Simulations of Marine Ecosystem Response to Climate Variation with a One Dimensional Coupled Ecosystem/Mixed Layer Model

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Abstract. Existing observations are inadequate to identify and to understand the processes by which oceanic and atmospheric variability affect the marine biota at climate scales. To aid in the identification and study of important processes, we employ a one-dimensional coupled mixed layer / planktonic ecosystem (Nutrient-Phytoplankton-Zooplankton-Detritus) model of the subarctic Pacific Ocean. Increasing evidence indicates that the subarctic Pacific, along with the Southern Ocean and the equatorial Pacific, are High Nutrient-Low Chlorophyll (HNLC) regimes because of the scarcity of the micronutrient iron. Under the assumption that the availability of iron might vary as the climate varies, we test the response of our model to a simple formulation of iron limitation. Simulations with and without iron limitation of primary production by phytoplankton yield a difference of about a factor of two in the standing stock of zooplankton during the productive season, although changes in phytoplankton biomass are small. A similar difference in zooplankton biomass has been observed over a 30 year period in the eastern subarctic Pacific (*Brodeur and Ware*, 1992). The modelled result occurs whether we employ a linear or a quadratic formulation for zooplankton losses. An important implication of this result is that a doubling in zooplankton biomass would mean more food for fish populations, yet contemporary plans to monitor ocean productivity from satellites would detect only minor changes in phytoplankton biomass.

1. Introduction

The North Pacific Ocean has long been associated with large scale anomalies on climatic scales in related atmospheric and oceanic patterns, e.g., *Horel and Wallace* (1981), *Wallace and Gutzler* (1981), *Namias et al*. (1989). More recently, some large changes have been interpreted as step-like 'regime shifts', e.g., *Trenberth* (1990), *Hanawa* (1991), *Trenberth and Hurrell* (1994), *Mantua et al*. (1997), *Zhang et al*. (1997), and references cited in other papers in this volume. There is evidence that sardine catches in this century have undergone large interdecadal fluctuations that are synchronous over the Pacific basin (*Kawasaki*, 1991; US GLOBEC Report 12, 1995), suggestive of a large scale climatic influence. *Beamish and Bouillon* (1993) have argued that N. Pacific salmon production trends over the period 1925-89 correlate with an Aleutian Low Pressure index based on area of surface pressure below 100.5 kPa during winter and spring months. *Beamish* (1993) and *Francis and Hare* (1994) have related changes in Northeast Pacific fish populations to the regime shift of 1976-77 and (in the second reference) to a reverse shift in the late 1940s.

Both phytoplankton and zooplankton also undergo interannual to interdecadal fluctuations. Phytoplankton biomass and primary production undergo both interannual fluctuation and trends (*Venrick et al*. (1987), *Wong et al*. (1995), *Sugimoto and Tadokoro* (1997)). However, from an analysis of Secchi depth records since 1907, *Falkowski and Wilson* (1992) concluded that there has been no significant change in either phytoplankton biomass or production over the whole North Pacific. *Brodeur and Ware* (1992) documented a doubling in zooplankton biomass in the subarctic Pacific between the periods 1956-62 and 1980-89, with a suggestion that zooplankton biomass correlates positively with Ekman transport (inferred from surface atmospheric pressure charts). Along the coastal margins, *Mackas* (1995) (and other investigators) have documented interannual variability in zooplankton community composition, again identifying possible correlations with interannual variation in upwelling intensity or other water transport properties. In a more general study, *Hofmann and Powell* (1998) document four case histories, ranging from Northern Cod to Antarctic Krill, where there is clear environmental control on the fisheries, albeit over a wide range of temporal scales. Finally, in an attempt to move from observing correlations to testing hypotheses of operative mechanisms, *Gargett* (1997) has hypothesized that the most productive ecosystems occur where there is optimum stability – sufficient to maintain phytoplankton in the sunlit surface layer of the ocean but not so strong as to suppress the transport of nutrients into the euphotic zone.

The natural question arises: are fish populations affected directly by changes in ocean conditions related to climate variability or are the effects propagated mainly through the marine foodweb, i.e., by affecting the food supply of the target fish species? The answer is undoubtedly that both direct and indirect effects are important. For example, *Welch* (this volume) has documented that oceanic thermal fronts clearly limit the southern extent of some salmon species – apparently a behavioral response. On the other hand, some of the references cited above present evidence of correlations between zooplankton and fish population abundances suggesting propagation of variability through the planktonic foodweb. Because existing simultaneous observations of oceanic conditions and the biotic responses are sparce, we are investigating the latter route – how climatic variability might affect fish populations by propagation through the planktonic foodweb – with a one-dimensional coupled mixed layer/planktonic ecosystem model.

To simulate the planktonic ecosystem at Ocean Station P (50°N, 145°W) and to examine the hypothesis that iron availability limits phytoplankton productivity and nutrient uptake in the subarctic North Pacific, we embedded a four-compartment Nutrient-Phytoplankton-Zooplankton-Detritus planktonic ecosystem model in a 60-level 1-d mixed layer model (Mellor-Yamada level 2.5; *Mellor and Yamada*, 1974, 1982), driven by annual forcing (winds, solar radiation, surface heat exchanges) characteristic of OSP. Both the physical and ecological models are forced with the same annual heat budget, i.e., sea surface temperature is an output, not a boundary condition of the model. In *Denman and Peña* (submitted), we found that for simulations with realistic sinking speeds and remineralization rates for sinking organic particles, some degree of iron limitation of phytoplankton growth and production was necessary so that surface nitrate concentrations did not drop below about half their late winter maximum concentrations, an historical observation from OSP.

In this paper we shall present model simulations which suggest that changes in the ocean associated with climate variation can result in foodweb modification. Specifically, changes in the degree of iron limitation in our model yield changes in zooplankton biomass on the same order as those observed by *Brodeur and Ware* (1992). At present, the source for bioavailable iron in the surface waters of the subarctic Pacific has not been identified. Long range atmospheric transport may be responsible (e.g., *Duce et al*., 1991; *Boyd et al*., submitted), but there are new observations suggesting the possibility of subsurface flow from the continental margins (J. K. Bishop, pers. comm.). Either pathway could be expected to vary in intensity with climate-related variability in the atmosphere and/or the ocean.

The results based on the simulations of *Denman and Peña* are no doubt model dependent: in particular, they may depend on the formulation used for zooplankton losses or mortality. To explore that possibility, here we also alter the form of the zooplankton loss term and rerun the simulations. While the fine features of the annual cycles change, the overall result – that a change in the intensity of iron limitation results in approximately a 2X change in the annual average biomass of zooplankton – remains a robust result. Interestingly, the annual cycle for the case without iron limitation, resembles an annual cycle characteristic of the western North Pacific (*Sugimoto and Tadokoro*, 1997).

2. The Ecological Model

The NPZD ecological model, consisting of four compartments, nitrogen *N*, phytoplankton *P*, zooplankton *Z*, and detritus *D*, is shown schematically in Figure 1. We use nitrogen as our 'currency' so *N* consists of nitrate, ammonium and urea. The model is similar to that of *Doney et al.* (1996). The arrows in Figure 1 represent the fluxes between the model compartments, and the subscripts denote the path of each flux. The double-ended arrows represent mixing fluxes across the 50-m horizon (+ve upwards). For example, the net primary

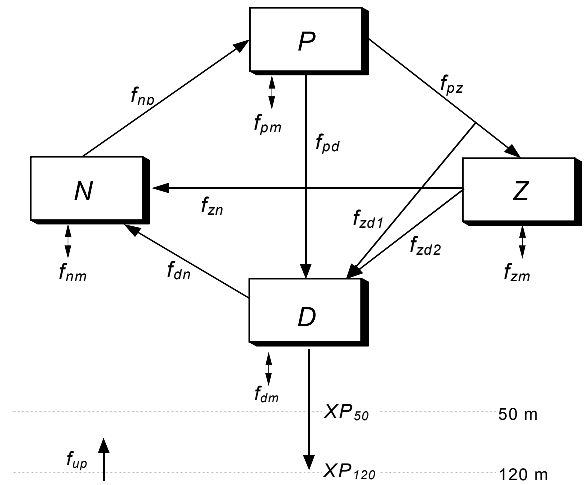

Figure 1. Schematic diagram for the NPZD ecosystem model. Fluxes from compartment *A* to compartment *B* are denoted by the symbol f_{ab}, mixing flux of *A* across the 50-m level (f_{am}) are shown with double ended arrows (positive upwards). The export of sinking particles across the 50-m level and out of the model domain are denoted by XP_{50} and XP_{120}. The addition of nitrate in the bottom 5 layers is denoted as f_{up}.

production is labelled as f_{np}, denoting a flux from *N* to *P*, and the mixing flux across 50 m of *Z* is labelled as f_{zm}. XP_{50} and XP_{120} represent the fluxes of sinking detritus *D* across the 50-m horizon and the 120-m horizon, which is the bottom of the model domain.

The formulation of the fluxes between the model compartments is given in the set of four coupled ordinary differential equations that define the model:

$$\frac{\mathrm{d}P}{\mathrm{d}t} = (\text{growth})\, P - (\text{grazing})\, Z - m_{pd} P \tag{1}$$

$$\frac{\mathrm{d}Z}{\mathrm{d}t} = g_a (\text{grazing})\, Z - (m_{zn} + m_{zd}) Z \tag{2}$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = -(\text{growth})\, P + m_{zn} Z + r_e D \tag{3}$$

$$\frac{\mathrm{d}D}{\mathrm{d}t} = (1 - g_a)\, (\text{grazing})\, Z + m_{pd} P + m_{zd} Z - r_e D + w_s \frac{\mathrm{d}D}{\mathrm{d}z} \tag{4}$$

where

$$\text{growth} = v_m \times \mathrm{Min}\left\{ \left(\frac{N}{k_n + N} \right), \left(1 - \exp(-\alpha\ I_{PAR}/v_m) \right),\ L_{Fe} \right\}$$

and

$$\text{grazing} = r_m \frac{P^2}{k_p^2 + P^2}\,. \tag{5a,b}$$

Under the assumption that only one factor limits phytoplankton growth at any time, the rate of phytoplankton growth is determined by the minimum value (evaluated each time step) of three functions, each ranging between 0 and 1, representing limitation by N, I_{PAR} (photosynthetically available radiation), or iron. The nitrogen uptake is given by the usual Michaelis-Menten (Monod) function, and the light function derives from *Webb et al.* (1974). For the attenuation coefficient of I_{PAR}, $k_t(z)$, we use a modification of the linear formulation used by *Evans and Parslow* (1985) and *Fasham* (1995):

$$k_t(z) = k_w + k_c(P(z) + D(z)) \tag{6}$$

where k_w is the attenuation coefficient of sea water and k_c is a single coefficient providing shading by both phytoplankton P and detritus D. The short wave penetrative radiation that provides heat in the mixed layer model uses the same attenuation coefficient; hence there is feedback from the ecological model back to the physical model making this a coupled model in both directions.

It is not yet clear what simple functional dependence to adopt for the effect of iron on phytoplankton growth. Instead we have chosen to model its possible effect by a constant factor L_{Fe}. We performed simulations with L_{Fe} taking on a series of (constant) values between 1 (no inhibition) and 0 (complete inhibition). As L_{Fe} is decreased, it initially limits nutrient uptake only in summer when there is lots of light, but as it takes on smaller values approaching 0, it limits uptake even in winter when it is less than the light function.

The linear loss term in the zooplankton conservation equation (3), $-(m_{zn} + m_{zd})Z$, allows for a straightforward equilibrium solution by setting all the time derivatives to zero in equations (1) – (4) (i.e., $dY_i/dt = 0$) when the particle sinking rate $w_s = 0$ and there is no Ekman upwelling:

$$P_e = k_p\sqrt{\frac{m_{zn} + m_{zd}}{g_a r_m - (m_{zn} + m_{zd})}} \tag{7}$$

$$\frac{Z_e}{P_e} = \frac{g_a}{m_{zn} + m_{zd}}\left[v_m MIN(L_N, L_{PAR}, L_{Fe}) - m_{pd}\right] \tag{8}$$

$$\frac{D_e}{P_e} = \frac{1}{r_e}\left[m_{pd} + \left(\frac{g_a m_{zd}}{m_{zn} + m_{zd}} + (1 - g_a)\right) \times \left(v_m MIN(L_N, L_{PAR}, L_{Fe}) - m_{pd}\right)\right] \tag{9}$$

and

$$N_e = N_T - (P_e + Z_e + D_e) \tag{10}$$

where N_T is the total nitrogen in the (closed) system. The equilibrium value for phytoplankton P_e depends only on constant parameter values representing the strength of zooplankton grazing and losses. Thus, for slowly varying forcing, this model might be expected to yield a nearly constant phytoplankton biomass, much like that observed historically at OSP. We used equation (7) to tune parameter values so as to give a phytoplankton biomass of about 0.3 mg-N m^{-3}, equivalent to the historical value of ~0.4 mg-Chl m^{-3} (e.g., *Wong et al.*, 1995). The equilibrium value for zooplankton Z_e depends on the net primary production, which varies with time according to the availability of nutrients, light and iron. The equilibrium value for detritus D_e also depends on the net primary production. This seemingly illogical dependence of phytoplankton abundances on zooplankton processes and zooplankton abundances on phytoplankton processes is known among ecological modellers and appears to derive from the formulation of predation rates as functions of prey abundances rather than as functions of carrying capacity or of ratios of masses or weights (e.g., *Berryman*, 1992; *Ginzburg and Akçakaya*, 1992). (The values of the parameters used in our simulations are given in Table 1.)

The loss term for zooplankton in equation (2) represents the 'closure' term in our model, much like the 'closure' term in models of turbulence. We recycle the losses to other compartments in the model, but usually some part of this term is assumed to flow to larger predators, not represented explicitly in the model. For both mathematical and ecological reasons, some modellers prefer to replace or augment this linear term with a quadratic mortalilty term (*Steele and Henderson*, 1992;

Table 1. Model parameters for OSP simulations

Parameter	Symbol	Units	Value Series A	Value Series B
Background diffusion coefficient	K_z	m^2 s^{-1}	4 ·10^{-5}	1·10^{-5}
PAR attenuation coefficient for sea water	k_w	m^{-1}	0.04	
PAR attenuation coefficient for (P+D)	k_c	m^{-1} (mmol-N m^{-3})$^{-1}$	0.06	
Initial slope of P-I curve	α	d^{-1} (W m^{-2})$^{-1}$ #	0.08	
Maximum phytoplankton growth rate	v_m	d^{-1}	2.0	
Nitrogen half saturation constant	k_n	mmol-N m^{-3}	0.1	
Phytoplankton mortality rate (to Detritus)	m_{pd}	d^{-1}	0.05	
Zooplankton maximum grazing rate	r_m	d^{-1}	1.0	
Zooplankton assimilation efficiency	g_a	-	0.7	
Zooplankton grazing half saturation constant	k_p	mmol-N m^{-3}	0.4	1.0
Zooplankton losses to Nutrient (linear)	m_{zn}	d^{-1}	0.20	-
Zooplankton losses to Detritus (linear)	m_{zd}	d^{-1}	0.05	-
Zooplankton losses to Nutrient (quadratic)	κ_{zn}	(mmol-N m^{-3})$^{-1}$ d^{-1}	-	0.08
Zooplankton losses to Detritus (quadratic)	κ_{zd}	(mmol-N m^{-3})$^{-1}$ d^{-1}	-	0.02
Detritus sinking speed	w_s	m d^{-1}	6	
Detritus remineralization rate	r_e	d^{-1}	0.06	

d^{-1} ≡ day^{-1}

Fasham, 1995). We will present simulations from our model for both cases: with a linear mortality term (as shown) and with a quadratic mortality term.

3. Results

3.1 Series A: Linear zooplankton loss term

The model was run for 3 years for each standard simulation, with a time step of 15 minutes. A "leap frog" time differencing scheme is used, with weak smoothing each time step to connect solutions between the even and odd time steps. Each simulation starts on 1 March (year day 60) at the end of winter, with the initial values $N_0+P_0+Z_0+D_0$ = 15 mmol-N m^{-3}. For the range of parameter values used in the biological model, the coupled model 'spins up' within a couple of months. We balance the annual net solar heat input to the mixed layer model with a constant heat loss at the sea surface: hence, sea surface temperature and mixed layer *P*, *Z*, and *D* all repeat annually to at least 4 significant figures (when there is excess *N*).

Nitrogen is lost from the model domain due to particles sinking past the depth of 120 m (XP_{120} in Figure 1). For typical sinking rates of 3-10 m d^{-1} used in the model, the model will run out of nitrogen in 5-10 years (*Denman and Peña*, submitted). Thus for each simulation, we approximately match the annual loss XP_{120} with a constant addition of nitrate f_{up} introduced over the bottom five layers in a manner that does not create a gradient at the bottom (since MY2.5 minimizes the vertical gradient at the bottom when a no-flux bottom boundary condition is applied). This addition is meant to mimic the flux of nitrate to the surface layer via Ekman upwelling in the subarctic gyres. (We had previously applied Ekman upwelling that was everywhere divergent in the model domain. The results were similar to those shown here, but it was extremely difficult to calculate a budget for nitrogen and hence to estimate the upwelling speeds required to balance the losses from particle sinking.)

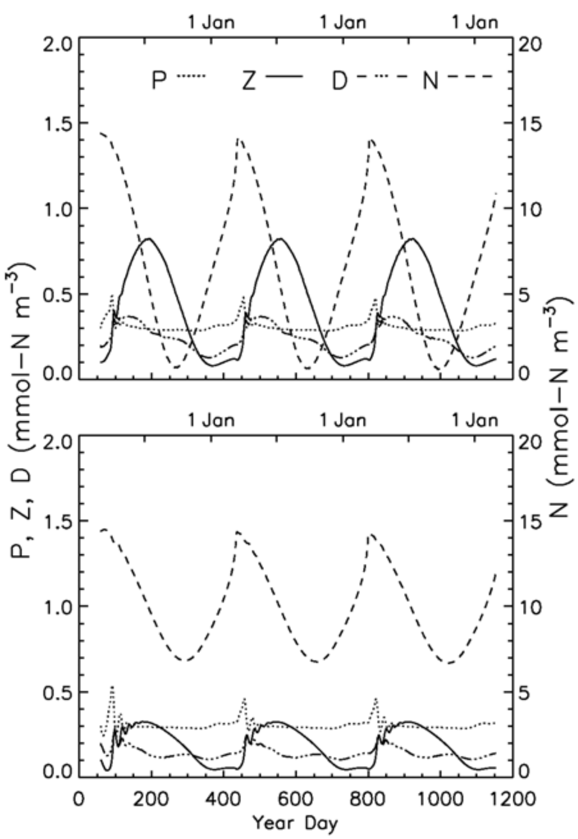

Figure 2. Simulated upper layer 3-year time series for iron limitation L_{Fe} = 1 (no limitation, top panel) and 0.35 (optimal limitation, bottom panel). The linear zooplankton loss term is employed as in equation (2).

For the model described by equations (1)-(5), we chose parameter values within ranges used by previous modellers and adjusted certain parameters using the equilibrium solutions to give realistic annual cycles of the state variables *P*, *Z*, *D* and *N* (*Denman and Peña*, submitted). With reasonable sinking speeds for the organic particles *D* of 3 – 10 m d^{-1} and without iron limitation (L_{Fe} = 1), we could not recover the annual cycle of surface nitrate at OSP: a winter maximum of ~15 mmol-N m^{-3} and a summer minimum of roughly half that value. This simulation is shown in the upper panel of Figure 2, where the right hand scale applied to the dissolved nitrate *N*. Note that the annual cycle of phytoplankton *P* is roughly constant except for a small peak (~30%) in the spring, not what would be considered a spring bloom. The zooplankton *Z* and detritus *D* concentrations follow smooth annual cycles.

In subsequent simulations, the iron limitation was applied in steps: an 'optimum' iron limitation (L_{Fe} = 0.35) was reached when the annual cycle of nitrate *N* approached the long term average annual cycle at OSP, as shown in the bottom panel of Figure 2. Note that the annual cycle of phytoplankton *P* remains essentially unchanged. Reducing the iron limitation factor further (increasing the iron limitation) caused further limitation of primary production in winter and significant blooms in spring and throughout the summer. To demonstrate changes in the vertical structure of the coupled mixed layer model over the annual cycle, we have plotted in Figure 3 (time-depth) contours for the temperature field (upper panel, no iron limitation), and for the zooplankton biomass fields (middle panel – no iron limitation, bottom panel – optimum iron limitation). The depth at which the photosynthetic available (short wave) radiation reaches 1% of its surface value ($Z_{1\%}$) is plotted on the temperature field. Because $Z_{1\%}$ will vary for each simulation depending on the *P* and *D* fields, the thermal structure also changes slightly between simulations.

More important in the context of 'Aha Huliko'a discussions, the summer peak in zooplankton biomass in the simulation without iron limitation (~0.8 mmol-N m^{-3}) is more than twice that for the case of optimal iron limitation (~0.3 mmol-N m^{-3}), reminiscent of the changes in zooplankton biomass over a 30-year period in the eastern subarctic Pacific, documented by *Brodeur and Ware* (1992).

3.2 Series B: Quadratic zooplankton loss term

Formulations of marine ecosystem models have not evolved to the stage where there is wide-spread consensus for any particular formulation (e.g., *Evans and Garçon*, 1997). In particular, changing the forms of grazing functions and of zooplankton loss terms is known to change the behavior of the

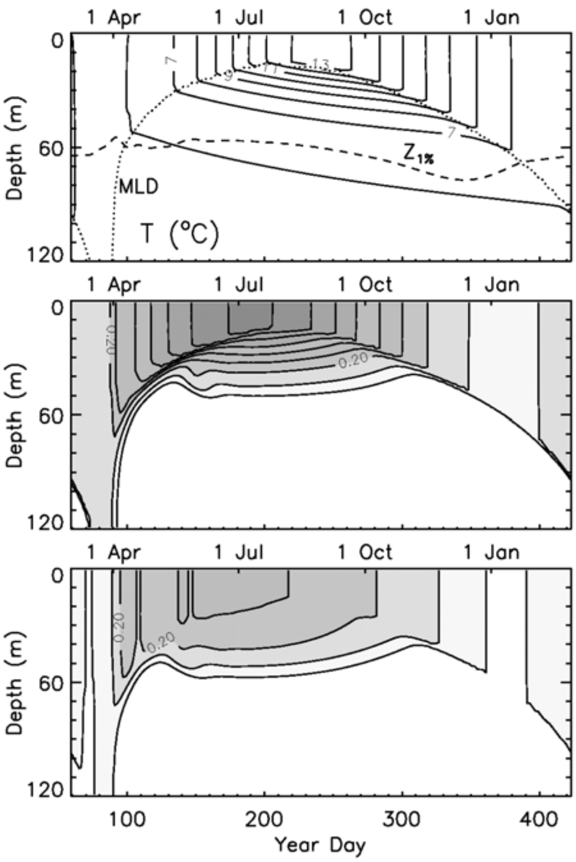

Figure 3. Time-depth plots for year 3 of the iron limitation simulations shown in Figure 2. Top panel: dotted line represents diagnosed mixed layer depth and dashed line represents 1% I_{PAR} penetration depth for no iron limitation. Middle panel: Z contours in units of mmol-N m^{-3} for no iron limitation. Maximum Z ~0.82. Bottom panel: Z contours in units of mmol-N m^{-3} for optimal iron limitation. Maximum Z ~0.32.

model output, even or especially the form of the annual cycle (e.g., *Steele and Henderson*, 1992). We thus did not know whether the change in zooplankton biomass with changing iron limitation would be a robust result if we changed the form of the zooplankton loss term to a quadratic form, which is also often used. When we replaced (in equation (2)) the linear loss term with a quadratic term of the form $-(\kappa_{zn} + \kappa_{zd})Z^2$, we were no longer able to obtain a simple algebraic form for the equilibrium solutions. With the help of a dynamic system solver, we were able to adjust the parameter values of the ecological model somewhat, but, for simulations without iron limitation, we were unable to avoid the model undergoing nutrient limitation during at least part of the summer.

The Mellor-Yamada models tend to under-mix at the base of the mixed layer (e.g., *Martin*, 1985; *Large et al.*, 1994). To increase the diffusion of nitrate into the mixed layer during the summer, we increased the background diffusion in the Mellor-Yamada model from 0.1x10^{-4} m^2 s^{-1} to 0.4x10^{-4} m^2 s^{-1} (in line with values used by *Large et al.*), but this change still did not totally eliminate summer nitrate limitation. The simulations for the quadratic zooplankton loss term are shown in Figure 4. The 3-month depression each summer in P, Z, and D in the upper panel (no iron limitation) results from the nitrate concentration N falling so low as to cause nutrient limitation of primary production. The case with optimum iron limitation (bottom panel) does not result in nutrient limitation because primary production in summer is limited instead by iron availability. The annual cycles of all four state variables are smooth, with the nitrate field N varying in a manner consistent with the average annual cycle at OSP. The phytoplankton annual cycle in nitrogen may be consistent with a roughly constant value of chlorophyll if, as expected, the Chl:Nitrogen cycle varies annually with a winter peak (*Taylor et al*., 1997). Unfortunately, there are no reliable published values of that ratio in winter for the subarctic Pacific.

More importantly, the summer peak in zooplankton biomass for no iron limitation (~2 mmol-N m^{-3}), while higher than in the first simulation, is still roughly twice that for optimum iron limitation (~0.95 mmol-N m^{-3}). This model result, that we might expect lower standing stocks of zooplankton in the eastern subarctic Pacific with greater iron limitation, is a robust result of the model, occurring in simulations that use both standard forms of the loss term for zooplankton.

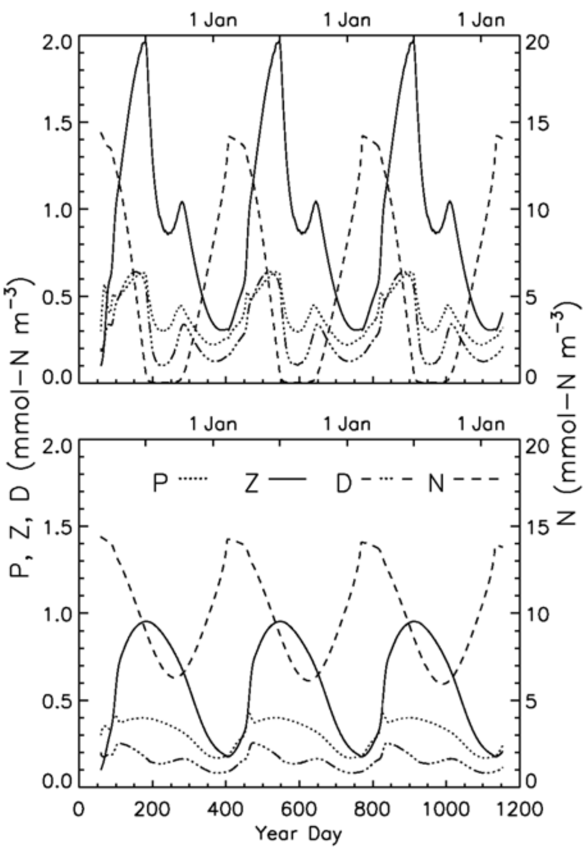

Figure 4. Simulated upper layer 3-year time series for iron limitation L_{Fe} = 1 (no limitation, top panel) and 0.30 (optimal limitation, bottom panel). A quadratic zooplankton loss term is employed in equation (2) instead of the linear term.

4. Summary and Future Work

Detecting 'Biotic impacts of extratropical climate change in the Pacific' (the title of this Workshop) requires simultaneous long term observations of both the climate system (atmospheric and /or oceanic) and of the marine biota. Not only are such data sets rare and incomplete, but attributing cause and effect relationships from statistical analysis of existing observations alone, is difficult if not impossible. To test ideas about what mechanisms might connect marine ecosystem response with oceanic (and atmospheric) forcing on climate scales, we have employed a simple coupled one-dimensional mixed layer / ecosystem model. This model has been developed to help understand planktonic ecosystem dynamics at Ocean Station P in the eastern subarctic Pacific Ocean (*Denman and Peña*, submitted). Here we have assumed that a single forcing function changes on climatic scales, namely the supply of the micronutrient iron.

Simulations with our model suggest that the standing stock of zooplankton might change by a factor of two, depending on whether there is a surplus of iron or whether it is sufficiently scarce to limit primary production by phytoplankton, as recent studies in the eastern subarctic Pacific seem to indicate (e.g., *Martin and Fitzwater*, 1988; *Boyd et al*., 1996). *Brodeur and Ware* (1992) have reported such a change in zooplankton biomass in the subarctic Pacific between the periods 1959-62 and 1980-89. In our model, two different commonly-used formulations for zooplankton losses yield the same outcome, suggesting that it may be a relatively robust result.

What should be done next? First, we have simulated only one process that might change as the climate changes. The next obvious step is to explore the possible effects in our model of global warming. Growth and respiration rates of phytoplankton, zooplankton and bacteria all vary with temperature (e.g., *Eppley*, 1972; *Huntley and Lopez*, 1992). We plan to introduce these dependencies one at a time and evaluate how, say, a 2°C warming would affect the output of our model simulations. By introducing the effects incrementally, we should be able to evaluate the relative importance of different mechanisms and forcing functions that might be expected to change with a changing climate.

Obviously, our model is too simple. It is known that a 1-D mixed layer model cannot adequately balance either the annual heat or salinity budgets at OSP (*Archer et al*. 1993; *Large et al*. 1994). In addition, *Freeland et al*. (1997) have detected long term trends at OSP in surface temperature and salinity, and maximum winter mixed layer depth – changes which may be affecting the plankton ecosystem. We are testing a version of our ecosystem model embedded in the MICOM isopycnal model (*Bleck et al*., 1992), which we have implemented over the whole North Pacific Ocean. We hope to explore the relative importance of vertical (local) processes and horizontal advective processes on the ecosystem model at several key locations in the North Pacific. We also plan to introduce a life stage or developmental submodel for large zooplankton predators. In all this work, we plan to proceed incrementally so that we might be able to evaluate each increase in complexity as it is introduced.

Finally, an important implication of the main result of these simulations is that varying the iron supply to the subarctic ecosystem might change the zooplankton biomass by a factor of two while changing the phytoplankton biomass only a negligible amount. Specifically, a doubling in zooplankton biomass would mean more food for fish populations, yet contemporary plans to monitor ocean productivity from satellites would yield only minor changes in phytoplankton biomass and hence might lead to conclusions that the marine ecosystem was unchanged.

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