Responses of the ocean planktonic ecosystem to finite-amplitude perturbations

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Abstract The responses of the ocean planktonic ecosystem to finite-amplitude perturbations are investigated using an ocean planktonic ecosystem model. Through changing the higher predation rate on zooplankton, multiple equilibria of the model, namely "high-nutrient" and "low-nutrient" states, are obtained under certain parameter values. Based on these states, the perturbations with maximum nonlinear growth are determined using the conditional nonlinear optimal perturbation (CNOP) method. The linear and nonlinear evolutions of the CNOP perturbation are compared. The results show that the nonlinear evolution of the perturbation leads to predator–prey oscillations with larger amplitude than the linear evolution. Besides, after the perturbation amplitude exceeds a critical value, the nonlinear evolution of the perturbation will induce the linearly stable ecosystem state to lose the stability and become nonlinearly unstable. This implies that nonlinear processes have important impacts on the stability of the ecosystem. Specifically, we identify the nonlinear processes related to zooplankton grazing to impact the stability most for the high-nutrient state, while for the low-nutrient state the main nonlinear process affecting the stability is the uptake process. These results help to improve our understanding of the sensitivity of the oceanic ecosystem model to finite-amplitude perturbations and the underlying nonlinear stability properties.

1. Introduction

Ocean plankton is the basis of the marine food chain. The variations of the planktonic ecosystem have important effects on marine fisheries production and thus affect economic resources. Oceanic plankton also plays an important role in the global carbon cycle, through transferring atmospheric carbon dioxide (CO2) into the deep ocean, which may influence global climate change. Hence, studies of the ocean planktonic ecosystem have attracted attention of both scientists and ecosystem managers.

Numerical modeling is a useful tool for studying the planktonic ecosystem, especially for investigating the effects of various environmental conditions on the ecosystem. A number of different models with varying levels of complexity have been developed to study the planktonic ecosystem in different marine regions. Their complexity ranges from simple three-variable nutrient–phytoplankton–zooplankton (NPZ) type models [Steele and Henderson, 1981; Franks et al., 1986; Ruan, 1993; Edwards and Brindley, 1996; Franks, 2002] to four-variable nutrient–phytoplankton–zooplankton–detritus (NPZD) type models [Edwards, 2001; Ji et al., 2008; Heinle and Slawig, 2013], and to even more complex models containing multiple nutrients and different plankton types [Gregg et al., 2003; Moore et al., 2004]. In the last decade, researchers mainly focused on understanding the effects of physical ocean processes on the planktonic ecosystem in different regions by coupling some of these ecosystem models with physical models [e.g., Franks and Chen, 2001; Losa et al., 2006; Ji et al., 2008]. However, the investigation for the intrinsic dynamics of the planktonic ecosystem model without coupling to a physical model has not been widespread, as noted by Lima et al. [2002].

Fortunately, a few studies have started to investigate the steady states of some simple ecosystem models (such as the NPZ and NPZD type models) and their linear stabilities [Edwards and Brindley, 1996; Newberger et al., 2003; Spitz et al., 2003; Lüptien, 2011; Heinle and Slawig, 2013]. Besides, Truscott and Brindley [1994] examined the rapid transient growth of the plankton based on a steady state of a phytoplankton–zooplankton model. However, the nonlinear processes in the planktonic ecosystem model make it difficult to analytically study the internal dynamics of the model. So Healey et al. [2009] linearized a simple nonlinear model around a steady state and then examined the responses of the linearized model to optimally initial perturbations to reveal the basic dynamics of the model. They regarded the perturbations as small changes to the stable state that may be induced by eddy advection, mixing, or mixed layer depth variability and so on.
It is worth noting that the aforementioned studies are based on a linear theory analysis which implicitly assumes that the nonlinearities of the system are relatively weak, and that the perturbations are sufficiently small so that the linear approximation is valid. However, strong nonlinear interactions among state variables in planktonic ecosystem model are known to exist. The perturbations caused by external forcing variations are generally not infinitely small, but finite-amplitude. So the linear method may not accurately represent the basic dynamics of the ecosystem model.

We also note that previous studies have shown that many planktonic ecosystem models can exhibit multiple linearly stable equilibria for certain parameter values and hysteresis behavior [Edwards and Brindley, 1996; Edwards, 2001; Yoshiyama and Nakajima, 2002; Collie et al., 2004]. Much attention has been paid to the abrupt transitions between the different ecosystem states that occur in some marine regions such as the North Pacific Ocean, the English Channel, and the Georges Bank [e.g., Scheffer et al., 2001; Collie et al., 2004]. In theory, the linear evolution of a small perturbation should not induce a transition, because the equilibria are linearly stable; however, it is interesting to investigate if the transition could occur because of nonlinear instability caused by nonlinear evolution of finite-amplitude perturbations. Several questions need to be answered. How much is the minimal amplitude of the perturbation that causes the transition? What is the nonlinear stability boundary of linearly stable ecosystem state? What roles do the nonlinear processes play in the abrupt transition? These difficult nonlinear problems, which have otherwise received little attention, are addressed in this study.

Here, we use a nonlinear approach, called Conditional Nonlinear Optimal Perturbation (CNOP) [Mu et al., 2003; see subsection 2.2], to study the response of a planktonic ecosystem model to finite-amplitude perturbations, an attempt to overcome the limitations of linear approximation method and reveal the importance of nonlinear processes. The planktonic ecosystem model used here is a NPZD type model proposed by Edwards [2001], which will be introduced in subsection 2.1. Although the model framework is relatively simple, this type of model has been shown to be able to capture the essential features of realistic marine ecosystem dynamics, as discussed by Ji et al. [2008], and is the core of some complex planktonic ecosystem models. We believe that the present study can provide insight into the nonlinear stability of the ecosystem model and the associated sensitivity, allowing us to understand the simulation results when the model is coupled to a physical model.

This paper is organized as follows. The NPZD model and the CNOP method are introduced in section 2. Section 3 investigates the linear and nonlinear responses of the planktonic ecosystem to finite-amplitude perturbations and reveals the impact of the nonlinearities on the evolution of the perturbations. Section 4 gives a summary. A discussion is presented in section 5.

2. Methods

2.1. Model Formulations

In this study, all the numerical experiments are performed using a zero-dimensional (0D) NPZD ecosystem model simulating the interactions between the four variables: nutrients, phytoplankton, zooplankton, and detritus. This model was developed by Edwards [2001] following Steele and Henderson [1981]. Similar models have frequently been coupled to a variety of physical models to reproduce a realistic planktonic ecosystem in some marine regions [e.g., Chen et al., 1999; Olascoaga et al., 2005; Ji et al., 2008; Tsiaras et al., 2008].

Assuming that the mixed layer is spatially homogeneous, the changes in nutrients, phytoplankton, zooplankton, and detritus are represented by,

$$\frac{dN}{dt} = \frac{a}{e+N} a \frac{P}{b+P} \text{uptake} - \frac{b_1 N P^2}{\mu^2 + P^2} \frac{Z}{excretion} + \gamma m Z^2 + \phi D \text{remineralization} + k (N_0 - N)$$

$$\frac{dP}{dt} = \frac{N}{e+N} a \frac{P}{b+P} \text{uptake} - \frac{P}{\mu^2 + P^2} \frac{Z}{growth} - \frac{r P}{\mu^2 + P^2} \frac{Z}{mortality} - \frac{P}{\mu^2 + P^2} \frac{Z}{sinking} - \frac{P}{\mu^2 + P^2} \frac{Z}{higher \ predation}$$

$$\frac{dZ}{dt} = \frac{2 b_1 P^2}{\mu^2 + P^2} \frac{Z}{growth} - \frac{m Z^2}{higher \ predation}$$

(1) (2) (3)
where $N, P, Z,$ and $D$ are, respectively, the concentrations (units in g C m$^{-3}$) of nutrients, phytoplankton, zooplankton, and detritus; $t$ represents the time in days. The concentrations and parameters have been converted to the appropriate units using the equivalences

$1 \text{ g carbon} \equiv 20 \text{ mg chlorophyll} \equiv 10 \text{ mmol nitrogen},$ as used by Steele and Henderson [1981].

The function of each term in the equations (1–4) is labeled. A detailed description was given by Edwards and Brindley [1996] and Edwards [2001]. Here, we repeat some essential aspects of the functional forms and the definitions of the parameters to be self-contained. The concentration of nutrients below the mixed layer is assumed to be a constant $N_0.$ The depth of the mixed layer is fixed at 12.5 m, a value derived from the observational data at Bermuda Station “S” (32° 10′ N, 64° 30′ W) and Ocean Weather Station “India” (59° N, 19° W) in the North Atlantic Ocean during summer [Fasham, 1993; Steele and Henderson, 1993]. The mixed layer depth is implicitly incorporated into the parameters $a, k, s,$ and $\psi,$ as pointed out by Edwards [2001].

Following Steele and Henderson [1981], the Michaelis-Menten function $N/(e+N)$ simulates the nutrient uptake by the phytoplankton with a half-saturation constant $e.$ The term $a/(b+cP)$ represents the nonnutrient-limited phytoplankton growth, which decreases due to light attenuation by water $b,$ and the self-shading effect of the phytoplankton $c.$ The parameter $a$ is defined by $a=2.58G_p/\text{MLD}$ according to Steele and Frost [1977], where $G_p$ is the maximum phytoplankton growth rate under optimal light conditions and MLD is the depth of the mixed layer. $G_p$ is taken as 1.25 d$^{-1},$ a value used by Fasham [1993] to reproduce the observed features at the Ocean Weather Station “India.” This approximately results in $a=0.2$ m$^{-1}$ d$^{-1},$ which makes the maximum phytoplankton growth rate $a/b=1.$ The Holling Type III function $G_pZ^\beta/(\mu^2 + P^\beta)$ represents zooplankton grazing on phytoplankton, with a maximum grazing rate $\lambda,$ and half-saturation constant $\mu.$ A fraction $\alpha$ of the grazed phytoplankton contributes to the zooplankton growth and a fraction $\beta$ is excreted by zooplankton and is converted into nutrient. The remaining fraction $1-\alpha-\beta$ enters the detritus compartment. The higher predation on zooplankton has a quadratic form $mZ^2.$ A fraction $\gamma$ of this term is regenerated as nutrient and the remaining fraction $1-\gamma$ fuels the growth of higher predators. In this model, nutrients can enter the system from below the mixed layer by diffusive mixing at a rate $k,$ and phytoplankton and detritus are allowed to sink out of the mixed layer at rates $s$ and $\psi,$ respectively. Detritus increases due to the phytoplankton mortality and respiration $rP$ at a rate $r.$ Besides, detritus can be converted into nutrient via remineralization at a rate $\psi.$

In general, the precise values of the above parameters are unknown and have to be determined empirically. Moreover, different models often use differing values. In this study, the default values of the parameters are listed in Table 1. These values are the same as those in Edwards [2001] except the nutrient concentration below the mixed layer $N_0; in the present study, N_0$ is set to 1.5 g C m$^{-3}.$ Based on the fact that the higher predation rate on zooplankton $m$ is difficult to measure and its different values have significant effects on the behaviors of planktonic ecosystem model [Edwards and Brindley, 1999; Steele and Henderson, 1981], we use it as a control parameter to examine the bifurcation behavior of the model. The subsection 3.1 will show that the model exhibits multiple linearly stable equilibria for certain values of $m,$ which forms the basis of the present study of which an important aim is to investigate the shift between the equilibria.

To obtain the steady states of the model, let the right-hand sides of equations (1–4) be equal to zero. By some simple algebraic operations, we can get a 10th-order polynomial with respect to $P.$ The detailed derivations for the polynomial and how to obtain the roots of the polynomial are shown in Appendix A. We only focus on the solution with strictly positive values of all four variables in this study. In the following discussion, we will investigate the nonlinear evolutions of perturbations. For this purpose, we need to obtain the time-dependent numerical solutions of the model. Here, the fourth-order Runge-Kutta scheme is employed to numerically discretize the equations (1–4). To compare the nonlinear evolutions of perturbations to the linear evolutions, we need to run the tangent linear version of the NPZD model, which is derived in Appendix B.

2.2. The CNOP Approach

The CNOP method is employed to determine the nonlinearly optimal finite-amplitude perturbations. This approach was first proposed by Mu et al. [2003] and has been utilized to study El Niño-Southern Oscillation
(ENSO) predictability [Duan et al., 2004; Mu et al., 2007], the stability of the thermohaline circulation [Mu et al., 2004], and the response of terrestrial ecosystem to climate change [Sun and Mu, 2012a, 2012b, 2013]. We will briefly introduce this approach in this subsection.

In general, the planktonic ecosystem model derived from equations (1)–(4) can be formally written as,

$$X(t) = M_t(X(0)),$$

where $X(t) = (N(t), P(t), Z(t), D(t))^T$ is the planktonic ecosystem state at time $t$ in which the “$T$” represents the transpose; $X(0) = (N(0), P(0), Z(0), D(0))^T$ denotes the initial ecosystem state, and $M_t$ is the nonlinear propagator that propagates the initial state to the state at time $t$. If there exists a perturbation $x(0) = (N(0), P(0), Z(0), D(0))^T$ on the initial state $X(0)$, then the equation (5) becomes,

$$X(t) + x(t) = M_t(X(0) + x(0)),$$

where $x(t) = (N(t), P(t), Z(t), D(t))^T$ denotes the perturbation at time $t$ obtained by a nonlinear evolution of the initial perturbation $x(0)$. To find the conditional nonlinear optimal perturbation (CNOP) $x^*(0) = (N^*(0), P^*(0), Z^*(0), D^*(0))^T$ resulting in the largest nonlinear evolution at a given optimization time $t$, the following constraint optimization problem is defined,

$$J(x^*(0)) = \max_{x(0) \in C_0} J(x(0)) = \max_{x(0) \in C_0} \frac{\| M_t(X(0) + x(0)) - M_t(X(0)) \|^2_2}{C_0}$$

where $C_0$ represents a constraint condition, $J(x(0))$ is an objective function.

In the NPZD model, the concentration of the plankton is nonnegative, so each component of $X(0) + x(0)$ is greater than or equal to zero. Besides, the amplitude of initial perturbation should be finite. Hence, the constraint condition is,

$$C_0 = \{ x(0) = (N(0), P(0), Z(0), D(0))^T | (N(0))^2 + (P(0))^2 + (Z(0))^2 + (D(0))^2 \leq \delta;$$

$$N(0) + N(0) \geq 0, P(0) + P(0) \geq 0, Z(0) + Z(0) \geq 0, D(0) + D(0) \geq 0 \}$$

where $\delta$ is the constraint radius that controls the amplitude of initial perturbation. The objective function $J(x(0)) = \| M_t(X(0) + x(0)) - M_t(X(0)) \|^2_2$ is defined as,

$$J(x(0)) = \frac{1}{2} \left[ (N(\tau))^2 + (P(\tau))^2 + (Z(\tau))^2 + (D(\tau))^2 \right].$$

By calculating the optimal perturbations with different constraint radii and comparing the values of the objective function, we find that the value of the objective function monotonically increases as the constraint radius increases. Furthermore, when the objective function value is small, the abrupt transition does
3. Results

3.1. Marine Planktonic Ecosystem Responses to Finite-Amplitude Perturbations

The bifurcation behavior of the NPZD model (equations (1–4)) has been analyzed in detail by Edwards [2001]. Using the higher predation rate on zooplankton \( m \) as the control parameter, we only show the bifurcation diagram related to our study in Figure 1. The solid curves denote the linearly stable steady states (equilibria) while the dashed curves indicate the unstable equilibria. The figure indicates that there exists only one stable equilibrium, when \( m < 1.08 \) and \( m > 1.34 \), and the model exhibits three equilibria for the interval \( 1.08 < m < 1.34 \), in which there are two linearly stable equilibria and one unstable equilibrium when \( 1.093 \leq m \leq 1.199 \). The nutrient concentrations of the equilibria on the upper solid curves are high, whereas those on the lower solid curves are low. For simplicity, the steady states on the upper and lower solid curve branches are, respectively, abbreviated as the “high-nutrient” and “low-nutrient” states. The Hopf bifurcation occurs at \( m = 1.093 \) and \( m = 1.199 \), as labeled with two solid squares. In this study, we will compare the linear and nonlinear responses of the planktonic ecosystem to optimally finite-amplitude perturbations (CNOPs) in the multiple equilibria regime located in the interval \( 1.093 \leq m \leq 1.199 \).

Two linearly stable equilibria for \( m = 1.14 \) m\(^3\) g\(^-1\) d\(^-1\), labeled as Cases A and B in Figure 1, are taken as the reference states used for calculating the CNOP. These two cases, respectively, correspond to the high-nutrient and low-nutrient states. They are chosen as representatives of the two stable branches in the bifurcation diagram. The concentrations of nutrients, phytoplankton, zooplankton, and detritus for these two states are listed in Table 2. To choose the optimization time, a group of numerical experiments are performed. We use the steady state of Case A as the reference state and fix the constraint radii as \( \delta = 0.0085 \) g C m\(^-2\). Then, we calculate the CNOPs with different optimization times \( \tau = 3.6.9, \ldots, 18 \) days and compare the values of the objective function. The results show that the objective function value is largest when \( \tau = 15 \) days. This implies that the optimal perturbation for \( \tau = 15 \) days results in the largest amplification. Hence, we choose \( \tau = 15 \) days as the optimization time.

To investigate the responses of the planktonic ecosystem to the perturbations with different amplitudes, we calculate the CNOPs with different constraint radii. Here, we only show the CNOPs with three constraint radii as the representatives for each case (Table 3). The constraint radii will be given in the following discussion involving the amplitude of perturbations. It is worth pointing out that the condition that each component of \( x(0) + x(0) \) should be greater than zero (see equation (8)) is automatically satisfied under all constraint radii considered in this study.

Note that the obtained CNOPs have the maximal permitted amplitude, i.e., \( \sqrt{(N^+(0))^2 + (P^+(0))^2 + (Z^+(0))^2 + (D^+(0))^2} = \delta \). Hence we are able to study the response of the ecosystem to perturbations with the fixed amplitude. Table 3 indicates that the absolute values of concentrations of phytoplankton and zooplankton in each CNOP perturbation are much larger than those of nutrient and detritus. Besides, the CNOP perturbation distributions depend on the amplitude, namely the proportion of \( N^+(0) : P^+(0) : Z^+(0) : D^+(0) \) changes with amplitude of the CNOPs. But the linear perturbation method without accounting for the effects of nonlinear processes tells us that the optimal perturbation structures are independent from the magnitude of the perturbation, as mentioned by Healey et al. [2009]. The above differences indicate that the structures of the optimal perturbations obtained from the linear method and the CNOP method are different, which implies that nonlinear processes have important effects on the perturbation structures.
To investigate the nonlinear evolutions of the CNOPs, we superimpose the CNOPs on the corresponding reference states as the initial conditions and then integrate the NPZD model. Simultaneously, we take the CNOPs as the initial conditions of the tangent linear model and integrate the model to examine the linear evolutions of the CNOPs.

We first explore the evolutions of the CNOPs with small amplitudes \( \delta = 0.0085 \text{ g C m}^{-3} \) for Case A and \( \delta = 0.015 \text{ g C m}^{-3} \) for Case B. For Case A, the amplitude \( \delta = 0.0085 \) is about 0.7% of the magnitude of the steady state. Figure 2 shows the variations in \( N, P, Z, \) and \( D \) induced by the nonlinear and linear evolutions of the CNOP. It illustrates that both the nonlinear and linear evolutions of the CNOP cause damped oscillations. But the periods of oscillations are about 35 days for the nonlinear evolution and 27 days for the linear evolution. Moreover, the amplitude of the oscillation caused by nonlinear evolution is much larger than that caused by the linear evolution. The time taken to recover to the original equilibrium is longer in the nonlinear evolution than the linear evolution.

Similarly, Figure 3 indicates the nonlinear and linear evolutions of the CNOP with \( \delta = 0.015 \text{ g C m}^{-3} \) (Table 3) for Case B. The amplitude \( \delta = 0.015 \) is equivalent to about 3.6% of the magnitude of the steady state. The results are broadly similar to Case A. The nonlinear evolution also results in an oscillation with a larger magnitude than the linear evolution. But it is worth mentioning that the magnitude of the oscillation induced by nonlinear evolution of the CNOP is not negligible with concentration of the nutrient increasing to almost double of the steady state value.

To further quantify the evolution of the CNOP perturbation, we use the following norm as a measure,

\[
\Pi = \frac{1}{2} \left[ (N_p(t))^2 + (P_p(t))^2 + (Z_p(t))^2 + (D_p(t))^2 \right]
\]

where \( (N_p(t), P_p(t), Z_p(t), D_p(t))^T \) denotes the

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**Table 2.** Linearly Stable Steady States of the Planktonic Ecosystem Model for Cases A and B*  
<table>
<thead>
<tr>
<th>Case</th>
<th>( N )</th>
<th>( P )</th>
<th>( Z )</th>
<th>( D )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Case A</td>
<td>1.1496</td>
<td>0.0424</td>
<td>0.0782</td>
<td>0.0786</td>
</tr>
<tr>
<td>Case B</td>
<td>0.1446</td>
<td>0.2313</td>
<td>0.1286</td>
<td>0.2886</td>
</tr>
</tbody>
</table>

*Units in g C m\(^{-3}\).*
Furthermore, Figure 6 shows the time series of the function perturbations. Early stable, they have the potential to become nonlinearly unstable due to relatively small finite-amplitude bria (Figure 5c), while the linear evolution does not (Figure 5d). Hence, although the steady states are linearly stable, the nonlinear evolution of the CNOP results in an opposite shift between two linearly stable equilibria (Figure 5b). Similarly, for Case A, the nonlinear evolution of the CNOP only induces an oscillation with small amplitude (Figure 5a). However, the linear evolution of the CNOP only induces a great decrease in the high-nutrient and low-nutrient states while the linear evolution does not. For Case B, the nonlinear evolution of the CNOP induces a shift between two linearly stable equilibria (Figure 5c), while the linear evolution does not (Figure 5d). Hence, although the steady states are linearly stable, they have the potential to become nonlinearly unstable due to relatively small finite-amplitude perturbations.

Furthermore, Figure 6 shows the time series of the function perturbations at time $t$ obtained by the nonlinear or linear evolutions of the CNOPs. For nonlinear evolutions, the perturbations are the differences between the results obtained by integrating the nonlinear model (equations (1)–(4)) with and without the CNOP perturbations. For linear evolutions, the perturbations are obtained by integrating the tangent linear model (equations (B1)–(B4)). The time series of the function $\Pi$ are plotted in Figure 4. Obviously, there are significant differences between the oscillations induced by nonlinear and linear evolutions for both Cases A and B, indicating that the nonlinear processes have important effects on the evolution of the perturbations.

We also examine the evolutions of the CNOPs with the slightly larger amplitude $\delta = 0.0089$ g C m$^{-3}$ for Case A and $\delta = 0.017$ g C m$^{-3}$ for Case B (Table 3). But these two amplitudes are still relatively small compared to the steady states. They are, respectively, about 0.8% and 4.1% of magnitudes of the corresponding steady states. Note that the amplitudes of the phytoplankton concentrations of the obtained CNOPs for both, Cases A and B, are well within the range of observed seasonal fluctuations of the phytoplankton at Ocean Weather Station “India” given by Fasham et al. [1993]. Figure 5 shows the time series of $N, P, Z,$ and $D$ induced by the perturbations. It is found that the nonlinear evolution of the CNOP induces a shift between the high-nutrient and low-nutrient states while the linear evolution does not. For Case A, the nonlinear evolution of the CNOP causes a great decrease in $N$, and the significant increases in $P, Z,$ and $D$ in the first 40 days. It finally induces an abrupt transition from the high- to low-nutrient equilibrium (Figure 5a). However, the linear evolution of the CNOP only induces an oscillation with small amplitude (Figure 5b). Similarly, for Case B, the nonlinear evolution of the CNOP results in an opposite shift between two linearly stable equilibria (Figure 5c), while the linear evolution does not (Figure 5d). Hence, although the steady states are linearly stable, they have the potential to become nonlinearly unstable due to relatively small finite-amplitude perturbations.

<table>
<thead>
<tr>
<th>Cases</th>
<th>Constraint Radii $\delta$</th>
<th>$N'(0)$</th>
<th>$P'(0)$</th>
<th>$Z'(0)$</th>
<th>$D'(0)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Case A</td>
<td>$0.008$</td>
<td>$-3.39 \times 10^{-3}$</td>
<td>$2.41 \times 10^{-3}$</td>
<td>$-7.63 \times 10^{-3}$</td>
<td>$-2.14 \times 10^{-3}$</td>
</tr>
<tr>
<td></td>
<td>$0.0085$</td>
<td>$-2.34 \times 10^{-3}$</td>
<td>$2.75 \times 10^{-3}$</td>
<td>$-8.04 \times 10^{-3}$</td>
<td>$-1.67 \times 10^{-3}$</td>
</tr>
<tr>
<td></td>
<td>$0.0089$</td>
<td>$-1.70 \times 10^{-3}$</td>
<td>$3.03 \times 10^{-3}$</td>
<td>$-8.37 \times 10^{-3}$</td>
<td>$-1.39 \times 10^{-3}$</td>
</tr>
<tr>
<td>Case B</td>
<td>$0.01$</td>
<td>$-2.23 \times 10^{-3}$</td>
<td>$-3.66 \times 10^{-3}$</td>
<td>$9.01 \times 10^{-3}$</td>
<td>$-6.20 \times 10^{-4}$</td>
</tr>
<tr>
<td></td>
<td>$0.015$</td>
<td>$-3.01 \times 10^{-3}$</td>
<td>$-6.18 \times 10^{-3}$</td>
<td>$1.33 \times 10^{-2}$</td>
<td>$-7.11 \times 10^{-4}$</td>
</tr>
<tr>
<td></td>
<td>$0.017$</td>
<td>$-3.29 \times 10^{-3}$</td>
<td>$-7.27 \times 10^{-3}$</td>
<td>$1.50 \times 10^{-2}$</td>
<td>$-7.32 \times 10^{-4}$</td>
</tr>
</tbody>
</table>

*Units in g C m$^{-3}$.

**Figure 2.** The (a, c) nonlinear and (b, d) linear responses of the planktonic ecosystem to CNOP perturbation with $\delta = 0.0085$ g C m$^{-3}$ for Case A.

**Table 3.** CNOP Perturbations With Different Constraint Radii (Amplitudes, g C m$^{-3}$) for Cases A and B.
weak oscillations, which eventually decay back to the original equilibria, while the CNOPs cause the regime shifts between equilibria as the amplitudes increase (red lines).

The above results imply that there exists a critical value of the constraint radius $d_c$, denoted $\delta_c$, such that a linearly stable equilibrium becomes nonlinearly unstable. Here $\delta_c$ is defined as the minimal amplitude of perturbation resulting in an abrupt transition between two linearly stable equilibria. From this definition, we infer that the larger $\delta_c$ is, the more stable the equilibrium is. We calculate the CNOPs with many different constraint radii to determine $\delta_c$ for each value of $m$ in the multiple equilibria regime. Figure 7a gives the critical value $\delta_c$ near the Hopf bifurcation point for the high-nutrient branch in the bifurcation diagram (Figure 1), indicating that the perturbations with the amplitudes located in the region above the curve will result in an abrupt transition from high-nutrient to low-nutrient states; on the contrary, the perturbations with the amplitudes under the curve cannot lead to the transition. This implies that the nonlinear stability of the equilibrium depends on the amplitude of the perturbation. Besides, as the parameter $m$ increases and approaches the Hopf bifurcation point at $m=1.199$, the value of $\delta_c$ decreases sharply. This reflects that the closer the steady state is to the bifurcation point, the easier it is to lose the stability. Similarly, for the low-nutrient branch (Figure 1), Figure 7b shows that the perturbations with the amplitudes above the curve will lead to the nonlinear instability of the steady state; while for the perturbation with the amplitudes under the curve, the steady state is nonlinearly stable. As $m$ decreases from 1.16 to the Hopf bifurcation point, $\delta_c$ decreases monotonically and tends to zero. This implies that the steady states lose their stabilities after the Hopf bifurcation point.

The above results are obtained based on Cases A and B for $m=1.14$. In fact, other equilibria on the high-nutrient and low-nutrient branches for $m=1.13$, 1.15, 1.16 are also used as reference states to compute the CNOPs. The obtained results for the high-nutrient and low-nutrient states are broadly similar to those for Cases A and B. That is, nonlinear processes play important roles in the evolutions of the finite-amplitude

![Figure 3](image-url) Figure 3. The (a) nonlinear and (b) linear responses of the planktonic ecosystem to CNOP perturbation with $\delta=0.015 \text{ g C m}^{-3}$ for Case B.

![Figure 4](image-url) Figure 4. The time series of the function $P$ caused by the nonlinear and linear evolutions of the CNOP perturbations with (a) $\delta=0.0085 \text{ g C m}^{-3}$ for Case A and (b) $\delta=0.015 \text{ g C m}^{-3}$ for Case B. The function $P$ is calculated using equation (10).
perturbations and may induce the instability of the planktonic ecosystem. In the following subsection, we will investigate the precise effects of the nonlinear processes and reveal the nonlinear response mechanism of the planktonic ecosystem to finite-amplitude perturbations.

3.2. How Do The Nonlinear Processes Promote the Evolution of Perturbation?

Note that the nonlinear processes in this study refer to nonlinear terms in the nonlinear evolution equations of perturbation, i.e., the perturbation-perturbation interactions. To investigate the precise effects of the nonlinear processes, we need to derive each nonlinear term. In the NPZD model (equations (1)–(4)), there are three terms related to the nonlinear processes: \(N/(e+N)\times aP/(b+cP)\), \(\lambda P^2 Z/(\gamma^2 + P^3)\), and \(mZ^2\). The derivation for the nonlinear processes is given in Appendix C. As we can see from the appendix, there are three nonlinear processes in the \(N\) evolution equation (C(5)), two in the \(P\) and \(Z\) evolution equations (C(6) and C(7)), and one in the \(D\) evolution equation (C(8)).

For Case A, Figure 8 shows each nonlinear process and their summations in the corresponding evolution equation for the CNOP perturbation with \(\delta = 0.0085\) g C m\(^{-3}\). It is found that the dominant contributions of the nonlinear processes appear in the \(P\) equation (see the blue line in Figure 8b), while those in other equations are relatively weak. Besides, Figure 8b indicates that the total tendency of nonlinear processes is positive, implying that the nonlinearities intensify perturbations of phytoplankton. Concretely, the initial perturbation consists primarily of a positive anomaly in \(P\), and a negative anomaly in \(Z\) (Table 3). For the nonlinear evolution of the perturbation, an initial decrease of \(Z\) results in an increase of \(P\). Because the combined contribution of nonlinear processes is positive in the \(P\) equation (blue line in Figure 8b), the increase of phytoplankton lasts for 15 days although the zooplankton anomaly changed sign relative to the original steady state at Day 5 (see Figure 2c). As \(P\) increases, \(Z\) and \(D\) correspondingly increase while \(N\) decreases (Figure 2a). We note that the nonlinear tendency terms are negative in Figures 8c and d, indicating that the effects of the nonlinear processes tend to suppress the evolutions of \(Z\) and \(D\). But the effects are weak and could not cancel the increases of \(Z\) and \(D\) induced by the increase of \(P\). Because of the continuing increase in \(Z\), the biomass of phytoplankton will decrease. This forms a predator–prey oscillation (Figures 2a and c). For the linear evolution, however, the increase of \(P\) only lasts for 5 days because the intensification due to nonlinear processes does not exist. So the amplitude of the predator–prey oscillation caused by the linear evolution of the perturbation is smaller than that caused by the nonlinear evolution.

The effect of the nonlinear process on the shift between linearly stable equilibria is also investigated. Figure 9 shows each nonlinear process for the evolution of the CNOP with \(\delta = 0.0089\) g C m\(^{-3}\) for Case A. Comparing with the case for \(\delta = 0.0085\) g C m\(^{-3}\), the results are qualitatively similar. That is, the combined contributions of the nonlinearities are also dominant and positive in the \(P\) equation for the first 20 days and close to zero in the other equations, implying that the nonlinearities promote the increase in \(P\). But the value of each nonlinear term for \(\delta = 0.0089\) g C m\(^{-3}\) is much greater than that for \(\delta = 0.0085\) g C m\(^{-3}\). For example, the summation of all the nonlinear processes in the \(P\) equation is about \(8.0 \times 10^{-3}\) g C m\(^{-3}\) d\(^{-1}\) on Day 14 (blue line in Figure 9b), while it is only \(5.0 \times 10^{-3}\) g C m\(^{-3}\) d\(^{-1}\) for \(\delta = 0.0085\) g C m\(^{-3}\) (blue line in Figure 8b). This results in an increase of biomass of phytoplankton. The maximum value of \(P\) is about 0.43 g C m\(^{-3}\) (Figure 5a), but the value is less than 0.12 g C m\(^{-3}\) for \(\delta = 0.0085\) g C m\(^{-3}\) (Figure 2c). With the increase of \(P\), zooplankton and detritus also increase while the nutrients decrease (Figure 5a). It is worth noting that, although the combined contribution of the nonlinear processes is positive after 20 days in the \(N\) evolution equation (Figure 9a), which tends to promote the increase of \(N\), this tendency is too small to offset the decrease of \(N\) induced by the increase of \(P\). Hence the system is driven to enter the domain of another attractor (i.e., a linearly stable low-nutrient steady state). The planktonic ecosystem eventually shifts to the low-nutrient equilibrium. Without accounting for the nonlinearities, the regime shift between linearly stable equilibria does not occur (Figure 5b).

The above discussion shows that for Case A, large changes in the planktonic ecosystem mainly result from the increase of phytoplankton, induced by nonlinear processes. Interestingly, Figures 8b and 9b show that the combined contribution of the nonlinear processes is mainly determined by the nonlinear term \(-nl_{grazing}\) (green lines). This means, for the high-nutrient state, that the nonlinearity related to the process of zooplankton grazing on phytoplankton has a dominant effect on the stability of the planktonic ecosystem.

Next we explore the effects of nonlinear processes for Case B. Initially, the CNOP perturbation with \(\delta = 0.015\) g C m\(^{-3}\) consists primarily of a negative anomaly in \(P\) and a positive anomaly in \(Z\) (Table 3). The biomass of
phytoplankton correspondingly reduces due to the increase in $Z$. For the nonlinear evolution of the perturbation, as shown in Figure 10, the combined contribution of the nonlinear processes promotes the decrease of phytoplankton (Figure 10b). So the concentration of the phytoplankton continues to decrease for 14 days (Figure 3a). Due to the decrease of $P$ and the positive effects of the nonlinear processes (Figure 10a), the nutrient concentration rapidly increases. Besides, due to the lack of food (i.e., a decrease in $P$), the biomass of zooplankton decreases. Correspondingly, the biomass of detritus also decreases. Then the biomass of phytoplankton increases because of the increase in nutrient and decrease in zooplankton. A predator-prey oscillation is eventually formed. Comparing to the nonlinear evolution of the perturbation, the linear evolution only causes the decrease of $P$ to last for about 6 days (Figure 3b). As a result, the formed predator-prey oscillation has smaller amplitude.

For the dramatic shift case caused by the CNOP perturbation with $\delta=0.017 \text{ g C m}^{-3}$, Figure 11 indicates that the summations of the nonlinear processes are much larger than those shown in Figure 10. They are negative for the evolution of the phytoplankton anomaly and positive for the evolution of the nutrient anomaly, which strongly promotes the decrease in $P$ and the increase in $N$. Consequently, $Z$ and $D$ greatly

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**Figure 5.** The nonlinear and linear responses of the planktonic ecosystem to CNOP perturbation with (a, b) $\delta=0.0089 \text{ g C m}^{-3}$ for Case A and (c, d) $\delta=0.017 \text{ g C m}^{-3}$ for Case B. For the nonlinear responses, the shifts occur between linearly stable equilibria (a, c).

**Figure 6.** The time series of the function $\Pi$ caused by the nonlinear evolutions of the CNOP perturbations with different constraint radii for (a) Case A and (b) Case B. The function $\Pi$ is calculated using equation (10).
decrease. This causes the system to eventually shift to the high-nutrient steady state (Figure 5c). However, for the linear evolution of the perturbation, there is no promoting role of the nonlinear processes, so the finite-amplitude perturbation cannot cause the shift to occur (Figure 5d). Note that the combined contribution of the nonlinearities is mainly determined by the nonlinear process related to uptake (red lines in Figures 10 and 11). Hence, for the low-nutrient state, the nonlinear uptake process is more likely to induce nonlinear instability of the planktonic ecosystem, which is different from the result for the high-nutrient state. A question arises naturally: why is the nonlinear uptake process (the nonlinear zooplankton grazing process) not important to induce the instability of the ecosystem for the high-nutrient (low-nutrient) state? This can be partly explained as follows.

For the high-nutrient state, the concentration of nutrient is $N = 1.1496$, while the half-saturation constant for nutrient is only $e = 0.03$, which means that $N$ is much greater than $e$. Simultaneously, the concentration of phytoplankton is $P = 0.0424$. So $cP$ is much less than $b$. Hence, both $N/(e+N)$ and $a/(b+cP)$ will barely change as $N$ and $P$ are perturbed from 1.1496 and 0.0424. In this situation, the term $nl_uptake$ in the equation (C2) is close to zero in the first 20 days of the evolution process of the perturbation, as shown by the

![Figure 8](image)

Figure 8. The nonlinear tendency terms in the (a) $N$, (b) $P$, (c) $Z$, and (d) $D$ evolution equations ((C(5))–(C(8))) and their summations (the blue line) in the nonlinear evolution of CNOP perturbation with $\delta = 0.0085$ g C m$^{-2}$ d$^{-1}$ for Case A. The nonlinear processes $nl_uptake$, $nl_grazing$, and $nl_predation$ are listed in Appendix C. Units in $10^{-2}$ g C m$^{-2}$ d$^{-1}$.
red lines in Figure 9b. This implies that the nonlinear process related to the uptake is not important to the evolution of the perturbation for the high-nutrient state. Similarly, for the low-nutrient state, the concentration of phytoplankton is $P_{\text{low}} = 2313$, but the zooplankton grazing half-saturation constant is only $I = 0.035$. So $P^2$ is much greater than $I^2$, which causes $J P^2/(I^2 + P^2)$ to be close to the constant $I$ although $P$ is perturbed. So the term $n_{\text{nl_grazing}}$ in the equation (C(3)) is close to zero (green lines in Figure 11b). Hence, the nonlinear process related to zooplankton grazing process does not play a dominant role in causing the nonlinear instability of the ecosystem.

4. Summary

A simple NPZD model is employed to investigate the responses of planktonic ecosystem to finite-amplitude perturbations. Specifically, we analyze the developments of the perturbations in the multiple equilibria regime which occurs across limited regions of the model parameter space. Two kinds of linearly stable steady states, the “high-nutrient” and “low-nutrient” states, are obtained. Based on these states, the perturbations with optimally nonlinear evolution are determined using the conditional nonlinear optimal perturbation (CNOP) method.

The nonlinear evolutions of the CNOP perturbations with different amplitudes are examined. The results show that nonlinear processes play important roles in the evolutions of the perturbations. For the high-nutrient state (Case A), the total contribution (i.e., summation) of nonlinear processes, mainly determined by the nonlinear process related to process of zooplankton grazing on phytoplankton, promotes the increase of the phytoplankton biomass. Zooplankton and detritus correspondingly increase while the nutrients decrease. This results in a damped predator-prey oscillation when the CNOP perturbation has small amplitude (i.e., 0.7% of the magnitude of the steady state). As the amplitude of the CNOP perturbation increases to about 0.8% of the magnitude of the steady state, the nonlinear evolution of the perturbation causes an abrupt transition from the high-nutrient to low-nutrient state.

For the low-nutrient state (Case B), the combined contribution of the nonlinearities, determined by the nonlinear process related to the uptake, tends to cause the biomass of phytoplankton to decrease and the...
biomass of nutrient to increase. This leads to the decreases of zooplankton and detritus. Hence, the damped predator-prey oscillation occurs when the amplitude of the initial perturbation is about 3.6% of the magnitude of the low-nutrient steady state. When the amplitude of perturbation increases to 4.1% of the magnitude of the steady state, the regime shift occurs from the linearly stable low-nutrient to high-nutrient state.

It is worth noting that the effects of the nonlinear processes depend on the underlying planktonic ecosystem state as mentioned above. The nonlinear stability of the planktonic ecosystem is dominantly affected by the nonlinear component of zooplankton grazing on phytoplankton for the high-nutrient state, and the nonlinear uptake process for the low-nutrient state.

Comparing the linear to the nonlinear evolutions of the perturbations, the linear evolutions also result in the damped predator–prey oscillations. But the amplitudes of the oscillations are much smaller than those caused by the nonlinear evolutions (see Figures 2 and 3). Besides, due to the absence of nonlinear processes, the linear evolutions of the perturbations cannot induce a transition between the linearly stable low-nutrient and high-nutrient states although the magnitudes of the perturbations are sufficiently large (Figure 5). Overall, nonlinear processes have important impacts on the evolution of finite-amplitude perturbation in the planktonic ecosystem.

5. Discussion

Healey et al. [2009] did an interesting work on the perturbation dynamics of ocean planktonic ecosystem using linear perturbation theory. The present study overcomes the limitations of the linear theory. The CNOP method is utilized to reveal that the nonlinear processes play important roles in the responses of planktonic ecosystem to finite-amplitude perturbation. We illustrate that the distribution of the values of $N'(0)$, $P'(0)$, $Z'(0)$, and $D'(0)$ in CNOP perturbation (as shown in Table 3) is very important. We investigate the nonlinear evolutions of 40 random perturbations with the amplitude $\delta=0.015 \text{ g C m}^{-3}$ for Case B. The results show that these random perturbations do not induce a shift from the low-nutrient to high-nutrient state (figure not shown). Hence, if a perturbation does not have the distribution similar to CNOP, it may be difficult to cause the regime shift in the system. It is thus very difficult to find the minimal amplitude of the perturbation that causes the shift by running the model with randomly chosen initial perturbation. So the
CNOP method appears to be well suited to investigate the sensitive, stability, and predictability of the planktonic ecosystem. It is important to note that the parameter values lead to modeled concentrations of nutrients and phytoplankton which are close to the observed values at Ocean Weather Station “India” during summer 1972. For example, the observed concentration of nutrient is about 1.0–2.0 mmol nitrogen m\(^{-3}\) in the top 20 m and the concentration of phytoplankton is about 0.1–3.1 mg chlorophyll m\(^{-3}\) over the period from April to October [Fasham et al., 1993]. For Case B, the modeled concentrations of nutrient and phytoplankton are, respectively, 0.1446 g C m\(^{-3}\) and 0.2313 g C m\(^{-3}\), as shown in Table 2, which can be converted to about 1.4 mmol nitrogen m\(^{-3}\) for N and 4.6 mg chlorophyll m\(^{-3}\) for P by using the assumed conversion equivalences 1 g carbon \(\equiv\) 20 mg chlorophyll \(\equiv\) 10 mmol nitrogen in our model. It appears that the modeled concentration of phytoplankton is slightly larger than the observational value. However, considering the simplicity of the model and the uncertainty in observational data, the model is able to reproduce the concentrations of nutrients and phytoplankton reasonably well. But for Case A, the modeled concentration of nutrient is about 11.5 mmol nitrogen m\(^{-3}\), which is much greater than the observational value. So the observations do not appear to capture the high-nutrient state predicted by the model. One possible reason is that the regime shift between multiple equilibria does not occur at the station “India” over the relatively short-observational period from April to October in 1972.

Of course, it is very difficult to observe the regime shift between two equilibria because one important characteristic of the shift is that the system will go to different steady states with different starting conditions. As pointed out by Collie et al. [2004], it is almost impossible to directly conduct experiments for marine ecosystems that allow the use of different starting conditions. But the regime shift indeed is seen to occur in the freshwater lake ecosystem experiments [Scheffer et al., 2001]. And Collie et al. [2004] also inferred the occurrence of the regime shift in the real ocean from ecological theory. On the other hand, it is difficult to judge whether common ecosystem models can represent realistic regime shifts. The regime shifts exhibited by the models might be realistic but might as well be artificial. Still it is important to investigate the sudden occurrence of the modeled regime shifts, especially for the current model which can reproduce some observational features of plankton concentrations.

Figure 11. The same as in Figure 8, but for the nonlinear evolution of CNOP perturbation with \(\delta=0.017\) g C m\(^{-3}\) for Case B.
Our results highlight the important effects of the nonlinear ecological interactions on the regime shift, which will help improve our understanding of ecological processes that affect the dynamics of the planktonic ecosystem. Additionally, we have shown that the nonlinear processes have important effects on the growths of the perturbations. This has some implications for the practical ecological modeling and prediction. For instance, when a more realistic three dimension (3D) ecosystem model is used, more nonlinear ecological processes will be taken into account. These processes may amplify the uncertainties in the initial condition or external forcing, which will impact the stability of the system and limit its simulation and prediction skills. But the precise effects of nonlinear processes on the simulations and predictability of a 3-D planktonic ecosystem need to be further investigated in the future.

Appendix A: Derivation of the Polynomial Related to Steady States of the Model

A steady state of the model (equations (1–4)) is a solution that satisfies \( \frac{dN}{dt} = \frac{dP}{dt} = \frac{dZ}{dt} = \frac{dD}{dt} = 0 \). Hence, the steady state can be obtained by solving the following four equations

\[
\frac{dN}{dt} = a \frac{N}{e+N} b + cP + \frac{\beta N P}{\mu^2 + P^2} Z + \gamma m Z^2 + \phi D + k(N_0 - N) = 0 \quad (A1)
\]

\[
\frac{dP}{dt} = a \frac{P}{e+N} b + cP + \frac{\gamma P^2}{\mu^2 + P^2} Z - sP - kP = 0 \quad (A2)
\]

\[
\frac{dZ}{dt} = 2 \frac{\alpha P^2}{\mu^2 + P^2} Z - m Z^2 = 0 \quad (A3)
\]

\[
rP + (1 - x - \beta) \frac{\gamma P^2}{\mu^2 + P^2} Z - \phi D - \psi D - kD = 0. \quad (A4)
\]

We only focus on the solution with nonzero values. In this situation, we can get from equation (A3),

\[
Z = \frac{\alpha P^2}{m(\mu^2 + P^2)} \quad (A5)
\]

From equation (A4), we have

\[
D = \frac{1}{\phi + \psi + k} \left[ rP + (1 - x - \beta) \frac{\alpha P^2}{m(\mu^2 + P^2)} \right] \quad (A6)
\]

Using equations (A1) and (A2), the following expressions can be obtained

\[
N = N_0 + \frac{(\beta - 1) \gamma P^2}{k(\mu^2 + P^2)} Z + \frac{\gamma m Z^2}{k} + \frac{\phi D}{k} \left( \frac{r + s + k}{k} \right) P \quad (A7)
\]

If substituting equations (A5) and (A6) into equation (A7), \( N \) can be expressed in term of \( P \). Finally, through substituting equations (A5)–(A7) into equation (A2) and rearranging, we obtain a 10th-order polynomial with respect to \( P \). For simplicity, we only give the coefficient of \( P^{10} \) as follows,

\[
a_{10} = \frac{(r + s + k) \phi rc}{k(\phi + \psi + k)} \left( \frac{r + s + k}{k} \right) \quad (A8)
\]

The steady states of the model are the roots of the above 10th-order polynomial. To obtain the roots, the “roots” function of Matlab 7.1 (Mathwork, Inc) is used. Only the steady states with strictly positive values of all four variables are discussed in this study.

Appendix B: The Tangent Linear Model of the Planktonic Ecosystem Model

In order to investigate the linear evolution of a perturbation, we need to obtain the tangent linear model of the planktonic ecosystem model. Based on the reference state \( (N_r, P_r, Z_r, D_r)^T \), the differential operation for each term in equations (1–4) with respect to each variable is performed. The obtained tangent linear model is shown as follows,
\[
\frac{dN_i}{dt} = - \left[ \frac{N_i}{e+N_i \left( b+c P_i \right)^2} \right] P_i^* + \frac{aP_i}{b+cP_i \left( e+N_i \right)^2} N_i \tag{B1}
\]

\[
\frac{dP_i}{dt} = \frac{N_i}{e+N_i \left( b+c P_i \right)^2} P_i^* + \frac{aP_i}{b+cP_i \left( e+N_i \right)^2} N_i - r P_i \tag{B2}
\]

\[
\frac{dZ_i}{dt} = \frac{2 \beta_i \mu Z_i P_i^*}{\left( \mu^2 + P_i^2 \right)^2} Z_i^* + \frac{2 \beta_i \mu^3 Z_i^2 P_i^*}{\left( \mu^2 + P_i^2 \right)^2} P_i^* - m Z_i^* \tag{B3}
\]

\[
\frac{dD_i}{dt} = \left( 1 - \alpha - \beta \right) \left[ \frac{\beta_i P_i^* Z_i^*}{\mu^2 + P_i^2} \right] P_i^* + 2 \beta_i \mu^3 P_i^* Z_i^2 P_i^* - \left( \phi + \psi + k \right) D_i \tag{B4}
\]

where \( N_i, P_i, Z_i, \) and \( D_i \) are the tangent linear variables of \( N, P, Z, \) and \( D, \) respectively; the subscript \( r \) denotes the reference state of the corresponding variables.

**Appendix C : The Nonlinear Processes in the Evolution Equations of Perturbation**

There are three functions related to the nonlinear processes in the planktonic ecosystem model: the uptake function, \( N/(e+N) \times aP/(b+cP), \) the Holling-type III function of zooplankton grazing on phytoplankton, \( \beta P^2Z/(\mu^2 + P^2), \) and the higher predation on zooplankton or mortality function of zooplankton, \( mZ^2. \) Here, the nonlinear processes refer to the perturbation-perturbation interaction processes (i.e., the perturbation terms with higher order than first), which can be obtained by Taylor expansions. For example, performing the Taylor expansions for the uptake term about the reference state \( (N_0, P_0, Z_0, D_0)^T \) with respect to each variable, we have

\[
\frac{N_i + N'}{e+N_i+N' b+(P_i+P')} = \frac{N_i}{e+N_i b+cP_i} + \frac{N_i aP_i e}{b+cP_i \left( e+N_i \right)^2} \tag{C1}
\]

where \( (N, P, Z, D)^T \) represents the perturbation obtained from a nonlinear evolution of finite-amplitude perturbation, which is different from \( (N_i, P_i, Z_i, D_i)^T \) in Appendix B, which is obtained from the linear evolution of the perturbation. The higher-order terms, namely the nonlinear uptake process, can be attained by the term on the left-hand side of the equation (C1) minus the first three terms on the right-hand side. Similarly, the other nonlinear processes can also be obtained. The related nonlinear processes are, respectively, abbreviated as \( \text{nl}_\text{uptake}, \text{nl}_\text{grazing}, \) and \( \text{nl}_\text{predation}, \) which are shown as follows,

\[
\text{nl}_\text{uptake} = \frac{N_i}{e+N_i b+cP_i} - \frac{aP_i}{b+cP_i \left( e+N_i \right)^2} \tag{C2}
\]

\[
\text{nl}_\text{grazing} = \frac{\beta P_i^2 Z_i^*}{\mu^2 + P_i^2} \left( Z_i + Z' \right) - \frac{\beta P_i^2}{\mu^2 + P_i^2} Z_i \tag{C3}
\]

\[
\text{nl}_\text{predation} = mZ_i^2 \tag{C4}
\]

Hence, the nonlinear evolution equations of perturbation can be written as,
\[ \frac{d\bar{N}}{dt} = - \left[ \frac{N_r}{e + N_r} \frac{rP}{(b + cP)^2} \frac{e}{b + cP} \left( \frac{e}{e + N_r} \right)^2 \bar{N} \right] - \text{nl_uptake} \]
\[ + \frac{2 \lambda \lambda P Z}{m + P Z} \frac{dH}{dP} + \frac{2 \lambda \lambda P Z}{(m + P Z)^2} \left( \frac{e}{e + N_r} \right)^2 \bar{N} + \bar{N} \cdot \text{nl_grazing} \]
\[ + 2 \gamma mZ \bar{Z} \cdot \bar{n} \cdot \text{nl_predation} + \phi \bar{D}^2 - k \bar{N} \]
\[ \frac{d\bar{P}}{dt} = \frac{N_r}{e + N_r} \frac{rP}{(b + cP)^2} \frac{e}{b + cP} \left( \frac{e}{e + N_r} \right)^2 \bar{N} + \text{nl_uptake} \]
\[ - \frac{\lambda \lambda P Z}{m + P Z} \bar{Z} \cdot \bar{P} \cdot \bar{P} + \bar{N} \cdot \text{nl_grazing} \]
\[ + 2 \gamma mZ \bar{Z} \cdot \bar{P} \cdot \bar{P} - \phi \bar{D}^2 - k \bar{N} \]
\[ \frac{d\bar{Z}}{dt} = \frac{\lambda \lambda P Z}{m + P Z} \bar{Z} \cdot \bar{P} + \bar{N} \cdot \text{nl_grazing} \]
\[ - 2 \gamma mZ \bar{Z} \cdot \bar{P} \cdot \bar{P} - \phi \bar{D}^2 - k \bar{N} \]
\[ \frac{d\bar{D}}{dt} = r \bar{P} + (1 - \alpha - \beta) \left[ \frac{\lambda \lambda P Z}{m + P Z} \bar{Z} \cdot \bar{P} + \bar{N} \cdot \text{nl_grazing} \right] \]
\[ + (1 - \alpha - \beta) \cdot \text{nl_grazing}, \]
\[ - (\phi + \psi + \kappa) \bar{D}^2 \]

The above equations show that there are three nonlinear terms in equation (C5), two in equations (C6) and (C7), and one in equation (C8), respectively.

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