

## Review

# NPZ Models of Plankton Dynamics: Their Construction, Coupling to Physics, and Application

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**Nutrient-phytoplankton-zooplankton (NPZ) models have been in use in oceanography for at least three decades, and are still a common research tool. Given the discoveries of the last two decades, particularly concerning the role of bacteria in the plankton, there are questions as to whether NPZ models can still be supported as a useful tool in planktonic research. Here I review the construction of NPZ models, and some of the physical platforms they have been coupled to. I then discuss the applications of NPZ-physical models, and conclude that they still constitute an important and viable research tool, provided that the questions being explored are clearly stated.**

Keywords:

- NPZ models,
- plankton models,
- physical-biological models,
- plankton ecosystem models.

## 1. Introduction

The nutrient-phytoplankton-zooplankton (NPZ) model is a common tool in oceanographic research. The NPZ model incorporates one of the simplest sets of dynamics that usefully describe oceanic plankton dynamics. Their acceptability as a research tool is by no means universal, however. In a review of a recent manuscript in which we used an NPZ model (now published as Franks and Chen, 2000), one of our anonymous reviewers commented, "The real world cannot be modeled with a 3-compartment NPZ model that agrees (possibly fortuitously) with satellite images. ... even in open ocean systems the scientific community has long-abandoned the use of 3-compartment models." This attitude reflects a common bias in modelling—that a more complicated model is necessarily a better model. While there are fine examples of detailed models in the literature (e.g., Baretta *et al.*, 1995; Carlotti and Wolf, 1998), I would argue that *there is no compelling reason to reject the NPZ model until it is clear that it cannot describe the system being studied*. The choice of the biological model (and indeed the physical model) should be determined by the questions being asked, and data available—not driven by the fact that more complicated models exist. Modelling studies should proceed from a thorough understanding of the simplest models, to detailed investigations of more complicated models when it is clear that a simple model cannot work for

the given problem.

NPZ models have the useful attributes that they have few parameters (and can thus be more reliably parameterized with existing data than a more complicated model), the limited number of state variables ( $N$ ,  $P$  and  $Z$ ) allows for analytical solutions under some circumstances, they are more easily explored and understood, and they are more easily initialized and tested against data than more complicated models. While these attributes may render them less realistic, they still allow for a wide range of model behaviors which are sufficient to give realistic simulations of some ecosystem dynamics.

In the sections that follow I review almost three decades of research using NPZ models. This review is by no means exhaustive, and I apologize to those whose work I have slighted by not including it here. I am quite restrictive in my analysis, considering only 3-compartment NPZ models. Still, many of the observations and conclusions apply equally to more complex models. First I explore the construction of an NPZ model, describing the mathematical forms used to simulate the ecosystem dynamics. I then explore how NPZ models have been coupled to physical models, and how these coupled models have been used to explore physical-biological interactions in the ocean. Finally, I discuss some of the philosophical issues associated with using NPZ models in research.

## 2. Constructing an NPZ Model

An NPZ model has, by definition, three state variables: nutrients, phytoplankton and zooplankton. These are usually modelled in terms of their nitrogen content,

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Table 1. Some functional forms for  $f(I)$ , the phytoplankton response to irradiance  $I$ . In some implementations, a second parameter  $P_{\max}$ , the maximal photosynthetic rate, will be multiplied by the functional forms below.

Functional form	Description
$\frac{I}{I_o}$	Linear response
$\frac{I}{I_o + I}$	Saturating response
$1 - \exp\left(-\frac{I}{I_o}\right)$	Saturating response
$\tanh\left(\frac{I}{I_o}\right)$	Saturating response
$\frac{I}{I_o} \exp\left(1 - \frac{I}{I_o}\right)$	Saturating and photo-inhibiting response. Parameter $I_o$ determines irradiance at photosynthesis maximum.

since nitrogen is often limiting to primary production in the ocean. The first issue in putting an NPZ model together is the choice of transfer functions—the functional forms joining the various state variables to each other. The choice of functional form is critical to the dynamics of the model, and may constrain the parameterization of the model (the choice of coefficients such as the maximal grazing rate, or half-saturation constant for nutrient uptake).

A general set of NPZ model equations can be written:

$$\begin{aligned} \frac{dP}{dt} &= f(I)g(N)P - h(P)Z - i(P)P, \\ \frac{dZ}{dt} &= \gamma h(P)Z - j(Z)Z, \\ \frac{dN}{dt} &= -f(I)g(N)P + (1 - \gamma)h(P)Z + i(P)P + j(Z)Z. \end{aligned} \quad (1)$$

In an NPZ model there are 5 transfer functions to consider: phytoplankton response to light  $f(I)$ , phytoplankton nutrient uptake  $g(N)$ , zooplankton grazing  $h(P)$ , and phytoplankton  $i(P)$  and zooplankton  $j(Z)$  loss terms due to death, excretion, and predation by organisms not included in the model. Zooplankton assimilation  $\gamma$  may also be important, though it is typically modelled as a simple linear function of food ingested.

Some of the functional forms that have been used to describe phytoplankton response to irradiance  $f(I)$  are given in Table 1. These range from a simple linear response to incident light, to nonlinear forms with a saturating and photoinhibiting response. Some forms are chosen for their ease of integration over a diel period, while

others are attempts to more accurately parameterize the nonlinear response of photosynthesis to irradiance. While all the functional forms in Table 1 can be written with 1 parameter, several parameters are often used. For example,  $\alpha P_{\max}$  is sometimes used in place of  $I_o$ , though mathematically unnecessarily. The use of multiple parameters may, however, aid in parameterizing the transfer functions based on laboratory data.

Most commonly nutrient uptake by phytoplankton  $g(N)$  is modelled by a saturating rectangular hyperbola—the Michaelis-Menten formulation (Table 2). This formulation was introduced to phytoplankton ecology by Dugdale in 1967, in analogy with chemical reaction kinetics. Droop (1973, 1983) argued that phytoplankton show luxury uptake of nutrients—they are stored in an internal pool  $Q$  before they are used for growth, allowing uptake to be uncoupled from growth. It has also been argued that only the most limiting process (photosynthesis or nutrient uptake) should determine the growth rate, allowing for switching between the two types of limitation depending on circumstances.

Zooplankton grazing ( $h(P)$  in Eq. (1)) has always presented a problem in NPZ models. Though most formulations show a saturating response to increasing food (Table 3) (e.g., the Ivlev response), they may also include grazing thresholds (usually denoted  $P_o$  or  $P_i$ ), varying degrees of nonlinearity, and acclimation of the grazing rate to changing food conditions. This nonlinear coupling between  $Z$  and  $P$  is a strong determinant of the dynamics displayed by the NPZ model. Franks *et al.* (1986a) showed that the use of an acclimating grazing response led to more highly damped oscillations in the model, a trait which was felt to be desirable. Parsons *et al.* (1967) introduced the use of a grazing threshold which can stabilize the model, allowing the phytoplankton populations to persist even when grazed to low levels. Murray and Parslow

Table 2. Some common functional forms for  $g(N)$ , the phytoplankton nutrient uptake.

Functional form	Description
$\frac{V_m}{k_s + N}$	Michaelis-Menten uptake: saturating response. Two parameters, $V_m$ and $k_s$ .
$V_m \min(\mu_p, \mu_N)$	Uptake rate determined by the process most limiting to growth ( $\mu$ ): light or nutrients. Potential growth rates usually calculated using Michaelis-Menten uptake, and a functional form from Table 1.
$V_m \left(1 - \frac{k_Q}{Q}\right)$	Luxury uptake: nutrients stored in an internal pool $Q$ , then used up through growth. Requires an equation for nutrient uptake from $Q$ . Minimum cell quota for $Q$ is $k_Q$ .
$\frac{dQ}{dt} = V_m I - \mu_m (1 - k_Q) I$	

Table 3. Some of the functional forms used for  $h(P)$ , the zooplankton grazing on phytoplankton. Note that the units for  $R_m$  and  $\lambda$  are not the same in every case.

Functional form	Description
$R_m P$	Linear
$\min[cP, R_m]$	Bilinear with saturation at $R_m$
$\frac{R_m (P - P_o)}{\lambda + P - P_o}$	Saturating, with lower feeding threshold $P_o$
$\frac{R_m P^n}{\lambda + P^n}, n = 1, 2$	Saturating, with curvature determined by $n$
$R_m [1 - \exp(-\lambda P)]$	Saturating (Ivlev)
$R_m [1 - \exp(-\lambda(P - P_o))]$	Saturating with feeding threshold $P_o$
$R_m \lambda P [1 - \exp(-\lambda P)]$	Acclimating to ambient food—relatively linear at high $P$

(1999) explored the steady-state behavior of 4 different grazing formulations (both saturating and non-saturating), and found that the details of the function were less important than whether the function saturated or not.

The death or loss terms of the phytoplankton  $i(P)$ , and zooplankton  $j(Z)$ , are the “closure” terms of the model (Table 4). These transfer functions allow nutrients in particulate form (phytoplankton and zooplankton) to be recycled back to the dissolved pool, potentially to be taken up again during photosynthesis. While phytoplankton death is almost always modelled as a linear process (though see Murray and Parslow, 1999), zooplankton death is sometimes more complicated. Including a nonlinear death rate usually implies a density-dependent loss rate—higher death rates at higher zooplankton densities. While there is little field evidence supporting the use of such a functional form (but see Ohman and Hirche, 2001), the use of a density-dependent loss rate has significant implications for the model behavior. Steele and Henderson (1992) suggested that the NPZ model was stable with quadratic zooplankton mortality, but showed unforced oscillations with linear mortality. Edwards and

Brindley (1996, 1999; see also Edwards and Yool, 2000) however, showed that both the linear and quadratic mortality terms allowed unforced oscillations, though the linear term allowed oscillations over a wider parameter range. Caswell and Neubert (1998) showed that nonlinear closure terms could cause chaotic oscillations, while Murray and Parslow (1999) explored the ecological relevance of an NPZ model’s behavior with linear vs. nonlinear mortality in relation to nutrient loading of the planktonic ecosystem. They showed that the steady-state phytoplankton biomass did not vary with nutrient loading under linear zooplankton mortality, until limit cycles were reached at the highest loadings. Under quadratic zooplankton mortality, steady-state phytoplankton biomass increased with the loading until phytoplankton uptake or zooplankton grazing became saturated at the highest loads. Such model dynamics call for careful field experimentation and analysis to aid in developing criteria for choosing a particular model formulation.

### 3. Coupling an NPZ Model to a Physical Model

In the most general form, the NPZ model is coupled

Table 4. Some of the functional forms for  $i(P)$ , the phytoplankton death rate, and  $j(Z)$ , the zooplankton death rate.

Form of $i(P)$	Description
$\varepsilon$	Linear
$\varepsilon P$	Quadratic (nonlinear)—density-dependent
Form of $j(Z)$	Description
$\varepsilon$	Linear
$\varepsilon Z$	Quadratic (nonlinear)—density-dependent
$\frac{\varepsilon Z}{b + Z}$	Nonlinear, density dependent but saturating rate (linear) at high zooplankton densities

Table 5. Examples of physical model architectures used to force NPZ models.

Model type	Reference
1D no spatial resolution (only mixed layer forcing)	Evans and Parslow (1985)
1D with turbulence-closure mixed-layer model	Denman and Gargett (1995), Edwards <i>et al.</i> (2000b)
1D mixed-layer model with horizontal resolution	Dippner (1993), Wroblewski <i>et al.</i> (1988), Wroblewski (1989)
1D mixed-layer Lagrangian model coupled to 1.5 layer quasi-geostrophic contour dynamics model	Flierl and Davis (1993)
2D kinematic models (vertical and horizontal)	Evans <i>et al.</i> (1977), Franks <i>et al.</i> (1986b), Klein and Steele (1988), Ishizaka (1990)
2D primitive-equation with turbulence-closure	Chen <i>et al.</i> (1997), Franks and Chen (1996), Franks and Walstad (1997), Edwards <i>et al.</i> (2000a)
3D quasigeostrophic model	Yoshimori and Kishi (1994), McGillicuddy <i>et al.</i> (1995a, b)
3D primitive-equation model	Kishi (1994), Lewis <i>et al.</i> (1994)
3D primitive equation with turbulence-closure	Franks and Chen (2000)

to a physical model through the advection-diffusion equation. Each state variable of the NPZ model will have a separate equation describing its motion in space and time, of the form

$$\begin{aligned} \frac{\partial C}{\partial t} + u \frac{\partial C}{\partial x} + v \frac{\partial C}{\partial y} + (w + w_s) \frac{\partial C}{\partial z} \\ = \kappa_h \left( \frac{\partial^2 C}{\partial x^2} + \frac{\partial^2 C}{\partial y^2} \right) + \kappa_v \frac{\partial^2 C}{\partial z^2} + \text{biological dynamics} \end{aligned} \quad (2)$$

where  $C$  is the concentration of the state variable ( $N$ ,  $P$ , or  $Z$ ),  $u$ ,  $v$  and  $w$  are the horizontal and vertical water velocities determined by the physical model,  $w_s$  is the vertical swimming or sinking speed of the state variable, and  $\kappa_h$  and  $\kappa_v$  are the horizontal and vertical eddy diffusivities. The biological dynamics are given by Eq. (1). As it stands, Eq. (2) is not trivial to solve, even when  $u$ ,  $v$  and  $w$  are prescribed. Typically  $u$ ,  $v$  and  $w$  are obtained from a physical model run simultaneously with the

biological dynamics (though this is by no means necessary if sufficient computer storage is available to retain the physical model results). Some of the physical model platforms that have been used to couple to NPZ models are given in Table 5. These models range from simple one-dimensional (1D) models with biological dynamics averaged over the mixed layer, to full 3D models with high-order turbulence-closure submodels.

Many researchers cast the physical coupling in a simplified form to facilitate finding solutions to the problem. For example, Evans and Parslow (1985) explored a 1D (vertical) model in which the plankton were affected by shoaling and deepening of the mixed layer. For a mixed layer of depth  $z_{ml}$ , the rate of change of mixed layer depth was

$$\frac{dz_{ml}}{dt} = \zeta(t), \quad \text{with } \zeta^+(t) = \max(\zeta(t), 0).$$

With mixing rate  $m$ , this gave physically driven rates of change of  $N$ ,  $P$ , and  $Z$  of

$$\frac{dN}{dt} = \frac{m + \zeta^+}{z_{ml}} (N_o - N),$$

$$\frac{dP}{dt} = -\frac{m + \zeta^+}{z_{ml}} P,$$

$$\frac{dZ}{dt} = \frac{\zeta}{z_{ml}} Z.$$

This set of equations allowed nutrients to be injected into the mixed layer during entrainment (deepening), while the phytoplankton became diffused throughout the mixed layer  $z_{ml}$ . During stratification, the phytoplankton below the new mixed layer  $z_{ml}$  were lost, while the zooplankton density increased as they swam upward with the new pycnocline. This simple physical model allowed Evans and Parslow (1985) to simulate annual cycles of mixing and entrainment.

Flierl and Davis (1993) used a conceptually similar coupling of physics and biology to simulate plankton dynamics along convoluted water parcel trajectories. As the water parcels moved along the curving path, the pycnocline could rise and sink, giving entrainment and mixing with the waters below. This was modelled as a dilution term for the plankton concentration  $C$ , with deep concentration  $C_o$  and entrainment velocity  $w^*$ :

$$\frac{dC}{dt} = \frac{w^*}{z_{ml}} H\left(\frac{w^*}{z_{ml}}\right) (C - C_o); \quad H(>0) = 0, \quad H(<0) = 1.$$

The entrainment velocity is the rate at which fluid crosses the moving base of the mixed layer,  $z_{ml}$ . If  $w^* > 0$ , the mixed layer is entraining, and  $C$  is diluted or increased, depending on the deeper concentration  $C_o$ . When water is downwelling through the mixed layer ( $w^* < 0$ ), the concentration is unaffected, similar to Evans and Parslow's (1985) formulation. Both these models average the biological dynamics over the mixed layer, potentially losing some spatial detail in favor of more simple solutions.

Other means of coupling biological to physical models (in addition to advection and diffusion) include the depth-dependence of irradiance, including the possibility of self-shading of the phytoplankton photosynthesis, and temperature effects on biological dynamics.

#### 4. How have NPZ Models been Used?

In a review of coupled physical-biological models in oceanography (Franks, 1995), I defined three applications of models: theoretical, heuristic, and predictive. These applications answer the questions, "What would

happen if ...?", "How did this happen?", and "What will happen ...?", respectively. The applications of NPZ models can be categorized in the same manner.

One of the most common uses of NPZ models is for theoretical investigations: how does the model behave if different transfer functions are used (e.g., Sjöberg, 1977; Steele and Henderson, 1981, 1992; Franks *et al.*, 1986a; Murray and Parslow, 1999; Ruan, 2001), if different parameters are used (e.g., Jernigan and Tsokos, 1979, 1980; Hastings and Powell, 1991; Ruan, 1993; Abrams and Roth, 1994; McCann and Yodzis, 1994; Truscott and Brindley, 1994; Edwards and Brindley, 1996, 1999; Edwards *et al.*, 2000a, b), or if different physical models are used (Franks, 1997). These investigations explored the array of possible dynamics inherent in the various NPZ model architectures, usually from a mathematical point of view rather than applying the equations to specific data sets. Such investigations are an essential element of any modelling program—without knowing the possible range of behaviors of the model, it is impossible to diagnose and interpret model behaviors in more complicated scenarios (e.g., when the NPZ model is coupled to a physical model). All these investigations have shown that NPZ models display a wide range of behaviors, from highly damped adjustments to initial conditions, to chaotic oscillations in time.

Other theoretical investigations have concentrated less on the model structure and parameterization, and more on the biological implications of the model. Evans (1978) and Evans *et al.* (1977) coupled the simple NPZ model to a kinematic physical model of vertical shear to explore how the interaction of vertical migration with vertical shear could lead to patchiness of plankton. Steele and Frost (1977) used an elaboration of an NPZ model to investigate the factors controlling the size structure of the phytoplankton. Kiefer and Atkinson (1984) used an NPZ model to study nitrogen cycling efficiency in the plankton. All these theoretical models used the NPZ framework as a hypothesis-testing tool. The model was used as a mathematical articulation of a hypothesis, which was then tested by running the model in various configurations and parameterizations.

More recently the NPZ model form has been used successfully in a heuristic sense, exploring the dynamics underlying particular observations in the field. Evans and Parslow (1985) used their model to understand the factors controlling the very different annual plankton cycles in the Atlantic and Pacific oceans. Using different forcing functions (vertical mixing cycles), they were able to reproduce the highly damped oscillations characteristic of the North Pacific, versus the strongly oscillatory North Atlantic spring phytoplankton bloom. A similar study was undertaken by Denman and Gargett (1995) using more elaborate physical models (see Table 5).

On shorter time scales, Marra and Ho (1993), Dippner (1993), Wroblewski *et al.* (1988), Wroblewski (1989), and McGillicuddy *et al.* (1995a, b) used NPZ models to explore the spring phytoplankton bloom. The NPZ model was usually the Franks *et al.* (1986a) formulation, coupled to a range of physical frameworks. Marra and Ho (1993) found that the Droop (1973, 1983) modification to the nutrient uptake (Table 2) was necessary to obtain a good simulation of the increase of phytoplankton biomass and the uptake of nutrients during the bloom.

Coupling the NPZ ecosystem model to a variety of physical models has allowed exploration of a range of physical-biological interactions in the ocean. Klein (1987), Lewis *et al.* (1994), and Franks and Chen (1996, 2000) have all explored the plankton dynamics on Georges Bank. The models have been used to investigate the importance of closed circulation around the bank, wind events over the bank, and the influence of tidal forcing on production on the bank. Similarly, Ishizaka (1990) and Chen *et al.* (1997) used coupled NPZ-physical models to study the influence of physical forcing on shelf ecosystems.

Mesoscale motions in the ocean are particularly suited for study using NPZ models, due to the close match of physical and biological spatial and temporal scales. Franks and Walstad (1997) coupled the Franks *et al.* (1986a) NPZ model to a primitive-equation model with turbulence-closure to investigate the effects of wind events on plankton patchiness at fronts. Flierl and Davis (1993) explored the plankton dynamics of Gulf Stream meanders using a clever reduction of a complex physical and biological model to a more tractable system. Franks *et al.* (1986b), Kishi (1994), and Yoshimori and Kishi (1994) used NPZ models to investigate the influences of mesoscale eddies on plankton dynamics in the ocean. Edwards *et al.* (2000a) coupled the Franks *et al.* (1986a) NPZ model to a physical model of wind-driven coastal upwelling to explore the types of patchiness generated in microzooplankton-dominated versus mesozooplankton-dominated plankton communities.

While many of the models discussed above made only qualitative comparisons to oceanographic data, some had success in making quantitative comparisons to various types of field data. There are three main types of data for comparing to model output: biomasses, rates, and derived quantities. Obtaining good agreement of field-measured biomasses and the values of the state variables is a primary (but not sole) requirement for accepting a model as a description of the system under investigation. NPZ models tend to be very good at reproducing biomasses of nutrients and phytoplankton. Comparison of modelled zooplankton with data tends to be less revealing, mainly because of the paucity of zooplankton data, and the difficulty in converting it to the modelled form (usually ni-

trogen content). The launching of new remote-sensing instruments (e.g., OCTS and SeaWiFS) is generating new, spatially resolved, synoptic data sets of surface phytoplankton biomass. These maps of phytoplankton provide a stronger constraint on coupled physical-biological models than point measurements of biomass, as they include a great deal of spatial detail. The level of detail that can be reproduced by the model depends on the physical model employed. Franks and Chen (2000) for example, had excellent success in comparing their 3D model to satellite images of the Gulf of Maine and Georges Bank. The model and satellite data had similar spatial resolution, and the model contained many (but clearly not all) of the dynamics necessary to reproduce the dominant biological features in this region.

Comparing biological rates between the model and data adds a further constraint on the model as a possible descriptor of the system. The rates usually chosen for comparison are primary production and nutrient uptake, though zooplankton grazing is also used. Rates of primary production are commonly measured in field programs, and should be used as a second test of model applicability. Nutrient uptake rates are less commonly measured, but also provide a strong constraint on the model. The more types of data used to test the model, the more confident the scientist can be in the model output. Franks and Chen (1996, 2000) showed that their simple NPZ model coupled to 2D and 3D physical models of tidally forced flows over Georges Bank gave excellent reproductions of primary productivity and nutrient uptake rates measured in that region. Furthermore, nutrient regeneration rates ( $h(P)$ ,  $i(P)$  and  $j(Z)$  in Eq. (1)) also agreed well with field data. Combining the biological and physical dynamics allowed quantification of the nutrient fluxes onto and off of the bank, which also gave good agreement with existing field data.

Derived quantities such as the  $f$  ratio (Eppley and Peterson, 1979) can also be used to test model output. The  $f$  ratio is the ratio of "new" production to total production. New production is primary production supported by nutrients from outside the local euphotic zone. The main source of new nutrients is physical mixing from the deep pool in the aphotic zone, particularly in regions of wind- and tidally dominated flows. New nutrients are usually in an oxidized form, typically nitrate. Nutrients lost from the particulate phase (phytoplankton death, zooplankton excretion and death) are usually in a reduced form—ammonium. While an NPZ model cannot (by definition) resolve nitrate and ammonium, it can follow the dynamics that would control the presence of these two forms in the euphotic zone. One technique is to assume that all nutrients below the euphotic zone are in the form of nitrate, while all biologically generated nutrients are in the form of ammonium. During the model runs the

physical and biological fluxes of these forms can be tracked and quantified for comparison to data (e.g., Franks *et al.*, 1986b). A second technique is to note that ammonium is taken up in preference to nitrate. Thus, if the phytoplankton nutrient uptake is balanced by excretion, new production will be negligible. However, if the excretion rate is too low to account for phytoplankton nutrient uptake, another source must be present—new nutrients. Thus the total production *not* accounted for by excretion ( $h(P)$ ,  $i(P)$  and  $j(Z)$  in Eq. (1)) must be new production. This term is relatively easy to calculate, and gives excellent agreement with data in some cases (e.g., Franks and Chen, 1996, 2000).

So far as I could find from the literature, NPZ models have not been used for predictive purposes. While they have been used successfully in hindcasting certain data types (e.g., Ishizaka, 1990), they have not, to my knowledge, been used in any operational sense to predict biological dynamics.

## 5. Discussion

I have described how NPZ models can be constructed, how they have been coupled to physical models, and how they have been employed in oceanographic studies. It is appropriate then, to revisit the original point concerning the general utility of NPZ models.

An NPZ model, like all mathematical models, is a mathematical manifestation of a hypothesis. The hypothesis concerns the dynamics that are presumed to underlie the observations. Inherent in the NPZ model is the assumption that the mathematical formulation captures the dominant dynamics of the biological system. So under what conditions is an NPZ model an appropriate description of the system?

Clearly an NPZ model cannot capture our best understanding of how the planktonic ecosystem works. On the other hand, there is no single model that does; nor would it necessarily be useful. The NPZ model is a simplification of an extremely complex system, and it must be used and applied carefully and appropriately. Before deciding what type of model to use, *it is essential to make a clear statement about the question being asked*. Very different models would be used, for example, to study patterns of primary production in mesoscale eddies versus studying the effects of turbulence on phytoplankton community structure. There are certainly occasions in which an NPZ model is a completely inappropriate tool. On the other hand, there are many instances in which the NPZ model is the best tool to begin the investigation.

Another way of putting the question posed above is, “When should we reject the NPZ model as an appropriate descriptor of the system under study?” The answer to this is not as obvious as it might seem at first. A simple answer would be that the NPZ model must be rejected

when it does not fit the data. But to do this in a practical sense, we must first decide which data are to be used as a test. These data should be independent of the data used to parameterize the model. Second, we have to decide on criteria by which the model will be judged. These criteria should be objective and quantitative. However, comparing a model to any particular data set will almost certainly give bad results—the data give a single realization of a few variables from a huge set of complex and nonlinear interactions. There is error associated with every measurement, and parallel experiments (if this is possible) will almost certainly give different results. Do we reject one of the experiments because it does not agree with the other? Typically not; we perform some statistical test to find a more robust descriptor of the system, such as the mean or median. We must be careful, then, in rejecting a model as a descriptor of the system. We need to find out how sensitive the model is to variations in parameters and transfer functions; to explore the conditions under which the model might accommodate the variability inherent in the data. It is only after the model has been exhaustively explored that it should be rejected, and a new model (hypothesis) sought. If the model cannot be rejected, then it can tentatively be accepted as an adequate descriptor of the system being studied *for the questions being asked*. The model may be a completely inappropriate system descriptor for other types of questions.

The relative simplicity of NPZ models makes them appealing tools for many questions. It becomes increasingly difficult to carry out the tests described above for models with more state variables. Finding analytical solutions becomes impossible (except in the cases when state variables go extinct), and exploring the range of possible behaviors and sensitivity of complex models is a daunting task. In addition, parameterizing, initializing, and testing a more detailed model is difficult with the data available from most field programs.

New techniques of data assimilation are proving fruitful for facilitating model-data comparisons. Ishizaka (1990) was probably the first to assimilate data into a coupled physical-biological model. He found that assimilating phytoplankton data into the NPZ model improved the model's skill at predicting future data. However, data assimilation is not just for improving model forecasts. Certain techniques can also be used to obtain more accurate parameterizations of the models, and used to give objective measures of the model's skill in describing the data. The adjoint method uses a cost function (the “adjoint”) to allow parameter estimation of a model using data. Lawson *et al.* (1995) used a model to generate data which were then subsampled and used to parameterize a model with the same number of state variables. The skill of the technique depended a great deal on the subsampling scheme used, as well as the form of the

generating model. A great deal more research is required to understand how we can exploit techniques such as these in improving our ability to model marine ecosystems.

My conclusion, then, is that NPZ models provide a robust platform for oceanographic research. They are particularly good tools for initial investigations of physical-biological dynamics, and give a good picture of the general planktonic community response to physical forcing. They constitute an appropriate tool for many scientific questions, and can give robust quantitative simulations of many types of dynamics. On the other hand, there is a great deal that NPZ models cannot tell us about the workings of the ocean, and it is important to continue to develop and test new models of planktonic dynamics.

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### References

- Abrams, P. A. and J. D. Roth (1994): The effects of enrichment of three-species food chains with nonlinear functional responses. *Ecology*, **75**, 1118–1130.
- Baretta, J. W., W. Ebenhoh and P. Ruardij (1995): The European Regional Seas Ecosystem Model, a complex marine ecosystem model. *Netherlands Journal of Sea Research*, **33**, 233–246.
- Carlotti, F. and K. U. Wolf (1998): A Lagrangian ensemble model of *Calanus finmarchicus* coupled with a 1-D ecosystem model. *Fish. Oceanogr.*, **7**, 191–204.
- Caswell, H. and M. G. Neubert (1998): Chaos and closure terms in plankton food chain models. *J. Plankton Res.*, **20**, 1837–1845.
- Chen, C., D. A. Wiesenburg and L. Xie (1997): Influences of river discharge on biological production in the inner shelf. A coupled biological and physical model of the Louisiana-Texas shelf. *J. Mar. Res.*, **55**, 293–320.
- Denman, K. L. and A. E. Gargett (1995): Biological/physical interactions in the upper ocean: the role of vertical and small scale transport processes. *Annu. Rev. Fluid. Mech.*, **27**, 225–255.
- Dippner, J. W. (1993): A Lagrangian model of phytoplankton growth dynamics for the Northern Adriatic Sea. *Cont. Shelf Res.*, **13**, 331–355.
- Droop, M. R. (1973): Some thoughts on nutrient limitation in algae. *J. Phycol.*, **9**, 264–272.
- Droop, M. R. (1983): 25 years of algal growth kinetics. *Botanica Marina*, **26**, 99–112.
- Dugdale, R. C. (1967): Nutrient limitation in the sea: dynamics, identification, and significance. *Limnol. Oceanogr.*, **12**, 685–695.
- Edwards, A. M. and J. Brindley (1996): Oscillatory behavior in a three-component plankton population model. *Dyn. Stab. Syst.*, **11**, 347–370.
- Edwards, A. M. and J. Brindley (1999): Zooplankton mortality and the dynamical behaviour of plankton population models. *Bull. Math. Biol.*, **61**, 303–339.
- Edwards, A. M. and A. Yool (2000): The role of higher predation in plankton population models. *J. Plankton Res.*, **22**, 1085–1112.
- Edwards, C. A., H. P. Batchelder and T. M. Powell (2000a): Modeling microzooplankton and macrozooplankton dynamics within a coastal upwelling system. *J. Plankton Res.*, **22**, 1619–1648.
- Edwards, C. A., T. A. Powell and H. P. Batchelder (2000b): The stability of an NPZ model subject to realistic levels of vertical mixing. *J. Mar. Res.*, **58**, 37–60.
- Eppley, R. W. and B. J. Peterson (1979): Particulate organic matter flux and planktonic new production in the deep ocean. *Nature*, **282**, 677–680.
- Evans, G. T. (1978): Biological effects of vertical-horizontal interactions. p. 157–179. In *Spatial Patterns in Plankton Communities*, ed. by J. H. Steele, Plenum Press, New York.
- Evans, G. T. and J. S. Parslow (1985): A model of annual plankton cycles. *Biol. Oceanogr.*, **3**, 327–347.
- Evans, G. T., J. H. Steele and G. E. B. Kullenberg (1977): A preliminary model of shear diffusion and plankton populations. Scottish Fisheries Res. Proj. Report #9.
- Flierl, G. R. and C. S. Davis (1993): Biological effects of Gulf Stream meandering. *J. Mar. Res.*, **51**, 529–560.
- Franks, P. J. S. (1995): Coupled physical-biological models in oceanography. *Rev. Geophys.*, Supp. July, 1177–1187.
- Franks, P. J. S. (1997): New models for the exploration of biological processes at fronts. *I.C.E.S. J. Mar. Sci.*, **54**, 161–167.
- Franks, P. J. S. and C. Chen (1996): Plankton production in tidal fronts: a model of Georges Bank in summer. *J. Mar. Res.*, **54**, 631–651.
- Franks, P. J. S. and C. Chen (2000): A 3-D prognostic numerical model study of the Georges Bank ecosystem. Part II: biological-physical model. *Deep-Sea Res. II*, **48**, 457–482.
- Franks, P. J. S. and L. J. Walstad (1997): Plankton patches at fronts: a model of formation and response to wind events. *J. Mar. Res.*, **55**, 1–29.
- Franks, P. J. S., J. S. Wroblewski and G. R. Flierl (1986a): Behavior of a simple plankton model with food-level acclimation by herbivores. *Mar. Biol.*, **91**, 121–129.
- Franks, P. J. S., J. S. Wroblewski and G. R. Flierl (1986b): Prediction of phytoplankton growth in response to the frictional decay of a warm-core ring. *J. Geophys. Res.*, **91C**, 7603–7610.
- Hastings, A. and T. Powell (1991): Chaos in a 3-species food chain. *Ecology*, **72**, 896–903.
- Ishizaka, J. (1990): Coupling of coastal zone color scanner data to a physical-biological model of the south-eastern U.S. Continental Shelf ecosystem 3. Nutrient and phytoplankton fluxes and CZCS data assimilation. *J. Geophys. Res.*, **95**, 20201–20212.
- Jernigan, R. W. and C. P. Tsokos (1979): Phytoplankton modeling involving random rate constants. Part I: Deterministic setting. *Intern. J. Env. Std.*, **14**, 97–105.
- Jernigan, R. W. and C. P. Tsokos (1980): Phytoplankton modeling involving random rate constants. Part II: stochastic



- formulation. *Intern. J. Env. Std.*, **15**, 217–227.
- Kiefer, D. A. and C. A. Atkinson (1984): Cycling of nitrogen by phytoplankton: a hypothetical description based upon efficiency of energy conversion. *J. Mar. Res.*, **42**, 655–675.
- Kishi, M. J. (1994): Prediction of phytoplankton growth in a warm-core ring using three dimensional ecosystem model. *J. Oceanogr.*, **50**, 489–498.
- Klein, P. (1987): A simulation of some physical and biological interactions. p. 395–402. In *Georges Bank*, ed. by R. H. Backus and D. W. Bourne, The MIT Press, Cambridge, Massachusetts.
- Lawson, L. M., Y. H. Spitz, E. E. Hofmann and R. B. Long (1995): A data assimilation technique applied to a predator-prey model. *Bull. Math. Biol.*, **57**, 593–617.
- Lewis, C. V. W., C. S. Davis and G. Gawarkiewicz (1994): Wind-forced biological-physical interactions on an isolated off-shore bank. *Deep-Sea Res. II*, **41**, 51–73.
- Marra, J. and C. Ho (1993): Initiation of the spring bloom in the northeast Atlantic (47°N, 20°W): a numerical simulation. *Deep-Sea Res. II*, **40**, 55–73.
- McCann, K. and P. Yodzis (1994): Nonlinear dynamics and population disappearances. *Am. Nat.*, **144**, 873–879.
- McGillicuddy, D. J., J. J. McCarthy and A. R. Robinson (1995a): Coupled physical and biological modeling of the spring bloom in the North-Atlantic. 1. Model formulation and one dimensional bloom processes. *Deep-Sea Res. I*, **42**, 1313–1357.
- McGillicuddy, D. J., A. R. Robinson and J. J. McCarthy (1995b): Coupled physical and biological modeling of the spring bloom in the North-Atlantic. 1. 3-dimensional bloom and post-bloom processes. *Deep-Sea Res. I*, **42**, 1359–1398.
- Murray, A. G. and J. S. Parslow (1999): The analysis of alternative formulations in a simple model of a coastal ecosystem. *Ecol. Modelling*, **119**, 149–166.
- Ohman, M. D. and H. J. Hirche (2001): Density-dependent mortality in an oceanic copepod population. *Nature*, **412**, 638–641.
- Parsons, T. R., R. J. LeBrasseur and J. D. Fulton (1967): Some observations on the dependence of zooplankton grazing on cell size and concentration of phytoplankton blooms. *J. Oceanogr. Soc. Japan*, **23**, 10–17.
- Ruan, S. G. (1993): Persistence and coexistence in zooplankton-phytoplankton-nutrient models with instantaneous nutrient cycling. *J. Math. Biol.*, **31**, 633–654.
- Ruan, S. G. (2001): Oscillations in plankton models with nutrient recycling. *J. Theor. Biol.*, **208**(1), 15–26.
- Sjöberg, S. (1977): Are pelagic ecosystems inherently unstable? A model study. *Ecol. Modelling*, **3**, 17–37.
- Steele, J. H. and B. W. Frost (1977): The structure of plankton communities. *Phil. Trans. R. Soc. Lond.*, **280**, 485–534.
- Steele, J. H. and E. W. Henderson (1981): A simple plankton model. *Am. Nat.*, **117**, 676–691.
- Steele, J. H. and E. W. Henderson (1992): The role of predation in plankton models. *J. Plankton Res.*, **14**, 157–172.
- Truscott, J. E. and J. Brindley (1994): Equilibria, stability and excitability in a general class of plankton population models. *Phil. Trans. R. Soc. Lond.*, **A347**, 703–718.
- Wroblewski, J. S. (1989): A model of the spring bloom in the North Atlantic and its impact on ocean optics. *Limnol. Oceanogr.*, **34**, 1563–1571.
- Wroblewski, J. S., J. L. Sarmiento and G. R. Flierl (1988): An ocean basin scale model of plankton dynamics in the North Atlantic 1. Solutions for the climatological oceanographic conditions in May. *Global Biogeochem. Cycles*, **2**, 199–218.
- Yoshimori, A. and M. J. Kishi (1994): Effects of interaction between two warm-core rings on phytoplankton distribution. *Deep-Sea Res. I*, **41**, 1039–1052.