Modeling microzooplankton and macrozooplankton dynamics within a coastal upwelling system

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Abstract. A simple nutrient–phytoplankton–zooplankton (NPZ) pelagic ecosystem model coupled to a two-dimensional primitive equation circulation model with explicit mixed-layer physics is configured in a coastal setting to study the biological response to idealized wind-driven upwelling conditions. Conventional ecosystem model parameterization, which assumes macrozooplankton as the target grazers, leads to upwelling-induced phytoplankton blooms that exhaust available nutrient supply and whose zonal scale increases with wind duration. Offshore zooplankton maxima result from upwelled water with greater total nitrogen concentrations than initial ambient surface water. Substantial vertical mixing in the surface boundary layer sets the vertical scale of the productivity. Phytoplankton sinking contributes to a nearshore accumulation of total nitrogen, and enhances the magnitude and duration of the phytoplankton bloom. The system responds differently when the zooplankton are parameterized to represent microzooplankton. The phytoplankton and zooplankton maxima have more limited zonal extent, are more independent of the duration of wind forcing, and near-surface nutrient levels remain high over most of the domain. When winds are relaxed, the diminished offshore transport reveals the underlying biological oscillations in the microzooplankton-parameterized ecosystem, and reduced vertical mixing decouples surface from subsurface dynamics. In contrast, the macrozooplankton system relaxes to a steady state supporting limited phytoplankton and large zooplankton levels in the upwelling region.

Introduction

Multi-component ecosystem models are widely applied in pelagic environments to simulate the response to external forcing and illustrate mechanisms of nitrogen and/or carbon cycling through the system. Such models exhibit various degrees of complexity, from the simple three-component nutrient–phytoplankton–zooplankton (NPZ) model of Franks et al. (Franks et al., 1986), through many examples ranging up to 20 compartments [e.g. (Hofmann and Ambler, 1988; Fasham et al., 1990; Moloney and Field, 1991; Moisan and Hofmann, 1996)]. Even in zero spatial dimensions, systems of greater than two coupled non-linear ordinary differential equations display a considerable range of dynamical behavior, from stable equilibria to chaos (Strogatz, 1994). While added complexity can often be argued on grounds of understood biological processes, it is not obvious that such enhancements quantitatively improve numerical solutions. Indeed, our ability to evaluate ecosystem models quantitatively remains inadequate to justify the added components on the sole basis of such improvement. Furthermore, accompanying the added model components are additional parameters that are usually poorly known from the literature and whose variation can significantly alter the dynamical response of the model. Added spatial dimensions and physical processes further complicate these systems. It is therefore prudent and
desirable to explore thoroughly even simple physical environments with mini-
mally simple ecosystem models. Only through a hierarchy of such models, from
simple to complex in both physics and biology, can the added contribution offered
by each stage be established.

The investigation of Carr exemplifies such a tiered approach (Carr, 1998). This
work compared an ecosystem containing single phytoplankton and zooplankton
populations (having 10 components in total) to one that distinguished between
different plankton size classes and included bacteria (having 20 components).
Models were configured in zero spatial dimensions and driven by prescribed
diffusive and advective nutrient and organism fluxes meant to parameterize trans-
fers into the surface mixed layer within a coastal upwelling environment. The 10-
and 20-component ecosystems responded differently to episodic upwelling, and
available datasets better supported the more complex model.

Coastal upwelling environments are well known for their high biological
productivity associated with seasonal wind forcing. Equatorward wind stress
drives an offshore Ekman transport in the surface waters, and this offshore flow
is compensated by nearshore upwelling of cold, nutrient-rich water into the
euphotic zone. However, coastal ecosystems are inherently spatially dependent,
with significant property variation in the offshore direction [e.g. (Strub et al.,
1991)]. This heterogeneity complicates the parameterization of fluxes into box
models. In upwelling systems, advection brings material into the domain from
below and removes it laterally. The downstream development of the ecosystem
is ignored in a box model. Indeed, vertical and offshore heterogeneity argue for
spatio-temporal coupling of biology and physical circulation models. The spa-
tially dependent response of a coastal ecosystem was first simulated using a
coupled biological–physical model by Wroblewski (Wroblewski, 1977). In that
work, a primitive equation physical model forced by upwelling-favorable wind
stress drove a limited domain, five-component NPZ model configured for the
Oregon coastal upwelling ecosystem. One limitation of that study was its omis-
sion of explicit mixed-layer physical effects on the biological model. Nonetheless,
model integration successfully demonstrated a phytoplankton bloom resulting
from nearshore upwelling followed by its offshore Ekman drift and sinking. It was
concluded that periodic upwelling events contribute significantly to primary
production within the coastal region.

With five or more ecosystem components, the Wroblewski (Wroblewski, 1977)
and Carr (Carr, 1998) models include considerable biological complexity. Here, we
revisit the coastal upwelling ecosystem using the more simple three-component
ecosystem model of Franks et al. (Franks et al., 1986), coupled to a two-dimensional
(x–z) circulation model which includes explicit mixed-layer physics. While surface
boundary layer models are increasingly incorporated into one-dimensional coupled
physical–biological models [e.g. (Doney et al., 1996; Lacroix and Nival, 1998;
Denman and Peña, 1999)], two dimensional coupled models that include complex
surface physics are less common. Franks (Franks, 1997) illustrated the significant
impact of enhanced surface physics on primary productivity in tidally forced frontal
regions. Our results reveal how surface mixing in the two-dimensional coupled
model impacts biological time scales, net productivity and vertical structure.
In particular, we examine two regimes in detail. Conventional parameterization of models that incorporate zooplankton into individual compartments generally consider macrozooplankton (e.g. copepods) to be the dominant grazers [e.g. (Franks and Walstad, 1997; Lacroix and Nival, 1998; Wroblewski et al., 1988)]. However, over the last 15 years, numerous studies have shown that microzooplankton, and not the copepods, are the predominant grazers in both nearshore and oceanic ecosystems (Gifford, 1988; Banse, 1992; Verity et al., 1993; Neuer and Cowles, 1994). Microzooplankton, predominantly ciliates and heterotrophic flagellates, have very different biological dynamics than copepods. First, protists undergo cell division, and thus their numbers can respond rapidly in response to favorable feeding conditions. Growth rates for microzooplankton can range from 0.5 to 2.0 day$^{-1}$, similar to that of their phytoplankton prey (Strom and Morello, 1998). Assuming gross growth efficiency (growth/ingestion) of micrograzers to be ~0.33 (range 0.15–0.64) (Straile, 1997; Strom and Morello, 1998), ingestion must be of the order of 1.5–6.0 day$^{-1}$—clearly sufficient to remove large amounts of phytoplankton and prevent substantial blooms. If only a third of microzooplankton ingestion contributes to Z biomass, then the remainder is remineralized immediately (through excretion and metabolism) to the dissolved nutrient pool. Thus, microzooplankton are efficient at converting phytoplankton biomass into dissolved nutrients, unlike the macrograzers. We explore the impacts of these Z-component differences (rapid ingestion, growth and remineralization) in our models.

Rather than focus on reconstructing a particular dataset, which might be accomplished through parameter tuning, the emphasis of this work is mechanistic. It is aimed at understanding the interaction of relatively simple biological dynamics within a well-understood advective and diffusive system. Elsewhere, Edwards et al. (Edwards et al., 2000) analyzed the stability properties of the Franks et al. (Franks et al., 1986) model in one physical (vertical) dimension to document the influence of diffusion alone on biological dynamics. While the macrozooplankton parameters led to a stable vertical profile with diffusion at or higher than background levels due to internal wave activity, the microzooplankton parameters exhibited limit cycle behavior, even at realistic mixed-layer diffusivities.

**The physical model**

The physical numerical model solves the time-dependent Navier–Stokes equations in two dimensions, x and z, and assumes no gradients perpendicular to the x–z plane. Specifically, the hydrostatic, Boussinesq model integrates the following equations on a staggered grid shown in Figure 1.

![Fig. 1. The grid stencil for the hydrodynamical model.](https://academic.oup.com/plankt/article-abstract/22/9/1619/1478094)
\[
\begin{align}
\frac{\partial u}{\partial t} + \frac{\partial}{\partial x} (\bar{u} \bar{u} x) + \frac{\partial}{\partial z} (\bar{w} \bar{w} z) - fv &= - \frac{1}{\rho_0} \frac{\partial \tilde{P}}{\partial x} - \frac{\partial}{\partial z} (\tilde{w} \tilde{u}) + \frac{\partial}{\partial x} \left( A_h \frac{\partial u}{\partial x} \right) \\
\frac{\partial v}{\partial t} + \frac{\partial}{\partial x} (\bar{u} \bar{v} x) + \frac{\partial}{\partial z} (\bar{w} \bar{v} z) + fu &= - \frac{\partial}{\partial z} (\tilde{w} \tilde{v}) + \frac{\partial}{\partial x} \left( A_h \frac{\partial v}{\partial x} \right) \\
\frac{\partial u}{\partial x} + \frac{\partial w}{\partial z} &= 0 \\
\frac{\partial T}{\partial t} + u \frac{\partial T}{\partial x} + w \frac{\partial T}{\partial z} &= - \frac{\partial}{\partial z} (\tilde{w} \tilde{T}) + \frac{\partial}{\partial x} \left( K_v \frac{\partial T}{\partial x} \right)
\end{align}
\]

where overbars with superscripts represent spatial averaging. The velocity field \( \mathbf{u} = (u, v, w) \) is oriented on a Cartesian grid with the origin located at the upper right corner of the domain. The temperature \( T \) contributes to a linear equation of state, and \( \rho_0 \) is a characteristic density. The Coriolis parameter is denoted as \( f \), and \( \tilde{P} \) is the total pressure.

The subgridscale processes are modeled using the K Profile Parameterization (KPP) of Large et al. (Large et al., 1994), which sets the vertical components of viscosity and diffusivity, as well as a non-local transport term, \( \gamma \). Specifically for temperature:

\[
(\tilde{w} \tilde{T}) = -A_v \left( \frac{\partial T}{\partial z} - \gamma T \right)
\]

and similar relationships apply to velocity fields. Experiments described in this study apply wind stress forcing only. In the absence of unstable thermal forcing, the non-local transport is always zero. KPP comprises separate parameterizations for dynamics within the surface well-mixed layer, defined above a dynamically determined boundary layer depth, \( h_{bl} \), as well as within the water column below. It does not provide an explicit mechanism for enhanced vertical mixing near the bottom, other than through gradient shear instability. To supplement this process, we allow the local mixing coefficients, \( K_v \) and \( A_v \), near the bottom to be determined by the larger of either KPP or that calculated using a simple mixing-length model in which

\[
K_v = A_v = \kappa \ell_* U_*
\]

Here, \( \kappa \) is the von Kármán constant, and at a distance \( z_b \) above the bottom:

\[
\ell_* = z_b \left( 1 - \frac{z_b}{d_0} \right)
\]

\[
U_* = \sqrt{C_d \left( u_b^2 + v_b^2 \right)}
\]

The drag coefficient \( C_d = 0.01 \), and \( d_0 = 10 \) m is a fixed boundary layer length scale. The velocity scales, \( u_b \) and \( v_b \), are the dynamically determined horizontal velocities at the first grid point up from the bottom. The constant horizontal eddy viscosity and diffusivity are:
Equations (1a–d) are solved subject to no flow and insulating boundary conditions:

\[ \mathbf{u} \cdot \hat{n} = 0 \]  
\[ \nabla_n T = 0 \]

where \( \hat{n} \) and \( \nabla_n \) represent a unit vector and gradient operator normal to the boundary, respectively. We apply the no slip condition at the bottom boundary:

\[ u = v = 0 \text{ on } z = 0 \]

Time stepping is achieved using a modified, second-order Adams–Bashforth algorithm. The model domain is 200 m deep and 100 km wide, and idealizes the topography off the Newport, OR, coast at latitude 44.65°N. The grid is stretched following Marti et al. (Marti et al., 1992) such that the minimum and maximum vertical resolutions are 1.5 m near the surface and 3.7 m at depth, and the horizontal resolution varies from 500 m inshore to just over 1.5 km offshore. A sponge layer extends over the western 20 km of the domain. All fields relax to their initial conditions with a 3 day time scale over the western 15 km, and the relaxation coefficient ramps linearly to zero over 5 km. The model is initialized with a horizontally uniform April 1962–69 temperature climatology and zero velocity.

The biological model

The biological model investigated is that of Franks et al. (Franks et al., 1986), which analyzes the interaction of nutrients (N), phytoplankton (P) and zooplankton (Z) components. In the absence of physical processes, it is expressed:

\[ \frac{\partial P}{\partial t} = \frac{V_m P}{k_s + N} e^{k_{ext} z} - R_m Z (1 - e^{-\Lambda P}) - mP - w_s \frac{\partial P}{\partial z} \]  
\[ \frac{\partial Z}{\partial t} = (1 - \gamma) R_m Z (1 - e^{-\Lambda P}) - gZ \]  
\[ \frac{\partial N}{\partial t} = -\frac{V_m P}{k_s + N} e^{k_{ext} z} + \gamma R_m Z (1 - e^{-\Lambda P}) + mP + gZ \]

in which the uptake is given by a Michaelis–Menten function, with \( V_m \) its maximum rate and \( k_s \) the half-saturation level. The light level influences the uptake directly and is assumed to decay with depth with an e-folding scale of \( k_{ext} ^{-1} \). With an aim toward simplicity, we keep the light function constant over time, as
in Franks and Walstad (Franks and Walstad, 1997). Moreover, we do not consider self-shading by phytoplankton (i.e. \( k_{ext} \) is independent of \( P \)). The grazing follows an Ivlev curve, with \( R_m \) its maximum rate and \( \Lambda \) its saturation constant. The assimilation efficiency is \((1 - \gamma)\) and phytoplankton and zooplankton mortalities are denoted \( m \) and \( g \), respectively. Phytoplankton sink at a speed \( w_s \).

When coupled to the physical model, each component may be considered an active tracer, modified by advection and diffusion. As a result, the dynamics for phytoplankton take the form:

\[
\frac{\partial P}{\partial t} + \mathbf{u} \cdot \nabla P = F + \frac{\partial}{\partial z} \left( K_v \frac{\partial P}{\partial z} \right) + \frac{\partial}{\partial x} \left( K_h \frac{\partial P}{\partial x} \right)
\]

where \( \nabla \) is the gradient operator and the active biological dynamics are represented by \( F \) [i.e. the right-hand side of equation (9a)]. Similar relationships exist for \( N \) and \( Z \).

Naturally, the biological model is subject to parameters that must be obtained through field observations and laboratory studies. Our increased understanding of pelagic ecosystems over the last decade has revealed the dominant role played by microzooplankton in open-ocean to nearshore environments (Gifford, 1988; Banse, 1992). However, the conventional parameters applied to ecosystem models generally represent macrozooplankton grazers. One purpose of this study is to examine the effect of applying a parameter set that assumes a microzooplankton-dominated ecosystem. We consider the two parameter sets in Table I. The macrozooplankton parameters have been used in the previous study of cross-frontal exchange (Franks and Walstad, 1997). The second set assumes that the zooplankton compartment is predominantly microzooplankton and includes three changes. Microzooplankton respond more quickly to food availability, with variable rates from 2 to 12 day\(^{-1}\). We have chosen an intermediate value, setting \( R_m = 4 \) day\(^{-1}\). The increased response is also reflected in the degree of non-linearity of the Ivlev function. We have set \( \Lambda = 0.3 \) (\( \mu \text{mol N l}^{-1} \))\(^{-1}\). The final modification is to the assimilation efficiency, which must be reduced to account for the remineralization capacity of microzooplankton [we choose \((1 - \gamma) = 0.3\)].

No flux boundary conditions are imposed at the free and solid surfaces:

\[
\nabla_n P = \nabla_n Z = 0
\]

Table I. Parameters used in this study assuming macro- and microzooplankton grazers

<table>
<thead>
<tr>
<th></th>
<th>Macro</th>
<th>Micro</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>( V_m )</td>
<td>2.0</td>
<td>2.0</td>
<td>( \text{day}^{-1} )</td>
</tr>
<tr>
<td>( k_s )</td>
<td>0.1</td>
<td>0.1</td>
<td>( \mu \text{mol N l}^{-1} )</td>
</tr>
<tr>
<td>( k_{ext} )</td>
<td>0.06</td>
<td>0.06</td>
<td>( \text{m}^{-1} )</td>
</tr>
<tr>
<td>( R_m )</td>
<td>0.5</td>
<td>4.0</td>
<td>( \text{day}^{-1} )</td>
</tr>
<tr>
<td>( \Lambda )</td>
<td>0.2</td>
<td>0.3</td>
<td>(( \mu \text{mol N l}^{-1} ))(^{-1})</td>
</tr>
<tr>
<td>( \gamma )</td>
<td>0.3</td>
<td>0.7</td>
<td></td>
</tr>
<tr>
<td>( m )</td>
<td>0.1</td>
<td>0.1</td>
<td>( \text{day}^{-1} )</td>
</tr>
<tr>
<td>( g )</td>
<td>0.2</td>
<td>0.2</td>
<td>( \text{day}^{-1} )</td>
</tr>
<tr>
<td>( w_s )</td>
<td>0 or -1</td>
<td>0 or -1</td>
<td>( \text{m day}^{-1} )</td>
</tr>
</tbody>
</table>
In the absence of phytoplankton sinking (i.e. $w_s = 0$), there exist no sources or sinks at the boundaries or in the interior, and the system advects and diffuses total nitrogen (i.e. $N_T = N + P + Z$) as a passive scalar. As a result, locally, the system reduces to a two-compartment predator–prey interaction, with $N$ set by the local total nitrogen, $N_T$. To reflect the reduced levels of total nitrogen typically found near the surface, we initialize the model with a vertical gradient in $N_T$, from 5 $\mu$mol N l$^{-1}$ at the surface to 20 $\mu$mol N l$^{-1}$ at 100 m, with the level remaining constant below this depth.

With $w_s = 0$, equations (9a–c) possess a well-known steady-state solution (Franks et al., 1986; Busenberg et al., 1990). The equilibrium solutions for the given total nitrogen gradient are shown in Figure 2 for the (a) macrozooplankton and (b) microzooplankton parameter sets. In both cases, phytoplankton and zooplankton are non-zero only above a particular level ($z \sim -50$ m). Above this depth, the phytoplankton level is constant, set through a balance of terms in equation (9b), which are depth independent. As the product of the grazing rate and assimilation efficiency increases, the equilibrium phytoplankton level decreases, and this effect is visible in a comparison of phytoplankton fields in Figure 2a.
and b. Note that in the surface waters, the macrozooplankton steady state is depleted in dissolved nitrogen. With the total nitrogen then split between the phytoplankton and zooplankton pools and the phytoplankton constant, the zooplankton profile must reflect the gradient in total nitrogen. The subsurface zooplankton maximum does not occur in the microzooplankton case because the total nitrogen gradient is manifested instead in the nitrogen compartment, which remains significantly non-zero, even near the surface.

Model runs are initialized with these steady states, although zero levels at depth are shifted to small positive values (0.1 µmol N l⁻¹), which then relax toward zero over the course of the integrations. A lower bound of 0.005 µmol N l⁻¹ is imposed on each biological field. The steady solution applied neglects the effect of diffusive mixing, which modifies the profiles particularly in the vicinity of the sharp discontinuity at depth. However, it is clear from the numerical calculations that the adjustment to these initial conditions is sufficiently small to be neglected relative to biological features that develop as a result of the larger upwelling circulation.

Results

Physical response

To contrast macro- and microzooplankton ecosystems in an upwelling context, we compare numerical runs in a standard physical context. The simulations extend for 30 days, using a constant southward, upwelling-favorable wind stress of 0.05 N m⁻². The physical response to a two-dimensional coastal upwelling scenario of this type has been thoroughly examined by Allen et al. (Allen et al., 1995) using the sigma-coordinate Blumberg and Mellor (Blumberg and Mellor, 1987) model and the Mellor and Yamada (MY) (Mellor and Yamada, 1982) level 2.5 turbulence closure scheme. As in that study, all fields presented here have been averaged over an inertial period to highlight the development of subinertial phenomena.

The physical fields from days 4, 12 and 20 over a limited portion of the full domain are shown in Figure 3. In the left column is the streamfunction field, which provides the general progression of the cross-shelf circulation. In each field, the offshore Ekman transport is evident near the surface. Mass transport offshore is balanced by a return flow that initially extends over the full ocean depth (days 1 and 2, not shown), but steadily collapses to the boundary layer adjacent to the topography. By day 4, the return flow on the shelf is largely against the topography, and by day 12 this is also true on the slope. The temperature fields, found in the middle column, reveal the influence of the bottom-trapped flow through a strong deformation of the temperature contours near the topography. Also shown in the middle panel as the heavy dashed line is the boundary layer depth as determined by KPP. The surface mixed layer deepens nearshore, and this feature penetrates further and broadens over the course of the run. The substantially larger diffusion of the surface mixed layer is reflected in the vertical isotherms that extend over this distance. At the surface, upwelled cold water is
found nearshore, and the sequence reveals the development of an upwelling front that moves offshore with the Ekman flow. Coincident with the strong horizontal temperature gradient is an alongshore flow as expected from thermal wind balance (right column).
This sequence can be compared directly with those of Allen et al. (Allen et al., 1995). The major quantitative difference is in the magnitude of the alongshore flow. At day 20, the maximum southward velocity is 29 cm s\(^{-1}\). Our reduction by roughly a factor of two results from the weaker stratification and wider shelf topography used in this study than in their basic case. Otherwise, the qualitative agreement is very good, including the dip in the streamfunction field near the upwelling front. The depths of the bottom boundary layers are somewhat different, with ours wider as set through equation (4) rather than MY 2.5. Associated with the bottom boundary layer on the slope is a large excursion of isotherms, which leads to a substantial horizontal temperature gradient. As a result, an alongshore thermal wind develops over the upper slope that is greater at depth than near the surface.

Concerned with possible influence of the sponge layer near the western boundary on the nearshore circulation, we evaluated model output using a domain extending 200 km zonally and found only modest quantitative variations in each representative field. The general structure of the upwelling circulation is quite robust.

Biological fields

Wind forcing, no sinking. We first address experiments with no phytoplankton sinking (i.e. \(w_s = 0\)). Accompanying the upwelled cold subsurface water in Figure 3 are high nutrient values and low plankton concentrations. Within the euphotic zone, a significant biological response follows for both macrozooplankton and microzooplankton parameters.

Within a limited portion of the domain, this sequence is revealed for the macrozooplankton run in Figure 4. From left to right are columns of phytoplankton, zooplankton and total nitrogen fields on days 4, 12 and 20. Respective gray scales for each column are located beneath. Note the different scale for zooplankton features as for phytoplankton. The vertical gradient of the total nitrogen field associated with the initial conditions is clearly visible away from the coast and topography (Figure 4c). The distortion of the total nitrogen field near topography is similar to that of the temperature field shown in Figure 3, and reflects the strong onshore advection of subsurface water in the bottom boundary layer. A sizeable horizontal gradient in total nitrogen is established within 10 km of shore. The zooplankton field on day 4 also reflects both the initial conditions and its modification due to the upwelling. Beyond 10 km from shore, the zooplankton retains a subsurface maximum (Figure 4b) from its initial conditions (Figure 2), although this feature is vertically aligned near \(x = -8\) km. While the most recently upwelled water inshore of this zooplankton front has low concentrations of zooplankton, it is increasingly rich in phytoplankton (Figure 4a). The emerging phytoplankton bloom extends ~5 km zonally, and has a maximum over 11 \(\mu\text{mol N l}^{-1}\), more than twice its initial value of 4.2 \(\mu\text{mol N l}^{-1}\) further offshore. The vertical variation of the phytoplankton initial conditions is still visible in the sharp gray scale variation near 50 m depth over much of the domain.

The features present on day 4 develop further as the upwelling continues. By
day 12, the phytoplankton bloom has spread zonally, and its maximum exceeds 16 µmol N l⁻¹. The zooplankton maximum is now displaced offshore, with a maximum of nearly 4 µmol N l⁻¹ near x = -20 km. The front in total nitrogen has been advected offshore a few kilometers, and values >17 µmol N l⁻¹ occur in the
newly upwelled surface water adjacent to the coast. By day 20, further small increases in phytoplankton and zooplankton and additional offshore advection are visible (Figure 4g–i). Homogenization of all tracers above the boundary layer depth (determined by KPP) reveals the influence of mixed-layer physics in setting the vertical scale of the productivity. Though not shown, the nitrogen pool \((N = N_T - P - Z)\) is severely depleted throughout the mixed layer, as it is in the initial conditions of Figure 2.

The different terms for physical and biological processes in the phytoplankton budget are shown for day 12 in Figure 5. In sequence top to bottom are (a) advection, (b) diffusion, (c) uptake, (d) grazing, (e) mortality and (f) the sum of all components, which gives an indication of the current time rate of change of the phytoplankton. The fields are in units of \(\mu\text{mol N l}^{-1}\text{ day}^{-1}\), and gray scales which are different for each panel are shown immediately below. The different magnitudes of the gray scales indicate that the predominant balance in the vicinity of the upwelling is between advection, diffusion and uptake. Deep, phytoplankton-poor water is advected into the near-coastal region, but this loss is balanced by new production near the surface that is mixed downward in the surface boundary layer. In this region, an advective loss is also found near the surface, associated with offshore advection toward the existing phytoplankton maximum. Grazing and phytoplankton mortality are negligible compared to the physical processes and uptake in this region, but enter into the balance further downstream. This offshore region is characterized by vertical shear in the Ekman flow, substantial mixing above the boundary layer depth, and no new nitrogen supply. As a result, all terms contribute to the phytoplankton time rate of change, as presented in Figure 6 for a depth near 10 m. Uptake (heavy solid) is positive everywhere, and off the scale of the figure in the upwelling region nearshore. The light dashed curve is phytoplankton mortality, highest negative inshore accompanying the phytoplankton maximum. Grazing (dotted) is negligible inshore with limited zooplankton concentration, but contributes to the balance west of \(x \sim -10 \text{ km}\). Local change due to both vertical and horizontal diffusion (dot–dashed) is very large in the upwelling region, and small and negative at this depth further offshore. Advection (light solid) reveals the offshore transport of high phytoplankton water in the Ekman layer and its replacement nearshore by phytoplankton-depleted deep water. Net phytoplankton concentrations (heavy dashed) at 10 m are increasing at all distances offshore at this time and depth in the model run. Thus, the balance of terms changes dramatically within this heterogeneous environment, with all processes, physical and biological, contributing significantly to the total budget, though with relative importance dependent on location. It is clear from Figure 5f that net phytoplankton increases at this time in the uptake region and at the base of the deepening mixed layer.

Since secondary production responds not to nitrogen input, but to the phytoplankton field, the zooplankton budget does not show an immediate response in the upwelling region (Figure 7). As in the offshore budget for phytoplankton, all terms contribute to the total budget. The mortality term (Figure 7d) is largest negative at the maximum of the zooplankton concentration, \(\sim 20 \text{ km offshore}\). Ingestion (Figure 7c) is large over a slightly wider domain, reflecting the increased
phytoplankton concentrations inshore of the zooplankton maximum. Advection (Figure 7a) reflects the Ekman transport of zooplankton-poor (-rich) water toward (from) its maximum. Diffusion (Figure 7b) is most important at the base of the mixed layer, it contributes weakly both positively and negatively to different regions above the boundary layer depth. As the largest of all terms, mixing...
Fig. 6. Zonal profile of terms in the phytoplankton budget from Figure 5 at depth near 10 m. Lines correspond to uptake (heavy solid), advection (light solid), diffusion (dot-dashed), grazing (dotted), mortality (light dashed) and their sum (heavy dashed).

Fig. 7. Zooplankton budget for the macrozooplankton run on day 12. In units of μmol N l⁻¹ day⁻¹ are (a) advection, (b) diffusion, (c) assimilated ingestion and (d) mortality.
at the base of the surface boundary layer dominates the sum total time rate of change of zooplankton at this time (not shown).

The microzooplankton parameter regime presents an opportunity to explore the range of behavior possible with this model (Figures 8 and 9). The evolution

![Phytoplankton and Zooplankton Concentrations](image)

**Fig. 8.** Phytoplankton and zooplankton concentrations (in $\mu$mol N l$^{-1}$) on days 4, 12 and 20 for the microzooplankton run. Gray scales for each column are located at the bottom. Total nitrogen concentrations are identical to those in Figure 4. Contour levels at 7 and 14 $\mu$mol N l$^{-1}$ for phytoplankton and 2 and 4 $\mu$mol N l$^{-1}$ for zooplankton have been superimposed.
of the total nitrogen field is identical to the previous run (Figure 4), and so is not shown. The qualitative development of the biological fields is initially similar to the macrozooplankton run. In the upwelling region, a phytoplankton bloom develops and persists through the sequence. Zooplankton are greatest just

Fig. 9. Phytoplankton budget for the microzooplankton run on day 12. Individual components (in µmol N l⁻¹ day⁻¹) are (a) advection, (b) diffusion, (c) uptake, (d) grazing, (e) mortality and (f) their sum. Gray scales for each panel are located immediately beneath.
offshore of the phytoplankton peak. This is similar to the results for the macrozooplankton scenario, but here the zonal (offshore) breadth of the peaks is considerably narrower than in Figure 4.

The phytoplankton budget for day 12 is shown in Figure 9. Uptake (Figure 9c) is redistributed through diffusion and advection (Figure 9b and a, respectively), as in the macrozooplankton run. These processes occur somewhat offshore, revealing a prolonged development time for the bloom. As before, phytoplankton mortality (Figure 9e) in the uptake region is small. However, in contrast to the macrozooplankton run, losses due to zooplankton grazing are large (Figure 9d). The net balance of terms (Figure 9f) most clearly resembles the changes due to advection, though at smaller magnitude. Evidence of the deepening boundary layer in the net balance is present, though small in comparison to other parts of the upwelling region.

Phytoplankton peaks on day 17 with a maximum value of $17.1 \mu$mol N l$^{-1}$, with a subsequent, steady decline. By day 20, it is reduced to a maximum of $14.9 \mu$mol N l$^{-1}$ (Figure 8e), and on day 25 the maximum is $8.2 \mu$mol N l$^{-1}$. That grazing would contribute significantly to the phytoplankton budget and slow the development, and the zonal extent of the initial bloom could be anticipated by the multipled increase in grazing rate of the microzooplankton parameter set. That it would ultimately overwhelm the phytoplankton growth process entirely, and lead to declining surface concentrations, is less obvious. In fact, it is not a purely biological result, but rather reflects the coupled biophysical nature of the problem. Under uniform advection only, downstream (i.e. offshore) development would directly follow the temporal evolution of the purely biological system. Diffusion complicates the scenario, transporting zooplankton upstream into the uptake region, where it can directly affect phytoplankton growth. Sensitivity studies at higher horizontal diffusion levels reveal primary productivity blooms of reduced magnitude and with shorter temporal duration.

The microzooplankton parameter set specifically examined how zooplankton with different growth and remineralization rates would affect the ecosystem. To assess also the possibility that the phytoplankton compartment might change in a microzooplankton-dominated ecosystem, we examined the sensitivity of the microzooplankton-parameterized ecosystem model to different phytoplankton uptake/growth rates. Decreasing the half-saturation constant $k_s$ by a factor of two, which increases the uptake rate at low nutrient levels, resulted in only small quantitative modifications to the upwelling sequence. The added modification of doubling the maximal uptake rate $V_m$ significantly hastens the phytoplankton response time to upwelled nutrients and therefore leads to an upwelling bloom that reaches its maximum more quickly and is found inshore of that obtained using smaller $V_m$. Consistently, halving the maximal uptake rate to 1 day$^{-1}$ leads to an offshore shift of the phytoplankton maximum, but more importantly slows phytoplankton growth so that only low phytoplankton levels ($<3 \mu$mol N l$^{-1}$) are observed by day 30 of the upwelling.

Wind relaxation, no sinking. The simulations presented above are idealized, consisting of a constant equatorward wind forcing for 30 days. Wind measurements
within eastern boundary regions show substantial variability of the wind stress, often with short durations of a few days [e.g. (Halpern, 1976)]. It thus is of interest to monitor the response of our system to a relaxation of the wind forcing. We emphasize again that our purpose is not to reproduce a dataset, but rather to understand model response under idealized conditions. As a result, we begin wind relaxation on day 30 of the integration, long after the upwelling field and associated biological features are well developed.

Once the wind relaxes, cross-shelf transport subsides. This occurs first in the Ekman layer, and subsequently in the bottom boundary layer. The position of the upwelling front remains largely fixed; it is no longer advected offshore by the Ekman flow, but it is also unable to relax back toward shore as it is geostrophically balanced by the alongshore velocity field. This sequence is seen in Figure 10 for days 31 and 40 (i.e. 1 and 10 days after 30 days of wind-forced spin-up). Once the surface forcing vanishes, the surface boundary layer depth quickly returns to zero, leading to small interior levels of mixing throughout the water column. Only mild erosion of the density gradient and the associated alongshore jet is observed over 10 days.

The temporal progression of the ecosystem components at 0.75 m depth for the macrozooplankton run is presented versus zonal position in Figure 11. The total nitrogen field (Figure 11c) shows the offshore Ekman transport of high total nitrogen during the first 30 days forced by equatorward winds, followed by 30 days of relaxation in which the zonal gradient of $N_T$ remains essentially constant. The phytoplankton field reveals a nearshore bloom, widening during wind forcing and contracting during relaxation. The expansion and contraction may be interpreted considering the near coincidence of the heavy dashed and light solid curves in Figure 6, representing net and advective changes, respectively. The time derivative of phytoplankton concentration due to offshore advection is positive, consistent with the positive zonal gradient, and is slightly larger than the net change at most longitudes. Once the Ekman transport subsides, other terms in the balance dominate, and the net rate of change of phytoplankton is negative. Finally, the zooplankton field shows the steady development of the offshore maximum, reaching levels exceeding 11 µmol N l$^{-1}$ at day 60.

Figure 11 supports the simple interpretation that, once perturbed, the macrozooplankton model undergoes a return to equilibrium through a phytoplankton peak. That is, nitrogen moves through the phytoplankton pool before both phytoplankton and zooplankton relax monotonically to their equilibrium values. The steady-state phytoplankton concentration is determined through equation (9b) and is independent of total nitrogen. Its value under macrozooplankton parameters is $P_{ss} = 4.24$ µmol N l$^{-1}$, as determined by the assimilation efficiency $(1 - \gamma)$, grazing rate $R_m$, Ivlev constant $\Lambda$ and zooplankton mortality $g$. Since total nitrogen is conserved, equilibrium zooplankton concentrations are determined directly from the local $N_T$. Figure 11 indicates that by day 60, the biological distributions further than 20 km from shore are nearly at steady state, whereas the most recently upwelled concentrations are still far from equilibrium.

In contrast, the microzooplankton run shows very different long-term behavior (Figure 12). During the first 17 days, the development of the phytoplankton
bloom is observed within 10 km of the shore. As discussed above, the bloom is then governed by the secondary production. Once the wind relaxes and the mixing levels are reduced, the system abruptly shifts into a dynamical state dominated by local biological dynamics, a limit cycle with a roughly 20 day period.

**Fig. 10.** Physical fields after 30 days of wind-forced spin-up followed by 1 and 10 days of calm. As in Figure 3. (a) and (d) Streamfunction field ($\Delta \omega = 0.1$ m$^2$ s$^{-1}$). (b) and (e) Temperature ($\Delta T = 0.25$°) and the boundary layer depth is heavily dashed. (c) and (f) A longshore velocity ($\Delta v = 0.05$ m s$^{-1}$).
in which new production consumes most available nitrogen followed by a weaker zooplankton peak. The wave-like nature of the fields reflects the combination of zonally varying 'initial' states on day 30 and a zonal diffusive propagation.

Wind relaxation, by reducing surface mixing levels, serves to decouple surface
from deeper biological processes. For example, the mild slope observed in phyto-
plankton concentration on day 35 (Figure 13, upper left panel) is consistent with
the emergence of a longer period oscillation at depth than at the surface. Such
oscillations were found in the purely one-dimensional model (Edwards et al.,
Horizontal and vertical gradients of the ecosystem state variables at the time winds cease, together with vertically dependent rate processes, can result in complex vertical, horizontal and temporal patterns (e.g. note the phytoplankton maximum visible on day 42 in the lower left panel of Figure 13). Zooplankton fields also show substantial structure in their progression (Figure 13, right panels).

Sinking. While the conservation of total nitrogen within the Franks et al. (Franks et al., 1986) model that follows from $w_s = 0$ simplifies the dynamics of the system, it limits the realism of long-term integrations. Upwelled waters remain nitrogen rich indefinitely, with no mechanism for vertical transport besides advection and diffusion. Setting $w_s \neq 0$ relieves this limitation without introducing the complexity of a detrital component to the model. In this section, we investigate the role of phytoplankton sinking at 1 m day$^{-1}$ on the response of an upwelling ecosystem. All other ecosystem model parameters remain unchanged from those presented earlier.

Fields at days 4 and 20 for the macrozooplankton parameters are presented in Figure 14, and show marked similarity to those of Figure 4. The phytoplankton maximum on day 4 is nearly 10% larger than in the non-sinking case, and this effect is amplified by day 20 when the maximum is 22.1 $\mu$mol N l$^{-1}$. This increase

![Fig. 13.](https://academic.oup.com/plankt/article-abstract/22/9/1619/1478094)
is also found in the total nitrogen field, which on day 20 has a maximum concentration of 24.6 $\mu$mol N l$^{-1}$. Changes in the zooplankton field are small.

Without advection, uniform sinking can only modify relative concentration distributions near the boundaries. However, in an active physical environment, advection and diffusion can redistribute those concentrations. In the upwelling sequence, phytoplankton sink to the depth layer where they contribute to a local maximum. Nearshore deep currents return this enhanced seed population to the surface waters, creating a nearshore loop of enhanced productivity. Further offshore, a subsurface maximum develops and settles in time. It is worth noting that the time scale for loss out of the surface waters is not the advective time given by $T = \frac{h_{bl}}{w_s}$, as it would be in a quiescent ocean. Rather, continual vertical homogenization within the mixed layer replenishes surface phytoplankton and reduces levels at the mixed-layer base, thereby reducing losses from the mixed layer due to sinking.

Biological fields after 30 days of wind-forced spin-up, followed by 5 and 15 days of relaxation, are shown in Figure 15. On day 35, large phytoplankton concentrations extend over a range of subsurface depths, reflecting the uniform sinking

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**Fig. 14.** Phytoplankton, zooplankton and total nitrogen concentrations (in $\mu$mol N l$^{-1}$) on days 4 and 20 for the macrozooplankton run including $w_s = 1$ m day$^{-1}$ phytoplankton sinking. Gray scales for each column are located at the bottom. Contour levels of 7, 14 and 21 $\mu$mol N l$^{-1}$ for phytoplankton and total nitrogen and of 2 and 4 $\mu$mol N l$^{-1}$ for zooplankton have been superimposed.
of a mixed-layer bloom present on day 30. By day 45, peak phytoplankton concentrations in excess of 50 µmol N l⁻¹ are found nearshore at the bottom, associated with the sinking-induced local convergence along the topography. Phytoplankton levels near the surface, despite high light levels, remain vanishingly small due to severe nutrient depletion in the absence of an upwelling circulation.

Fig. 15. As in Figure 14, but after 30 days of wind forcing and then 5 and 15 days of calm. Contour levels of 15, 30 and 45 µmol N l⁻¹ have been superimposed for phytoplankton and total nitrogen, and of 2, 4 and 6 µmol N l⁻¹ for zooplankton.
The microzooplankton run subject to sinking is not presented, but peak phytoplankton concentration occurs on day 15 with sinking, as opposed to day 17 in the non-sinking run. In addition, sinking weakens the phytoplankton bloom, inducing a more transient response which subsides to $\leq 5$ µmol N l$^{-1}$ by day 21. While the addition of phytoplankton sinking enhances the seed population at depth, as in the macrozooplankton run, the qualitative description of the ecosystem development is not significantly altered.

Summary and discussion

Numerical integrations of a simple three-component ecosystem model in a wind-driven, coastal upwelling circulation with explicit mixed-layer physics support the well-known relationship between nutrient supply and primary production. Advection draws nutrient-rich water into the euphotic zone where uptake becomes significant, followed by secondary production further offshore.

With identical physical scenarios consisting of 30 days of northerly winds followed by 30 days of calm, we have compared integrations using two biological parameter sets, representing macrozooplankton and microzooplankton grazers. Beyond the basic generation of an initial phytoplankton maximum in the upwelling region, similarities between the two model runs are limited. In the macrozooplankton scenario, the bloom expands zonally with the offshore Ekman transport of nutrient-rich upwelled water, whereas in the microzooplankton scenario the phytoplankton bloom has relatively narrow zonal extent. These differences point to the fundamental role that biological processes have in combination with the physics in setting horizontal scales in this ecosystem model. This relationship has not been well defined by observations. Statistical analysis of temperature and ocean color from satellite images of the California Current region by Denman and Abbott (Denman and Abbott, 1994) suggests that physical processes primarily control biological scales. More recent evidence (Abbott and Letelier, 1998) using data from surface drifters in the CODE region off Northern California suggest that while physical processes may be dominant nearshore, the role of biological processes may increase offshore (e.g. beyond 400 km from shore).

The limited offshore zonal extent of the phytoplankton bloom in the microzooplankton experiments results from the enhanced grazing pressure, but it also reflects a dynamical shift between the two systems as a result of the parameter change. Following parcels of water, macrozooplankton parameter integrations show monotonic transfer of nitrogen first to the phytoplankton followed by the zooplankton pools toward a stable steady state. In contrast, the microzooplankton simulations indicate an underlying limit cycle in which the transfer between ecosystem compartments is periodic (Edwards et al., 2000). However, the amplitude and period of the oscillation are modified significantly by horizontal mixing absent in that one-dimensional study.

The different dynamics of the microzooplankton and macrozooplankton simulations reflect variability typically observed in systems of coupled non-linear equations, even those with a few compartments only. Furthermore, added spatial dimensions allow for heterogeneity in dynamical state even with a single
parameter set. As discussed in Edwards et al. (Edwards et al., 2000) for the Franks et al. (Franks et al., 1986) model, dynamical stability can be depth dependent, if uptake is parameterized to be light sensitive with light varying with depth. Diffusion can modify the profile stability. For the macrozooplankton parameters, background levels of diffusion were sufficient to stabilize an otherwise unstable portion of the water column, whereas the microzooplankton steady-state profile remained unstable even at high surface mixed-layer levels. In multiple spatial dimensions, other equally plausible rate dependencies (e.g. on temperature) will contribute to horizontal and potentially time-dependent variability in model dynamical state as well.

Although easily explained, the presence of a phytoplankton bloom under constant wind conditions is not always borne out in numerical experiments. For example, Carr studied two more complicated multi-component ecosystem models (in zero spatial dimensions) forced by advective and diffusive property fluxes meant to represent input from subsurface water driven by local upwelling-favorable winds (Carr, 1998). While periodic nutrient fluxes produced phytoplankton blooms, fluxes from constant wind forcing produced no blooms. We speculate that those results arise because of limitations of single box-model formulations for studying inherently spatially dependent processes rather than aspects of those biological models themselves. It would be interesting to couple those more complex biological models into a multi-dimensional physical model.

Our work also relates to that of Wroblewski, in which a phytoplankton bloom was generated in a similar two-dimensional coastal upwelling scenario (Wroblewski, 1977). Inclusion of the KPP mixed-layer model in our work reveals the central role that strong vertical mixing can play in setting the vertical structure of the bloom, and influencing its magnitude. More importantly, in contrast to the previous work, we find an offshore zooplankton maximum present in both parameter scenarios discussed. We should note, however, that the secondary production peak is not a robust aspect of the Franks et al. (Franks et al., 1986) model under all conditions, but is rather a consequence of the rate parameters and of the initial distribution of total nitrogen. Using the microzooplankton parameters, we expect the zooplankton peak to occur under a wide range of initial conditions because of the cyclic nature of the biology. This is not the case, though, for the macrozooplankton parameters. The peak results from the injection of total nitrogen concentrations in excess of those found in the ambient surface water. The monotonic route to stable equilibria under the macrozooplankton parameters results in zooplankton levels that are always below their steady-state values. If, for example, upwelled concentrations of \( N_T \) equal those of the ambient surface fluid, zooplankton levels only approach those of the surrounding fluid and no peak occurs. Our model initial conditions purposely set \( N_T \) at the surface less than that at depth to mimic real oceanic conditions better, and therefore we observe a downstream zooplankton bloom. We also note that mechanisms for exporting nitrogen to depth (e.g. phytoplankton sinking) would create nitrogen-depleted surface waters necessary for the zooplankton bloom, and so it may be considered a robust aspect of the modified model. Though subtle, this point emphasizes the sensitivity of even simple biological models to choices of the modeler.
That the macrozooplankton model in the absence of phytoplankton sinking has a stable profile justifies applied initial conditions and greatly simplifies interpretation of simulations. However, to be consistent with observations, long-term integrations require mechanisms to transport nitrogen to depth. Allowing phytoplankton to sink at a mild 1 m day\(^{-1}\) rate resulted in a local recirculation of phytoplankton in the upwelling region. This feedback led to enhanced magnitudes of the nearshore phytoplankton blooms, largely a result of the dynamically increased total nitrogen of the inshore waters.

Oscillations are not new in ecosystem models. For example, Steele and Henderson found that implementing a quadratic closure (\(Z^2\) term on zooplankton mortality which leads to higher mortality effects when grazer concentrations are large) reduced oscillatory behavior in simple NPZ models (Steele and Henderson, 1992). The current model, when parameterized for macrozooplankton, does not exhibit oscillations. However, when the model is parameterized for microzooplankton grazers, oscillations occur. Applying \(Z^2\) closure to the microzooplankton model, and using the same numerical value of the mortality coefficient, eliminates oscillations, and provides time-dependent results qualitatively similar to the macrozooplankton scenario (without quadratic closure). However, the amplitude and zonal scales of the resulting maxima are considerably smaller. Such features can be modified through substantial parameter tuning, but this is contrary to the intent of the present work. Furthermore, the \(Z^2\) mortality formulation does not in general eliminate oscillations within the present model. For example, shifting the maximum uptake rate from \(V_m = 2\) day\(^{-1}\) to \(V_m = 3\) day\(^{-1}\) reintroduced cyclic behavior in the state variable dynamics. We elected not to implement the \(Z^2\) closure in order to investigate an established model structure with both established parameters and those specifically modified to represent a microzooplankton ecosystem. This choice also demonstrates the implications of both stable and unstable steady-state profiles in an upwelling circulation.

Ryabchenko et al. (Ryabchenko et al., 1997) have also investigated oscillations in a seven-component model. They interpreted short-term (i.e. damped) fluctuations to potentially reflect natural temporal variability over an annual cycle at OWS I. Our model studies further demonstrate how vertical and horizontal structure in phytoplankton and zooplankton can result from predator–prey interactions in combination with advection and diffusion in coupled biological–physical systems.

These model simulations lead us to speculate how nearshore marine ecosystems are structured in nature, and what is the best way to represent that structure in ecological models. For decades, the paradigm of pelagic marine ecosystems was that under favorable light, mixing and nutrient conditions, large phytoplankton (diatoms) took up nutrients, causing a bloom. A local imbalance between phytoplankton production and losses, caused by the inability of the presumed dominant grazers, e.g. copepods, to respond numerically and immediately to increased phytoplankton concentrations, caused a bloom. Ecosystem modelers adopted this paradigm [see the early models of Steele (Steele, 1974), Landry (Landry, 1976) and Steele and Frost (Steele and Frost, 1977)] and used experimentally measured rates from copepods to parameterize the zooplankton component of simple NPZ models [see (Franks et al., 1986; Franks and Walstad,
Our macrozooplankton model exhibits these features, with nearshore introduction of nutrient to surface waters, a phytoplankton bloom developing offshore of the upwelling front, and a maximum zooplankton concentration further offshore.

However, we now know from investigations of many nearshore and oceanic ecosystems that the dominant consumers of pelagic primary productivity are not copepods, but rather much smaller microzooplankton, such as ciliates and microflagellates (Gifford, 1988; Banse, 1992). Those fauna have quite different ecological dynamics to copepods; two quantities for which there is now considerable evidence are (i) their maximum growth rates and (ii) their gross growth efficiency (growth/ingestion). These results stimulated our explorations using a zooplankton parameterization more consistent with microzooplankton dynamics. Qualitatively, we obtain similar spatial patterns with highest surface nutrients inshore, a phytoplankton bloom just offshore, and maximum microzooplankton biomass just offshore of the phytoplankton bloom. However, the spatial extents of peak phytoplankton and zooplankton concentrations are quite different from the macrozooplankton scenario. Significantly, offshore nutrient concentrations near the surface differ substantially, with high values found in the microzooplankton case and nearly complete nutrient depletion in the macrozooplankton scenario.

Observations of coastal upwelling provide support for certain aspects of both models. Satellite imagery [e.g. Figure 17 of Strub et al. (Strub et al., 1991)] and some hydrographic surveys [e.g. Line A described in Hood et al. (Hood et al., 1991)] reveal spatially broad (several tens of kilometers), temporally persistent (Chavez et al., 1991) blooms, more consistent with the macrozooplankton model. In contrast, surveys with higher spatial resolution (Small and Menzies, 1981) reveal responses of finer scale (<10 km), more in line with the features of the microzooplankton parameter set. Moreover, except for in the vicinity of the zonally limited phytoplankton bloom, near-surface nutrient concentrations offshore are quite high (exceeding 19 µmol N l⁻¹) in the microzooplankton simulation, far exceeding observed concentrations offshore of coastal regions of upwelling. Large nearshore nutrient levels are found shortly after upwelling events (Small and Menzies, 1981; Chavez et al., 1991). Moreover, there is little field evidence for the substantial temporal oscillations that characterize the microzooplankton run, though identifying such oscillations from field surveys would be a difficult task. Although the NPZ only ecosystem as formulated here can produce arguably plausible features it seems insufficient to describe the complexity of the real ecosystem. Other formulations, or extensions of this model that include detritus, other nutrients, or multiple size classes of both P and Z, appear necessary to model ecosystem dynamics effectively.

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