{l}^{-1}, \epsilon = 8.6 \times 10^{-4} \text{ hr}^{-1},$

if $P_5 \geq 25.85 \mu\text{g at C} \cdot \text{l}^{-1}, \epsilon = 1.8 \times 10^{-2} \text{ hr}^{-1},$

if $P_5 < 1.2 \mu\text{g at C} \cdot \text{l}^{-1},$ the grazing threshold, $\epsilon = 0.$

This expression is used in the model as the phytoplankton carbon ingestion function for the large zooplankton ($> 500 \mu\text{m}$) with carbon concentration, q_5 . It yields a maximum biomass-specific ingestion rate of 0.42 d^{-1} and probably underestimates the ingestion rates of the smaller zooplankton which have higher specific metabolic rates.

Many studies have shown metabolic rates of organisms to be power functions of body weight. Ikeda (1974) showed for zooplankton found in an $11.7 - 17.5^\circ \text{C}$ temperature regime, similar in range to an upwelling habitat, that

$$\log \gamma = 0.756 \log \omega + 0.127 \quad [3.25]$$

where

γ = respiration rate $(\mu\text{l O}_2 \text{ animal}^{-1} \text{ hr}^{-1});$

ω = body dry weight $(\text{mg animal}^{-1}).$

If the mean dry weights per individual of the 100-500 μ and $> 500 \mu$ size fractions are 0.00254 mg and 0.304 mg, respectively (Smith and Whitledge 1977), the weight specific respiration rate for the smaller zooplankton may be a factor $\lambda = 3.22$ times greater than the rate for the larger zooplankton. Assuming equivalent assimilation efficiencies, and saturating food concentrations, the weight specific ingestion rate of the smaller zooplankton is $\lambda = 3.22$ times greater than the ingestion rate of the larger zooplankton and results in a maximum biomass specific ingestion rate of 1.34 d^{-1} . In other words, the small zooplankton may ingest as much as 134% of their biomass per day. The fraction, Z, of the phytoplankton standing stock consumed by the large and small zooplankton combined can then be defined as

$$Z = (q_5 L_5 + \lambda j_5 L_5) / P_5. \quad [3.26]$$

The products ZP_1 , ZP_4 , ZP_5 , ZP_6 , ZN express the losses due to zooplankton grazing of phytoplankton silica, nitrogen, carbon, chlorophyll and cell numbers, respectively.

Some fraction of the nutrients contained in the phytoplankton biomass consumed by herbivorous zooplankton and fish is excreted and returned to the environment as inorganic regenerated nutrient. This regenerative process has been identified as an important source of nutrients in both oligotrophic (Dugdale and Goering 1967; Eppley, et al. 1973) and eutrophic (Whitledge 1972) regions of the oceans. Ammonium is commonly observed to be the most important form of regenerated nitrogen. Urea is also excreted, but average molar ratios of urea to ammonium excretion commonly range between 1:5 and 1:7, although

Eppley, et al. (1973) do report a ratio of 1:2. Both urea and ammonium can be assimilated by phytoplankton (McCarthy 1972) so neglecting urea excretion underestimates somewhat the potential effects of regeneration in sustaining primary production. Nitrogen is excreted in other forms as well, but these appear to be relatively minor sources (T. Whitledge, personal communication). The contributions to the regenerated nitrogen pool by urea and other nitrogen species are probably of second order importance and will not be included in this model.

Although some zooplankton regeneration measurements were made during JOINT-I (Smith and Whitledge 1977), the rates were not methodologically related to measured amounts of food consumed. Experiments with Calanus zooplankton species (Butler, et al. 1970) have shown, however, that of the total quantity of nitrogen ingested each day, about 36% was excreted in a soluble form. If 80% of zooplankton-regenerated nitrogen is ammonium (Smith and Whitledge 1977), then 29% of the total particulate nitrogen ingested could be excreted as ammonium.

Excretion rates have been observed to be closely related in time to feeding activity (Corner, et al. 1965; Ikeda 1977), but excretion is probably not instantaneous. The function used in the model,

$$X_3 = \beta_3 \cdot Z \cdot P_4 \quad [3.27]$$

where

$$X_3 = \text{the ammonium excretion rate } (\mu\text{g at l}^{-1} \text{ hr}^{-1})$$

β_3 = the zooplankton ammonium excretion efficiency

$(.29 \mu\text{g at excreted} \cdot (\mu\text{g at phyto-N ingested})^{-1}$ based

on Calanus excretion experiments (Butler, et al. 1970);

$Z \cdot P_4$ = the rate of ingestion of phytoplankton nitrogen by

zooplankton ($\mu\text{g at phyto-N} \cdot \text{l}^{-1} \cdot \text{hr}^{-1}$),

instantaneously relates excretion and ingestion and does not allow for a time lag between the two processes. The effect on the system, however, is probably quite insignificant. This function yields excretion rates equivalent to the mean measured rates of 0.0017 and 0.026 $\mu\text{g atom NH}_3\text{-N}(\text{mg dry wt})^{-1} \cdot \text{hr}^{-1}$ (Smith and Whitledge 1977) when the simulated ingestion rates equal 79% and 62% of assumed maximum rates for the small and large zooplankton size classes, respectively. In other words, the mean measured excretion rates occur within the range of rates attainable in the model as functions of phytoplankton nitrogen concentration.

3.2d Fish. Acoustic surveys made during JOINT-I identified two spatially distinct congregations of fish (Thorne, et al. 1977). One was found associated with the upper continental slope and the other was found over the continental shelf. Egg and larval data indicated that the upper continental slope congregation was primarily horse mackerel (Trachurus spp.) and that the shelf congregation was primarily sardine (Sardina pilchardus) with some anchovy (Engraulis encrasicolus) present (Blackburn and Nellen 1976).

Trachurus spp. in this area are known to be primarily zooplanktivorous (Blackburn 1976b) and are not included in the model. Sardina, however, are known to be functional herbivores and may have fed primarily on phytoplankton (Blackburn 1976b). The food requirements of the Sardina population can be estimated if the population biomass is known. A mean value of 48 g m^{-2} (wet weight) was calculated from the average fish biomass observed with the 120-kHz acoustic system during JOINT-I, between 6 April and 6 May, 1974 (Thorne, et al. 1977) over the shelf region. If the fish are 10% carbon by weight (Gulland 1970), the mean carbon biomass is 4.8 g C m^{-2} . Mathisen, et al. (in press) estimate that the pelagic fish of the JOINT-I area consume between 4 and 8% of their body weight per day. If the Sardina consume 4% of their body weight per day as phytoplankton, they require approximately $0.2 \text{ g C m}^{-2} \text{ day}^{-1}$ to sustain growth and meet metabolic requirements.

Mathisen, et al. (in press) show that food supply may not directly control the size of adult fish populations in the northwest African upwelling system. The $0.2 \text{ g C m}^{-2} \text{ day}^{-1}$ requirement, therefore represents a maximum ration obtainable when food is relatively abundant. In general, however, the quantity of food eaten increases as the concentration of food increases until a maximum ration is reached (Ivlev 1945). In order to relate the amount ingested to the amount available, it is assumed that the fish obtain a maximum ration at the same concentration of phytoplankton carbon as the zooplankton, $25.5 \mu\text{g at C l}^{-1}$, and that the feeding threshold, $1.2 \mu\text{g at C}^{-1}$, is also the same

as for the zooplankton. The carbon-specific ingestion rate of the fish, expressed as a function of phytoplankton carbon concentration may then be written as

$$M_5 = \theta P_5 + \tau \quad [3.28]$$

where

M_5 = carbon specific ingestion rate of the fish

(μg at phytoplankton carbon (μg at fish carbon) $^{-1}$ hr $^{-1}$);

θ = a filtering constant ($l(\mu\text{g}$ at fish carbon) $^{-1}$ hr $^{-1}$),

if $P_5 < 25.85 \mu\text{g}$ at C l^{-1} , $\theta = 6.9 \times 10^{-5}$,

if $P_5 \geq 25.85 \mu\text{g}$ at C l^{-1} , $\theta = 1.7 \times 10^{-3}$,

if $P_5 < 1.2 \mu\text{g}$ at C l^{-1} , the grazing threshold, $\theta = 0$;

τ = a constant (hr $^{-1}$),

if $P_5 < 25.85 \mu\text{g}$ at C l^{-1} , $\tau = 8.2 \times 10^{-5}$,

if $P_5 \geq 25.85 \mu\text{g}$ at C l^{-1} , $\tau = 0$,

if $P_5 < 1.2 \mu\text{g}$ at C l^{-1} , the grazing threshold, $\tau = 0$.

The fraction

$$F = (w_5 M_5) / P_5 \quad [3.29]$$

of phytoplankton carbon ingested by the fish is calculated at each iteration for each spatial segment. Equivalent fractions expressed as FP_1 , FP_4 , FP_5 , FP_6 , FN are then subtracted from standing stocks of phytoplankton silica, nitrogen, carbon, chlorophyll, and cell numbers respectively in [3.5-3.9].

Ammonia excretion by the Sardina off northwest Africa is estimated from data for Engraulis mordax (McCarthy and Whitledge 1972) used by Walsh (1975) in a model of the Peru upwelling system. Walsh calculates

that of the 725 μg at N day^{-1} ingested by each fish, 486 μg at $\text{N}\cdot\text{day}^{-1}$ is excreted. If 68% of the total nitrogen excreted is ammonia (McCarthy and Whitledge 1972), then 46% of the nitrogen ingested is excreted as ammonium. This 46% fraction is included as the constant, γ_3 , in the following function for ammonia excretion by fish

$$Y_3 = \gamma_3 \cdot F \cdot P_4 \quad [3.30]$$

where

Y_3 = the ammonia excretion rate (μg at $\text{NH}_3\text{-N}\cdot\text{l}^{-1}\cdot\text{hr}^{-1}$);

γ_3 = a constant ($0.46 \mu\text{g}$ at $\text{NH}_4\text{-N}$ excreted $\cdot (\mu\text{g}$ at phyto-N ingested) $^{-1}$);

$P F_4$ = the rate of ingestion of phytoplankton by fish (μg at phyto-N $\cdot \text{l}^{-1} \cdot \text{hr}^{-1}$).

3.2e Benthos. Benthic remineralization of organic matter has been identified as a significant nutrient cycling process in the region off northwest Africa (Rowe, et al. 1977). The dynamics of the process are presently poorly understood, so benthic regeneration is treated in this model as a boundary process occurring at a constant rate insensitive to changes in the dynamic variables of the simulated system. Rates of nutrient flux from the bottom are assumed equal to the mean rates reported by Rowe, et al. (1977). In units of $\mu\text{g atoms}\cdot\text{m}^{-2}\cdot\text{hr}^{-1}$ the mean fluxes are 550 for silicate, 160 for nitrate and 235 for ammonium. For spatial segments having the continental shelf as a bottom boundary, benthic nutrient fluxes contribute to nutrient concentration changes in a manner dependent on the vertical dimension of the spatial segment (i.e. in a unit of time the concentration change

in a segment 5 m deep bounded by the shelf is proportionally greater than in a segment 20 m deep). Accordingly, the benthic regeneration functions, r_1 , r_2 , and r_3 are defined as

$$r_n = h_n \Omega \quad [3.31]$$

where

h_n = areal nutrient fluxes ($\mu\text{g at} \cdot \text{m}^{-2} \text{hr}^{-1}$),

for $n = 1$, silicate, $h_1 = 550$,

$n = 2$, nitrate, $h_2 = 160$,

$n = 3$, ammonium, $h_3 = 235$;

Ω = a vertical scaling factor, constant for each spatial segment of a given vertical dimension;

for a segment 20 m deep, Ω is defined as

$$\Omega = (1/20 \text{ m}) \times (1 \text{ m}^3/1000 \text{ liters}) = 5 \times 10^{-5} \text{ m}^2 \cdot \text{liter}^{-1};$$

for spatial segments not bounded below by the continental shelf, $\Omega = 0$.

3.3 Results

Results from three simulated cases are presented below. Recall that these cases are related by a common set of boundary and initial conditions and functional relationships among the biological components. (Boundary and initial conditions common to the three cases are defined in Tables 5 and 6 of Appendix II.) The differences among cases are due to the absence or occurrence of simulated upwelling and differences in the intensity of vertical mixing occurring over a ten day period. During the 10 day simulation period, the distribution of

variables do not, in general, reach steady states. However, the observed variability in the physical forcing of the system occurs at 10 day or shorter intervals, so a comparison of theoretical steady states, if and when they are reached in the model, would be of limited value.

A comparison of results from the first and second cases illustrates the effects of upwelling. The first case was run with weak mixing and no advection and the second case was run with weak mixing and the time sequence of advective fields generated by the physical submodel. In both of these simulations, vertical eddy coefficients are set as constants to $1 \text{ cm}^2 \text{ s}^{-1}$. This value is equivalent to those used in previous simulation studies of the upwelling systems off Peru (Walsh 1975) and Oregon (Wroblewski 1977). Vertical mixing may have been more intense off Africa during JOINT-I than off Oregon and Peru. Accordingly, results are presented for a third simulation case run with the same circulation scheme as the second case, but with vertical eddy coefficients of $40 \text{ cm}^2 \text{ s}^{-1}$. The results presented from the three simulation cases are limited to variables routinely measured at hydrographic stations during JOINT-I to permit comparisons between simulated and observed distributions. The discussion will therefore focus on the distributions of nitrate, ammonium and chlorophyll.

3.3a A Case with Weak Mixing and No Advection. Figures 24 to 30 show nitrate, ammonium and chlorophyll distributions after 0, 120, and 240 hours (0, 5 and 10 days) time in the case with no advection.

Figure 24. The initial nitrate distribution. Above 30 m the concentration is $1.48 \mu\text{g at liter}^{-1}$ and below 30 m, $2.84 \mu\text{g at liter}^{-1}$. Contour interval is $2 \mu\text{g at liter}^{-1}$.

Figure 25. The nitrate distribution after 5 days in the case without upwelling, $K_z = 1 \text{ cm}^2 \text{ s}^{-1}$. Contour interval is $2 \mu\text{g at liter}^{-1}$.

Figure 26. The nitrate distribution after 10 days in the case without upwelling, $K_z = 1 \text{ cm}^2\text{s}^{-1}$. Contour interval is $2 \mu\text{g at liter}^{-1}$.

Figure 27. The ammonium distribution after 5 days in the case without upwelling, $K_z = 1 \text{ cm}^2\text{s}^{-1}$. Contour interval is $1 \mu\text{g at liter}^{-1}$.

Figure 28. The ammonium distribution after 10 days in the case without upwelling, $K_z = 1 \text{ cm}^2\text{s}^{-1}$. Contour interval is $1 \mu\text{g at liter}^{-1}$.

Figure 29. The chlorophyll a distribution after 5 days in the case without upwelling, $K_z = 1 \text{ cm}^2\text{s}^{-1}$. Contour interval is $3 \mu\text{g at liter}^{-1}$.

Figure 30. The chlorophyll a distribution after 10 days in the case without upwelling, $K_z = 1 \text{ cm}^2 \text{ s}^{-1}$. Contour interval is $3 \mu\text{g at l}^{-1}$.

Figure 24 is an example of the initially horizontal two layer distributions represented in Tables 5 and 6 of Appendix II describing the initial conditions for all cases simulated. With no upwelling, nitrate becomes depleted in the upper 20 m due to phytoplankton uptake, except in the nearshore region where phytoplankton growth is reduced by turbidity in the water column (Figure 25-26). Nitrate concentrations increase at depth and near the continental shelf due to benthic regeneration and some diffusion through the lower boundary off the shelf. As a consequence of the high uptake of nitrate by phytoplankton, seaward of the turbid region near shore and the benthic regeneration of nitrate over the shelf, the nitrate isolines tend to slope upwards near the coast as if upwelling were occurring. The concentrations of ammonium also increases near the bottom over the shelf. From an initial concentration of $0.35 \mu\text{g at NH}_3 \text{ l}^{-1}$ below 30 m, ammonium increases to greater than $3 \mu\text{g at NH}_3 \text{ l}^{-1}$ in the turbid nearshore region near the bottom (Figure 28).

Diagnostic information listed during the simulation (see Appendix III) indicated that chlorophyll concentrations, initially $1.45 \mu\text{g Chl l}^{-1}$ above 30 m, increase until phytoplankton growth is limited by a lack of inorganic nitrogen. Growth is reduced due to turbidity in the extreme inshore region, but a subsurface chlorophyll maximum develops over the shelf where benthic regeneration and vertical mixing supply nutrients to the base of the euphotic zone (Figure 30). The mean net primary production in the upper 20 m initially exceeds, by a factor of 8.3 the mean vertically integrated ingestion of phytoplankton carbon

by all zooplankton and fish. As phytoplankton production decreases due to nutrient limitation, herbivorous ingestion eventually equals primary production. Total herbivorous ingestion subsequently exceeds net primary production by a factor of 2.7 during day 5 and by a factor of 11.1 during day 10.

3.3b A Case with Advection and Weak Vertical Mixing. The effects of upwelling are most evident when the results of this simulation (Figures 31-34), run with the sequence of upwelling flow fields generated in the physical submodel, are compared with the results of the case with no advection in the previous section (Figures 24-30). After 10 days in the case without upwelling, the initial $1.48 \mu\text{g at l}^{-1}$ nitrate concentration in the 0-30 m layer declines to a mean $0.35 \mu\text{g at l}^{-1}$ and the mean concentration from 30-100 m increases slightly from 2.84 to $3.09 \mu\text{g at l}^{-1}$. After an equivalent period with upwelling, the mean nitrate concentration is $1.44 \mu\text{g at l}^{-1}$ above 30 m and $4.39 \mu\text{g at l}^{-1}$ below. Chlorophyll concentrations also increase in response to upwelling. Figures 33-34 show a region of maximum concentrations developing over the outer shelf and spreading seaward with time. From an initial concentration of $1.45 \mu\text{g Chl l}^{-1}$ mean chlorophyll concentrations above 30 m increase to $4.88 \mu\text{g l}^{-1}$ after 10 days time.

Increases in chlorophyll concentrations are accompanied by increases in the rate of primary production over the shelf. After 5 days in the case without upwelling, net primary productivity integrated over the 20 m surface layer averages $0.16 \text{ g C m}^{-2} \text{ d}^{-1}$ and continues to decline in the case without upwelling. In contrast, net production

Figure 31. The nitrate distribution after 5 days in the case with upwelling $K_z = 1 \text{ cm}^2\text{s}^{-1}$. Concentrations exceeding $10 \mu\text{g at l}^{-1}$ appear near the intersection of the shelf with the bottom boundary. Contour interval is $2 \mu\text{g at l}^{-1}$.

Figure 32. The nitrate distribution after 10 days of upwelling with $K_z = 1 \text{ cm}^2\text{s}^{-1}$. Contour interval is $2 \mu\text{g at l}^{-1}$.

Figure 33. The chlorophyll a distribution after 5 days of upwelling with $K_z = 1 \text{ cm}^2 \text{ s}^{-1}$. Contour interval is $3 \mu\text{g l}^{-1}$.

Figure 34. The chlorophyll a distribution after 10 days of upwelling with $K_z = 1 \text{ cm}^2 \text{ s}^{-1}$. Contour interval is $3 \mu\text{g l}^{-1}$.

across the shelf ranges between 0.7 to $3.7 \text{ g C m}^{-2} \text{ d}^{-1}$ after the tenth day in the upwelling case. The highest rates occur about 20 km offshore over the midshelf region.

Vertically integrated herbivorous ingestion averages $0.25 \text{ g C m}^{-2} \text{ d}^{-1}$ after 10 days of upwelling, and is slightly less than the average of $0.33 \text{ g C m}^{-2} \text{ d}^{-1}$ after the same time in the non-upwelling case. Herbivorous ingestion is a function of phytoplankton carbon concentration and the small difference between cases is due mainly to the presence of slightly higher phytoplankton carbon concentrations at mid-depths in the case without upwelling. Mean phytoplankton carbon concentrations between 30 and 50 m average $4.48 \text{ } \mu\text{g at C l}^{-1}$ without upwelling and $3.70 \text{ } \mu\text{g at C l}^{-1}$ with upwelling. Phytoplankton carbon concentrations are all above the $1.2 \text{ } \mu\text{g at C l}^{-1}$ grazing threshold in the case without upwelling between 30 and 50 m , but in the case with upwelling they are below the threshold in 18% of the $30\text{--}50 \text{ m}$ depth region nearest the coast where upwelling and consequent dilution of phytoplankton concentration is most intense. The ammonium distribution is also affected by dilution due to upwelling. Concentrations exceeding $2.0 \text{ } \mu\text{g at l}^{-1}$ occur only within 5 km of the coast after 10 days in the case with advection.

3.3c A Case with Advection and Strong Vertical Mixing. Simulated distributions of nitrate (Figures 35,36) and chlorophyll (Figures 37, 38) illustrate the effects of upwelling accompanied by strong vertical mixing parameterized in vertical eddy coefficients of $40 \text{ cm}^2 \text{ s}^{-1}$. Strong vertical mixing results in higher nitrate concentrations in the

Figure 35. The nitrate distribution after 5 days of upwelling with $K_z = 40 \text{ cm}^2\text{s}^{-1}$. Contour interval is 2 $\mu\text{g at liter}^{-1}$.

Figure 36. The nitrate distribution after 10 days of upwelling with $K_z = 40 \text{ cm}^2\text{s}^{-1}$. Contour interval is 2 $\mu\text{g at liter}^{-1}$.

Figure 37. The chlorophyll a distribution after 5 days of upwelling with $K_z = 40 \text{ cm}^2 \text{ s}^{-1}$. Contour interval is $3 \mu\text{g l}^{-1}$.

Figure 38. The chlorophyll a distribution after 10 days of upwelling with $K_z = \text{cm}^2 \text{ s}^{-1}$. Contour interval is $3 \mu\text{g l}^{-1}$.

offshore subsurface regions. In the previous weak mixing case with vertical eddy coefficients equal to $1 \text{ cm}^2 \text{ s}^{-1}$, the mean nitrate concentration below 30 m after day 5 is $3.48 \mu\text{g l}^{-1}$ and $4.39 \mu\text{g l}^{-1}$ after day 10. With vertical eddy coefficients of $40 \text{ cm}^2 \text{ s}^{-1}$, the mean 30-100 m nitrate concentration is $5.36 \mu\text{g l}^{-1}$ after day 5 and $5.41 \mu\text{g l}^{-1}$ after day 10.

The increased nutrient flux supports higher rates of primary production in the case with strong vertical mixing. After 5 and 10 days of upwelling in the weak mixing case, the mean net primary productivity integrated over the surface 20 m is affected by nitrogen limitation and the mean was 0.62 and $0.89 \text{ g C m}^{-2} \text{ d}^{-1}$, respectively. With the eddy coefficients increased to $40 \text{ cm}^2 \text{ s}^{-1}$, productivity averages $3.92 \text{ g C m}^{-2} \text{ d}^{-1}$ after day 5 and $5.28 \text{ g C m}^{-2} \text{ d}^{-1}$ after day 10. Apparently the growth-stimulating effects of an improved nutrient environment are greater than the adverse effects that increased mixing has on the light environment for the phytoplankton.

The higher rates of primary production result in generally higher chlorophyll concentrations in the strong mixing case. With eddy coefficients of $1 \text{ cm}^2 \text{ s}^{-1}$, the mean chlorophyll concentrations above 30 m increases from $3.91 \mu\text{g Chl l}^{-1}$ after the first day to $4.88 \mu\text{g Chl l}^{-1}$ after the tenth day. With the higher vertical eddy coefficients, the mean chlorophyll concentration above 30 m is $7.23 \mu\text{g Chl l}^{-1}$ after day 5 and $12.56 \mu\text{g Chl l}^{-1}$ after day 10.

The vertically integrated ingestion of phytoplankton carbon by zooplankton and fish averages $0.79 \text{ g C m}^{-2} \text{ d}^{-1}$ after 10 days time. Ingestion is greatest in this case because relatively high phytoplankton concentrations above the grazing threshold ($1.2 \text{ } \mu\text{g at C l}^{-1}$) occur over a broad depth range. The upwelling-induced dilution of phytoplankton concentrations at mid-depths which occurred in the previous case is apparently compensated for by the downward mixing of phytoplankton from the surface layers. Strong vertical mixing also results in a reduction of the ammonium concentration maximum near the coast and bottom over the shelf. Maximum concentrations do not exceed $1 \text{ } \mu\text{g at l}^{-1}$ during the 10 day simulation period.

3.4 Discussion

The three cases depict responses of initially identical biological systems to different physical regimes, which are at times observed within the eastern boundary currents. The results from the first case without upwelling describe the transition towards an oligotrophic state. Without an advective nutrient input the phytoplankton remove nutrients from the euphotic zone until population growth is limited by nutrient supply from regenerative sources and slow turbulent input from below. An interesting feature of this simulation with eddy coefficients of $1 \text{ cm}^2 \text{ s}^{-1}$ is the development of a subsurface chlorophyll maximum at the base of the euphotic zone where the rate of nutrient supply is relatively high. The subsurface maximum extends offshore, but is most apparent over the shelf where the vertical nutrient gradient is greatest. These results suggest that subsurface chlorophyll

maxima in oligotrophic systems may be biologically dynamic features not necessarily associated with vertical density gradients. A topic for future investigation is the extent to which the vertical position and intensity of density gradients as expressed in spatially variable eddy coefficients modify the subsurface chlorophyll maximum and the availability of nutrients higher in the euphotic zone.

A qualitative comparison of the first case with either of the cases run with advection shows that the model represents a number of expected differences between non-upwelling and upwelling regimes. Simulated upwelling increases nutrient concentrations in the euphotic zone and supports higher rates of primary production. Although the model may qualitatively depict an intuitively satisfactory biological response to upwelling, it was designed to quantitatively assess the effects of upwelling off northwest Africa. A comparison of simulated results with observations from the actual system reveals that significant differences exist between the actual and simulated systems.

The differences occur in both the weak and strong mixing cases with upwelling as phytoplankton concentrations become higher and nutrient concentrations become lower than observed during JOINT-I. As an example, compare the measured nitrate (Figure 39) and chlorophyll (Figure 40) distributions taken on 23-24 March 1974 after a 10-12 day period of strong equatorward wind stress with the nitrate (Figures 32 and 36) and chlorophyll (Figure 34 and 38) distributions after 10 days of simulated upwelling in the weak and strong mixing cases. In both cases, simulated chlorophyll concentrations in the surface layers are

generally higher and nitrate concentrations lower than observed.

A comparison of the mean measured onshore-offshore distributions of nitrate and chlorophyll in the euphotic zone with the mean euphotic zone concentrations after 10 days of simulated time also illustrates similar differences (Figures 41 and 42). The purpose of the following discussion is to identify possible physical or biological factors in the model that may be responsible for these differences.

During JOINT-1, one of the characteristic features of the distribution of nutrients was the occurrence of elevated ammonium concentrations ranging from 0.5 to 3.0 μg at 1^{-1} within approximately 15 km of the coast. Codispoti and Friedrich (in press) have attempted to explain the origins of this feature and identify the reasons for its variability. They conclude its origins are probably related to a local net regenerative production of ammonium in excess of losses due to biological and physical transport processes. Other possible, but discounted, origins are alongshore advection of ammonium into the region from a nonlocal source or ammonium release from wind blown Sahara sand. A consideration of the observed and simulated ammonium distributions will show that the relatively high simulated phytoplankton biomass and low simulated nutrient concentrations cannot reasonably be attributed to differences between the actual and simulated physical regimes.

Results from the simulation experiments support the hypothesis that the high ammonium concentrations could be a locally generated feature. Neither the alongshore advection feature nor the dissolution of ammonium from sand are included in the model formulation.

Figure 39. The distribution of nitrate at 21°40'N on 23-24 March, 1974, during JOINT I.

Figure 40. The distribution of chlorophyll at 21°40'N on 23-24 March, 1974, during JOINT-I.

Figure 41. Observed and simulated onshore-offshore distributions of nitrate concentrations. Measured concentrations are averages over the euphotic zone for the JOINT-I cruise period, March-May, 1974 (From Huntsman and Barber, 1977.) Simulated concentrations are mean euphotic zone concentrations after 10 days simulation time. The depth of the euphotic zone in the simulation cases is defined for each column as the depth of the bottom boundary of the deepest segment where daily phytoplankton carbon fixation exceeds respiration.

Figure 42. Observed and simulated onshore-offshore distributions of chlorophyll a concentrations. Measured concentrations are averages over the euphotic zone for the JOINT-I cruise period, March-May, 1974 (From Huntsman and Barber, 1977). Simulation concentrations are averages for the euphotic zone as defined for Figure 41.

From initial concentrations of $0.24 \mu\text{g at l}^{-1}$ above 30 m, and $0.35 \mu\text{g at l}^{-1}$ below, and despite dilution from upwelling source waters with $0.13 \mu\text{g at l}^{-1}$, all simulation experiments show a net production of ammonium occurring over some of the shelf region. Increases in simulated ammonium concentration tend to be greatest in the nearshore highly turbid region where maximum concentrations ranging from 0.81 to $3.04 \mu\text{g at l}^{-1}$ occurred in all three cases simulated (e.g., Figures 27 and 28). In agreement with the possible sources of variability suggested by Codispoti and Friedrich, the higher simulated concentrations occur when physical transport processes and phytoplankton growth are lowest (Figure 28). Conversely, lower concentrations occur when phytoplankton uptake rates and dilution by upwelling of low ammonia water are maximized. Although some characteristics of the high ammonium concentrations beneath the euphotic zone are accounted for by the model, the simulated ammonium concentrations in the surface layers are generally lower than the observed concentrations. Mean simulated ammonium concentrations in the surface 10 meters do not exceed $1.5 \mu\text{g at l}^{-1}$ in any of the simulation experiments, although concentrations of that magnitude were common in the surface layers near the coast.

More intense upwelling would improve the agreement between observed and simulated distributions of nitrate and chlorophyll because higher nitrate concentrations and lower chlorophyll concentrations would occur in the simulations if advection were increased (Walsh 1975). However, the comparison of the simulated cases shows that increased advection or mixing would further decrease the already

low surface ammonium concentrations. It is unlikely, therefore, that the illustrated differences between observed and simulated distributions of nutrients and phytoplankton can be attributed to differences between actual and simulated physical conditions. The alternative explanations remaining are that the simulated phytoplankton growth rates are greater and/or the phytoplankton loss rates are lower than the actual rates.

Given a set of initial conditions comparable to the mean JOINT-I conditions, simulated rates of net primary production do not significantly overestimate the rates measured by Huntsman and Barber (1977). They report that primary production generally varied between 1 and 3 g C·m⁻²·d⁻¹. In a separate short term simulation, initialized with the JOINT-I mean observed values listed in Table 4 (Appendix II), net carbon production occurring during 24 hours ranges from 0.98 g C·m⁻² d⁻¹ inshore to 3.3 g C·m⁻²·d⁻¹ over most of the shelf and offshore areas. Simulated assimilation numbers ranging from 11 mg C·(mg Chl a)·d⁻¹ in the inshore turbid region to 31 mg C (mg Chl a) d⁻¹ further offshore are calculated from the 24 hour net primary production integrated over the surface 20 m and a mean chlorophyll concentration estimated from initial and final chlorophyll concentrations integrated over the same depth interval in the model. Assimilation numbers measured by Huntsman and Barber over the interval between 0900 and 1500 hours normally range from 2 to 4 mg C·(mg Chl a)⁻¹·hr⁻¹. The relationship they found between incubations in natural light at 6 and 24 hour periods ($C_{24} = 1.72 \times C_6 \cdot 0.27$) can be used to convert the

observed range of hourly rates to average daily rates of approximately 20 to 41 $\text{mg C} \cdot (\text{mg Chl a})^{-1} \cdot \text{d}^{-1}$. Observed rates in these units compare more directly with the 11 to 31 $\text{mg C} \cdot (\text{mg Chl a})^{-1} \cdot \text{d}^{-1}$ range calculated in the model for average JOINT-I conditions.

A broad range of environmental conditions, including onshore-offshore nutrient gradients within the surface layers is created in some of the other cases simulated. For example, after 10 days simulation time in the upwelling case with weak vertical mixing, the mean nitrate concentration in the upper 20 m was $4.10 \mu\text{g at l}^{-1}$ within 20 km of the coast and $1.06 \mu\text{g at l}^{-1}$ from 25 to 45 km offshore. The mean assimilation numbers calculated from simulated net primary productivity and chlorophyll concentrations integrated over these same regions are $50.1 \text{ mg C} \cdot (\text{mg Chl a})^{-1} \cdot \text{d}^{-1}$ in the high nutrient area and $11.2 \text{ mg C} \cdot (\text{mg Chl a})^{-1} \cdot \text{d}^{-1}$ in the lower nutrient area further offshore. The greater of these rates, for the high nutrient area, exceeds the average observed values, but is within the 40 to 80 $\text{mg C} (\text{mg Chl a}) \text{ d}^{-1}$ range observed during periods of diminished winds and presumably moderate mixing. The high simulated assimilation number in the weak mixing case exceeds the short term simulated number for the mean JOINT-I conditions and a similar number calculated for the strong mixing case because most of the chlorophyll is near the surface in the weak mixing case. More light is attenuated by non-chlorophyll components and less remains for photosynthesis when the chlorophyll is more evenly distributed throughout the euphotic zone.

Huntsman and Barber (1977) report that some variability in assimilation efficiency can be attributed to light-shade adaptation, but this process is not entirely represented in the current formulation of the model. For a given light intensity and vertical chlorophyll distribution, changes in the simulated carbon-specific rate of photosynthesis ($\text{mg C} \cdot (\text{mg C})^{-1} \cdot \text{d}^{-1}$) do occur when the chlorophyll per cell changes. However, the chlorophyll-specific rate of photosynthesis ($\text{mg C} \cdot (\text{mg Chl a})^{-1} \cdot \text{d}^{-1}$) does not change if Q_{max} and I_{max} are constants in [2.03]. These parameters remain constant in this formulation, because the light-shade adaptation process has not yet been adequately theoretically resolved. The problem of parameterizing the process has been encountered by others and one solution used in simulation studies by Jamart, et al. (1977) and Steele and Frost (1977) is to force photosynthetic parameters to change as a function of maximum daily incident light intensity on a seasonal time scale. This solution unfortunately leaves the mechanism for the change undefined in biological terms and, in any event, is probably not appropriate for light-shade adaptation occurring at the time scale of this model. The absence of a light-shade adaptation mechanism in this model is not, however, particularly significant. Without the light-shade adaptation process, simulated rates underestimate light-adapted primary production rates measured on JOINT-I during the infrequent and brief calm periods.

The above analysis suggests that the formulation of environmental characteristics and phytoplankton growth functions of the model are reasonable and should not intrinsically overestimate the observed rates of primary production. If the simulated rate of phytoplankton increase

is not intrinsically high, then the loss rates must be low. Rates of phytoplankton physiological mortality are generally assumed to be slow in comparison to rates of growth and uptake. The rate used in this model ($m = 0.0042 \text{ hr}^{-1}$) is equivalent to the rate used by Wroblewski (1977) in a model of upwelling off Oregon and is similar to sinking loss rates assumed by other authors. For example, Steels and Frost (1977) assume the sinking rate to be a function of nutrient concentration and refer to Epley, et al. (1967) to obtain a maximum sinking rate of 1 m d^{-1} for non-growing cells 10μ in diameter. In the 5, 10, and 20, thick layers of this model, a 1 m d^{-1} sinking rate could result in local losses of phytoplankton as high as 0.008, 0.005, and 0.002 hr^{-1} , respectively. These sinking rates approximate the assumed mortality rate for non-growing phytoplankton in this model and would not significantly alter the simulated results if they were used in place of the assumed mortality function. Unless phytoplankton physiological mortality occurs at a rate much higher than presently believed, it has a relatively minor effect on the distribution of phytoplankton and nutrients at the time and space scales of this model.

Losses of phytoplankton to herbivorous zooplankton and fish are the possible processes remaining in the model's formulation which could reduce the rates of simulated primary production. The amount of phytoplankton lost to grazing is dependent on the areal biomass, vertical distribution and species and age composition of the herbivorous population. Data are available for estimates of areal biomass, but lacking for estimates of vertical distribution and population composition. Specifications for the vertical distribution and composition of the

herbivores in the model are based on simple assumptions and allow for the vertically homogenous distributions of one type of herbivorous fish and two size classes of herbivorous zooplankton. More elaborate specifications in the absence of a more complete data set would be arbitrary and unwarranted.

If zooplankton and fish were concentrated in the upper layers of the model where phytoplankton growth rates and biomass are greatest, losses to grazing would increase and agreement between calculated and observed distributions in the previous examples would improve. The magnitude of the effects on phytoplankton and nutrient distributions resulting from a vertical migration of the herbivore biomass varies as a function of the vertical phytoplankton distribution and concentration. If all herbivores were concentrated in the upper 30 m after 10 days time in the simulation experiments, losses to grazing would approximately triple in the weak mixing case and approximately double in the strong mixing case. The rates of net primary production in the surface layers of these cases remain greater than the increased ingestion rates. It is unlikely, therefore, that migratory behavior alone can completely account for the differences between observed and simulated results.

The species and age composition of the zooplankton population are parameterized in the model as a function of the size of the organisms. Two size classes are represented and size-specific ingestion rates are defined in relation to the expected size-specific metabolic rate estimates for each class. Differences in grazing behavior related to the composition of the zooplankton may be even larger than assumed in the

model. Steele and Frost (1977) have recently published a more detailed formulation for the size-specific characteristics of filter feeding zooplankton. They propose an ingestion function which, if used in this model would yield, for the smaller zooplankton, a size-specific ingestion rate, a factor $\lambda = 4.9$ (see [3.26] greater than rates for the large zooplankton; a size-specific effect 53% greater than the value assumed. The effects of size may be further underestimated, because unweighted arithmetic mean weights are used to describe the two classes of grazers whose ingestion rates increase geometrically as an inverse function of size. Simulated ingestion rates may also be low if very small or soft bodied herbivores have been inefficiently sampled and represented. Unfortunately, the magnitude of size, species, or age specific effects not included in this model cannot be reliably estimated with the available data.

A number of previous simulation studies concerned with lower trophic level dynamics have encountered, but not necessarily emphasized, the problems associated with representing the herbivorous components of marine ecosystems. O'Brien and Wroblewski (1973) in a study of a region off West Florida cited data for zooplankton biomass-specific ingestion rates ranging from 0.10 to 0.60 day⁻¹, but apparently found it necessary to use a value of 1.51 day⁻¹ to produce reasonable ecological efficiencies with a simulated final zooplankton biomass approximately one half of the phytoplankton biomass. A sensitivity analysis of a non-spatial version of the model at steady state suggests the importance of grazing control and it shows their results

to be more sensitive to parameter changes related to zooplankton processes than any others.

In a subsequent study of the upwelling system off Oregon, Wroblewski (1977) cites and uses a maximum zooplankton ingestion rate of 0.48 d^{-1} . His analysis of the model equations "show the parameters describing zooplankton grazing, egestion, and excretion are the most important... in determining the steady state concentrations" of nitrate, ammonium, detritus and phytoplankton and zooplankton biomass. He concludes that his model successfully reproduces several of the observed biological and chemical features off Oregon, but does not discuss or quantitatively compare with observations his remarkably high simulated distributions of zooplankton biomass. After 10 days simulation time, the zooplankton biomass is approximately equal to or double the phytoplankton biomass over most of the euphotic zone. Data for Oregon were not available, but a comparison of the Peru, Baja California and northwest Africa upwelling ecosystems by Walsh (1976) suggests that phytoplankton concentrations in the euphotic zones of these upwelling systems may exceed mean zooplankton biomass concentrations by a factor of ten or more.

In Walsh's (1975) simulation model of the Peru upwelling system both herbivorous zooplankton and fish are represented. As in the present model of upwelling off northwest Africa, Walsh uses field measurements of zooplankton biomass and laboratory measurements of grazing (a maximum ingestion rate of 0.29 d^{-1}) to estimate losses of phytoplankton to the zooplankton. The anchoveta are assumed to have a maximum specific ingestion rate of 0.65 d^{-1} ; a rate similar to the 0.04 d^{-1}

rate for Sardina in the model of upwelling off northwest Africa. The wet weight estimate of fish biomass Walsh uses in the autumn upwelling plume off Peru is approximately $1 \times 10^3 \text{ g m}^{-2}$ or a factor of 20 larger than the estimated Sardina population off Africa. Walsh makes the biomass estimates from echogram and schooling geometry arguments that, according to his figures, would place half of the total Peruvian anchoveta biomass in a single upwelling plume constituting 8% of the total Peruvian upwelling area estimated by Ryther (1969) or 1% of the total area estimated by Cushing (1960). Walsh then found it necessary to arbitrarily introduce a grazing threshold of $3.0 \text{ } \mu\text{g atoms phyto-plankton nitrogen } \cdot \text{l}^{-1}$ (equivalent to a chlorophyll concentration of $3.8 \text{ } \mu\text{g Chl l}^{-1}$, assuming a N/Chl ratio of 11.1 by weight). He speculates that such a large threshold "is essentially a parameterization of the inability of the herbivore submodel to resolve horizontal scales of prey patchiness of less than 10 km," but a simpler alternative explanation is that the anchoveta biomass is too high. Whatever the explanation, it is clear that a more objective definition of the grazing stress for the Peru upwelling system is needed.

In a study of phytoplankton growth and nutrient distribution off the northwestern U.S. coast, Jamart, et al. (1977) also acknowledged that one of the less satisfying aspects of their work was the necessity of "altering the grazing pressure to make fine adjustments during the numerical simulations." They specified a somewhat arbitrary maximum zooplankton ingestion rate of 2.0 d^{-1} and even then the values of zooplankton biomass used in the model were about two to three times greater than the observed values. When the sensitivity of this type

of lower trophic level model to changes in grazing parameters is considered, the uncertainties associated with the estimates of the zooplankton biomass and rate parameters are unacceptably large for predictive analysis. They suggest that one of the contributions of their theoretical study is that it "emphasizes the need for a more accurate knowledge of the feeding rate and the spatial and temporal distribution of zooplankton." The results from this simulation study of upwelling off northwest Africa reinforces the statement of Jamart, et al. (1977). This analysis has shown that the behavioral characteristics of the herbivores fundamentally affect the biological response to upwelling and that uncertainties associated with estimates of herbivore biomass and vertical migratory and feeding behavior are critical to an adequate representation of ecosystem functions. While O'Brien and Wroblewski (1973) and Wroblewski (1977) showed that grazing may be the most dynamic process of marine ecosystems, this analysis, by a process of elimination, shows that it may also be the most poorly understood.

3.5 Summary and Conclusions

A two dimensional model of upwelling and its effects on nutrient and phytoplankton fields has been developed. In it, a phytoplankton population is defined by a set of variables for cell numbers and particulate carbon, nitrogen, chlorophyll and silica. Phytoplankton growth rate is simulated as a function of concentrations of nitrate, ammonium, and silicate and intensity of photosynthetically active radiation. Grazing losses occur to one species of herbivorous fish and two size classes of zooplankton.

Several simulation experiments have been run to study the effects of upwelling in the northwest African coastal ecosystem. Time varying habitat characteristics are defined by independent submodels for physical circulation and solar radiation.

Comparisons of simulation results with measurements made during the JOINT-I expedition during 1974 suggest that some observed characteristics may occur as consequences of interactions expressed in the model. Simulations show a flux of nutrient rich water into the euphotic zone supporting high rates of primary production seaward of a turbid nearshore region. High ammonium concentrations, observed in the nearshore region, are shown in the simulations to be sensitive to physical circulation processes and phytoplankton uptake rates.

Given comparable environmental conditions, simulated and observed intrinsic rates of phytoplankton growth are approximately equal. However, rates of primary production during simulated upwelling exceed significantly the losses attributed in the model to phytoplankton physiological mortality and ingestion by herbivores. An underestimate of the significance of grazing related to the vertical distribution of biomass and feeding behavior of the zooplankton is identified as the factor responsible for the discrepancy between observed and simulated conditions.

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APPENDIX I

BIOCEAN, A FORTRAN Program for Simulation in a Biological Oceanography

The state equations of the models discussed in this study were solved with a FORTRAN program named BIOCEAN. Although BIOCEAN is similar in principal to its predecessor AUGUR (Morishima, et al. 1974), it is different in several operational respects. Like AUGUR, BIOCEAN is designed as a program for 3-dimensional simulation and analysis in biological oceanography. Both programs use a similar spatial segmentation system and operate on a simulated space divided into I,J,K columns, rows and layers of rectilinear segments, each with a linear subscript or numerical sequence identifier. Unlike AUGUR, BIOCEAN begins each iteration at the surface; it is not dependent on installation-specific assembly language subroutines and it does not iteratively transfer all computational information to and from mass storage. Use-interraction with BIOCEAN is more direct than with AUGUR, because BIOCEAN lacks the lengthy code necessary to interpret a complex set of input instructions intended to automatically direct program execution. With a reduced operating overhead, BIOCEAN is more compact, easier to use and operates at approximately 1/30 the cost of AUGUR for simulations on the scale of the northwest African upwelling study. Smaller scale simulations with fewer equations are run even more efficiently.

I.A The Numerical Integration Scheme

The numerical method used in BIOCEAN to integrate model equations over time is the improved Euler predictor-corrector scheme discussed by McCracken and Dorn (1964) and Beckett and Hurt (1967). Most models consist of a set of equations in several variables to be solved simultaneously, but as a simple example to illustrate the solution methodology, consider the equation for a single variable, y , where

$$\frac{dy}{dx} = f(x,y) \quad . \quad [A.1]$$

Given an initial condition (x_n, y_n) , Euler's method is used to start the procedure and obtain an initial approximation y_{n+1}^o to the actual solution at x_{n+1} , where $x_{n+1} - x_n = h$ as follows:

$$y_{n+1}^o = y_n + hf(x_n, y_n) \quad [A.2]$$

Equation [A.2] is re-evaluated at x_{n+1} , using the initial approximation y_{n+1}^o to estimate $f(x_{n+1}, y + hf(x, y))$. Then with the improved Euler method the second approximation or corrected value y_{n+1}^c is given by

$$y_{n+1}^c = y_n + (h/2) (f(x_n, y_n) + f(x_{n+1}, y_n + hf(x_n, y_n))) \quad . \quad [A.3]$$

The iteration counter is advanced, y_n becomes y_{n-1} and y_{n+1} becomes y_n . New values of y_{n+1} at the new x_{n+1} are approximated by

$$y_{n+1}^p = y_{n-1} + 2h (x_n, y_n) \quad [A.4]$$

This predicted value is substituted into equation [A.1] and $f(x_{n+1}, y_{n+1}^p)$ determined in order to obtain a corrected value y_{n+1}^c in

$$y_{n+1}^c = y_n (h/s) (f(x_n, y_n) + f(x_{n+1}, y_{n+1}^p)) \quad [A.5]$$

This corrected value can be substituted into equation [A.1], the derivative evaluated, and a presumably better estimate of y_{n+1}^c obtained by reiterating equation [A.5]. In a series of tests (to be discussed more fully below) designed to examine the stability characteristics of

the predictor-corrector scheme, it was found that reiteration of the corrector equation produced less than a 0.2% difference in an integrated total over 10 days simulation time with a time step of 0.5 hours. Reiteration increases execution time by about 50%, produces a negligible difference in output for the timestep size used in these simulations and was, therefore, judged unnecessary in the present study.

McCracken and Dorn (1964, p. 340) do show, however, that on the basis of an estimate of the truncation error made possible by the choice of predictor and corrector expression one simple further correction can be made

$$y_{n+1}^{c*} = (4 y_{n+1}^c + y_{n+1}^p)/5 \quad [A.6]$$

and this is included in the simulation calculations.

The predictor-corrector scheme is more difficult to program and requires more computer memory and time to execute than a simple predictor method, but it is significantly more accurate. As an example, consider the simple exponential growth at a rate, g , of 0.08 hr^{-1} of a variable, p , whose initial value, p_0 , is 1.0 beginning at time $t_0 = 0$. Then

$$\frac{dp}{dt} = gP \quad [A.7]$$

and

$$P_t = P_0 \exp [g \cdot (t - t_0)]. \quad [A.8]$$

For such a simple example it is possible to calculate an exact solution, $P_t = 54.598$ after $t = 50$ hours. With one hour time steps, a simple Euler method predicts 46.902 and the predictor-corrector method used in the model gives a value of 54.586. The results of the simple

Euler method are affected by the summation or propagation of successive errors of approximation over time, and the predicted solution tends, as in this example, to diverge further and further from the actual solution. The method used in the model corrects itself and so diminishes the tendency to diverge from the actual solution.

In another model of phytoplankton growth, Jamart, et al. (1977) experimented with time step length using a different numerical procedure (Crank-Nicholson) and noticed unacceptable errors arising from inaccuracies associated with the photosynthetic production relationship at time steps greater than 0.1 hours over an integration period of 10 days time. Tests were run with the production relationship and integration scheme used in this model to determine whether or not special corrective measures would need to be taken for cases run with time steps of 0.5 hours.

For the tests, solar radiation values were generated as a truncated sine function of time, with $470 \text{ g cal cm}^{-2} \text{ d}^{-1}$ as the total incident radiation and a 15% reflection correction for photosynthetically active radiation applied as assumed by Jamart, et al. The production relationship tested is essentially the same as in the complete model, but P_{max} is treated as a constant for these single variable test calculations. After 10 days simulation time the chlorophyll in a simulated 50 meter depth region in the 0.1 and 0.5 hour time step tests differed by only 1.6% and no corrective measures were judged necessary.

I.B The Finite Difference Scheme

The grid in Figure 43 illustrates the scheme used to identify state variable values, current velocities and diffusion coefficients

Figure 43. A schematic diagram showing the convention used in the model to define the relative and absolute locations of state variables (S), eddy coefficients (K) and horizontal (u) and vertical (w) current velocities. A segment whose center is at i, k has a dimension x_i on the horizontal i axis and a dimension z_k on the vertical k axis. Current velocities and eddy coefficients are defined on the faces between the centers of the rectangular spatial segments.

used in the BIOCEAN model of northwest African upwelling. The following finite difference functions for dispersive transport in the vertical and horizontal directions are based on the derivation of Thomann (1972).

$$\frac{\partial K_x}{\partial x} \frac{\partial s}{\partial x} \approx [(K_{i-\frac{1}{2},k}/x_i) (S_{i-1,k}-S_{i,k}) / ((x_i + x_{i-1})/2)] + [(K_{i+\frac{1}{2},k}/x_i) (S_{i+1,k}-S_{i,k}) / ((x_i + x_{i+1})/2)] \quad [A.9]$$

and in the vertical, or z direction, the function is

$$\frac{\partial K_z}{\partial z} \frac{\partial s}{\partial z} \approx [(K_{i,k-\frac{1}{2}}/z_k) (S_{i,k+1}-S_{i,k}) / ((z_k + z_{k-1})/2)] + [(K_{i,k+\frac{1}{2}}/z_k) (S_{i,k+1}-S_{i,k}) / ((z_k + z_{k+1})/2)] \quad [A.10]$$

The finite difference functions for advection are discussed by Harbaugh and Bonham-Carter (1970) and recommended by Piacsek and Williams (1970). In the horizontal, or x dimension, the approximation is given as

$$\frac{-\partial(uS)}{\partial x} \approx \frac{-\Delta(uS)}{\Delta x} \quad [A.11]$$

$$\Delta x = x_i$$

$$\begin{aligned} -\Delta(uS) &= (uS)_{i-\frac{1}{2},k} - (uS)_{i+\frac{1}{2},k} \\ (uS)_{i-\frac{1}{2},k} &= u_{i-\frac{1}{2},k} S_{i,k} \quad , \text{ if } u_{i-\frac{1}{2},k} \leq 0 \\ &= u_{i-\frac{1}{2},k} S_{i-1,k} \quad , \text{ if } u_{i-\frac{1}{2},k} > 0 \end{aligned}$$

$$\begin{aligned}
(uS)_{i+\frac{1}{2},k} &= u_{i+\frac{1}{2},k} S_{i+1,k} \quad , \text{ if } u_{i+\frac{1}{2},k} \leq 0 \\
&= u_{i+\frac{1}{2},k} S_{i,k} \quad , \text{ if } u_{i+\frac{1}{2},k} > 0
\end{aligned}$$

A functionally similar approximation is used for advection in the vertical direction,

The problem with these and other finite difference methods for advection is the existence of an error arising from the division of the simulated space into finite spatial segments. The nature of the error can be visualized by considering the advection in one dimension of a concentration peak through a series of initially empty segments. During the first iteration some material is advected from a starting segment into a second adjacent spatial segment. On the assumption that the contents of each spatial segment are completely mixed, some material in the second spatial segment will be advected to the third spatial segment at the next iteration even though the advection velocity may be too slow for a particle to have actually traversed the second segment. This effect results in a spreading of concentration through space in excess of the true advective flux, and has been described as numerical mixing (Orlob, et al. 1967), pseudo-dispersion (Bella and Grenney 1970) or implicit diffusion (Walsh 1975a). The magnitude of the error, expressed as a mixing coefficient, K_{pseudo} , has been quantified (Bella and Grenney 1970), in the x dimension for example, as

$$K_{\text{pseudo}} = (u/2) (\Delta x - u\Delta t) \quad [A.12]$$

where

u is current velocity ($\text{cm}\cdot\text{sec}^{-1}$);

Δx is spatial segment length (cm);

Δt is iteration time (sec).

For the velocities and spatial segmentation scheme used in meso-scale models of marine systems, the magnitude of the pseudo-mixing coefficient may be of the same order as the specified mixing coefficients, $K_{i,k}$. Walsh (1975), for example, did not explicitly include expressions for turbulent diffusion in the plane of his model. He assumed that the pseudo-mixing process implicitly associated with the finite difference function for advection adequately expressed turbulent diffusion effects. The problem with this assumption is that the size of the mixing coefficient is directly dependent on the magnitude and direction of advective flow, i.e., in the absence of flow in a given direction, there is no mixing in that direction. Accordingly, there is no vertical mixing, either specified or pseudo, in Walsh's (1975) model at distances greater than 30 km offshore.

A solution to the pseudo-mixing problem, suggested by Bella and Grenney (1970) and used by Harper (1972), is to estimate the pseudo-dispersion coefficient and subtract it from the specified coefficient. This solution was used in the northwest African upwelling model. The coefficients, $K_{i,k}$, used in the finite difference expressions are calculated as

$$\begin{aligned} K_{i,k} &= K_{\text{specified}} - K_{\text{pseudo}}, \text{ if } K_{\text{specified}} > K_{\text{pseudo}} & [\text{A.13}] \\ &= 0, \text{ otherwise} \end{aligned}$$

where

$K_{\text{specified}}$ is the specified diffusion coefficient;

K_{pseudo} is the pseudo-diffusion coefficient.

Necessary conditions for stability are

$$u_{i,k} (\Delta t / \Delta x) < 1$$

$$w_{i,k} (\Delta t / \Delta z) < 1$$

$$K_{i,k+\frac{1}{2}} (\Delta t / \Delta z^2) < \frac{1}{2}$$

$$K_{i+\frac{1}{2},k} (\Delta t / \Delta x^2) < \frac{1}{2}$$

For $\Delta t = 1.8 \times 10^3$ sec ($\frac{1}{2}$ hour), $\Delta x = 5 \times 10^5$ cm, and $\Delta z = 5 \times 10^2$ cm,

these conditions are met when $u < 278$ cm sec⁻¹, $w < 0.28$ cm sec⁻¹,

$K_{i,k+\frac{1}{2}} < 69$ cm² sec⁻¹, $K_{i+\frac{1}{2},k} < 6.9 \times 10^6$ cm² sec⁻¹. These

stability requirements have been developed from an analysis of the behavior of solutions to equations describing advection only or diffusion only. Although the processes of advection and diffusion occur simultaneously in a real marine environment, Bella and Dobbins (1968) state that summing the finite-difference effects of diffusion and advection introduces serious errors. They suggest a multistep procedure, adopted in this model, to eliminate the errors. During the first step, the change in concentration due to advection alone is determined and a new concentration distribution calculated. Next, the changes due to diffusion are evaluated, and the resulting distribution of concentrations is used when the effects of biological interactions are evaluated and a final new distribution calculated.

APPENDIX II

Boundary and Initial Conditions

Boundary conditions for nitrate, ammonium, silicate and chlorophyll are specified at the offshore and lower boundaries only. Along-shore gradients are considered negligible and no flux is permitted through the east or upper boundary. Specified boundary conditions are constant through time and are averages based on data taken throughout the JOINT-I cruise period. Data taken between $18^{\circ}30'W$ and $18^{\circ}48'W$ define the offshore boundary conditions 105 km from the coast and data taken between 100 and 150 m depth define the lower boundary conditions listed in Table 5. Offshore boundary conditions are used as initial conditions throughout the simulated space.

Values of phytoplankton variables other than chlorophyll are based on the chlorophyll measurements and assumptions concerning the cell size (T. Smayda, pers. comm.) and state of the phytoplankton population. An estimated maximum carbon quota of $7.3 \text{ pg at C} \cdot \text{cell}^{-1}$ is based on the assumptions that phytoplankton are individually $10 \text{ } \mu\text{m}$ spheres and that the maximum carbon quota is twice the estimate of cell carbon suggested by Strathman (1967). Other phytoplankton quotas are specified to be values halfway between maximum (c_i) and minimum (d_i) limits. The initial and boundary chlorophyll values divided by the chlorophyll quota gives cell numbers, N , in units of $10^6 \text{ cells} \cdot \text{l}^{-1}$. The product of N and the quotas of carbon, silica, and nitrogen define the values for the phytoplankton variable values listed in Table 6.

Table 4. Initial values for a short term simulation of the mean JOINT-I conditions.

	Depth Range	
	0-30 m	30-100 m
Nitrate ($\mu\text{g at}\cdot\text{l}^{-1}$)	3.43	7.06
Ammonium ($\mu\text{g at}\cdot\text{l}^{-1}$)	0.54	0.34
Silicate ($\mu\text{g at}\cdot\text{l}^{-1}$)	2.27	3.02
Chlorophyll ($\mu\text{g}\cdot\text{l}^{-1}$)	3.74	1.98
Silica ($\mu\text{g at}\cdot\text{l}^{-1}$)	0.46	0.24
Nitrogen ($\mu\text{g at}\cdot\text{l}^{-1}$)	1.35	0.72
Carbon ($\mu\text{g at}\cdot\text{l}^{-1}$)	13.06	6.91
Cell Numbers ($10^6 \text{ cells}\cdot\text{l}^{-1}$)	2.88	1.52

Table 5. Offshore and lower boundary conditions of nutrients and chlorophyll a based on JOINT-I observations.

	Nitrate ($\mu\text{g at}\cdot\text{l}^{-1}$)	Ammonium ($\mu\text{g at}\cdot\text{l}^{-1}$)	Silicate ($\mu\text{g at}\cdot\text{l}^{-1}$)	Chl. <u>a</u> ($\mu\text{g}\cdot\text{l}^{-1}$)
Offshore (0-30 m)	1.48	0.24	0.93	1.45
Offshore (30-100 m)	2.84	0.35	1.37	0.95
Lower Boundary (35-55 km offshore)	13.59	0.13	4.88	0.42
Lower Boundary (55-105 km offshore)	9.85	0.24	3.6	0.39

Table 6. Estimates of offshore and lower boundary phytoplankton variable concentrations and cell numbers

	Silica ($\mu\text{g at}\cdot\text{l}^{-1}$)	Nitrogen ($\mu\text{g at}\cdot\text{l}^{-1}$)	Carbon ($\mu\text{g at}\cdot\text{l}^{-1}$)	Cell Numbers ($\times 10^6 \text{ l}^{-1}$)
Offshore (0-30 m)	0.18	0.52	3.06	1.12
Offshore (30-100 m)	0.12	0.34	3.32	0.73
Lower Boundary (35-55 km offshore)	0.05	0.15	1.47	0.32
Lower Boundary (55-105 km offshore)	0.05	0.14	1.36	0.30

APPENDIX III

Computer Methods for Results Post-Processing

The computational results of simulation models are often difficult to interpret without some form of processing. In the models discussed in this study, some diagnostic information was listed during execution. In addition to printed maps of variable concentration, items output during execution for each spatial segment (where appropriate) included printed maps of the factor most limiting to phytoplankton growth, the fraction of phytoplankton standing stock consumed per hour, the phytoplankton growth rate, an estimate of zooplankton body-carbon ingestion rate per day, and the process causing the largest absolute changes in nitrate and chlorophyll. Also, in each spatial segment, net photosynthetic carbon production and total herbivore carbon ingestion were integrated over 24 hour periods ending at midnight.

Once generated, simulation results were post-processed in an interactive data base management system developed for this study. Data were selected from the output file to be vertically integrated or prepared as an input file for a general statistics program package. Grid points in the ecosystem model are unevenly distributed in space and before statistical calculations were begun, data associated with each point were arithmetically weighted according to the area of the spatial segment from which the data originated.

Model output was also graphically post-processed to show the changing simulated distributions of variables. A file management system was developed to process the results generated on a CDC 7600 and

interactively create contour maps on a Tektronix 4014 cathode ray display terminal with a CDC 6600 using DISSPLA, a general plotting package (Integrated Software Systems Corp.) and a Brookhaven National Laboratory Central Scientific Computing Facility contouring program, CMRBR, modified to contour unevenly spaced data. Copies of the graphics were recreated on microfilm with an FR-80 (Information International, Inc.) and processed photographically to produce the final illustrations.

APPENDIX IV

Definition of Symbols

- a_3 = a proportionality constant expressing the reduction in the maximum specific uptake of nitrate as a function of ammonium concentration ($0.1 \text{ l} \cdot (\mu\text{g at NH}_4)^{-1} \text{ hr}^{-1}$)
- b_5 = a proportionality constant relating cell division rate and carbon specific respiration rate (0.11)
- $c_n, n = 1,4,5,6$ = cell quotas of particulate silica, nitrogen, carbon, and chlorophyll a, respectively ($\text{pg at} \cdot \text{cell}^{-1}$ and $\text{pg} \cdot \text{cell}^{-1}$ for chlorophyll only)
- $c_n, n = 1,4,5$ = maximum cell quotas of silica, nitrogen and carbon, respectively ($\text{pg at} \cdot \text{cell}^{-1}$)
- $d_n, n = 1,4,5$ = minimum cell quotas of silica, nitrogen and carbon, respectively ($\text{pg at} \cdot \text{cell}^{-1}$)
- e_6 = a proportionality constant relating nitrogen uptake to chlorophyll synthesis ($0.875 \text{ pg chlorophyll/pg total nitrogen uptake}$) when nitrogen is limiting cell division rate
- F = the fraction of phytoplankton biomass ingested by fish (hr^{-1})
- f_5 = carbon-specific basal respiration rate of phytoplankton (0.003 hr^{-1})

G	= cell division rate (hr^{-1})
g	= maximum cell division rate (0.08 hr^{-1})
I_0	= light intensity at the upper boundary of a segment of thickness z meters ($\text{einstein} \cdot \text{m}^{-2} \text{ hr}^{-1}$)
I_{max}	= optimal light intensity for photosynthesis. Photosynthesis rate is maximum when light intensity is equal to I_{max} ($2.07 \text{ einstein} \cdot \text{m}^{-2} \text{ hr}^{-1}$)
I_z	= light intensity at the lower boundary of a segment of z meters thickness ($\text{einstein} \cdot \text{m}^{-2} \text{ hr}^{-1}$)
j_5	= small zooplankton carbon concentration ($\mu\text{g at C} \cdot \text{l}^{-1}$)
$k_n, n = 1, 2, 3$	= half-saturation constants for uptake of silicate, nitrate and ammonia, respectively ($1.0 \mu\text{g at l}^{-1}$)
K_c	= average spectral extinction coefficient ($\text{m}^2(\text{mg} \cdot \text{Chl } \underline{a})^{-1}$) per unit of phytoplankton concentration, where phytoplankton concentration is expressed as concentration ($\text{mg} \cdot \text{m}^{-3}$) of chlorophyll <u>a</u> ($0.016 \text{ m}^2 \cdot (\text{mg Chl } \underline{a})^{-1}$)
K_dX	= average spectral extinction (m^{-1}) for dissolved and suspended substances other than chlorophyll

K_t	= average total spectral extinction coefficient (m^{-1}) for seawater and all light attenuating components
K_w	= average spectral extinction coefficient for seawater ($0.04 m^{-1}$)
L_5	= carbon-specific ingestion rate of large zooplankton ($\mu g \text{ at zoo. C}^{-1} \cdot hr^{-1}$)
M_5	= carbon-specific ingestion rate of fish
m	= physiological mortality rate of phyto- plankton ($0.0042 hr^{-1}$)
N	= phytoplankton cell concentration (in units of $10^6 \text{ cells} \cdot l^{-1}$)
$P_n, n = 1,4,5,6$	= phytoplankton particulate silica, nitrogen, carbon and chlorophyll, respectively (in units of $\mu g \text{ at} \cdot l^{-1}$ and $\mu g \cdot l^{-1}$ for chlorophyll only)
Q_{max}	= maximum quantum yield ($60 \text{ mg at carbon} \cdot \text{einstein}^{-1}$)
q_5	= large zooplankton carbon concentration
R	= a general inclusive symbol for nonconservative effects
R_5	= phytoplankton carbon respiration rate (hr^{-1})
$r_n, n = 1,2,3$	= benthic nutrient flux terms ($\mu g \text{ at} \cdot l^{-1} \cdot hr^{-1}$)
S	= a generalized nonconservative variable. $P_n, n = 1,4,5,6$ and $S_n, n = 1,2,3$ define non- conservative variables in this model

S_n , $n = 1,2,3$	= nutrient concentrations of silicate, nitrate and ammonium, respectively (in units of $\mu\text{g at} \cdot \text{l}^{-1}$). Concentrations expressed as $\mu\text{g at} \cdot \text{l}^{-1}$ refer to $\mu\text{g at}$ of the nutrient element per liter
V_n , $n = 1,2,3,4,5,6$	= specific rates of phytoplankton nutrient uptake, photosynthesis or chlorophyll synthesis (hr^{-1})
$u_{i,k}$	= east-west current velocity at the i^{th} column and k^{th} layer of the model. u is positive towards the west
v_n , $n = 1,2,3$	= maximum specific uptake rates (0.12 hr^{-1}) of silicate, nitrate, and ammonium, respectively. The maximum effective nitrate uptake rate, v_2 , is varied as a function of ammonium concentration
$w_{i,k}$	= vertical current velocity of the i^{th} column and k^{th} layer of the model. w is positive downward
w_5	= carbon concentration of herbivorous fish ($\mu\text{g at C l}^{-1}$)
x_i	= horizontal dimension of a column (m)
Y_3	= ammonium excretion rate ($\mu\text{g at NH}_3\text{-N l}^{-1} \text{ hr}^{-1}$)
Z	= the fraction of the phytoplankton biomass ingested by fish (hr^{-1})
z	= depth (m)

$\alpha_n, n = 1,2,3$	= the change in nutrient concentration caused by the addition of nutrients to an experimental container. In general, $\alpha_n = 0$, except at the time when nutrients are added. When $\alpha_n \neq 0$, the starter sequence of the numerical method (Appendix I.A) is used to continue the simulation
β_3	= zooplankton ammonium excretion efficiency ($0.29 \mu\text{g}$ at ammonium excreted $\cdot (\mu\text{g}$ at phyto-nitrogen ingested) $^{-1}$)
γ_3	= fish ammonium excretion efficiency ($0.46 \mu\text{g}$ at ammonium excreted $\cdot (\mu\text{g}$ at phyto-nitrogen ingested) $^{-1}$)
ϵ	= zooplankton grazing constant
θ	= fish filtering constant
λ	= small zooplankton size-specific weighting factor (3.22)
τ	= fish grazing constant
ψ	= zooplankton filtering constant
Ω	= constant vertical scaling factor

APPENDIX V

Equations of the Physical Circulation Submodel

The equations of continuity, advection and diffusion of density and conservation of momentum, using the Boussinesq approximation and assuming that all longshore gradients may be neglected, are (Hamilton and Rattray 1978), respectively

$$\frac{\partial \zeta}{\partial t} + \frac{\partial}{\partial x} \int_{-\zeta}^h u dz = 0$$

$$\frac{\partial u}{\partial x} + \frac{\partial w}{\partial z} = 0$$

$$w = \frac{\partial}{\partial x} \int_z^h u dz$$

$$\frac{\partial \rho}{\partial t} + u \frac{\partial \rho}{\partial x} + w \frac{\partial \rho}{\partial z} - \frac{\partial}{\partial x} \left(K_x \frac{\partial \rho}{\partial x} \right) - \frac{\partial}{\partial z} \left(K_z \frac{\partial \rho}{\partial z} \right) = 0$$

$$\frac{\partial u}{\partial t} + u \frac{\partial u}{\partial x} + w \frac{\partial u}{\partial z} - fv = - \frac{g}{\rho_0} \frac{\partial \rho}{\partial x} - g \frac{\partial \zeta}{\partial x} + \frac{\partial}{\partial z} \left(N_z \frac{\partial u}{\partial z} \right)$$

$$\frac{\partial v}{\partial t} + u \frac{\partial v}{\partial x} + w \frac{\partial v}{\partial z} + fu = - g \frac{\partial \zeta}{\partial y} + \frac{\partial}{\partial z} \left(N_z \frac{\partial v}{\partial z} \right)$$

The symbols in the above equations are defined as follows

x, y, z	a right-handed coordinate set with x positive offshore,, y in the plane of the undisturbed sea surface and z vertically upward, respectively
t	time
u, v, w	velocity components in the x, y, z directions, respectively
ζ	elevation of the sea surface above the undisturbed plane
ρ	density
h	depth
N_z	coefficient of vertical eddy viscosity
K_z, K_x	coefficients of vertical and horizontal eddy diffusivity, respectively
f	Coriolis parameter [$= 2 \sin$]
Ω	angular velocity of the earth
ϕ	latitude
g	acceleration due to gravity
$\bar{u}, \bar{v}$	vertically integrated transports
$\tau_{xs}(\tau_{ys}), \tau_{xb}(\tau_{yb})$	surface and bottom stresses in the x(y) direction, respectively.