Ecosystem response to upwelling off the Oregon coast:
Behavior of three nitrogen-based models

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[1] The behavior of three ecosystem models is analyzed for upwelling off the Oregon coast as a function of the number of model components. The first ecosystem model includes dissolved inorganic nitrogen-phytoplankton-zooplankton (NPZ), the second (NPZD) adds detritus, and the third (NNPZD) splits the nutrients into nitrate and ammonium. The models are made as equivalent as possible by choosing the same parameterizations for the biological interactions and are coupled to a two-dimensional physical circulation model. Simulations with wind forcing from summer 1973 lead to similar spatial and temporal patterns for the three models. The mean phytoplankton concentration is maximum onshore of the upwelling jet while the mean zooplankton concentration is maximum farther offshore. The main difference among the models is a larger maximum zooplankton concentration for the NPZ simulation. This difference is attributed to the sinking of phytoplankton rather than detritus. We repeat the NNPZD summer 1973 simulation with wind forcing from 1999 and with constant wind stress. We also use the 1973 wind forcing and vary model parameters. The zooplankton maximum grazing rate is increased, the detritus sinking rate is reduced, and the inhibition of nitrate uptake by ammonium is removed. In all cases, the maximum of the zooplankton concentration is found offshore of the phytoplankton maximum. The locations and magnitudes depend upon the nature of the time variability of the wind forcing and on the biological parameters. The wind variability and the parameter values have little effect on the mean primary productivity, but have a larger effect on the f-ratio.

INDEX TERMS: 4815 Oceanography: Biological and Chemical: Ecosystems, structure and dynamics; 4279 Oceanography: General: Upwelling and convergences; 4842 Oceanography: Biological and Chemical: Modeling; 4845 Oceanography: Biological and Chemical: Nutrients and nutrient cycling; 4255 Oceanography: General: Numerical modeling; KEYWORDS: ecosystem modeling, nitrogen cycling, coastal upwelling, Oregon coast


1. Introduction

[2] Ecosystem models are increasingly being applied to a variety of regions in the ocean [Hofmann and Lascara, 1998]. Most of these models are nitrogen-based models and vary greatly in their complexity, from the simple three-component Nitrogen-Phytoplankton-Zooplankton (NPZ) models [e.g., Franks et al., 1986] to more than 10 components [e.g., Fasham et al., 1990; Spitz et al., 2001; Chai et al., 2001; Dugdale et al., 2001].

[3] While ecosystem models, which have been developed for almost 3 decades, are generally tending to become more complex and to include a larger number of components, the fundamental question concerning the minimum number of components that the model should include to test a given hypothesis still remains without a clear answer. We will assume that the simplest model that may be relevant is a three-component NPZ model, while the next most complicated is a four-component model where a detritus pool has been added. The addition of a detritus pool takes into account the fact that remineralization is not instantaneous. The next step in complexity is to separate the dissolved inorganic pool into nitrate and ammonium pools to distinguish new versus regenerated production. This step is also motivated by the observation that phytoplankton preferentially take up ammonium over nitrate [Dortch, 1990; Wheeler and Kokkinakis, 1990; Varela and Harrison, 1999]. The complexity can then be increased by introducing several different phytoplankton species, zooplankton species, and detritus pools, or by including a complete microbial loop. One has to recognize that increasing the number of components also leads to an increase in the number of model parameters that are needed to describe a given ecosystem. Most of these parameters are poorly known, and specifying values for an appropriate set of parameters can quickly become a challenging task. The number of observations required to properly calibrate the model also increases. Unfortunately, the observations are not always available for all the components of the ecosystem. Finally,
the mathematical behavior of these nonlinear models is incompletely known, especially when coupled to complicated circulation fields.

[4] In this paper, we consider several different models in a study of the ecosystem response to upwelling off the Oregon coast, where the physical circulation model is forced by observed winds. We limit the comparison to three ecosystem models that comprise three, four and five components, respectively. To keep the comparisons as straightforward as possible, the same parameterizations of various processes are used where possible in all three models. We also test the sensitivity of the five-component model results to variations in the wind forcing and to variations in some of the model parameters. The models are described in section 2 with the equations recorded in Appendix A. In section 3, differences of model results for a one-dimensional problem are examined. In section 4, the results when the various models are coupled to a two-dimensional circulation model are presented. A summary and discussion are given in section 5.

2. Ecosystem Models

[5] The three ecosystem models considered in this study are described by Newberger et al. [2003]. The equations are given in Appendix A, and the models are shown schematically in Figure 1. The first, three-component model (referred to as NPZ) is based on the Franks et al. [1986] model. It includes a dissolved inorganic nitrogen pool DIN, one phytoplankton species P and one zooplankton species Z. The second, four-component model (referred to as NPZD) is similar to the Denman and Peña [1999] model and includes in addition to the NPZ model a detritus pool D. The third, five-component model (referred to as NNPZD) is based on the ecosystem model developed by Wroblewski [1977],

where the DIN pool has been split into nitrate NO$_3$ and ammonium NH$_4$. We refer to the total nitrogen in each model as T$_3$, T$_4$ and T$_5$, respectively. The three models are made as nearly equivalent as possible by choosing the same parameterizations for the various pathways such as nitrogen uptake (Michaelis-Menten), light limitation (multiplicative law), grazing (Ivlev), mortality (linear) and egestion (constant percentage of grazing). Most of the parameters (Table 1) were taken from the Wroblewski [1977] ecosystem model since it was calibrated for upwelling off the Oregon coast. The ammonium oxidation rate of 0.25 d$^{-1}$ was chosen based upon the observations in the California coastal waters by Ward et al. [1982].

[6] While the original NPZ model of Franks et al. [1986] does not include any sinking of nitrogen from the upper layer, it was later found necessary to add sinking to avoid accumulation at frontal regions [Franks and Chen, 1996; Franks and Walstad, 1997] and during coastal upwelling [Edwards et al., 2000]. Sinking of nitrogen is modeled by adding a phytoplankton sinking term in the NPZ model. In the other two models, the sinking of nitrogen is naturally modeled via sinking of detritus. To compare the behavior of the three models, we consider two sets of experiments that are described in the two following sections.

3. One-Dimensional Simulations

[7] The behavior and differences of the three models in a one-dimensional framework that includes spatial variations with depth and small background vertical diffusivity, but no sinking, have been analyzed by Newberger et al. [2003]. They examine solutions for times that are large compared to the timescales for biological adjustment, but short compared to those for vertical diffusion. They find in those experiments that the three models give similar results. With the vertical profile of total nitrogen the same for the three models, the NPZ model gives a somewhat larger pool of NV phytoplankton exist in a shallower layer when

\[
\begin{align*}
\text{Light attenuation due to sea water} & : k_w = 0.067 \text{ m}^{-1} \\
\text{Light attenuation by phytoplankton} & : \kappa_p = 9.5 \times 10^{-4} \text{ m}^2 \text{ mmol N}^{-1} \\
\text{Initial slope of P-I curve} & : \alpha = 0.025 \text{ d}^{-1} \text{ (W m}^{-2})^{-1} \\
\text{Surface photosynthetically available radiation} & : I_0 = 158.075 \text{ W m}^{-2} \\
\text{Phyto. maximum uptake rate} & : V_m = 1.5 \text{ d}^{-1} \\
\text{Half-sat. for phyto. NO}_3\text{ uptake} & : K_a = 1 \text{ mmol N m}^{-3} \\
\text{NH}_4\text{ uptake NH}_4\text{ inhibition parameter} & : \Psi = 1.46 \text{ (mmol N m}^{-3})^{-1} \\
\text{NH}_4\text{ oxidation coefficient} & : \Omega = 0.25 \text{ d}^{-1} \\
\text{Detritus decomposition rate} & : \phi = 1.03 \text{ d}^{-1} \\
\text{Phyto. specific mortality rate} & : \Gamma = 0.145 \text{ d}^{-1} \\
\text{Zoo. specific excretion, mortality rate} & : R_m = 0.52 \text{ d}^{-1} \\
\text{Ivlev constant} & : \gamma = 0.06 \text{ mmol N m}^{-3} \\
\text{Fraction of zoo. grazing egested} & : \gamma = 30\% \\
\text{Detritus sinking rate} & : w_d = 8. \text{ m d}^{-1} \\
\text{Phytoplankton sinking rate} & : w_p = 0.65 \text{ m d}^{-1} \\
\end{align*}
\]
there is inhibition of nitrate uptake by ammonium. With these differences in mind, we extend the studies in the work of Newberger et al. [2003] and consider a one-dimensional (1D) simulation with sinking of phytoplankton (NPZ) or detritus (NNPZD, NNPZD).

[8] In order to include effects of sinking as well as those of vertical mixing, we performed the 1D experiments with sinking and wind-forced surface mixing in addition to the background diffusion used by Newberger et al. [2003]. Vertical mixing is modeled by the Mellor and Yamada [1982] level 2.5 turbulence closure scheme, as in the two-dimensional model simulations with the Princeton Ocean Model (POM) [Blumberg and Mellor, 1987] and a background diffusivity of $D_s = 2 \times 10^{-5}$ m$^2$ s$^{-1}$. The wind stress corresponds to a typical 61-day period of upwelling off the Oregon coast; that is, the stress is calculated from winds measured during summer 1973 (Figure 2). Two distinct upwelling events are observed. The first event, starting around day 190, is quite short and strong (10-day duration with a maximum alongshore wind stress of $-0.35$ N m$^{-2}$) while the second, starting around day 207, is longer and weaker with intermittent relaxation periods (~25-day duration with a maximum alongshore wind stress of $-0.25$ N m$^{-2}$). The initial vertical distributions of the variables for the 1D experiments are taken from the respective NNPZD concentrations after a 1-year run with small background diffusivity and without sinking [Newberger et al., 2003].

Total nitrogen $T_2$ and $T_3$ are 11.36 mmol N m$^{-3}$ at the surface increasing linearly to about 30 mmol N m$^{-3}$ at 100 m and 35 mmol N m$^{-3}$ at 500 m. Total nitrogen $T_3$ is 10.45 mmol N m$^{-3}$ at the surface and increases linearly with depth as $T_4$ and $T_5$. The NPZD and NNPZD detritus sinking rate $w_d = 8$ m d$^{-1}$ is imposed such that, with the chosen remineralization rate ($\phi = 1.03$ d$^{-1}$) (Table 1), we obtain a remineralization length scale of 8 m. This sinking rate is smaller than the values found in the literature for fecal pellet sinking rate and marine snow [Shanks and Trent, 1980], since a large fraction of the model single detritus pool consists of nonsinking suspended particles and dissolved organic nitrogen (DON) that is not explicitly included in the model.

[8] Figure 3 shows the solutions, after forcing for 61 days with the wind stress in Figure 2, for DIN, phytoplankton and zooplankton profiles of the NNPZD and the NPZ runs when various phytoplankton sinking rates are chosen for the NPZ model. Increasing the NPZ phytoplankton sinking rate from 0.5 to 1 m d$^{-1}$ decreases the phytoplankton at the surface. The deep maximum increases and deepens, and DIN between 20 and 40 m decreases while it increases between 40 and 80 m. This is accompanied by a decrease of the surface zooplankton. We find that a phytoplankton sinking rate of 0.65 m d$^{-1}$ in the NPZ model gives the best match with the NNPZD phytoplankton concentrations in the upper 30 m of the water column and leads to a surface NPZ zooplankton concentration slightly larger than the NNPZD zooplankton concentration. This sinking rate also gives a good match in terms of nitrogen flux from the euphotic zone. The phytoplankton flux (NPZ model) from the euphotic zone after 61 days of forcing is equal to 0.14, 0.22, 0.51 and 0.33 mmol N m$^{-2}$ d$^{-1}$ for sinking rates of 0.5, 0.65, 0.8 and 1 m d$^{-1}$, respectively. The detritus flux (NNPZD model) from the euphotic zone is equal to 0.19 mmol N m$^{-2}$ d$^{-1}$. The results from NPZD (not shown) are very close to those from NNPZD. The solutions of the NNPZD model after 61 days of forcing (Figure 4) are used as initial conditions for the two-dimensional experiments discussed in section 4. Since the euphotic depth in the upwelling region near the Oregon coast is about 30 m and the best match for the NPZ and NNPZD phytoplankton concentration in the upper 30 m and for nitrogen flux from the euphotic zone is found with a phytoplankton sinking rate of 0.65 m d$^{-1}$ in NPZ, we choose to pursue the two-dimensional simulations (section 4) with NPZ using a phytoplankton sinking rate of 0.65 m d$^{-1}$.

[10] While we notice some differences between the results from the three models in a one-dimensional framework with sinking, the differences are small. The question is then: Will the differences remain small for an upwelling system?

4. Two-Dimensional Simulations

[11] We consider coastal upwelling with a two-dimensional approximation, variations across-shore and with depth; uniformity alongshore. We choose topography corresponding to the Oregon shelf at 45.25°N and force with measured winds at Newport (44.7°N) from summer 1973. The three ecosystem models are coupled to a two-dimensional circulation model.

4.1. Circulation Model

[12] We utilize the Blumberg-Mellor [Blumberg and Mellor, 1987] finite-difference, sigma-coordinate model for the hydrostatic primitive equations with potential density used in place of temperature and salinity. A full description and an application of the model for two-dimensional (2D) simulations of upwelling off Oregon are given by Allen et al. [1995] and Federiuk and Allen [1995]. In model simu-
lations forced by measured winds during the 1973 Coastal Upwelling Experiment (CUE-2), Federiuk and Allen [1995] achieved some success with the 2D-circulation model in representing features of the observed flow field. Since the physical response of the model to upwelling-favorable winds has been well documented by Federiuk and Allen [1995], we focus our attention on the comparison of the results from the three ecosystem models for the 61-day period, 29 June through 28 August 1973 (year days 180–240), of the CUE-2 experiment.

The model domain (Figure 5) is an across-shelf section extending 200 km offshore and bounded by a solid wall at the coast and offshore. The shelf and slope topography represents the Oregon shelf at 45.25°N with a minimum depth of 10 m at the coast and an offshore maximum depth of $H_0 = 500$ m. The grid spacing is uniform with 60 sigma levels in the vertical and a horizontal grid size of 250 m. The wind forcing applied at the surface is the hourly wind stress calculated from the observed wind from June 29 (day 180) through August 28 (day 240) 1973 at Newport, Oregon (44.7°N), using the method of Large and Pond [1981]. The hourly wind stress is first filtered with a 6-hour low-pass Fast Fourier Transform (FFT) filter and then interpolated to the 45-s model time step using a cubic spline (Figure 2).

Figure 3. Comparison of 1D solutions after forcing for 61 days with the 1973 wind stress (Figure 2) from the three-component NPZ model with various phytoplankton sinking rates and the five-component NNPZD model solution (basic case) with detritus sinking rate of $8 \text{ m d}^{-1}$. DIN equals nitrate plus ammonium in the five-component model results.

Figure 4. Initial conditions for the two-dimensional simulations corresponding to the 1D NNPZD basic case experiment (Figure 3).
circulation model starts from rest with an initial horizontally uniform potential density corresponding to the horizontal average of the CUE-II density field of 29 June 1973.

Figure 6 shows the mean and standard deviation of the potential density \( \sigma_0 \), the alongshore velocity \( v \), the streamfunction \( \psi \) for the cross-shelf flow and 2 times the turbulent kinetic energy \( q^2 \) over the 48-day upwelling period (year days 188–235), referred to as the upwelling analysis period. The first 8 days of the simulation, days 180–187, are not included in the mean since the physical model is spun-up from rest. The last 5 days (days 236–240) are omitted from the upwelling analysis period since northward, downwelling-favorable winds were present at that time. In the mean fields, we find a shallow mixed layer (less than 20 m deep) that deepens onshore. A southward alongshore jet extends roughly 40 km offshore with a maximum speed of \(-0.58 \text{ m s}^{-1}\) located 14 km offshore. The streamlines indicate mean offshore flow near the surface with a downward excursion as the offshore flow crosses the frontal region at about 10 km from the coast. The mean upwelling into the surface layer occurs primarily close to the coast (roughly within 5 km) through the bottom boundary layer. On average, near-surface turbulent kinetic energy \( \frac{1}{2} q^2 \) is larger offshore and larger deeper in the core of the jet than offshore. The highest \( q^2 \) standard deviation is located at the frontal region of the jet about 10 km from the coast and around 20 m depth. The largest standard deviations in \( \sigma_0 \), \( v \) and \( q^2 \) are found within 50 km from the coast and above a depth of 60 m. As verified below, we expect that most of the biological production will happen in this region. We focus the comparison of the three ecosystem models on the upper 60 m of the water column and the first 75 km from shore.

### 4.2. Ecosystem Response

For the two-dimensional runs, the three ecosystem models (NPZ, NPZD and NNPZD) are coupled to the two-dimensional circulation model described in the previous subsection. The advection of the various concentrations is discretized using a Smolarkiewicz upstream scheme [Smolarkiewicz, 1984]. The detritus (NPZD, NNPZD) and phytoplankton (NPZ) sinking terms are discretized using an upstream scheme in the vertical. No-flux conditions are imposed at the free surface and at the solid lateral boundaries. A no-flux condition is imposed at the bottom except for the sinking. The initial concentrations are taken from the one-dimensional NNPZD run with sinking and wind forcing (Figure 4). The initial DIN concentrations for the NPZ and the NPZD model runs are the sum of the nitrate and ammonium concentrations from the NNPZD model. The initial NPZ total nitrogen, lacking a contribution from detritus, is slightly less than the initial NNPZD total nitrogen. These initial concentrations are intended to approximate pre-upwelling concentrations, where nutrients are depleted at the surface and across-shore variations are small.

[14] Mean fields over the upwelling analysis period (days 188–235) of the biological variables from the three models are shown in Figure 7. The three models lead to similar mean spatial distributions of the corresponding concentrations, but with larger zooplankton and phytoplankton pools in the NPZ model run. In all three model runs, the phytoplankton concentrations are maximal at the onshore side of the jet and the zooplankton concentrations are maximal at the offshore side of the jet. The formation of the observed spatial patterns can be explained as follows. During the southward upwelling-favorable wind events, the DIN (NPZ, NPZD models) and NO\(_3\) (NNPZD model) rich water reaches the surface at the coast through the bottom layer. This water, however, has low concentrations of phytoplankton and zooplankton, which leaves a small region (a few kilometers) near the coast with almost no phytoplankton and zooplankton. The surface nutrient rich water at the coast is transported offshore at the surface where the phytoplankton grow rapidly, reaching a maximum concentration about 9 km offshore. The mixed layer is relatively shallow; thus mixing does not remove much of the phytoplankton from the surface. The region with phytoplankton extends, however, deeper in the jet where mixing is stronger. Sinking of nitrogen from the surface layer controls the decrease of phytoplankton offshore of the maximum. Due to the slow grazing rate chosen in this simulation, the zooplankton are not important in limiting the phytoplankton concentration. The zooplankton reach a maximum value well offshore of the phytoplankton maximum. The relative location of the phytoplankton and zooplankton maxima depends upon the speed at which the upwelled water is advected offshore and the zooplankton grazing rate. The offshore extent of the zooplankton patch is limited by the availability of phytoplankton. As seen in Figure 7, the NPZ maximum mean phytoplankton value is slightly larger than the corresponding values of the NNPZD and NNPZD models, while the maximum mean zooplankton in the NPZ model is about twice the maximum mean value of the other two models. More precisely, the maximum mean phytoplankton (21.39 mmol N m\(^{-3}\)) from the NPZ model is located at 8 m depth and 7.5 km offshore, while the maximum mean phytoplankton from NPZD (19.6 mmol N m\(^{-3}\)) and from NNPZD (19.5 mmol N m\(^{-3}\)) are located at 4 m depth and 9 km offshore. The maximum mean values of zooplankton (0.23, 0.14, 0.12 mmol N m\(^{-3}\)) for the three model (NPZ, NPZD, and NNPZD) are coupled to the two-dimensional circulation model described in the previous subsection. The advection of the various concentrations is discretized using a Smolarkiewicz upstream scheme [Smolarkiewicz, 1984]. The detritus (NPZD, NNPZD) and phytoplankton (NPZ) sinking terms are discretized using an upstream scheme in the vertical. No-flux conditions are imposed at the free surface and at the solid lateral boundaries. A no-flux condition is imposed at the bottom except for the sinking. The initial concentrations are taken from the one-dimensional NNPZD run with sinking and wind forcing (Figure 4). The initial DIN concentrations for the NPZ and the NPZD model runs are the sum of the nitrate and ammonium concentrations from the NNPZD model. The initial NPZ total nitrogen, lacking a contribution from detritus, is slightly less than the initial NNPZD total nitrogen. These initial concentrations are intended to approximate pre-upwelling concentrations, where nutrients are depleted at the surface and across-shore variations are small. [15] For the two-dimensional runs, the three ecosystem models (NPZ, NPZD and NNPZD) are coupled to the two-dimensional circulation model described in the previous subsection.
NPZD, NNPZD) runs are located at 9 m depth and 36.5, 35, and 35.25 km offshore, respectively.

[17] The increased NPZ maximum zooplankton compared to the other two models is due in part to the sinking of phytoplankton from the surface layer into the water that is advected onshore and then upwelled. This leads to enhancement of the phytoplankton concentration in the surface layer and consequently to increased zooplankton. An additional two-dimensional experiment (not shown) with the NPZ model and an increased phytoplankton sinking rate of 0.8 m d^{-1} shows similar increased zooplankton and phytoplankton compared to the other two models. The fact that this is not observed in the equivalent one-dimensional simulation (section 3) or in the mixed-layer model from Newberger et al. [2003] supports the reasoning that upwelling near the coast of subsurface water richer in phytoplankton due to sinking is one of the mechanisms leading to larger zooplankton concentrations in NPZ. Another possible reason for the increased NPZ phytoplankton and zooplankton is related to the instantaneous remineralization in subsurface water rich in phytoplankton. In the NPZ model, the dead phytoplankton and zooplankton as well as the zooplankton egestion are added instantaneously to the DIN pool. During upwelling, that pool of nitrogen is advected onshore and upwelled to the surface. It is directly available for phytoplankton growth and consequently for zooplankton growth. Farther offshore (≈60 km), the surface NNPZD phytoplankton and zooplankton concentrations are slightly larger than the corresponding ones from the NPZD and the NPZ models. Offshore, the sinking of NPZ phytoplankton removes phytoplankton from the upper layer, but there is no mechanism to replace the surface phytoplankton in a manner similar to upwelling in the nearshore region. Thus the offshore NPZ phytoplankton concentration is smaller than in the other models at the surface but larger around 40 m depth (Figure 7).

[18] The standard deviations of DIN, phytoplankton and zooplankton for the three models are shown in Figure 8. Similar spatial distributions are observed for the three models. For the DIN, two regions of high variability are present. The first one is located within the first 5 km from the coast where the effect of upwelling is to bring nutrient rich water to the surface. The second region is a subsurface layer that corresponds to high production of DIN (NPZ and

Figure 6. Mean and standard deviation of the density $\sigma_0$ (kg m^{-3}), the onshore velocity $v$ (m s^{-1}), the streamfunction for the cross-shelf flow $\psi$ (m^2 s^{-1}) and 2 times the kinetic energy $q^2$ (m^2 s^{-2}) over the 48-day upwelling analysis period, i.e., from July 6 through August 22, 1973 (year days 188–235).
NPZD) or ammonium (NNPZD). The source of $\text{DIN}$ is phytoplankton mortality in NPZ or remineralization of detritus in NPZD (as shown later in Figure 11). In NNPZD, the pool of ammonium comes from remineralization of detritus. At depth, part of this ammonium pool is oxidized and becomes a source of nitrate. High variability of phytoplankton is seen in three regions. The first one near the coast corresponds to an increase of phytoplankton taking up nutrient from the upwelled water. The second region is located at the surface, and it extends offshore about 25 km. It corresponds to an increase of phytoplankton due to offshore advection of nutrient as well as of phytoplankton. The third region is located around 40 m depth and extends to about 25 km offshore. This region is characterized by an increase of phytoplankton mixed down from the surface and growing on regenerated nutrients. Three regions of high zooplankton standard deviation are also apparent for all the models. The first one near the coast corresponds to a loss of zooplankton due to upwelling of zooplankton poor water and to offshore advection during upwelling events. The second region, located around 35 km offshore, is the result of the growth of zooplankton near the mean maximum (Figure 7). This is consistent with the mixed-layer horizontal advection results from Newberger et al. [2003]. The region offshore of the maximum mean zooplankton concentration experiences a decrease of zooplankton directly through vertical mixing with water poor in zooplankton, but also primarily from a lack of phytoplankton. For the chosen set of parameters, zooplankton mortality exceeds growth if the phytoplankton concentration is less than 8.468 mmol N $m^{-3}$.

[19] The three regions of high phytoplankton and zooplankton standard deviation can be further characterized by analyzing the balance of biological and physical processes in the phytoplankton and zooplankton budgets. In our discussion we only present the NNPZD budgets. Figure 9 displays the mean biological processes from Appendix A equations (A14) and (A15), the physical processes for NNPZD phytoplankton and zooplankton, and the time variations of the concentrations over the upwelling analysis period. All terms, except the time rate of change, are evaluated as if written on the right-hand side of the equations. The source-sink term represents the sum of the biological terms, and the physics term represents the sum of diffusion and advection. Grazing of phytoplankton by zooplankton is not shown in the phytoplankton biological terms since this term is 2 orders of magnitude smaller than the others.

[20] In the phytoplankton balance, at the surface and within 5 km from the coast, a negative physics term, dominated by vertical advection of deep phytoplankton poor water and offshore advection, is balanced by a positive source term, due to larger uptake of nitrate than mortality. This balance leads to an increased phytoplankton at day 235.
compared to day 188. Near the coast and close to the bottom, there is a decrease of phytoplankton due to vertical advection of deep phytoplankton poor water (negative physics term). At the surface between 5 and 30 km, the uptake of ammonium is of the same order of magnitude as nitrate uptake and their sum is larger than mortality, resulting in a positive source term. This positive source term is balanced by a negative physics term that is dominated by vertical mixing. Since the biological source is larger than the physical term, an increase of phytoplankton is also found in that region, but it is smaller than the increase at the coast. Below 20 m in the upwelling jet, mortality is the dominant biological process and is balanced by a positive physics term dominated by vertical mixing. The resulting increase of phytoplankton is smaller than in the surface layer.

Similar to the phytoplankton budget, the contributions of the source-sink and the physics terms in the zooplankton budget are of the same order of magnitude. The source-sink term is maximum where the maximum of zooplankton is found and is a balance between grazing, egestion and excretion. A negative physics term with contribution from both vertical mixing and offshore advection dominates the budget near the surface to about 30 km offshore. The resulting increase of phytoplankton is smaller than in the surface layer.

Figure 8. Standard deviation of dissolved inorganic nitrogen (DIN) (mmol N m\(^{-3}\)), phytoplankton (mmol N m\(^{-3}\)) and zooplankton (mmol N m\(^{-3}\)) over the 48-day upwelling analysis period, i.e., from July 6 through August 22, 1973 (year days 188–235), for (left column) the five-component model, (middle column) the four-component model and (right column) the three-component model. Note that the maximum of the zooplankton standard deviation scale corresponds to the NNPZD maximum. The maxima are 0.054, 0.075, 0.17 mmol N m\(^{-3}\) for NNPZD, NPZD and NPZ models, respectively.

Since most of the biological variability occurs in the upper 60 m and within 75 km from shore (Figures 7 and 8), we examine the time evolution (Figure 10) and the net changes over the upwelling analysis period (Figure 11 and Tables 2 and 3) of the spatially-averaged concentrations in this region, which we call the upper-ocean coastal (UOC) region. The temporal evolution (Figure 10) is very similar for the three models. The time series for DIN, phytoplankton, and detritus show clearly the response to the succession of upwelling and intermittent relaxation periods in the wind stress. This can be seen by comparing the time variation of these terms with that of the time integrated alongshore component of the wind stress, \( F(t) = -\int_0^t \tau_l'(t) dt \). Over the upwelling analysis period (days 188–235), there is a net increase of total nitrogen (Table 2). This increase is due to
physical circulation processes since there is no net change of the total nitrogen due to biological sources and sinks (Table 3) other than from vertical sinking of detritus (NNPZD, NPZD) or phytoplankton (NPZ). Over the analysis period, physical and biological processes lead to an accumulation of phytoplankton and a decrease of $\text{DIN}$ for all the models. The phytoplankton maximum is slightly larger for the NPZ model, however, than for the other two models, and the $\text{DIN}$ decrease is slightly smaller. A small increase in zooplankton occurs in NPZ while there is a decrease for the other two models. If we consider the gains and losses due to biological sources and sinks only (Table 3 and Figure 11), we find that there is a greater loss of $\text{DIN}$ for the NPZ that is accompanied by a larger gain of phytoplankton and zooplankton.

23] The biological fluxes typically measured in the field are primary productivity and $f$-ratio. Averaged in time over the upwelling analysis period and in space over the UOC region (Figure 11), the primary productivity, i.e., flux from $\text{DIN}$ (or $\text{NO}_3$ and $\text{NH}_4$) to phytoplankton, increases as the number of ecosystem components decreases. The $f$-ratio is the fraction of primary productivity that is supported by new nitrogen [Dugdale and Goering, 1967]. In other words, it is the ratio of the new to the total productivity, where the total productivity is the sum of new plus regenerated productivity. In the field, the technique used to separate new from
regenerated production is based on isotopic tagging by stable \(^{15}\text{N}\) of ammonium and nitrate in solution and on the measurement of the relative uptake of nitrate and ammonium by phytoplankton. One of the main advantages of having the DIN pool split into nitrate and ammonium (NNPZD model) is that it allows computation of the \(f\)-ratio in a way directly comparable to that calculated from shipboard measurements. In the NPZ and NPZD models, the DIN uptake represents total productivity. New productivity can in this case be estimated as the difference between total productivity and regenerated productivity that is approximated by the fluxes entering the DIN compartment [Franks and Chen, 1996; Denman and Peña, 1999]. Equations for the \(f\)-ratio for the different models are given in Appendix A. The mean NPZ and NPZD \(f\)-ratio averaged over the upwelling analysis period and the UOC region are equal to 0.29 and 0.34, respectively, and the NNPZD \(f\)-ratio calculated in a similar fashion, \(f_{r}(1)\) in (A19), equals 0.33. These values suggest that the primary productivity is on average mainly regenerated productivity. On the other hand, calculated as with in situ measurements, \(f_{r}(2)\) in Appendix A equation (A20), the NNPZD \(f\)-ratio is equal to 0.57, which indicates that the primary productivity is, on average, dominated by new productivity. The difference between the results using \(f_{r}(1)\) and \(f_{r}(2)\) can be explained as follows. As shown in Figure 11, ammonium oxidation (nitrification) averaged over the upwelling analysis period and the UOC region corresponds to about 37% of the phytoplankton NO\(_3\) uptake. Consequently, a large part of NO\(_3\) uptake does not correspond to new production but rather to regenerated production. Thus, the use of \(f_{r}(2)\) and shipboard measurements may lead to a larger estimate of new productivity and therefore to a larger \(f\)-ratio.

In all three models, about 98% of the total regenerated productivity is due to detritus regeneration (NPZD and NNPZD) or phytoplankton mortality/exudation (NPZ), while the rest is due to zooplankton excretion. Most of the detritus pool in NPZD and NNPZD is made of dead phytoplankton. [24] As also found in the mixed-layer horizontal advection study from Newberger et al. [2003], we find that two-dimensional physical processes (i.e., advection and diffusion) amplify the differences among the three models. Even though we identified a phytoplankton sinking rate in a one-dimensional simulation (Figure 3) such that the phytoplankton concentrations from the NPZ and NNPZD models

![Figure 10](image-url)
agree in the surface layer, advection and diffusion during upwelling lead to noticeable differences in the corresponding two-dimensional phytoplankton fields. These findings are also valid for the zooplankton fields where the mean NPZ zooplankton concentration is larger than in the other two models. The positions of the maxima in zooplankton and in phytoplankton are found at about the same locations for the three models. This indicates that the mean spatial distributions in Figure 7 are robust features of all the models. Of course, these spatial distributions may vary depending upon the wind events and the chosen model parameters.

4.3. Sensitivity to Wind Stress

We focus now on a study of the sensitivity of the NNPZD model results to the characteristics of the wind

Table 2. Net Changes Due to Both Physical Circulation Processes and Biological Sources and Sinks Between Day 188 and 235 of the Spatially-Averaged Concentrations From the Surface to 60 m Depth and From the Coast to 75 km Offshore (mmol N m\(^{-3}\))

<table>
<thead>
<tr>
<th></th>
<th>NNPZD</th>
<th>NPZD</th>
<th>NPZ</th>
</tr>
</thead>
<tbody>
<tr>
<td>DIN ((\text{NO}_3^-))</td>
<td>(-2.0036)</td>
<td>(-0.7925)</td>
<td>(-0.7354)</td>
</tr>
<tr>
<td>DIN ((\text{NH}_4^+))</td>
<td>(1.2111)</td>
<td>(0.5907)</td>
<td>(0.5868)</td>
</tr>
<tr>
<td>Det</td>
<td>6.2411</td>
<td>6.1763</td>
<td>7.2253</td>
</tr>
<tr>
<td>Phyto</td>
<td>0.3398</td>
<td>0.3398</td>
<td>0.3398</td>
</tr>
<tr>
<td>Zoo</td>
<td>0.0494</td>
<td>0.0494</td>
<td>0.0494</td>
</tr>
<tr>
<td>Total</td>
<td>6.0089</td>
<td>6.0020</td>
<td>6.6188</td>
</tr>
</tbody>
</table>
forcing. In section 4.2, we found that during the 48-day upwelling analysis period (days 188–235) in 1973, there was an increase of total nitrogen via an increase of phytoplankton, ammonium, and detritus and a decrease of zooplankton and nitrate in the UOC region (Figure 10). We also found characteristic spatial patterns in the mean distributions of these biological variables (Figure 7). The sensitivity of the qualitative nature of those results to the specific time variability of the wind stress forcing is examined here with additional experiments.

We repeat the basic case experiment with a constant wind stress corresponding to the mean of the 1973 wind stress for the 56-day forcing period from day 180 to day 235 ($\tau^{(3)} = 0.0048$ N m$^{-2}$, $\tau^{(3)} = -0.0299$ N m$^{-2}$) and also with wind stress from summer 1999 computed from wind measurements at the NDBC Yaquina Bay buoy in the same manner as used to calculate the 1973 wind stress. The 1999 wind stress (Figure 12) is generally upwelling favorable, but with a different temporal evolution than during 1973. Several periods of strong upwelling favorable wind interrupted by a few days of almost no wind or weak downwelling favorable wind are observed in July 1999, while a shorter upwelling period (about 10 days) is found in July 1973. On the other hand, in late July and August 1973, there were more upwelling-favorable winds in 1973 than during the same period in 1999. To be consistent in the model result comparison, we analyze the circulation and ecosystem model results from the constant 1973 wind stress cases. Compared to the 1973 basic case experiment (Figure 6), the surface density is increased near the coast where the phytoplankton is almost zero since the upwelled water is poor in phytoplankton. This region is narrower in the 1973 and 1999 variable wind cases than in 1973CW due to periods of relaxation or downwelling (1999). Evidently, as a result of the shallower offshore mixing in 1973CW, less phytoplankton and zooplankton are found offshore.

$\sigma_{ib}$ is the alongshore velocity $v$, the streamfunction $\psi$ for the cross-shelf flow and two times the turbulent kinetic energy $q^2$ over the upwelling analysis period for the constant 1973 wind stress (referred to as 1973CW case) and the variable 1999 wind stress cases. Compared to the 1973 basic case experiment (Figure 6), the surface density is increased near the coast in the 1973CW case. The offshore mixing is shallower and the turbulent kinetic energy is weaker offshore, but stronger in the jet. In 1999, a larger band of high density is found at the surface, compared to the 1973 basic case experiment. The values of $q^2$ are generally larger, reflecting stronger mixing. The southward jet is located farther offshore and extends to a greater depth. The transport through the bottom boundary layer is also stronger. Overall, the differences in the mean physical fields between the three wind stress scenarios are small, but they result in appreciable differences in the ecosystem behavior (Figure 14).

Figure 12. Wind stress (N m$^{-2}$) from June 29 through August 29, 1999, at the NDBC Yaquina Bay buoy. Negative N-S wind stress corresponds to an upwelling favorable wind. The mean values of the (alongshore (N-S), across-shore (E-W)) wind stress components (N m$^{-2}$) are $(-0.0294, 0.0046)$ with standard deviations of $(0.0482, 0.0072)$. 

$\text{DIN} = 15.2688 - 15.8448 - 16.3776$

$\text{Det} = 2.3712 - 2.472$

$\text{Phyto} = 12.8976 - 13.368 - 16.3776$

$\text{Zoo} = 0 - 0.0048 - 0.0672$

$\text{Total} = 0 - 0 - 0$

<table>
<thead>
<tr>
<th></th>
<th>NNPZD</th>
<th>NPZD</th>
<th>NPZ</th>
</tr>
</thead>
<tbody>
<tr>
<td>Det</td>
<td>2.3712</td>
<td>2.472</td>
<td></td>
</tr>
<tr>
<td>Phyto</td>
<td>12.8976</td>
<td>13.368</td>
<td>16.3104</td>
</tr>
<tr>
<td>Zoo</td>
<td>0</td>
<td>0.0048</td>
<td>0.0672</td>
</tr>
<tr>
<td>Total</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
smaller increase of ammonium in 1999. The net gain of zooplankton is the largest in the 1973CW. The primary productivity increases from 0.90 mmol N m\(^{-3}\) d\(^{-1}\) for 1973CW to 0.95 for the variable 1973 case and to 1.05 in 1999. The mean \(f\) -ratios, computed as \(f(2)\) in Appendix A equation (A20) are equal to 0.57, 0.54 and 0.56 for the basic 1973, the 1973CW, and the 1999 cases, respectively. Computed as \(f(1)\) in Appendix A equation (A19), the respective \(f\) -ratios are equal to 0.33, 0.34 and 0.32. From the computation of \(f(2)\), there is an indication that the primary productivity is mainly new productivity. From the computation as \(f(1)\), the primary productivity is mainly regenerated productivity. These computations again illustrate the discrepancy between the two formulations discussed in section 4.2. The comparison between the three experiments leads us to conclude that the time variability of the forcing affects the amount of primary productivity in the UOC region.

To illustrate the spatial and temporal variability of the biological and physical variables, we plot the time evolution of the surface values for the physical and biological fields in Figures 16 and 17, respectively. In 1999, the surface jet reaches a width of approximately 50 km by day 12. In the 1973CW case, it takes about 60 days and in the variable 1973 wind stress case about 30 days to reach a width of 50 km. The maximum of the alongshore velocity is the largest for the 1973 variable wind stress. Results of the succession of upwelling and non-upwelling events in the wind stress in 1973 and 1999 may be seen clearly in the physical surface fields. During wind relaxation periods, the alongshore velocity near the coast approaches zero. In 1973, phytoplankton start to increase around 10 km offshore during the first upwelling event (day 14) and are transported onshore during the following relaxation period. Starting around day 40, there is a band of high phytoplankton that remains located at around 10 km offshore for the next 20 days. Phytoplankton start to accumulate earlier in the 1973CW case than in the 1973 variable wind and 1999. For 1973CW, the phytoplankton start increasing as early as the second day, and after about 10 days a band of high phytoplankton remains located around 10 km offshore for the rest of the simulation. Similar behavior starting around day

Figure 13. Mean of the density \(\sigma_0\) (kg m\(^{-3}\)), the alongshore velocity \(v\) (m s\(^{-1}\)), the streamfunction for the cross-shelf flow \(\psi\) (m\(^2\) s\(^{-1}\)) and 2 times the kinetic energy \(q^2\) (m\(^2\) s\(^{-2}\)) over the 48-day upwelling analysis period, i.e., from July 6 through August 22 (year days 188–235) for (left column) the constant 1973 wind stress case and (right column) the 1999 wind stress run.
20 is found in 1999, but with more variability due to the relaxation events. In the three cases, the zooplankton concentration decreases to about day 10. The zooplankton start to accumulate earlier in the 1973CW case. In 1999, there is formation of two patches of higher zooplankton. The first one is located around 40 km offshore and starts forming around day 30 while the second one is located around 10 km and starts forming about day 45. The importance of the succession of upwelling and relaxation events is clearly illustrated when comparing the surface zooplankton evolution in 1973 and 1999. The results of the 1973CW case also agree with the results given by Newberger et al. [2003] when horizontal

![Figure 14. Mean nitrate, ammonium, detritus, phytoplankton and zooplankton (mmol N m$^{-3}$) over the 48-day upwelling analysis period, i.e., from July 6 through August 22 (year days 188–235) for (left column) the variable 1973 wind stress case, (middle column) the 1973 constant wind stress case, and (right column) the 1999 wind stress run.](image)
diffusion is added to the mixed-layer model. The location of the zooplankton maximum is located around 35 km offshore in both studies. In the two-dimensional simulations however, the zooplankton first decrease due to decreased grazing during the spin-up period (first 9 days of the simulation).

4.4. Sensitivity to Parameters

[31] An analysis of the sensitivity to model parameters for the 0D- and 1D-simulations is given by Newberger et al. [2003]. For the 2D case with the NNPZD model forced by winds from 1973 as in the basic case experiment, we limit the analysis to the parameters that have shown the largest sensitivity in the 0D- and 1D-calculations. Newberger et al. [2003] find that the grazing rate has a large impact on the response of the ecosystem. We should recall that in the 0D model the value of the steady state phytoplankton concentration is determined solely by the zooplankton parameters, and therefore the choice of those parameters is critical. Edwards et al. [2000] utilized a three-component ecosystem to study both microzooplankton and macrozooplankton dynamics in an idealized coastal upwelling system. They find similar patterns in both cases, but the offshore extent of phytoplankton is smaller for the faster growing microzooplankton case. They also find that the surface dissolved inorganic nitrogen is nearly depleted in the macrozooplankton case, but not with the microzooplankton. While the grazing formulations follow an Ivlev curve in their study as well as in the present one, the microzooplankton and the macrozooplankton, with parameter values from Edwards et al. [2000], reach a maximum grazing rate for smaller values of the phytoplankton concentration and grow faster than in our study. Consequently, in one experiment we increase the maximum zooplankton grazing rate from \( R_m = 0.52 \text{ d}^{-1} \) in the basic case to \( R_m = 1.5 \text{ d}^{-1} \) corresponding to the simulation of microzooplankton instead of macrozooplankton. We keep the other parameters at the basic case values. The mean fields of the biological variables that result in this experiment are shown in Figure 18 while the \( (x, t) \) variations at the surface for the variable and the constant wind stress case are plotted in Figure 19. The differences between the \( R_m = 1.5 \text{ d}^{-1} \) experiment and the basic case are appreciable for all the mean concentrations. While most concentrations are in the same range as the basic case values (Figure 14), the zooplankton concentration is more than 10 times the value of that in the basic case. As in the basic case, a maximum of zooplankton is found offshore of the maximum of phytoplankton but is located closer to the coast. A second weaker peak of zooplankton is observed at approximately 35 km offshore. This peak value is also larger than the basic case maximum. While most concentrations are in the same range as the basic case values (Figure 14), the zooplankton concentration is more than 10 times the value of that in the basic case. As in the basic case, a maximum of zooplankton is found offshore of the maximum of phytoplankton but is located closer to the coast. A second weaker peak of zooplankton is observed at approximately 35 km offshore. This peak value is also larger than the basic case maximum. The phytoplankton is limited to a small region onshore by the increased grazing. Consequently, the nitrate is depleted at the surface in that region, and a band of higher nitrate is found in the jet just offshore of the region of high phytoplankton. The surface phytoplankton concentration also increases in the region between the zooplankton maxima (Figure 19). The subsurface ammonium pool is larger onshore but does not extend as far offshore. A corresponding similar change is observed for the detritus pool. By comparing the average fluxes for the same region and period as the basic case (Figure 11), we find that with \( R_m = 1.5 \text{ d}^{-1} \) the primary productivity (0.986 mmol N m\(^{-3}\) d\(^{-1}\)) is slightly higher than in the basic case (0.9547 mmol N m\(^{-3}\) d\(^{-1}\)). Also, since \( f_r(2) = 0.48 \) (Appendix A equation (A20)) compared to \( f_r(2) = 0.57 \) in the basic case, the system tends toward one of regenerated production rather than new production.

[32] The plot of surface values (Figure 19) reveals zooplankton growth over the entire domain starting at day one. Indeed, if we suppose that there is no advection and diffusion is added to the mixed-layer model. The location of the zooplankton maximum is located around 35 km offshore in both studies. In the two-dimensional simulations however, the zooplankton first decrease due to decreased grazing during the spin-up period (first 9 days of the simulation).

Table 4. Value and Location of the Maximum of the Mean Phytoplankton and Zooplankton Concentration (mmol N m\(^{-3}\)) for the 1973 Basic Case, the 1973 Constant Wind Stress and the 1999 Cases

<table>
<thead>
<tr>
<th>Year</th>
<th>Phytoplankton</th>
<th>Zooplankton</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Maximum</td>
<td>Location (km, m)</td>
</tr>
<tr>
<td>1973</td>
<td>19.1282</td>
<td>(8.75, 3.8)</td>
</tr>
<tr>
<td>1973CW</td>
<td>24.5310</td>
<td>(6.00, 0.0)</td>
</tr>
<tr>
<td>1999</td>
<td>21.6767</td>
<td>(6.75, 0.0)</td>
</tr>
</tbody>
</table>

The means are computed over the 48 day analysis period (day 188 to 235) (mmol N m\(^{-3}\)). The location \((x, z)\) is given as distance from the coast (km) and depth (m).

Figure 15. Fluxes (mmol N m\(^{-3}\) d\(^{-1}\)) as in Figure 11 but for (left) the constant 1973 wind stress case and (right) the 1999 wind stress case.
diffusion, the zooplankton will accumulate if the phytoplankton concentration is larger than 2.478 mmol N m^{-3}, which is the case with the chosen initial conditions. Due to upwelling of water poor in zooplankton, the zooplankton do not accumulate near shore. In that region, the phytoplankton will increase as in the basic case since there are not enough grazers to control them. The offshore extent of the high phytoplankton region is limited by grazing of the rapidly growing zooplankton. An accumulation of nitrate is found in the first 5 km offshore during the upwelling events. Additionally, a region of elevated nitrate is found around 20 km offshore after day 30. This region corresponds to a region of lower phytoplankton concentration and hence lower grazing, and is located in the interior of the jet where there is stronger vertical mixing that brings water rich in nutrients to the surface. We can then see a region of higher phytoplankton concentration offshore of that region of high nutrient after day 40 resulting from grazing on phytoplankton advected offshore. This simulation demonstrates that the grazing rate plays a major role in determining the spatial distribution of the phytoplankton and zooplankton.

Figure 16. Surface across-shore ($u$) and alongshore ($v$) velocity and $\sigma_0$ as a function of distance from the coast and from June 29 (day 1) through August 28 (day 61) for (left column) the case of 1973 variable wind stress, (middle column) the case of a constant wind stress equal to the mean wind stress between June 29 and August 22, 1973, and (right column) the 1999 wind stress case. Note the change of scale for the 1973CW $u$-velocity.
The locations of the zooplankton and phytoplankton maxima and of the secondary peaks agree well with those given by Newberger et al. [2003] with the mixed-layer advection model. The two-dimensional circulation seems to have less influence on the spatial and temporal evolution of the ecosystem response in the case of a larger grazing rate. The spatial patterns are basically determined by the biological interactions.

[33] The effective detritus sinking rate is an important parameter that is poorly known. Most modelers choose it based upon data from sediment traps. However, the detritus pool in a NNPZD model represents not only dead material, but also non-sinking suspended particles and dissolved organic nitrogen (DON) that are not explicitly included in the model. Consequently, we vary the detritus sinking rate and repeat the basic case experiment ($w_d = 8 \text{ m d}^{-1}$) with a smaller value of $w_d = 1 \text{ m d}^{-1}$ (remineralization length scale = 1 m). Due to the reduction of the sinking rate, higher detritus concentrations are found in the mixed-layer, leading to increased remineralization of the detritus near the surface. The ammonium concentration thus increases at the surface, which allows increased growth of phytoplankton. Higher phytoplankton and zooplankton concentrations are found offshore of the jet (Figure 18) compared to the basic case (Figure 7). Since the slower sinking of detritus results in more phytoplankton and consequently more zooplankton...
earlier in the upwelling season, the maximum of the phytoplankton and of the zooplankton concentrations averaged over the upwelling analysis period is higher in this experiment. Nearshore, the zooplankton concentration remains very small since it is controlled by the upwelling of water poor in zooplankton. Due to remineralization of the detritus pool near the surface, we have a reduction of ammonium at the base of the euphotic zone. Offshore, we also have reduction of the nitrate level around 50 m deep since the phytoplankton concentration is larger and the utilization of nitrate is higher.

**Figure 18.** Mean nitrate, ammonium, detritus, phytoplankton and zooplankton (mmol N m\(^{-3}\)) over the upwelling analysis period, i.e., from July 6 through August 22, 1973, for (left column) a grazing rate \(R_m\) of 1.5 d\(^{-1}\), (middle column) a detritus sinking rate \(w_d\) of 1 m d\(^{-1}\), and (right column) a case without inhibition of nitrate uptake by ammonium, i.e., \(\psi = 0\).
of the nutrient uptake by phytoplankton. In the NNPZD model, there are two pools of nutrients and an inhibition of nitrate uptake by ammonium while there is only one pool of nutrient in the NPZD model. An experiment without inhibition, i.e., $\psi = 0$, (Figures 18 and 19) shows higher mean concentrations of phytoplankton and zooplankton over the upwelling analysis period than in the basic case ($\psi = 1.46$ (mmol N m$^{-3}$)$^{-3}$). Since the phytoplankton are allowed to take up a larger amount of nitrate, increased phytoplankton are found near the coast around day 30 when the second upwelling event starts. Phytoplankton are also advected offshore, which leads to an increase of zooplankton earlier than in the basic case. Note that the mean phytoplankton and zooplankton concentrations are also larger than in the NPZD case where there is only one pool of nutrient (Figure 7). This experiment demonstrates an important impact of the inhibition of nitrate uptake, not only on the phytoplankton, but also on the zooplankton concentration in an upwelling system. Several field observations and model results support our finding of the importance of inhibition of nitrate uptake by ammonium. Wheeler and Kokkinakis [1990] found that concentrations of $NH_4$ between 0.1 and 0.3 $\mu$M caused complete inhibition of $NO_3$ assimilation in the subarctic Pacific. Field observations in the equatorial Pacific [McCar-

**Figure 19.** Surface nitrate, phytoplankton and zooplankton (mmol N m$^{-3}$) as a function of distance from the coast and from June 29 (day 1) through August 28 (day 61) for (left column) the basic case with increased maximum grazing rate, (middle column) the 1973 constant wind case with increased maximum grazing rate, and (right column) the basic case with $\psi = 0$. 
thy et al., 1996] and model studies using various parameterizations of inhibition of nitrate uptake by ammonium [Leonard et al., 1999; Friedrichs and Hofmann, 2001; Christian et al., 2002] have shown that, due to inhibition, ammonium uptake can exceed nitrate uptake. Future process oriented field studies will be necessary to determine the appropriate inhibition parameter or parameterization for model applications off Oregon.

5. Summary and Discussion

[35] The solutions of three nitrogen-based ecosystem models have been compared in one- and two-dimensional experiments. The first model (NPZ) includes dissolved inorganic nitrogen (DIN), phytoplankton and zooplankton, the second (NPZD) has in addition detritus, and the third has detritus and splits DIN into nitrate and ammonium. The three models are made as close as possible by choosing the same parameterizations for the biological interactions. First, we compare the response of the three ecosystem models in a one-dimensional vertical model with sinking of detritus (NPZD, NNPZD) or phytoplankton (NPZ). Second, we study the response of the three ecosystem models to upwelling off the Oregon coast when coupled to a two-dimensional version of the Princeton Ocean Model (POM).

[36] Several zero- and one-dimensional studies [Edwards, 2001; Newberger et al., 2003] have shown that the addition of a detritus component to an NPZ model to make it an NPZD model does not greatly change the ecosystem dynamics when the zooplankton do not graze on detritus and when no sinking of the detritus or the phytoplankton is introduced. In the one-dimensional simulations with sinking, we were able to find a phytoplankton sinking rate for NPZ such that the NPZ surface phytoplankton matches the surface phytoplankton from the other two models with a fixed detritus sinking rate. In that case, with forcing corresponding to wind stress from Oregon in summer 1973 and with the same initial concentrations for the NPZ variables, DIN, phytoplankton and zooplankton, as for the other two models, the values of the NPZ surface zooplankton and the subsurface DIN are slightly larger than the corresponding values from the NPZD and NNPZD models at the end of 61 days. The lack of detritus in NPZ is equivalent to an instantaneous remineralization. In the low light region, this leads to an accumulation of DIN while, in the surface layer, zooplankton increase due to an increased net grazing.

[37] The three ecosystem models result in similar spatial patterns for the various concentrations when coupled to a two-dimensional circulation model simulating the 1973 summer upwelling off the Oregon coast. On average over the upwelling season, a patch of high phytoplankton concentration is found on the shoreward side of the jet, while the zooplankton concentration is the highest on the offshore side of the jet. This is consistent with the offshore distribution that Small and Menzies [1981] observed in summer 1972 and 1973. Phytoplankton patches with length scales of 5 to 10 km have also been observed in other coastal upwelling regions [Walsh et al., 1974; Kelley et al., 1975]. Similar spatial phytoplankton patterns were, however, not observed in the Wroblewski [1977] simulation, probably due to the limitation of the circulation model. Coupled to a two-dimensional model, we found that the NPZ zooplankton concentration in the upper ocean is larger than the NPZD and NNPZD zooplankton concentrations. In the NPZD and NNPZD models, sinking of detritus from the upper layer results in direct removal of nitrogen from the surface layer. Even though sinking detritus reach the water that is advected onshore and then upwelled, no effect will be seen in the zooplankton concentration since the zooplankton do not graze on detritus. On the other hand, in the NPZ model when the phytoplankton is allowed to sink, the removed nitrogen from the surface layer will be advected towards shore at depth as phytoplankton and will be mixed with the onshore pool of phytoplankton during upwelling. Upwelling events will then increase the phytoplankton values onshore. In addition, the NPZ model has an instantaneous remineralization rate since the dead phytoplankton are directly introduced to the DIN pool. This will also lead to an increase in DIN at the surface and hence to an increase of phytoplankton. In the surface layer, the higher NPZ phytoplankton concentration is grazed by zooplankton. Consequently, in NPZ, higher values of zooplankton are found offshore of the jet, compared to the NPZD and NNPZD.

[38] From experiments using the NNPZD model with constant 1973 wind stress and with variable wind stress from 1973 and 1999, we were able to illustrate important effects of the time dependence of the upwelling. Comparing the 1973 simulation to a simulation with a constant wind stress equal to the 1973 mean wind stress, we found that the primary productivity was increased with variable wind stress. The formation of zooplankton patches at the surface is also found to be related to the time-dependence of the upwelling events. Two regions of relatively high zooplankton are formed in 1999 while only one is found in 1973.

[39] One of the difficulties in ecosystem modeling is to choose an adequate set of model parameters. Additional experiments address the effect of some of the parameters on the ecosystem. The simulation with increased grazing rate \( R_m = 1.5 \text{ d}^{-1} \), corresponding to microzooplankton instead of macrozooplankton, showed very good agreement with the findings of Newberger et al. [2003] when using a simple mixed-layer horizontal advection model. In that case, the biological interactions determine the location and magnitude of the maximum of phytoplankton and zooplankton and the results are quite robust. The two-dimensional simulation with a smaller detritus sinking rate \( w_d = 1 \text{ m} \text{ d}^{-1} \), corresponding to a smaller remineralization length scale and removal of less detritus from the surface layer, leads to higher zooplankton and phytoplankton in the surface layer. Effective sinking rates, while difficult to measure, seem to be a key element in determining the location and value of the plankton maxima during upwelling. In a third parameter sensitivity experiment, the suppression with \( \psi = 0 \) of the inhibition of nitrate uptake by ammonium in the NNPZD model leads to increased plankton concentrations. The lack of inhibition seems to explain in part the larger phytoplankton and zooplankton found in the NPZD compared to the NNPZD model.

[40] In conclusion, from the experiments with the three models, we find that the maximum of zooplankton is always located offshore of the phytoplankton maximum and, with this choice of parameters, is the largest for NPZ model. The distance from shore and strength of the maxima depend
upon the succession of upwelling events as well as the biological parameters. To address the response of the ecosystem to upwelling, the addition of a sinking detritus pool to the NPZ model is found to be important. The sinking of detritus removes nitrogen from the coastal upwelling region without affecting the phytoplankton concentration in the upwelled water near the coast and avoids instantaneous remineralization, which in turn affects the zooplankton concentration. Analysis of observations from two field programs, the GLOBal Ocean Ecosystems Dynamics (GLOBEC) and the Coastal Ocean Processes (CoOP) programs, will be utilized in the near future to determine the dominant plankton species and to estimate the key parameters of the NNPZD model during the upwelling season off the Oregon coast.

Appendix A. Ecosystem Model Equations

[41] For simplicity, we record the biological term only and omit the physical advection and diffusion terms.

A1. Three-Component Model: NPZ

[42] The model equations consist of three partial differential equations representing dissolved inorganic nitrogen DIN, phytoplankton nitrogen P and zooplankton nitrogen Z:

\[
\frac{\partial \text{DIN}}{\partial t} = -V_m f(I) \left[ \frac{\text{DIN}}{K_u + \text{DIN}} \right] P + \frac{f_{np}}{\phi D + \Gamma Z} + R_m \left[ 1 - e^{-\lambda P} \right] Z, \quad (A1)
\]

\[
\frac{\partial P}{\partial t} = V_m f(I) \left[ \frac{\text{DIN}}{K_u + \text{DIN}} \right] P - R_m \left[ 1 - e^{-\lambda P} \right] Z - \Xi P, \quad (A2)
\]

\[
\frac{\partial Z}{\partial t} = R_m \left[ 1 - e^{-\lambda P} \right] Z - \Gamma Z. \quad (A3)
\]

[43] The light limitation \( f(I) \) is defined as

\[
f(I) = \frac{\alpha I}{\sqrt{(V_m^2 + \alpha^2 P)}}
\]

where

\[
I(\chi, z, t) = I_0 \exp \left[ k_u z + k_p \int_0^\chi P(z') \, dz' \right],
\]

and where \( -H_0 \leq z \leq 0 \), so that the (positive) water depth is \( -z \). For simplicity, the surface photosynthetically available radiation \( I_0 \) is defined as the daily mean and remains constant in time. In this model, the total nitrogen is

\[
T_3 = \text{DIN} + P + Z. \quad (A4)
\]

The \( f \)-ratio \( (f_r) \), the fraction of primary production that is supported by new, rather than regenerated, nitrogen \cite{Dugdale and Goering, 1967} is computed as

\[
f_r = \frac{f_{np} - (f_{zn} + f_{zn})}{f_{np}}. \quad (A5)
\]

where \( f_{np} \) represents the flux from DIN to phytoplankton, \( f_{zn} \) represents the flux from zooplankton to DIN and \( f_{zn} \) represents the flux from phytoplankton to DIN \cite{Franks and Chen, 1996}.

A2. Four-Component Model: NPZD

[44] The model equations consist of four partial differential equations representing dissolved inorganic nitrogen DIN, phytoplankton nitrogen \( P \), zooplankton nitrogen \( Z \), and detritus nitrogen \( D \):

\[
\frac{\partial \text{DIN}}{\partial t} = -V_m f(I) \left[ \frac{\text{DIN}}{K_u + \text{DIN}} \right] P + \frac{f_{np}}{\phi D + \Gamma Z}, \quad (A6)
\]

\[
\frac{\partial P}{\partial t} = V_m f(I) \left[ \frac{\text{DIN}}{K_u + \text{DIN}} \right] P - R_m \left[ 1 - e^{-\lambda P} \right] Z - \Xi P, \quad (A7)
\]

\[
\frac{\partial Z}{\partial t} = R_m \left[ 1 - e^{-\lambda P} \right] Z - \Gamma Z, \quad (A8)
\]

\[
\frac{\partial D}{\partial t} = R_m \left[ 1 - e^{-\lambda P} \right] Z + \Xi P - \phi D - w_d \frac{\partial D}{\partial z}, \quad (A9)
\]

\[
T_4 = \text{DIN} + P + Z + D. \quad (A10)
\]

[45] The \( f \)-ratio \( (f_r) \) is given by

\[
f_r = \frac{f_{np} - (f_{zn} + f_{zn})}{f_{np}}, \quad (A11)
\]

where \( f_{np} \) represents the flux from DIN to phytoplankton, \( f_{zn} \) the flux from zooplankton to DIN and \( f_{zn} \) the flux from detritus to DIN \cite{Denman and Peita, 1999}.

A3. Five-Component Model: NNPZD

[46] The model equations consist of five partial differential equations representing nitrate \( NO_3 \), ammonium \( NH_4 \), phytoplankton nitrogen \( P \), zooplankton nitrogen \( Z \), and detritus nitrogen \( D \):

\[
\frac{\partial \text{NO}_3}{\partial t} = \Omega \text{NH}_4 - V_m f(I) \left[ \frac{\text{NO}_3}{K_u + \text{NO}_3} e^{-\rho \text{NH}_4} \right] P, \quad (A12)
\]

\[
\frac{\partial \text{NH}_4}{\partial t} = \frac{f_{ln}}{\phi D + \Gamma Z} - V_m f(I) \left[ \frac{\text{NH}_4}{K_u + \text{NH}_4} \right] P - \Omega \text{NH}_4, \quad (A13)
\]

\[
\frac{\partial P}{\partial t} = V_m f(I) \left[ \frac{\text{DIN}}{K_u + \text{DIN}} \right] P - R_m \left[ 1 - e^{-\lambda P} \right] Z - \Xi P, \quad (A14)
\]

\[
\frac{\partial Z}{\partial t} = R_m \left[ 1 - e^{-\lambda P} \right] Z - \Gamma Z, \quad (A15)
\]

\[
\frac{\partial D}{\partial t} = R_m \left[ 1 - e^{-\lambda P} \right] Z + \Xi P - \phi D - w_d \frac{\partial D}{\partial z}, \quad (A16)
\]
\[ T_S = \text{NO}_3 + \text{NH}_4 + P + Z + D, \quad (A17) \]

and, here
\[ \text{DIN} = \text{NO}_3 + \text{NH}_4, \quad (A18) \]

[48] The $f$-ratio can either be computed based upon the fluxes ($f_s(1)$), similarly to the other two models,
\[ f_s(1) = \frac{f_{\text{up}} - (f_{\text{anz}} + f_{\text{dn}})}{f_{\text{up}}}, \quad (A19) \]

or based upon the uptake ratios in a similar fashion as the observed $f$-ratio ($f_s(2)$),
\[ f_s(2) = \frac{f_{\text{no3p}}}{{f_{\text{no3p}}} + {f_{\text{nh4p}}}} - \frac{f_{\text{up}} - f_{\text{nh4p}}}{{f_{\text{up}}}} \quad (A20) \]

where $f_{\text{no3p}}$ and $f_{\text{nh4p}}$ are the uptake of nitrate and ammonium by phytoplankton, $f_{\text{up}} = f_{\text{no3p}} + f_{\text{nh4p}}$ is the total flux from DIN to phytoplankton, $f_{\text{anz}}$ and $f_{\text{dn}}$ are the fluxes from zooplankton and detritus to ammonium.

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