Local and Global Sensitivity Analysis of a Nutrients-Phytoplankton-Oysters Mathematical Model of a Bay Ecosystem

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Abstract. *A parametrized mathematical model that is based on a chemostat model was developed and used to theoretically describe the interactions of nutrients (N), phytoplankton (P) and oysters (O) in a bay ecosystem. Using the theoretical Model (NPO), we derive verifiable conditions for the persistence or extinction of phytoplankton and oysters in a bay ecosystem. In addition, we use local and global sensitivity analysis and simulations to illustrate how human activities such as increased oyster harvesting and environmental factors such as increased nutrients flow and increased oyster filtration can generate phytoplankton blooms via Hopf bifurcation with corresponding oscillations in the oyster biomass and nutrients level in a bay ecosystem.*

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1 Introduction

Bay ecosystems provide critical habitats and environments for survival and growth of humans, animals and plants. The Chesapeake Bay, for example, provides important critical habitat for wildlife while serving as a recreational facility and important fishery for humans [1, 2]. However, increasing human activities in close proximity of bay ecosystems are causing changes to the water resources. For example, in the Chesapeake Bay, these changes have led to greater freshwater flows and increased fluxes of nutrients to the bay waters [3, 2]. In some coastal waters, the presence of moderate nutrients enrichment enhance fish production. However, episodes of excessive growth of phytoplankton are known to be promoted by excess nutrients. These enormous amounts of phytoplankton biomass combined with suspended material, in coastal waters, degrade water clarity, and as a result endanger the living of some of the critical habitats, for example seagrass habitat. Occasionally, some phytoplankton species produce toxins that cause harm to fish, shellfish, birds, humans and other mammals [4]. It has been established that, in the Chesapeake Bay, a large decline in the abundance of filter-feeders eastern oysters *Crassostrea virginica* has resulted in high phytoplankton biomass in the bay [5, 6, 7].

Several mathematical models have been used to theoretically study the dynamics of phytoplankton blooms [8, 9, 10]. Others have used models to study the interactions of nutrients, phytoplankton and zooplankton interactions [11, 12, 13, 15, 14, 16]. Some of these studies have focussed on the dynamics of suspension feeders [17] and oysters [18] in bay ecosystems. Saunders and Bazin, in [20], analyzed general nutrients-prey-predator chemostat type models.

In this article, we introduce a parameterized mathematical nutrients-phytoplankton-oysters (NPO) model, based on a chemostat model of Saunders and Bazin that is used to describe interaction dynamics of nutrients, phytoplankton and oysters. The theoretical model is a system of three ordinary differential equations. When the maximum values of nutrients uptake is less than the rate of phytoplankton loss, we show that both phytoplankton and oysters decline to zero and the nutrients level stabilizes at a positive steady state. However, when the maximum value of phytoplankton filtration by oysters is smaller than the rate of oysters removal, then the oysters go extinct and the model reduces to a system of nutrients-phytoplankton interactions (NP). For the reduced Model (NP), we introduce a threshold parameter, R_N, and use it to show that $R_N < 1$ implies phytoplankton extinction while $R_N > 1$ implies phytoplankton persistence.

In the full Model (NPO), we use the threshold parameter, R_N, to study persistence of phytoplankton with or without oysters in the system. In particular, we obtain that when $R_N < 1$, then both phytoplankton and oysters go extinct. However, when $R_N > 1$, we introduce a second threshold parameter R_{NPO} and use it to show that $R_{NPO} < 1$ implies extinction of oysters and the Model (NPO) exhibits a locally stable equilibrium point with positive values of nutrients level and phytoplankton biomass. In addition, we show that when the maximum value of phytoplankton filtration by oysters is larger than the rate of oysters removal, then it is possible for the Model (NPO) to exhibit an interior equilibrium with positive values of nutrients, phytoplankton and oysters (persistence dynamics).

We use specific examples to illustrate that the interior equilibrium of the full Model (NPO) is capable of undergoing a Hopf bifurcation; which results in phytoplankton blooms and corresponding oscillations in oyster biomass and nutrients levels. Others have shown similar oscillatory dynamics in NPZ models [11, 13, 15, 14]. Using local and global sensitivity index analysis, we study the effects of increasing the model parameters on the level of nutrients, phytoplankton and oysters biomass.

In Sections 2, we introduce our bay ecosystem nutrients-phytoplankton-oysters (NPO) mathematical model. In Section 3, we establish the well-posedness of the Model (NPO). Local and global sensitivity analysis of the nutrients only Model (N) and nutrients-phytoplankton Model (NP) are given in Sections 4 and 5; respectively. In Section 6, we perform local and global sensitivity analysis in the full Model (NPO). Also, illustrative examples of Hopf bifurcations in the Model (NPO) are given in Section 6. Our results are summarized in the conclusion section, Section 7.

2 Bay ecosystem NPO mathematical model

The following figure, illustrates simplified interactions of nutrients, phytoplankton and oysters in a bay ecosystem.
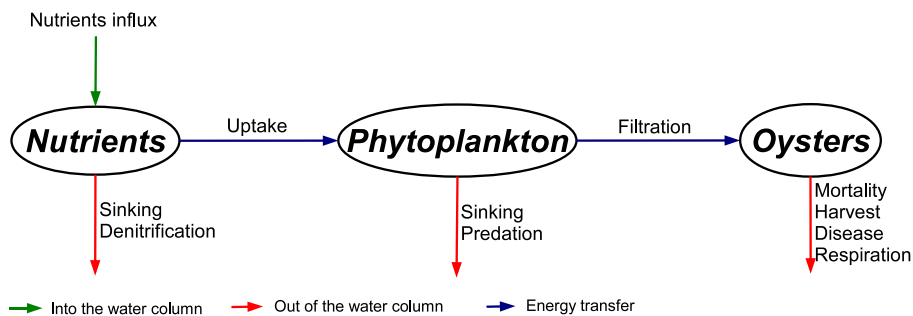
Fig. 1 Compartmental model of interactions of nutrients, phytoplankton and oysters in a bay ecosystem.

To model the interactions of Figure 1, we make the following simplifying assumptions.

- Water of the bay is shallow, well mixed and has the same depth.
- Nutrients flow rate into a bay is considered constant.
- Temperature, salinity and light intensity are not included in the model.
- Nutrients are nitrogen type.
- Phytoplankton are of *Prorocentrum minimum* species.
- Oysters are of *Crassostrea virginica* species.
- The NPO model will be formulated as a mass balance on nitrogen with working units of $mg\,N\,l^{-1}$.

The model variables are described in Table 1. To our knowledge, there is a shortage of daily measurements of nutrients, phytoplankton and oyster biomass. As a result of this, some of our parameters are estimates. Our model parameters are given in Table 2.

Table 1 List of model variables

Variable	Description	Units
t	Time	d (Days)
$N(t)$	Nutrients level at time t	$mg\,N\,l^{-1}$
$P(t)$	Phytoplankton biomass at time t	$mg\,N\,l^{-1}$
$O(t)$	Oysters biomass at time t	$mg\,N\,l^{-1}$

Table 2 Table of model parameters

Parameter	Description	Unit	Range	Baseline	Reference
γ	Nutrients inflow rate	$mgNl^{-1}d^{-1}$	$0.01-5$	2.505	estimated
k_n	Half saturation for nutrients uptake by phtoplankton	$mgNl^{-1}$	$0.005-0.5$	0.25025	[8]
k_p	Half saturation for filtration by oysters	$mgNl^{-1}$	$0.005-0.2$	0.10025	[8]
μ_n	Nutrients loss by sinking and denetrification	d^{-1}	$0.1-1.5$	0.8	[8]
μ_p	Removal of phytoplankton by sinking and predation	d^{-1}	$0.1-1$	0.55	[8]
μ_o	Removal of oysters by mortality, harvest, disease and respiration	d^{-1}	$0.01-0.1$	0.0505	estimated
α_{max}	Maximum nutrients uptake by phytoplankton	d^{-1}	$0.1-1.5$	0.8	[8]
f_{max}	Maximum phytoplankton filtration by oysters	d^{-1}	$0.1-2$	1.05	estimated

In [20], Saunders and Bazin introduced a chemostat model of an ecosystem with nutrients, a prey and a predator. In this paper, we study a system of three differential equations model of nutrients, phytoplankton (as prey) and oysters (as predator), Model (NPO). Our model is based on the chemostat model of [20] "with varying death rates".

Next, we introduce the Model (NPO) in three steps. First, we introduce the ordinary differential equation that describes the nutrients level of our Model (NPO).

(i) Nutrients level equation

The rate of change of nutrients level at time t in the bay ecosystem is modeled by

$$\frac{dN}{dt} = \underbrace{\gamma}_{N \text{ flow}} - \underbrace{\alpha(N)P}_{N \text{ loss by } P \text{ uptake}} - \underbrace{\mu_n N}_{\substack{N \text{ loss due to sinking} \\ \text{and denitrification}}} . \tag{2.1}$$

The first term of equation (2.1) is the constant flow of nutrients. The second and third terms model the loss of nutrients due to phytoplankton uptake and due to sinking and denitrification; respectively. The nutrients uptake by phytoplankton function α is defined by the Monod equation,

$$\alpha(N) = \frac{\alpha_{max}N}{N + k_n}, \tag{2.2}$$

where the model parameters α_{max}, γ, k_n and μ_n are defined in Table 2. In step 2, we introduce the ordinary differential equation that describes the phytoplankton biomass of the Model (NPO).

(ii) Phytoplankton biomass equation

The rate of change of phytoplankton biomass at time t in the bay ecosystem is modeled by

$$\frac{dP}{dt} = \underbrace{\alpha(N)P}_{P \text{ gain from } N \text{ uptake}} - \underbrace{f(P)O}_{P \text{ loss by } O \text{ uptake}} - \underbrace{\mu_p P}_{\substack{P \text{ loss due to sinking} \\ \text{and predation}}} . \tag{2.3}$$

The first term of equation (2.3) represents energy transfer from nutrients to phytoplankton. The second and third terms model the loss of phytoplankton due to oyster filtration and due to sinking and predation by other filter feeders and fish; respectively. As in [19, 20], an expression of the function f, that represents the oysters filtration of phytoplankton function, can be derived using the Monod equation

$$f(P) = \frac{f_{max}P}{P + k_p}, \tag{2.4}$$

where the model parameters f_{max}, k_p and μ_p are defined in Table 2. In step 3, we introduce the ordinary differential equation that describes the oysters biomass of the Model (NPO).

(iii) Oysters biomass equation

The rate of change of oysters biomass at time t in the bay ecosystem is modeled by

$$\frac{dO}{dt} = \underbrace{f(P)O}_{O \text{ gain from filtration of } P} - \underbrace{\mu_o O}_{\substack{O \text{ loss due to mortality,} \\ \text{harvest, respiration and disease}}}. \tag{2.5}$$

The first term of equation (2.5) represents gain from oysters filtration of phytoplankton. The second term models oysters loss due to natural mortality, harvest, respiration and disease.

Consequently, from equations (2.1), (2.3) and (2.5) the Model (NPO) is the following system of equations.

$$\begin{cases} \dfrac{dN}{dt} = \gamma - \alpha(N)P - \mu_n N, \\[2mm] \dfrac{dP}{dt} = \alpha(N)P - f(P)O - \mu_p P, \\[2mm] \dfrac{dO}{dt} = f(P)O - \mu_o O, \end{cases} \tag{NPO}$$

with nonnegative initial conditions $N(0) \geq 0$, $P(0) \geq 0$ and $O(0) \geq 0$.

The influence of nutrients on phytoplankton bloom has been studied by Fan and Glibert in [8] and Hood *et al.* in [21]. Huppert *et al.* in [9, 10] studied a nutrients-phytoplankton NP model with phytoplankton bloom. Others have studied nutrients-phytoplankton-zooplankton NPZ models [11, 13, 14, 15, 22, 23]. These investigations have shown that NPZ models are capable of exhibiting a wide range of dynamical behaviors from equilibrium to oscillatory dynamics. Saunders and Bazin [20] have studied stability analysis of general NPO type models. In this paper, we use local and global sensitivity analyses to illustrate the impact of human and environmental factors on Model (NPO) dynamics.

3 Boundedness of orbits

In this section, we show that the Model (NPO) is well-posed. In particular, we show that all orbits are nonnegative and there is no population explosion.

Theorem 1. All solutions of the Model (NPO) are nonnegative and bounded whenever the initial conditions are nonnegative.

Proof. If $N(0) = 0$, then from equation (2.1) we obtain that $\frac{dN}{dt}|_{t=0} = \gamma > 0$. Similarly, if $P(0) = 0$, then from equation (2.3) we obtain that $\frac{dP}{dt}|_{t=0} = 0$. If $O(0) = 0$, then from equation (2.5) we obtain that $\frac{dO}{dt}|_{t=0} = 0$. Hence, by a result of Smith[24], we conclude that for $t > 0$, $N(t) \geq 0$, $P(t) \geq 0$ and $O(t) \geq 0$ whenever $N(0) \geq 0$, $P(0) \geq 0$ and $O(0) \geq 0$. Next, we prove boundedness of orbits.

From equation (2.1), we have $\frac{dN}{dt} \leq \gamma - \mu_n N$. Hence, $\lim_{t \to \infty} N(t) \leq \frac{\gamma}{\mu_n} < \infty$. Therefore, $N(t)$ is bounded.

Note that α and f are nonnegative bounded functions. In fact $0 \leq \alpha(N) \leq \alpha_{max}$ and $0 \leq f(P) \leq f_{max}$.

Since N is bounded and $\alpha(N) \not\equiv 0$, if $\lim_{t \to \infty} P(t) = \infty$, then from equation (2.1), $\exists\, k_1 > 0$ and a sequence $\{t_n\}$ such that $\frac{dN(t_n)}{dt} < 0$, $\forall\, t_n \geq k_1$. However, this is a contradiction to $N(t) \geq 0$ when $N(0) \geq 0$. Hence, P is bounded.

Similarly, since P is bounded and $f(P) \not\equiv 0$, if $\lim_{t \to \infty} O(t) = \infty$, then proceeding exactly as above in equation (2.3), we obtain a contradiction to $P(t) > 0$ when $P(0) > 0$. Hence, O is also bounded.

4 Nutrients N model

In the Model (NPO), oysters feed on phytoplankton and they starve to death whenever the phytoplankton population dies out. From the phytoplankton equation, we obtain

$$\frac{dP}{dt} \leq (\alpha_{max} - \mu_p)P.$$

Therefore, when the maximum value of the nutrients uptake by phytoplankton, α_{max}, is less than the value of phytoplankton loss, μ_p, then the phytoplankton and oysters populations ultimately decline to zero and Model (NPO) reduces to the following nutrients only equation,

$$\frac{dN}{dt} = \gamma - \mu_n N. \tag{N}$$

Hence, for all $t \geq 0$

$$N(t) = (N(0) - \frac{\gamma}{\mu_n})e^{-\mu_n t} + \frac{\gamma}{\mu_n}$$

and

$$\lim_{t \to \infty} N(t) \equiv E_N^1 = \frac{\gamma}{\mu_n}.$$

In the absence of phytoplankton and oysters, the nutrients level in the Model (NPO) stabilizes at the unique positive equilibrium point E_N^1. We next perform sensitivity analysis to determine how crucial the parameters γ and μ_n are to the equilibrium nutrients level.

4.1 Sensitivity analysis of E_N^1

Local sensitivity analysis index allows us to measure the relative change in a state variable when a parameter changes. In this paper, we use the following definition of normalized forward sensitivity index to perform local sensitivity analysis and compute normalized sensitivity indices [25, 26, 27, 28].

Definition 1 ([25, 26, 27, 28]). The normalized forward sensitivity index of a variable, u, that depends differentiably on a parameter, q, is defined as:

$$\Upsilon_q^u := \frac{\partial u}{\partial q} \times \frac{q}{u}.$$

Others, [25, 26, 27, 28], have used normalized sensitivity indices to study the impact of model parameters on model input. To perform local sensitivity analysis at equilibrium nutrients level, E_N^1, we compute normalized sensitivity indices using Definition 1. We summarize our results in Table 3.

Table 3 Normalized sensitivity indices of equilibrium nutrients level, E_N^1, to parameters evaluated at baseline of Table 2 and order of importance.

Parameter	Sensitivity index of E_N^1	Order of importance
γ	1	1
μ_n	-1	2

We note that in the absence of phytoplankton and oysters, increasing (respectively, decreasing) nutrients flow, γ, by 1% will increase (respectively, decrease) equilibrium nutrients level, E_N^1, by 1%. Increasing (respectively, decreasing) nutrients loss, μ_n, will decrease (respectively, increase) nutrients equilibrium level, E_N^1, by 1%.

Global sensitivity analysis illustrates the impact generated by one parameter on the model variable, while all the other parameters vary [29]; allowing identification of interactions [30, 31]. We use the Sobol' sensitivity method that is based on ANOVA (ANalysis Of VAriance) decomposition [32]. In particular, we perform global sensitivity analysis using Sobol' method with a free software tool, named Global Sensitivity Analysis Toolbox (GSAT) [33]. GSAT is implemented using Matlab software. We compute Sobol' first-order and total-order sensitivity indices. Our model parameters sampling are based on quasi-random sequences, model parameter ranges are provided in Table 2 and the sampled parameter values are used to run 200,000 simulations.

Next, we perform the global sensitivity analysis at equilibrium nutrients level, E_N^1. We summarize our results in Table 4.
Sobol' sensitivity results of Table 4 indicate that nutrients loss, μ_n, is the most important parameter and contributes about 57% of the nutrients equilibrium level, E_N^1, total variance. The nutrients flow, γ, contributes about 24% of the nutrients equilibrium level, E_N^1, total variance. There is no very large difference between first and total Sobol' index for each parameter. Therefore, there is no significant interaction between the parameters.

Table 4   First-order and total-order Sobol sensitivity indices of equilibrium nutrients level, E_N^1, related to changes in parameters with ranges listed in Table 2 and their order of importance.

Parameter	Sobol' first-order sensitivity	Order of importance	Sobol' total-order sensitivity	Order of importance
γ	0.2412	2	0.4298	2
μ_n	0.5702	1	0.7588	1

5 Nutrients-phytoplankton NP model

From the oysters equation of the Model (NPO), we obtain

$$\frac{dO}{dt} \leq (f_{max} - \mu_o)O.$$

Thus, when the maximum phytoplankton filtration by oysters, f_{max}, is smaller than μ_o, the removal of oysters, then the oysters die out, and the Model (NPO) reduces to the following nutrients-phytoplankton system of two equations,

$$\begin{cases} \dfrac{dN}{dt} = \gamma - \alpha(N)P - \mu_n N, \\ \dfrac{dP}{dt} = \alpha(N)P - \mu_p P. \end{cases} \tag{NP}$$

For all model parameter values,

$$E_{NP}^1 \equiv (E_{NP}^{1,1}, E_{NP}^{1,2}) = (E_N^1, 0), \tag{5.1}$$

is the unique phytoplankton-missing boundary equilibrium point of Model (NP).

5.1 NP model phytoplankton-missing equilibrium: E_{NP}^1

To study the stability of the boundary equilibrium points of the Model (NP), we introduce the threshold parameter,

$$R_N = \frac{\alpha_{max}\gamma}{(\gamma + k_n\mu_n)\mu_p}.$$

$R_N < 1$ is equivalent to $\alpha_{max} < \mu_p(1 + \frac{k_n\mu_n}{\gamma})$ and $R_N > 1$ is equivalent to $\alpha_{max} > \mu_p(1 + \frac{k_n\mu_n}{\gamma})$.

When α_{max} is "small", then $R_N < 1$, and E_{NP}^1 is locally stable. However, when α_{max} is "large", then $R_N > 1$, and E_{NP}^1 is unstable. We capture this stability result in the following theorem.

Theorem 2. In Model (NP), the phytoplankton-missing boundary equilibrium point, E_{NP}^1, is locally stable when $R_N < 1$ and unstable when $R_N > 1$.

Proof.   The Jacobian matrix of Model (NP) evaluated at E_{NP}^1 is

$$\mathcal{J}_{|E_{NP}^1} = \begin{bmatrix} -\mu_n & -\frac{\alpha_{max}\gamma}{\gamma + k_n\mu_n} \\ 0 & \frac{\alpha_{max}\gamma}{\gamma + k_n\mu_n} - \mu_p \end{bmatrix}.$$

Hence, the eigenvalues of $\mathcal{J}_{|E_{NP}^1}$ are

$$\lambda_{1|E_{NP}^1} = -\mu_n \quad \text{and} \quad \lambda_{2|E_{NP}^1} = \frac{\alpha_{max}\gamma}{\gamma + k_n\mu_n} - \mu_p. \tag{5.2}$$

We see from (5.2) that $\lambda_{1|E_{NP}^1} < 0$. Furthermore,

$$R_N < 1 \Longleftrightarrow \lambda_{2|E_N} < 0 \quad \text{and} \quad R_N > 1 \Longleftrightarrow \lambda_{2|E_N} > 0.$$

Hence, if $R_N < 1$, E_{NP}^1 is locally stable and if $R_N > 1$, E_{NP}^1 is unstable.

Next, we establish the global stability of E_{NP}^1.

Corollary 1. In Model (NP), the phytoplankton-missing boundary equilibrium point, E_{NP}^1, is globally stable when $R_N < 1$.

Proof. Since α is an increasing function of N and $\lim\limits_{t \to \infty} N(t) \le \frac{\gamma}{\mu_n}$, then $\exists \, k_1 > 0$ such that

$$\frac{dP}{dt} \le \left(\alpha(\frac{\gamma}{\mu_n}) - \mu_p \right) P, \ \forall \, t \ge k_1.$$

Notice that

$$\alpha(\frac{\gamma}{\mu_n}) - \mu_p = \mu_p(R_N - 1),$$

and

$$P(t) \le P(0)e^{\mu_p(R_N - 1)t} \quad \text{for} \quad \forall \, t \ge k_1.$$

Hence, $\lim\limits_{t \to \infty} P(t) = 0$.

By Theorem (2), E_{NP}^1 is the only stable equilibrium point of Model (NP) with $P = 0$. Hence, E_{NP}^1 is globally stable.

When $\alpha_{max} < \mu_p(1 + \frac{\mu_n k_n}{\gamma})$, then $R_N < 1$ and the phytoplankton biomass decreases to zero. That is, when the maximum value of nutrients uptake by phytoplankton, α_{max}, is less than the product of phytoplankton removal, μ_p, and $(1 + \frac{\mu_n k_n}{\gamma})$, then the phytoplankton population goes extinct (Theorem 2 and Corollary 1).

We next perform sensitivity analysis of E_{NP}^1.

5.2 Sensitivity analysis of E_{NP}^1

Here, as in Table 3, we perform local sensitivity analysis of the equilibrium nutrients level, $E_{NP}^{1,1}$ of E_{NP}^1. We summarize our results in Table 5.

Table 5 Normalized sensitivity indices of equilibrium nutrients level, $E_{NP}^{1,1}$ of E_{NP}^1, to the five parameters evaluated at their baseline in Table 2 and order of importance.

Parameter	Sensitivity index of $E_{NP}^{1,1}$	Order of importance
γ	1	1
k_n	0	3
μ_n	-1	2
μ_p	0	4
α_{max}	0	5

In the absence of oysters, when $R_N < 1$, we see from the sensitivity indices in Table 5 that the most important parameters are the nutrients loss, μ_n, and the nutrients flow, γ. Furthermore, decreasing (respectively, increasing) nutrients flow, γ, by 1% will decrease (respectively, increase) nutrients level $E_{NP}^{1,1}$ of E_{NP}^1, by 1%, and increasing (respectively, decreasing) nutrients loss, μ_n, by 1% will decrease (respectively, increase) nutrients level, $E_{NP}^{1,1}$ of E_{NP}^1, by 1%.

Next, as in Table 4, we perform the global sensitivity analysis of equilibrium nutrients level, $E_{NP}^{1,1}$ of E_{NP}^1. We summarize our results in Table 6.

Table 6   First-order and total-order Sobol sensitivity indices of equilibrium nutrients level, $E_{NP}^{1,1}$ of E_{NP}^1, related to changes in parameters with ranges given in Table 2 and their order of importance.

Parameter	Sobol' first-order sensitivity	Order of importance	Sobol' total-order sensitivity	Order of importance
γ	0.2412	2	0.4298	2
k_n	0	3	0	3
μ_n	0.5702	1	0.7588	1
μ_p	0	4	0	4
α_{max}	0	3	0	5

Similar to the local sensitivity analysis, Sobol' sensitivity results show that the most important parameters are the nutrients loss, μ_n, and the nutrients flow, γ. Sobol' sensitivity results of Table 6 indicate that nutrients loss, μ_n, contributes about 57% of the nutrients equilibrium level, $E_{NP}^{1,1}$ of E_{NP}^1, total variance. The nutrients flow, γ, contributes about 24% of the nutrients equilibrium level, $E_{NP}^{1,1}$ of E_{NP}^1, total variance. There is no very large difference between first-order and total-order Sobol' indices for each parameter. Therefore, there is no significant interactions between the parameters. However, equilibrium phytoplankton biomass, $E_{NP}^{1,2}$ of E_{NP}^1, is not sensitive to parameter values change, and remains zero.

5.3 NP model nutrients-phytoplankton interior equilibrium: E_{NP}^2

When $R_N > 1$, then Model (NP) has a stable interior equilibrium with positive phytoplankton biomass and nutrients level at

$$E_{NP}^2 \equiv \left(E_{NP}^{2,1}, E_{NP}^{2,2} \right) = \left(\frac{k_n \gamma}{\gamma(R_N - 1) + R_N \mu_n k_n}, \frac{\gamma}{\mu_p} \left(\frac{(R_N - 1)(\gamma + \mu_n k_n)}{\gamma(R_N - 1) + R_N \mu_n k_n} \right) \right).$$

We capture this in the following result.

Theorem 3. When $R_N > 1$, then Model (NP) has a unique stable interior equilibrium, E_{NP}^2, and the phytoplankton population persists. However, the Model (NP) has no interior equilibrium point and the phytoplankton population goes extinct when $R_N < 1$.

Proof.   If $R_N > 1$, then $E_{NP}^{2,1} > 0$ and $E_{NP}^{2,2} > 0$ and E_{NP}^2 is the only interior equilibrium of (NP).
If $R_N < 1$, we have shown, in Corollary (1), that the boundary equilibrium E_{NP}^1 is globally stable. So, E_{NP}^2 does not exist if $R_N < 1$.
The eigenvalues of the Jacobian matrix of Model (NP) evaluated at E_{NP}^2 are

$$\lambda_{1|E_{NP}^2} = -\frac{1}{2\alpha_{max}k_n\mu_p}\left(\gamma(\alpha_{max}-\mu_p)^2 + \mu_n k_n\mu_p^2\right.$$

$$\left. -\sqrt{\left(\gamma(\alpha_{max}-\mu_p)^2 + \mu_n k_n\mu_p^2\right)^2 - 4\alpha_{max}k_n\mu_p^2(\alpha_{max}-\mu_p)(\gamma(\alpha_{max}-\mu_p) - \mu_n k_n\mu_p)}\right)$$

$$= -\frac{1}{2\alpha_{max}k_n\mu_p}\left[\frac{1}{\gamma}(\gamma\mu_p(R_N-1) + R_N k_n\mu_n\mu_p)^2 + \mu_n k_n\mu_p^2\right.$$

$$\left. -\sqrt{\left(\frac{1}{\gamma}(\gamma\mu_p(R_N-1) + R_N k_n\mu_n\mu_p)^2 + \mu_n k_n\mu_p^2\right)^2 - 4\alpha_{max}^2 k_n\mu_p^2(1-\frac{1}{R_N})(\gamma\mu_p(R_N-1) + R_N k_n\mu_n\mu_p)}\right]$$

$$\tag{5.3}$$

and

$$\lambda_{2|E_{NP}^2} = -\frac{1}{2\alpha_{max}k_n\mu_p}\left(\gamma(\alpha_{max}-\mu_p)^2 + \mu_n k_n\mu_p^2\right.$$

$$\left. +\sqrt{\left(\gamma(\alpha_{max}-\mu_p)^2 + \mu_n k_n\mu_p^2\right)^2 - 4\alpha_{max}k_n\mu_p^2(\alpha_{max}-\mu_p)(\gamma(\alpha_{max}-\mu_p) - \mu_n k_n\mu_p)}\right)$$

$$= -\frac{1}{2\alpha_{max}k_n\mu_p}\left[\frac{1}{\gamma}(\gamma\mu_p(R_N-1) + R_N k_n\mu_n\mu_p)^2 + \mu_n k_n\mu_p^2\right.$$

$$\left. +\sqrt{\left(\frac{1}{\gamma}(\gamma\mu_p(R_N-1) + R_N k_n\mu_n\mu_p)^2 + \mu_n k_n\mu_p^2\right)^2 - 4\alpha_{max}^2 k_n\mu_p^2(1-\frac{1}{R_N})(\gamma\mu_p(R_N-1) + R_N k_n\mu_n\mu_p)}\right].$$

$$\tag{5.4}$$

From equations (5.3) and (5.4) we obtain that

$$R_N > 1 \implies \mathcal{R}e(\lambda_{1|E_{NP}^2}) < 0 \quad \text{and} \quad \mathcal{R}e(\lambda_{2|E_{NP}^2}) < 0.$$

Hence, when $R_N > 1$, then interior equilibrium point E_{NP}^2 is stable. However, when $R_N < 1$, Model (NP) has no interior equilibrium.

When $\alpha_{max} < \mu_p(1 + \frac{k_n\mu_n}{\gamma})$, then phytoplankton removal is "stronger" than the maximum phytoplankton uptake of nutrients, and this results in phytoplankton extinction. Nutrients, however, do not decrease to zero and remain at positive levels because of the nutrients steady inflow. Moreover, Theorem (1) assures that nutrients level will not explode over time even when the phytoplankton population is extinct. When $\alpha_{max} > \mu_p(1 + \frac{k_n\mu_n}{\gamma})$, then the phytoplankton removal is "weaker" than the maximum phytoplankton filtration and this results in phytoplankton persistence (Theorem 3).
We next perform sensitivity analysis of E_{NP}^2.

5.4 Sensitivity analysis of E_{NP}^2

Sensitivity indices of equilibrium nutrients level, $E_{NP}^{2,1}$ of E_{NP}^2.

Proceeding as in Table 3, we compute normalized sensitivity indices of equilibrium nutrients level, $E_{NP}^{2,1}$ of E_{NP}^2. We summarize our results in Table 7.

Table 7 Normalized sensitivity indices of equilibrium nutrients level, $E_{NP}^{2,1}$ of E_{NP}^2, to parameters evaluated at their baseline in Table (2) and order of importance, where $R_N = 1.3469$.

Parameter	Sensitivity index of $E_{NP}^{2,1}$	Order of importance
γ	0	4
k_n	1	3
μ_n	0	5
μ_p	3.2	1
α_{max}	-3.2	2

The most sensitive parameters in the equilibrium nutrients level, $E_{NP}^{2,1}$ of E_{NP}^2, are the phytoplankton removal, μ_p, and the maximum phytoplankton filtration by oysters, α_{max}. Increasing (respectively, decreasing) phytoplankton removal, μ_p, by 1% will increase (respectively, decrease) equilibrium nutrients level, $E_{NP}^{2,1}$ of E_{NP}^2, by about 3.2%. Decreasing (respectively, increasing) phytoplankton filtration by oysters, α_{max}, by 1% will increase (respectively, decrease) equilibrium nutrients level, $E_{NP}^{2,1}$ of E_{NP}^2, by about 3.2%.

Next, as in Table 4, we perform the global sensitivity analysis of equilibrium nutrients level, $E_{NP}^{2,1}$ of E_{NP}^2. We summarize our results in Table 8.

Table 8 First-order and total-order Sobol sensitivity indices of equilibrium nutrients level, $E_{NP}^{2,1}$ of E_{NP}^2, related to changes in the five parameters at ranges given in Table 2 and their order of importance.

Parameter	Sobol' first-order sensitivity	Order of importance	Sobol' total-order sensitivity	Order of importance
γ	0	4	0.9900	3
k_n	0.0040	1	0.3361	4
μ_n	0.0022	3	0	5
μ_p	0.0029	2	0.9986	2
α_{max}	0	5	1.0037	1

Sobol' sensitivity analysis suggest that model parameters in Table 8 do not contribute significantly to variance of the equilibrium nutrients level, $E_{NP}^{2,1}$ of E_{NP}^2. However, some of the parameters interact strongly with others.

Sensitivity indices of equilibrium phytoplankton biomass, $E_{NP}^{2,2}$ of E_{NP}^2.

Proceeding as in Table 3, we compute normalized sensitivity indices of equilibrium phytoplankton biomass, $E_{NP}^{2,2}$ of E_{NP}^2. We summarize our results in Table 9.

Table 9 Normalized sensitivity indices of equilibrium phytoplankton biomass, $E_{NP}^{2,2}$ of E_{NP}^2, to parameters with baseline given in Table (2) and order of importance, where $R_N = 1.3469$.

Parameter	Sensitivity index of $E_{NP}^{2,2}$	Order of importance
γ	1.2133	2
k_n	-0.2133	4
μ_n	-0.2133	5
μ_p	-1.6827	1
α_{max}	0.6827	3

The most sensitive parameters in the equilibrium phytoplankton biomass, $E_{NP}^{2,2}$ of E_{NP}^2, are the phytoplankton removal, μ_p, and the nutrients flow, γ. Increasing (respectively, decreasing) phytoplankton removal, μ_p, by 1% will decrease (respectively, increase) equilibrium phytoplankton biomass, $E_{NP}^{2,2}$ of E_{NP}^2, by about 1.7%. Decreasing (respectively, increasing) nutrients flow, γ by 1% will decrease (respectively, increase) equilibrium phytoplankton biomass, $E_{NP}^{2,2}$ of E_{NP}^2, by about 1.2%.

Next, as in Table 4, we perform the global sensitivity analysis of equilibrium phytoplankton biomass, $E_{NP}^{2,2}$ of E_{NP}^2. We summarize our results in Table 10.

Sobol' sensitivity analysis suggest that model parameters in Table 10 do not contribute significantly to variance of the equilibrium phytoplankton biomass, $E_{NP}^{2,2}$ of E_{NP}^2. However, some of the parameters interact strongly with others.

We next perform sensitivity analysis to determine how parameters are important to R_N.

Table 10   First-order and total-order Sobol sensitivity indices of equilibrium phytoplankton biomass, $E_{NP}^{2,2}$ of E_{NP}^2, related to changes in parameters at ranges given in Table 2 and their order of importance.

Parameter	Sobol' first-order sensitivity	Order of importance	Sobol' total-order sensitivity	Order of importance
γ	0	1	1	1
k_n	0	2	0.0023	5
μ_n	0	3	0.0046	4
μ_p	0	4	0.9999	3
α_{max}	0	5	1	2

5.5 Sensitivity analysis of R_N

Proceeding as in Table 3, we compute normalized sensitivity indices at R_N. We summarize our results in Table 11.

Table 11   Sensitivity indices of R_N to parameters evaluated at their baseline given in Table 2 and order of importance.

Parameter	Sensitivity index of R_N	Order of importance
γ	0.0740	3
k_n	-0.0740	4
μ_n	-0.0740	5
μ_p	-1	2
α_{max}	1	1

The most sensitive parameters are the maximum nutrients uptake by phytoplankton, α_{max}, and the phytoplankton removal, μ_p. From Table (11), increasing (respectively, decreasing) the maximum nutrients uptake by phytoplankton, α_{max}, by 1% will increase (respectively, decrease) R_N by about 1%. Increasing (respectively, decreasing) the maximum nutrients uptake by phytoplankton, α_{max}, by 1% will decrease (respectively, increase) R_N by about 1%.

Next, as in Table 4, we perform the global sensitivity analysis at R_N. We summarize our results in Table 12.

Table 12   First-order and total-order Sobol sensitivity indices of R_N related to changes in parameters at ranges given in Table 2 and their order of importance.

Parameter	Sobol' first-order sensitivity	Order of importance	Sobol' total-order sensitivity	Order of importance
γ	0.0191	3	0.0434	3
k_n	0.0035	5	0.0122	4
μ_n	0.0026	4	0.0088	5
μ_p	0.5426	1	0.7007	1
α_{max}	0.2623	2	0.4127	2

Table 6 shows that the most important parameters to R_N are the phytoplankton removal, μ_p and the maximum nutrients uptake by phytoplankton, α_{max}. Sobol sensitivity results in Table 12 indicate that μ_p contributes about 54% of R_N total variance and α_{max} contributes about 26% of R_N total variance. There is no very large difference between first-order and total-order Sobol' indices for each parameter. Therefore, there is no significant interaction between the parameters.

6 Nutrients-phytoplankton-oysters NPO model

Now, we consider the full Model (NPO) where $f_{max} > \mu_o$ and $\alpha_{max} > \mu_p$. That is, in this section, we study the Model (NPO) with nutrients, phytoplankton and oysters present.

For all parameter values, the Model (NPO) has both phytoplankton and oysters-missing boundary equilibrium at

$$E_{NPO}^1 \equiv (E_{NPO}^{1,1}, E_{NPO}^{1,2}, E_{NPO}^{1,3}) = (E_N^1, 0, 0).$$

In addition, when $R_N > 1$, the Model (NPO) has an only oysters-missing equilibrium at

$$E_{NPO}^2 \equiv (E_{NPO}^{2,1}, E_{NPO}^{2,2}, E_{NPO}^{2,3}) = \left(\frac{k_n \gamma}{\gamma(R_N - 1) + R_N \mu_n k_n}, \frac{\gamma}{\mu_p} \left(\frac{(R_N - 1)(\gamma + \mu_n k_n)}{\gamma(R_N - 1) + R_N \mu_n k_n} \right), 0 \right).$$

6.1 NPO phytoplankton and oysters missing equilibrium: E_{NPO}^1

As in the Model (NPO), $R_N < 1$ implies extinction dynamics and the phytoplankton and oysters populations decrease to zero. We summarize these results in the following result.

Theorem 4. In Model (NPO), the phytoplankton and oysters-missing equilibrium point, E_{NPO}^1, is locally stable when $R_N < 1$ and unstable when $R_N > 1$.

Proof. The eigenvalues of the Jacobian matrix of Model (NPO) evaluated at E_{NPO}^1 are

$$\begin{aligned}
\lambda_{1|E_{NPO}^1} &= -\mu_n, \\
\lambda_{2|E_{NPO}^1} &= \frac{\alpha_{max}\gamma}{\gamma + k_n \mu_n} - \mu_p \\
\text{and} \quad \lambda_{3|E_{NPO}^1} &= -\mu_o.
\end{aligned} \tag{6.1}$$

We see from (6.1) that $\lambda_{1|E_{NPO}^1} = \lambda_{1|E_{NP}^1} < 0$, $\lambda_{2|E_{NPO}^1} = \lambda_{2|E_{NP}^1}$ and $\lambda_{3|E_{NPO}^1} < 0$. Furthermore,

$$R_N < 1 \iff \lambda_{2|E_{NPO}^1} < 0 \quad \text{and} \quad R_N > 1 \iff \lambda_{2|E_{NPO}^1} > 0.$$

Hence, when $R_N < 1$, E_{NPO}^1 is locally stable and when $R_N > 1$, E_{NPO}^1 is unstable.

Next, we establish the global stability of E_{NPO}^1.

Corollary 2. In Model (NPO), the phytoplankton and oysters-missing equilibrium point, E_{NPO}^1, is globally stable when $R_N < 1$.

Proof. Since α is an increasing function of N and $\lim_{t \to \infty} N(t) \leq \frac{\gamma}{\mu_n}$, then we have from the second equation of Model (NPO) that $\exists k_1 > 0$ such that

$$\frac{dP}{dt} \leq \left(\alpha(\frac{\gamma}{\mu_n}) - \mu_p \right) P, \quad \forall t \geq k_1.$$

Notice that $\alpha(\frac{\gamma}{\mu_n}) - \mu_p = \mu_p(R_N - 1)$. Hence

$$P(t) \leq P(0) e^{\mu_p (R_N - 1)t}, \quad \forall t \geq k_1. \tag{6.2}$$

Therefore, $\lim_{t \to \infty} P(t) = 0$. Since $f(0) = 0$, then $\exists 0 < \varepsilon < \mu_o$ and $k_2 > k_1$ such that $f(P(t)) \leq \varepsilon$ for $t \geq k_2$.
Consequently,

$$\frac{dO}{dt} \leq (\varepsilon - \mu_o)O, \quad \forall t \geq k_2$$

and

$$O(t) \leq O(0) e^{(\varepsilon - \mu_o)t}, \quad \forall t \geq k_2. \tag{6.3}$$

Hence, $\lim_{t \to \infty} O(t) = 0$.
E_{NPO}^1 is the only equilibrium point of Model (NPO) with $P = O = 0$. Hence, E_{NPO}^1 is a globally stable equilibrium point.

We next perform sensitivity analysis of E_{NPO}^1.

6.2 Sensitivity analysis of E_{NPO}^1

Proceeding as in Table 3, we compute normalized sensitivity indices at equilibrium nutrients level, $E_{NPO}^{1,1}$ of E_{NPO}^1. We summarize our results in Table 13.

Table 13 Normalized sensitivity indices of equilibrium nutrients level, $E_{NPO}^{1,1}$ of E_{NPO}^1, to parameters evaluated at their baseline given in Table 2 and order of importance.

Parameter	Sensitivity index of $E_{NPO}^{1,1}$	Order of importance
γ	1	1
k_n	0	3
μ_n	-1	2
μ_p	0	4
α_{max}	0	5
k_p	0	6
μ_o	0	7
f_{max}	0	8

When $R_N < 1$, we see from sensitivity indices in Table 13 that the most important parameters are the nutrients flow, γ, and the nutrients loss, μ_n. Furthermore, decreasing (respectively, increasing) equilibrium nutrients flow, γ, by 1% would decrease (respectively, increase) equilibrium nutrients level, $E_{NPO}^{1,1}$ of E_{NPO}^1, by 1%, and increasing (respectively, decreasing) nutrients loss, μ_n, by 1% would decrease (respectively, increase) equilibrium nutrients level, $E_{NPO}^{1,1}$ of E_{NPO}^1, by 1%.

Next, as in Table 4, we perform the global sensitivity analysis of equilibrium nutrients level, $E_{NPO}^{1,1}$ of E_{NPO}^1, We summarize our results in Table 14.

Table 14 First-order and total-order Sobol sensitivity indices of equilibrium nutrients level, $E_{NPO}^{1,1}$ of E_{NPO}^1, related to changes in parameters at ranges given in Table 2 and their order of importance.

Parameter	Sobol' first-order sensitivity	Order of importance	Sobol' total-order sensitivity	Order of importance
γ	0.2412	2	0.4297	2
k_n	0	3	0	3
μ_n	0.5703	1	0.7588	1
μ_p	0	4	0	4
α_{max}	0	5	0	5
k_p	0	6	0	6
μ_o	0	7	0	7
f_{max}	0	8	0	8

Similar to the local sensitivity analysis, Sobol' sensitivity results of Table 14 show that the most important parameters are the nutrients flow, γ, and the nutrients loss, μ_n. Sobol' sensitivity results of Table 14 indicate that nutrients loss, μ_n, contributes about 57% of the equilibrium nutrients level, $E_{NPO}^{1,1}$ of E_{NPO}^1, total variance. The nutrients flow, γ, contributes about 24% of the equilibrium nutrients level, $E_{NPO}^{1,1}$ of E_{NPO}^1, total variance. There is no very large difference between first-order and total-order Sobol' indices for each parameter. Therefore, there is no significant interactions between the parameters. However, equilibrium phytoplankton biomass, $E_{NPO}^{1,2}$ of E_{NPO}^1, and equilibrium oysters biomass, $E_{NPO}^{1,3}$ of E_{NPO}^1, are not sensitive to parameter values change, and remain zero.

6.3 NPO model oysters-missing equilibrium: E_{NPO}^2

The only oysters-missing equilibrium point, E_{NPO}^2, exists whenever $R_N > 1$. To study the stability of E_{NPO}^2, we assume that $R_N > 1$ and define the positive threshold parameter,

$$R_{NPO} \equiv \frac{f_{max}(R_N - 1)}{\mu_o\left((R_N - 1)\left(\frac{k_p\mu_p}{\gamma} + 1\right) + \frac{\mu_p\mu_n k_p k_n}{\gamma(\gamma + \mu_n k_n)}\right)}. \tag{6.4}$$

$R_{NPO} < 1$ is equivalent to $f_{max} < \mu_o\left(1 + \frac{k_p\mu_p(\alpha_{max} - \mu_p)}{\gamma(\alpha_{max} - \mu_p) - \mu_n k_n\mu_p}\right)$ and $R_{NPO} > 1$ is equivalent to $f_{max} > \mu_o\left(1 + \frac{k_p\mu_p(\alpha_{max} - \mu_p)}{\gamma(\alpha_{max} - \mu_p) - \mu_n k_n\mu_p}\right)$. When $R_{NPO} < 1$, then the filtration rate is "small" and oysters population dies out. However, when $R_{NPO} > 1$, then the filtration rate is "large" and the oysters population may persist. We collect this in the following result.

Theorem 5. Let $R_N > 1$ in Model (NPO). Then E_{NPO}^2 is locally stable when $R_{NPO} < 1$ and unstable when $R_{NPO} > 1$.

Proof. The eigenvalues of the Jacobian matrix of Model (NPO) evaluated at E_{NPO}^2 are

$$\lambda_{1|E_{NPO}^2} = -\frac{1}{2\alpha_{max}k_n\mu_p}\left(\gamma(\alpha_{max} - \mu_p)^2 + \mu_n k_n\mu_p^2\right.$$

$$\left. - \sqrt{\left(\gamma(\alpha_{max} - \mu_p)^2 + \mu_n k_n\mu_p^2\right)^2 - 4\alpha_{max}k_n\mu_p^2(\alpha_{max} - \mu_p)(\gamma(\alpha_{max} - \mu_p) - \mu_n k_n\mu_p)}\right)$$

$$= -\frac{1}{2\alpha_{max}k_n\mu_p}\left(\frac{1}{\gamma}\left(\gamma\mu_p(R_N - 1) + R_N k_n\mu_n\mu_p\right)^2 + \mu_n k_n\mu_p^2\right.$$

$$\left. - \sqrt{\left(\frac{1}{\gamma}(\gamma\mu_p(R_N - 1) + R_N k_n\mu_n\mu_p)^2 + \mu_n k_n\mu_p^2\right)^2 - 4\alpha_{max}^2 k_n\mu_p^2(1 - \frac{1}{R_N})(\gamma\mu_p(R_N - 1) + R_N k_n\mu_n\mu_p)}\right), \tag{6.5}$$

$$\lambda_{2|E_{NPO}^2} = -\frac{1}{2\alpha_{max}k_n\mu_p}\left(\gamma(\alpha_{max} - \mu_p)^2 + \mu_n k_n\mu_p^2\right.$$

$$\left. + \sqrt{\left(\gamma(\alpha_{max} - \mu_p)^2 + \mu_n k_n\mu_p^2\right)^2 - 4\alpha_{max}k_n\mu_p^2(\alpha_{max} - \mu_p)(\gamma(\alpha_{max} - \mu_p) - \mu_n k_n\mu_p)}\right)$$

$$= -\frac{1}{2\alpha_{max}k_n\mu_p}\left(\frac{1}{\gamma}\left(\gamma\mu_p(R_N - 1) + R_N k_n\mu_n\mu_p\right)^2 + \mu_n k_n\mu_p^2\right.$$

$$\left. + \sqrt{\left(\frac{1}{\gamma}(\gamma\mu_p(R_N - 1) + R_N k_n\mu_n\mu_p)^2 + \mu_n k_n\mu_p^2\right)^2 - 4\alpha_{max}^2 k_n\mu_p^2(1 - \frac{1}{R_N})(\gamma\mu_p(R_N - 1) + R_N k_n\mu_n\mu_p)}\right) \tag{6.6}$$

and

$$\lambda_{3|E_{NPO}^2} = -\frac{(\mu_o - f_{max})\left(\gamma(\alpha_{max} - \mu_p) - \mu_n k_n\mu_p\right) + k_p\mu_p\mu_o(\alpha_{max} - \mu_p)}{\left(\gamma(\alpha_{max} - \mu_p) - \mu_n k_n\mu_p\right) + k_p\mu_p(\alpha_{max} - \mu_p)}. \tag{6.7}$$

From equations (6.5) and (6.6), we have

$$R_N > 1 \implies \mathcal{R}_e(\lambda_{1|E_{NPO}^2}) < 0 \quad \text{and} \quad \mathcal{R}_e(\lambda_{2|E_{NPO}^2}) < 0.$$

When $R_N > 1$, then the following equivalences are immediate

$$f_{max} < \mu_o\left(1 + \frac{k_p\mu_p(\alpha_{max} - \mu_p)}{\gamma(\alpha_{max} - \mu_p) - \mu_n k_n\mu_p}\right) \iff \mathcal{R}_e(\lambda_{3|E_{NPO}^2}) < 0,$$

and

$$f_{max} > \mu_o\left(1 + \frac{k_p\mu_p(\alpha_{max} - \mu_p)}{\gamma(\alpha_{max} - \mu_p) - \mu_n k_n\mu_p}\right) \iff \mathcal{R}_e(\lambda_{3|E_{NPO}^2}) > 0.$$

Hence, E_{NPO}^2 is stable when $R_{NPO} < 1$, and E_{NPO}^2 becomes unstable when $R_{NPO} > 1$; where $R_N > 1$.

We next perform sensitivity analysis on E_{NPO}^2.

6.4 Sensitivity analysis of E_{NPO}^2

Sensitivity indices of equilibrium nutrients level, $E_{NPO}^{2,1}$ of E_{NPO}^2.

Proceeding as in Table 3, we compute normalized sensitivity indices at equilibrium nutrients level, $E_{NPO}^{2,1}$ of E_{NPO}^2. We summarize our results in Table 15.

Table 15   Normalized sensitivity indices of equilibrium nutrients level, $E_{NPO}^{2,1}$ of E_{NPO}^2, to parameters evaluated at their baseline given in Table 2 and order of importance.

Parameter	Sensitivity index of $E_{NPO}^{2,1}$	Order of importance
γ	0	4
k_n	1	3
μ_n	0	5
μ_p	3.2	1
α_{max}	-3.2	2
k_p	0	6
μ_o	0	7
f_{max}	0	8

The most sensitive parameters in the equilibrium nutrients level, $E_{NPO}^{2,1}$ of E_{NPO}^2, are the phytoplankton removal, μ_p, and the maximum phytoplankton filtration by oysters, α_{max}. Increasing (respectively, decreasing) phytoplankton removal, μ_p, by 1% will increase (respectively, decrease) equilibrium nutrients level, $E_{NPO}^{2,1}$ of E_{NPO}^2, by about 3.2%. Decreasing (respectively, increasing) phytoplankton filtration by oysters, α_{max}, by 1% will increase (respectively, decrease) equilibrium nutrients level, $E_{NPO}^{2,1}$ of E_{NPO}^2, by about 3.2%. Next, as in Table 4, we perform the global sensitivity analysis of equilibrium nutrients level, $E_{NPO}^{2,1}$ of E_{NPO}^2. We summarize our results in Table 16.

Table 16   First-order and total-order Sobol sensitivity indices of equilibrium nutrients level, $E_{NPO}^{2,1}$ of E_{NPO}^2, related to changes in parameters at ranges given in Table (2) and their order of importance.

Parameter	Sobol' first-order sensitivity	Order of importance	Sobol' total-order sensitivity	Order of importance
γ	0	1	1.0002	2
k_n	0	2	0.3289	4
μ_n	0	3	0	5
μ_p	0	4	0.9997	3
α_{max}	0	5	1.0006	1
k_p	0	6	0	6
μ_o	0	7	0	7
f_{max}	0	8	0	8

Sobol' sensitivity analysis suggest that model parameters in Table 16 do not contribute significantly to variance of the equilibrium nutrients level, $E_{NPO}^{2,1}$ of E_{NPO}^2. However, some of the parameters interact strongly with others.

Sensitivity indices of equilibrium phytoplankton biomass, $E_{NPO}^{2,2}$ of E_{NPO}^2.

Proceeding as in Table 3, we compute normalized sensitivity indices at equilibrium phytoplankton biomass, $E_{NPO}^{2,2}$ of E_{NPO}^2. We summarize our results in Table 17.

Table 17   Normalized sensitivity indices of equilibrium phytoplankton biomass, $E_{NPO}^{2,2}$ of E_{NPO}^2, to parameters with baseline given in Table 2 and order of importance.

Parameter	Sensitivity index of $E_{NPO}^{2,2}$	Order of importance
γ	1.2133	2
k_n	-0.2133	4
μ_n	-0.2133	5
μ_p	-1.6827	1
α_{max}	0.6827	3
k_p	0	6
μ_o	0	7
f_{max}	0	8

The most sensitive parameters in the equilibrium phytoplankton biomass, $E_{NPO}^{2,2}$ of E_{NPO}^2, are the phytoplankton removal, μ_p, and the nutrients flow, γ. Increasing (respectively, decreasing) phytoplankton removal, μ_p, by 1% will decrease (respectively, increase) equilibrium phytoplankton biomass, $E_{NPO}^{2,2}$ of E_{NPO}^2, by about 1.7%. Decreasing (respectively, increasing) nutrients flow, γ by 1% will decrease (respectively, increase) equilibrium phytoplankton biomass, $E_{NPO}^{2,2}$ of E_{NPO}^2, by about 1.2%.
Next, as in Table 4, we perform the global sensitivity analysis of equilibrium phytoplankton biomass, $E_{NPO}^{2,2}$ of E_{NPO}^2. We summarize our results in Table 18.

Table 18   First-order and total-order Sobol sensitivity indices of equilibrium phytoplankton biomass, $E_{NPO}^{2,2}$ of E_{NPO}^2, related to changes in parameters at ranges given in Table 2 and their order of importance.

Parameter	Sobol' first-order sensitivity	Order of importance	Sobol' total-order sensitivity	Order of importance
γ	0	1	1	2
k_n	0	2	0.0406	5
μ_n	0	3	0.0696	4
μ_p	0	4	1.0001	1
α_{max}	0	5	1	3
k_p	0	6	0	6
μ_o	0	7	0	7
f_{max}	0	8	0	8

Sobol' sensitivity analysis suggests that model parameters in Table 18 do not contribute significantly to variance of the equilibrium phytoplankton biomass, $E_{NPO}^{2,2}$ of E_{NPO}^2. However, some of the parameters interact strongly with others. However, equilibrium oysters biomass, $E_{NPO}^{1,3}$ of E_{NPO}^1, is not sensitive to parameter values change, and remains zero.
We next perform sensitivity analysis on R_N.

6.5 Sensitivity indices of R_N

Proceeding as in Table 3, we compute normalized sensitivity indices on R_N. We summarize our results in Table 19.

Table 19 Normalized sensitivity indices of R_N to parameters with baseline given in Table 2 and their order of importance.

Parameter	Sensitivity index of R_N	Order of importance
γ	0.0740	3
k_n	-0.0740	4
μ_n	-0.0740	5
μ_p	-1	2
α_{max}	1	1
k_p	0	6
μ_o	0	7
f_{max}	0	8

The most sensitive parameters are the maximum nutrients uptake by phytoplankton, α_{max}, and the phytoplankton removal, μ_p. From Table (19), increasing (respectively, decreasing) the maximum nutrients uptake by phytoplankton, α_{max}, by 1% will increase (respectively, decrease) R_N by about 1%. Increasing (respectively, decreasing) the maximum nutrients uptake by phytoplankton, α_{max}, by 1% will decrease (respectively, increase) R_N by about 1%.

Next, as in Table 4, we perform the global sensitivity analysis on R_N. We summarize our results in Table 20.

Table 20 First-order and total-order Sobol sensitivity indices of R_N related to changes in parameters at ranges given in Table 2 and their order of importance.

Parameter	Sobol' first-order sensitivity	Order of importance	Sobol' total-order sensitivity	Order of importance
γ	0.0191	3	0.0435	3
k_n	0.0035	5	0.0119	4
μ_n	0.0027	4	0.0088	5
μ_p	0.5425	1	0.7005	1
α_{max}	0.2624	2	0.4123	2
k_p	0	6	0	6
μ_o	0	7	0	7
f_{max}	0	8	0	8

Table 20 shows that the most important parameters on R_N are and the phytoplankton removal, μ_p and the maximum nutrients uptake by phytoplankton, α_{max}. Sobol sensitivity results in Table 20 indicate that μ_p contributes about 54% of R_N total variance and α_{max} contributes about 26% of R_N total variance. There is no very large difference between first-order and total-order Sobol' indices for each parameter. Therefore, there is no significant interaction between the parameters.

We next perform sensitivity analysis on R_{NPO}.

6.6 Sensitivity indices of R_{NPO}

Proceeding as in Table 3, we compute normalized sensitivity indices on R_{NPO}, We summarize our results in Table 21.

Table 21 Normalized sensitivity indices of R_{NPO} to parameters with baseline given in Table 2 and their order of importance.

Parameter	Sensitivity index of R_{NPO}	Order of importance
γ	0.0316	4
k_n	-0.0055	7
μ_n	-0.0055	8
μ_p	-0.0438	3
α_{max}	0.0178	6
k_p	-0.0260	5
μ_o	-1	2
f_{max}	1	1

Table 21 shows that the most sensitive parameters are the maximum phytoplankton filtration by oysters, f_{max}, and the oysters removal, μ_o. Increasing (respectively, decreasing) maximum phytoplankton filtration by oysters, f_{max}, by 1% will increase (respectively, decrease) R_{NPO} by about 1% and increasing (respectively, decreasing) oysters removal, μ_o, by 1% will decrease (respectively, increase) R_{NPO} by about 1%.

Next, as in Table 4, we perform the global sensitivity analysis on R_{NPO}. We summarize our results in Table 22.

Table 22 First-order and total-order Sobol sensitivity indices of R_{NPO} related to changes in parameters at ranges given in Table 2 and their order of importance.

Parameter	Sobol' first-order sensitivity	Order of importance	Sobol' total-order sensitivity	Order of importance
γ	0	1	0.9993	4
k_n	0	2	0.9984	5
μ_n	0	3	1.0367	1
μ_p	0	4	1.0028	2
α_{max}	0	5	0.9994	3
k_p	0	6	0.9980	6
μ_o	0	7	0.1262	8
f_{max}	0	8	0.3922	7

Sobol' sensitivity analysis suggests that model parameters in Table 22 do not contribute significantly to variance of R_{NPO}. However, some of the parameters interact strongly with others.

6.7 NPO model positive equilibrium: E_{NPO}^3

Recall that in the full Model (NPO), we assumed that $f_{max} > \mu_o$ and $\alpha_{max} > \mu_p$ so that the phytoplankton and oysters are present. To establish conditions for the existence of an interior equilibrium point, we let

$$\hat{R}_{NPO} = \frac{\alpha_{max}}{\mu_p\left(1 + \frac{k_n}{E_{NPO}^{3,1}}\right)} > 1,$$

where

$$E_{NPO}^{3,1} = \frac{\gamma - \frac{\alpha_{max}k_p\mu_o}{f_{max}-\mu_o} - \mu_n k_n + \sqrt{(\gamma - \frac{\alpha_{max}k_p\mu_o}{f_{max}-\mu_o} - \mu_n k_n)^2 + 4\mu_n\gamma k_n}}{2\mu_n}. \tag{6.8}$$

Then, the Model (NPO) has an equilibrium point with positive values of nutrients, phytoplankton and oysters at

$$E_{NPO}^3 = (E_{NPO}^{3,1}, E_{NPO}^{3,2}, E_{NPO}^{3,3}),$$

where

$$E_{NPO}^{3,2} = \frac{k_p\mu_o}{f_{max} - \mu_o}. \tag{6.9}$$

$$E_{NPO}^{3,3} = \frac{k_p\left(\alpha(E_{NPO}^{3,1}) - \mu_p\right)}{f_{max} - \mu_o}. \tag{6.10}$$

We capture this result in the following theorem.

Theorem 6. Let $f_{max} > \mu_o$. If $\hat{R}_{NPO} > 1$, then E_{NPO}^3 is a positive interior equilibrium point of the Model (NPO).

Proof. For all parameter values $E_{NPO}^{3,1} > 0$. It is clear from equation (6.9) that, if $f_{max} > \mu_o$, then $E_{NPO}^{3,2} > 0$. Furthermore, when $f_{max} > \mu_o$ and $\hat{R}_{NPO} > 1$, then $E_{NPO}^{3,3} > 0$.
Consequently, $E_{NPO}^3 > 0$ is a positive equilibrium point of the Model (NPO).

6.8 Illustrative examples

Now, we use specific examples to illustrate that the Model (NPO) exhibits a stable positive equilibrium. In addition, we use local and global sensitivity analysis to study the impact of the model parameters on the interior equilibrium point, E_{NPO}^3.

Example 1: Effects of increasing nutrients inflow rate

In the Model (NPO)*, we set the following parameter values.*

$$k_n = 0.25025, \quad k_p = 0.2, \ \mu_n = 0.8, \quad \mu_p = 0.1, \ \mu_o = 0.34, \quad \alpha_{max} = 0.8 \ \ and \ \ f_{max} = 1.3. \tag{6.11}$$

Figure 2 shows that for the inflow rate $\gamma \in (0.1, 1.8625)$, the Model (NPO) has a stable equilibrium point with positive values of nutrients, phytoplankton and oysters. As we increase the nutrients inflow rate, γ, nutrients level and oysters biomass increase while the phytoplankton biomass remains constant. As we further increase γ past $\gamma^* = 1.8625$, the interior equilibrium point undergoes a Hopf bifurcation which forces recurrent phytoplankton blooms with corresponding oscillations in the nutrients level and oyster biomass (see Figures 3 and 4).

Example 1 shows that the Model (NPO) is capable of supporting a stable equilibrium point with positive values of nutrients, phytoplankton and oysters. Furthermore, in the presence of oysters, increasing or decreasing values of nutrients inflow rate can lead to a Hopf bifurcation induced recurrent phytoplankton blooms with corresponding oscillations in the oysters biomass and nutrients level.
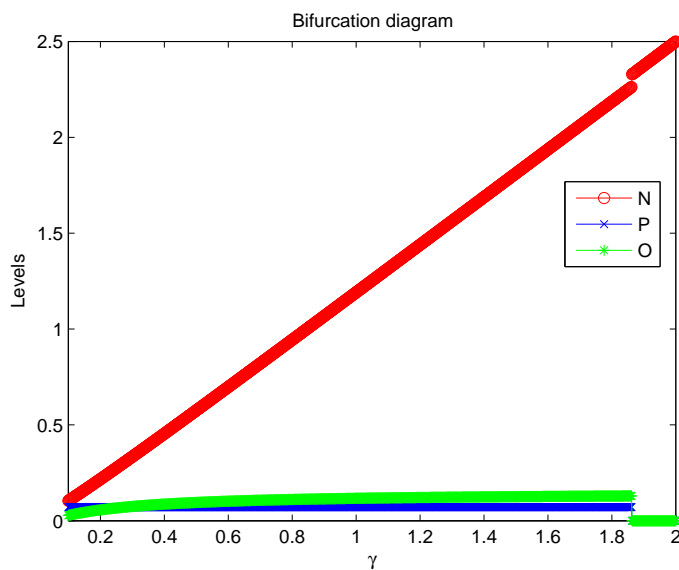
Fig. 2 Nutrients, phytoplankton and oysters levels in Example 1 as γ is varied in $(0.1, 1.8625)$. Nutrients level and oysters biomass increase while phytoplankton biomass remains constant as γ increases. At $\gamma^* = 1.8625$, a Hopf bifurcation occurs resulting in a sharp decline in phytoplankton and oysters biomasses, while nutrients level exhibits a sudden increase.
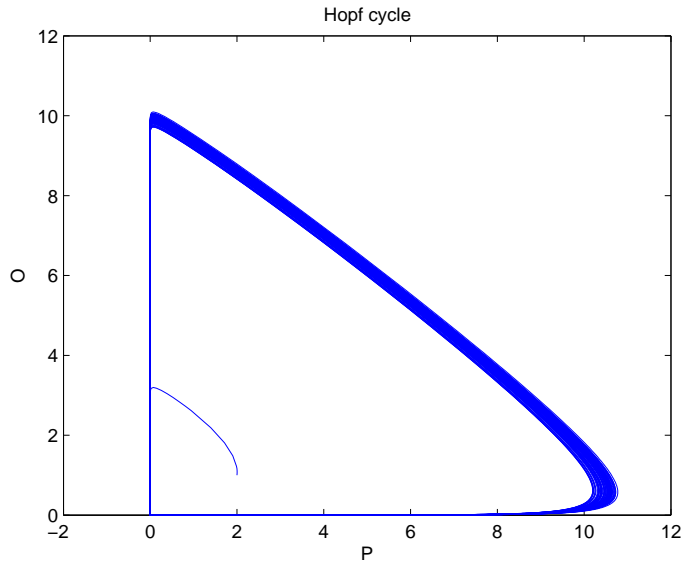

Fig. 3 A Hopf bifurcation closed curve emerges in the P-O plane at $\gamma^* = 1.8625$, where the other parameters are given in Example 1.
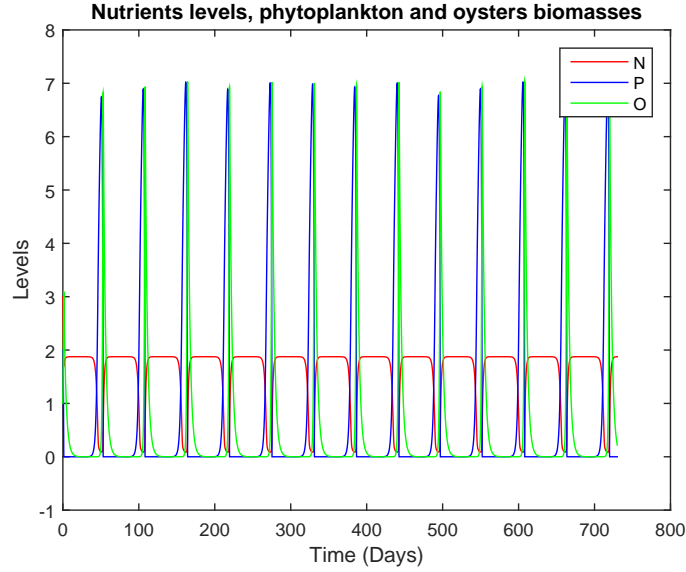
Fig. 4 Oscillations in phytoplankton, oysters and nutrients levels are observed, where Model (NPO) parameters are in Example 1 with $\gamma = \gamma^* = 1.8625$.

Sensitivity indices of E^3_{NPO} relative to γ:

Next, we perform local sensitivity analysis on E^3_{NPO} relative to the parameter γ. We summarize our results in Table 23.

Table 23 Sensitivity indices of E^3_{NPO} relative to γ, evaluated at the parameter values of Example 1.

Parameter	Sensitivity index of $E^{3,1}_{NPO}$	Sensitivity index of $E^{3,2}_{NPO}$	Sensitivity index of $E^{3,3}_{NPO}$
γ	1.0253	0	0.1185

Table 23 shows that equilibrium nutrients level, $E^{3,1}_{NPO}$ of E^3_{NPO}, is the most sensitive to changes in nutrients inflow, γ, and equilibrium phytoplankton biomass, $E^{3,2}_{NPO}$ of E^3_{NPO}, is not sensitive to changes in γ. Increasing γ by 1% increases both equilibrium nutrients level by about 1.03% and equilibrium oysters biomass by about 0.12%.

Example 1 shows that it is possible for an increase in nutrients inflow to lead to an increase in oysters biomass without a corresponding increase in phytoplankton biomass.

Next, we study the effects of increasing values of the maximum phytoplankton filtration constant, f_{max}, on the interior stable equilibrium point of Example 1.

Example 2: Effects of increasing maximum rate for filtration

Now, we let $\gamma = 1.5$ and keep all the other parameters fixed at their current values in Example 1 while we vary f_{max} in $(1.05, 1.7)$. With our choice of parameters, Example 2 has a stable interior equilibrium point when $f_{max} = 1.3$ (not shown here). As in Figure 2 and Figure 3, when we increase f_{max} past $f^*_{max} = 1.5962$, the interior equilibrium point undergoes a Hopf bifurcation which forces similar phytoplankton outbreaks with corresponding oscillations in nutrients and oysters values (not shown here).

Sensitivity indices of E^3_{NPO} relative to f_{max}:

Next, we perform local sensitivity analysis on E^3_{NPO} relative to the parameter f_{max}. We summarize our results in Table 24.

Table 24 Sensitivity indices of E^3_{NPO} relative to f_{max}, evaluated at the parameter values of Example 2.

Parameter	Sensitivity index of $E^{3,1}_{NPO}$	Sensitivity index of $E^{3,2}_{NPO}$	Sensitivity index of $E^{3,3}_{NPO}$
f_{max}	0.0330	-1.2706	-1.2660

Table 24 shows that phytoplankton biomass, $E^{3,2}_{NPO}$ of E^3_{NPO}, is the most sensitive to changes in maximum phytoplankton filtration by oysters rate, f_{max}, and nutrients level is the least sensitive to changes in f_{max}. Increasing f_{max} by 1% decreases phytoplankton biomass by about 1.27% and oysters by about 1.27% while it increases nutrients level by about 0.03%. That is, increase in oysters filtration rate is capable of decreasing the populations of phytoplankton and oysters while increasing nutrients level.

Next, we study the impact of oyster removal on the stable interior equilibrium point of Example 1.

Example 3: Effects of increasing oyster removal rate

In Example 3, we. let $\gamma = 1.6$, and keep all other parameter values fixed at their current values in Example 1 as we vary μ_o in $(0.32, 0.62)$.

When the removal rate of oysters $\mu_o \in (0.34, 0.588)$, the Model (NPO) has a stable positive equilibrium point. As in Examples 1 and 2, when we increase μ_o past $\mu_o^* = 0.588$, the equilibrium point undergoes a Hopf bifurcation which forces similar recurrent phytoplankton blooms with corresponding oscillations in the oysters biomasses and nutrients level (not shown here).

Sensitivity indices of E^3_{NPO} relative to μ_o:

Next, we perform local sensitivity analysis on E^3_{NPO} relative to the parameter μ_o. We summarize our results in Table 25.

Table 25 Sensitivity indices of E^3_{NPO} relative to μ_o, evaluated at the parameter values of Example 3.

Parameter	Sensitivity index of $E^{3,1}_{NPO}$	Sensitivity index of $E^{3,2}_{NPO}$	Sensitivity index of $E^{3,3}_{NPO}$
μ_o	-0.1433	1.8310	0.8111

Table 25 shows that equilibrium phytoplankton biomass, $E^{3,2}_{NPO}$ of E^3_{NPO}, is the most sensitive to changes in oysters removal rate, μ_o, and equilibrium nutrients level, $E^{3,1}_{NPO}$ of E^3_{NPO}, is the least sensitive to changes in μ_o. Increasing μ_o by 1% will increase both phytoplankton biomass by about 1.83% and oysters by about 0.81%, and will decrease nutrients level by 0.14%. That is, an increase in oysters removal rate is capable of decreasing the nutrients level while increasing phytoplankton and oysters biomass.

Example 4: Effect of increasing nutrients removal rate

Now, we let $\gamma = 1.6$ and keep all the other parameters fixed at their current values in Example 1 while we vary μ_n in $(0.79, 0.83)$.

When the removal rate of nutrients $\mu_n \in (0.79, 0.8239)$, the Model (NPO) has a stable positive equilibrium point. As in Examples 1 and 2, when we increase μ_n past $\mu_n^* = 0.8239$, the equilibrium point undergoes a Hopf bifurcation which forces similar recurrent phytoplankton blooms with corresponding oscillations in the oysters biomasses and nutrients level (not shown here).

Sensitivity indices of E_{NPO}^3 relative to μ_n:

Next, we perform local sensitivity analysis on E_{NPO}^3 relative to the parameter μ_n. We summarize our results in Table 26.

Table 26   Sensitivity indices of E_{NPO}^3 relative to μ_n, evaluated at the parameter values of Example 4.

Parameter	Sensitivity index of $E_{NPO}^{3,1}$	Sensitivity index of $E_{NPO}^{3,2}$	Sensitivity index of $E_{NPO}^{3,3}$
μ_n	-0.9962	0	-0.1363

Table 26 shows that equilibrium nutrients level, $E_{NPO}^{3,1}$ of E_{NPO}^3, is the most sensitive in changes in nutrients removal rate, μ_n, and the phytoplankton biomass, $E_{NPO}^{3,2}$ of E_{NPO}^3, is the least sensitive and remains not sensitive to changes in μ_n. Increasing μ_n by 1% will decrease both equilibrium oysters biomass by about 0.14% and equilibrium nutrients level by about 1%. That is increasing of nutrients removal rate is capable of decreasing both equilibrium nutrients level and equilibrium oysters biomass.

Example 5: Effect of increasing phytoplankton removal rate

Now, we let $\gamma = 1.6$ and keep all the other parameters fixed at their current values in Example 1 while we vary μ_p in $(0.09, 0.14)$. When the removal rate of phytoplankton $\mu_p \in (0.09, 0.14)$, the Model (NPO) has a stable positive equilibrium point. As in Examples 1 and 2, when we increase μ_p and past $\mu_p^* = 0.1013$, the equilibrium point undergoes a Hopf bifurcation which forces similar recurrent phytoplankton blooms with corresponding oscillations in the oysters biomasses and nutrients level (not shows here).

Sensitivity indices of E_{NPO}^3 relative to μ_p:

Next, we perform local sensitivity analysis on E_{NPO}^3 relative to the parameter μ_p. We summarize our results in Table 27.

Table 27   Sensitivity indices of E_{NPO}^3 relative to μ_p, evaluated at the parameter values of Example 5.

Parameter	Sensitivity index of $E_{NPO}^{3,1}$	Sensitivity index of $E_{NPO}^{3,2}$	Sensitivity index of $E_{NPO}^{3,3}$
μ_p	0	0	-0.1668

Table 27 shows that oysters biomass, $E_{NPO}^{3,3}$ of E_{NPO}^3, is the most sensitive to changes in phytoplankton removal rate, μ_p, and both equilibrium nutrients level, $E_{NPO}^{3,1}$ of E_{NPO}^3, and equilibrium phytoplankton biomass, $E_{NPO}^{3,2}$ of E_{NPO}^3, are not sensitive to changes in μ_p. Increasing μ_p by 1% will decrease equilibrium oysters biomass by about 0.17%. That is, an increase in phytoplankton removal rate is capable of decreasing equilibrium oysters biomass.

Example 6: Effect of increasing half saturation rate for filtration

Now, we let $\gamma = 1.6$ and keep all the other parameters fixed at their current values in Example 1 while we vary k_p in $(0.19, 0.2)$. When the half saturation rate for filtration $k_p \in (0.19, 0.2)$, the Model (NPO) has a stable positive equilibrium point. As in Examples 1 and 2, when we increase k_p past $k_p^* = 0.1949$, the equilibrium point undergoes a Hopf bifurcation which forces similar recurrent phytoplankton blooms with corresponding oscillations in the oysters biomasses and nutrients level (not shown here).

Sensitivity indices of E_{NPO}^3 relative to k_p:

Next, we perform local sensitivity analysis on E_{NPO}^3 relative to the parameter k_p. We summarize our results in Table 28.

Table 28   Sensitivity indices of E_{NPO}^3 relative to k_p, evaluated at the parameter values of Example 6.

Parameter	Sensitivity index of $E_{NPO}^{3,1}$	Sensitivity index of $E_{NPO}^{3,2}$	Sensitivity index of $E_{NPO}^{3,3}$
k_p	-0.0314	1	0.9958

Table 28 shows that equilibrium phytoplankton biomass, $E_{NPO}^{3,2}$ of E_{NPO}^3, is the most sensitive to changes in half saturation rate for filtration, k_p, and equilibrium nutrients level, $E_{NPO}^{3,1}$ of E_{NPO}^3, is the least sensitive to changes in k_p. Increasing k_p by 1% will decrease equilibrium nutrients level, by about 0.03%, and increase both equilibrium phytoplankton biomass, by a about 1%, and equilibrium oysters biomass, by 1%. That is, increasing half saturation rate for filtration is capable of increasing both equilibrium phytoplankton and oysters biomasses while decreasing equilibrium nutrients level.

Example 7: Effect of increasing half saturation rate for nutrients uptake

Now, we let $\gamma = 1.6$ *and keep all the other parameters fixed at their current values in Example 1 while we vary* k_n *in* $(0.2, 0.5)$. When the half saturation rate for nutrients uptake $k_n \in (0.2, 0.2583)$, the Model (NPO) has a stable positive equilibrium point. As in Examples 1 and 2, when we increase k_n and past $k_n^* = 0.2583$, the equilibrium point undergoes a Hopf bifurcation which forces similar recurrent phytoplankton blooms with corresponding oscillations in the oysters biomasses and nutrients level (not shown here).

Sensitivity indices of E_{NPO}^3 *relative to* k_n:

Next, we perform local sensitivity analysis on E_{NPO}^3 relative to the parameter k_n. We summarize our Table 29.

Table 29   Sensitivity indices of E_{NPO}^3 relative to k_n, evaluated at the parameter values of Example 7.

Parameter	Sensitivity index of $E_{NPO}^{3,1}$	Sensitivity index of $E_{NPO}^{3,2}$	Sensitivity index of $E_{NPO}^{3,3}$
k_n	0.0038	0	-0.1365

Table 29 shows that equilibrium oysters biomass, $E_{NPO}^{3,3}$ of E_{NPO}^3, is the most sensitive to changes in half saturation rate for nutrients uptake, k_n, and equilibrium phytoplankton, $E_{NPO}^{3,2}$ of E_{NPO}^3, is the least sensitive to changes in k_n, and is not sensitive in changes in k_n. Increasing k_n by 1% will decrease equilibrium oysters biomass by about 0.137% and increase equilibrium nutrients level by about 0.004%. That is, an increase in half saturation rate for nutrients uptake is capable of decreasing equilibrium oysters biomass while increasing equilibrium nutrients level.

Example 8: Effect increasing maximum nutrient uptake rate

Now, we let $\gamma = 1.6$ *and keep all the other parameters fixed at their current values in Example 1 while we vary* α_{max} *in* $(0.8, 0.9)$. When the maximum nutrient uptake rate $\alpha_{max} \in (0.8, 0.9)$, the Model (NPO) has a stable positive equilibrium point. As in Examples 1 and 2, when we increase α_{max} past $\alpha_{max}^* = 0.8945$, the equilibrium point undergoes a Hopf bifurcation which forces similar recurrent phytoplankton blooms with corresponding oscillations in the oysters biomass and nutrients level (not shown here).

Sensitivity indices of E_{NPO}^3 *relative to* α_{max}:

Next, we perform local sensitivity analysis on E_{NPO}^3 relative to the parameter α_{max}. We summarize our results in Table 30.

Table 30   Sensitivity indices of E_{NPO}^3 relative to α_{max}, evaluated at the parameter values of Example 8.

Parameter	Sensitivity index of $E_{NPO}^{3,1}$	Sensitivity index of $E_{NPO}^{3,2}$	Sensitivity index of $E_{NPO}^{3,3}$
α_{max}	-0.0362	0	1.1398

Table 30 shows that equilibrium oysters biomass, $E_{NPO}^{3,3}$ of E_{NPO}^3, is the most sensitive to changes in maximum nutrients uptake rate, α_{max}, and equilibrium phytoplankton biomass, $E_{NPO}^{3,2}$ of E_{NPO}^3, is the least sensitive to changes in α_{max}. Increasing α_{max} by 1% will increase equilibrium oysters biomass by about 1.14% and decrease equilibrium nutrients level by about 0.04%. Equilibrium phytoplankton biomass in not sensitive to changes in α_{max}. That is an increase in maximum nutrients uptake rate is capable of increasing oysters population while decreasing nutrients level.

Global sensitivity analysis of E_{NPO}^3

Proceeding as in Table 4 we perform the global sensitivity analysis of equilibrium nutrients level, $E_{NPO}^{3,1}$ of E_{NPO}^3. We summarize our results in Table 31.

Table 31   First-order and total-order Sobol sensitivity indices of $E_{NPO}^{3,1}$ related to changes in parameters at ranges given in Table 2 and their order of importance.

Parameter	Sobol' first-order sensitivity	Order of importance	Sobol' total-order sensitivity	Order of importance
γ	0.2420	2	0.4314	2
k_n	0	3	0	3
μ_n	0.5684	1	0.7578	1
μ_p	0	4	0	4
α_{max}	0	5	0	5
k_p	0	6	0	6
μ_o	0	7	0	7
f_{max}	0	8	0	8

Table 31 shows the most sensitive parameters to the equilibrium nutrients level, $E_{NPO}^{3,1}$ of E_{NPO}^3, are the nutrients loss, μ_n, and the nutrients flow, γ. Sobol' sensitivity indices of Table 31 indicate that nutrients loss, μ_n, contributes about 57% of the equilibrium nutrients level, $E_{NPO}^{3,1}$ of E_{NPO}^3, total variance. The nutrients flow, γ, contributes about 24% of the equilibrium nutrients level, $E_{NPO}^{3,1}$ of E_{NPO}^3, total variance. There is no very large difference between first-order and total-order Sobol' indices for each parameter. Therefore, there is no significant interactions between the parameters.

Proceeding as in Table 4, we perform the global sensitivity analysis of equilibrium phytoplankton biomass, $E_{NPO}^{3,2}$ of E_{NPO}^3. We summarize our results in Table 32.

Table 32 First-order and total-order Sobol sensitivity indices of $E_{NPO}^{3,2}$ related to changes in parameters at ranges given in Table 2 and their order of importance.

Parameter	Sobol' first-order sensitivity	Order of importance	Sobol' total-order sensitivity	Order of importance
γ	0	4	0	4
k_n	0	5	0	5
μ_n	0	6	0	6
μ_p	0	7	0	7
α_{max}	0	8	0	8
k_p	0.0087	3	0.2436	3
μ_o	0.0121	2	0.8301	2
f_{max}	0.1205	1	0.9746	1

Table 32 shows that the most important parameters to the equilibrium phytoplankton biomass, $E_{NPO}^{3,2}$ of E_{NPO}^3, is the maximum phytoplankton filtration by oysters, f_{max}. Sobol' sensitivity results of Table 32 indicate maximum phytoplankton filtration by oysters, f_{max}, contributes about 12% of the equilibrium phytoplankton biomass, $E_{NPO}^{3,2}$ of E_{NPO}^3, total variance. There is a large difference between first-order and total-order Sobol' indices for parameter f_{max}. This suggest parameter f_{max} interacts strongly with the other parameters.

Proceeding as in Table 4, we perform the global sensitivity analysis of equilibrium oysters biomass, $E_{NPO}^{3,3}$ of E_{NPO}^3. We summarize our results in Table 33.

Table 33 First-order and total-order Sobol sensitivity indices of $E_{NPO}^{3,3}$ related to changes in parameters at ranges given in Table 2 and their order of importance.

Parameter	Sobol' first-order sensitivity	Order of importance	Sobol' total-order sensitivity	Order of importance
γ	0.0020	4	0.1020	6
k_n	0	6	0.0025	8
μ_n	0	7	0.0036	7
μ_p	0.0109	3	0.3263	4
α_{max}	0.0191	1	0.1140	5
k_p	0.0012	5	0.5155	3
μ_o	0	8	0.8322	2
f_{max}	0.0116	2	0.9534	1

Table 33 shows that the most important parameters to the equilibrium oysters biomass, $E_{NPO}^{3,3}$ of E_{NPO}^3, is the maximum nutrients uptake by phytoplankton, α_{max}. Sobol' sensitivity results of Table 33 indicate maximum nutrients uptake by phytoplankton, α_{max}, contributes about 2% of the equilibrium oysters biomass, $E_{NPO}^{3,3}$ of E_{NPO}^3, total variance. There is a large difference between first-order and total-order Sobol' indices for the maximum phytoplankton filtration by oysters, f_{max}. This suggests parameter f_{max} interacts strongly with the other parameters.

7 Conclusion

To theoretically study the dynamics of nutrients-phytoplankon-oysters model of an ecosystem, we introduced a simple NPO ordinary differential equation model, based on a Chemostat model, that describes nutrients-phytoplankton-oysters interactions in a bay ecosystem. We used the model to show that when the maximum values of the nutrients uptake is less than the rate of phytoplankton loss, then both phytoplankton and oysters decline to zero in the model and the nutrients level stabilizes at a positive steady state. Furthermore, we established that when the maximum value of phytoplankton filtration by oysters is smaller than the rate of oysters removal in the system, then the oysters go extinct and the model reduces to a system of nutrients-phytoplankton (NP) interactions. For the reduced NP system, we show that $R_N < 1$ implies phytoplankton extinction while $R_N > 1$ implies phytoplankton persistence. Local and global sensitivity analysis on nutrients only Model (N) and nutrients-phytoplankton Model (NP) were performed.

In the full Model (NPO), we studied persistence of phytoplankton with or without oysters. We showed that when $R_N < 1$, then both phytoplankton and oysters go extinct and the Model (NPO) stabilizes at a positive value of nutrients. When $R_N > 1$ and $R_{NPO} < 1$ then oysters go extinct and the Model (NPO) exhibits a locally stable equilibrium point with positive values of nutrients and phytoplankton. In addition, we established that when the maximum value of phytoplankton filtration by oysters is larger that than the rate of oysters removal and $\hat{R}_{NPO} > 1$, then the full Model (NPO) exhibits an interior equilibrium with positive values of nutrients, phytoplankton and oysters.

We used examples to show that human activities such as increasing oysters removal rate can force the interior equilibrium, of the full Model (NPO), to undergo a Hopf bifurcation; which results in phytoplankton blooms and corresponding oscillations in oyster biomass and nutrients level.

In addition, we performed local and global sensitivity analysis on the model. Results of the local sensitivity analysis are the following :

- Increasing nutrients flow, γ, by 1% increases both equilibrium nutrients level by about 1.03% and oysters biomass by approximately 0.12% (see Example 1).
- Increasing maximum phytoplankton filtration by oysters, f_{max}, by 1% decreases phytoplankton biomass by approximately 1.27% and oysters biomass by about 1.27% while it increases nutrients level by about 0.03% (see Example 2).
- Increasing oysters removal, μ_o, by 1% will increase both phytoplankton biomass by about 1.83% and oysters by approximately 0.81%, and decrease nutrients level by 0.14% (see Example 3).
- Increasing nutrients loss, μ_n, by 1% will decrease both oysters biomass by about 0.14% and nutrients level by approximately 1%. (see Example 4)
- Increasing phytoplankton removal, μ_p, by 1% will decrease oysters biomass by approximately 0.17% (see Example 5).
- Increasing half saturation for filtration by oysters, k_p, by 1% will increase both oysters biomass by approximately 1% and phytoplankton biomass by about 1% and will decrease nutrients level by about 0.03% (see Example 6).
- Increasing half saturation for nutrients uptake by phytoplankton, k_n, by 1% will decrease oysters biomass by approximately 0.137% and increase nutrients level by about 0.004% (see Example 7).
- Increasing maximum nutrients uptake by phytoplankton, α_{max}, by 1% will increase oysters biomass by approximately 1.14% and decrease nutrients level by about 0.04% (see Example 8).

Results of the global sensitivity analysis are the following:

- Nutrients loss, μ_n, contributes approximately 57% of the equilibrium nutrients level total variance.
- Nutrients flow, γ, contributes approximately 24% of the equilibrium nutrients level total variance.
- Maximum phytoplankton filtration by oysters, f_{max}, contributes approximately 12% of the equilibrium phytoplankton biomass total variance.
- Maximum nutrients uptake by phytoplankton, α_{max}, contributes approximately 2% of the equilibrium oysters biomass total variance.

Local and global sensitivity analysis results may have important implications on bay ecosystem restoration programs such as the Chesapeake Bay restoration program [1].

Acknowledgments

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