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AN NPZ MODEL WITH STATE-DEPENDENT DELAY DUE TO SIZE-STRUCTURE IN JUVENILE ZOOPLANKTON*

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Abstract. The study of planktonic ecosystems is important as they make up the bottom trophic levels of aquatic food webs. We study a closed nutrient-phytoplankton-zooplankton (NPZ) model that includes size structure in the juvenile zooplankton. The closed nature of the system allows the formulation of a conservation law of biomass that governs the system. The model consists of a system of a nonlinear ordinary differential equation coupled to a partial differential equation. We are able to transform this system into one of delay differential equations where the delay is of threshold type and is state dependent. The system of delay differential equations can be further transformed into one with fixed delay. Using the different forms of the model, we perform a qualitative analysis of the solutions, which includes studying existence and uniqueness, positivity and boundedness, local and global stability, and conditions for extinction. Key parameters that are explored are the total biomass in the system and the maturity level at which the juvenile zooplankton reach maturity. Numerical simulations are also performed to verify our analytical results.

Key words. plankton, state-dependent delay, threshold, size structured, closed ecosystem

AMS subject classification. 37N25

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1. Introduction.

Nutrient-phytoplankton-zooplankton (NPZ) models are used to describe the bottom two trophic levels of an aquatic ecosystem. As is the case with many ecological models, they range from very simple to very complex. Simple models, such as the Lotka–Volterra system [22], are beneficial in that one can obtain analytical results more easily, but they often suffer from lack of realism. On the other hand, complex models may theoretically represent a more accurate description of reality, but may be difficult or impossible to understand in any general way, and may be useless without precise and accurate parameter values. A lot of structure can be given to an NPZ model, such as size dependence and spatial dependence, and this structure leads to rich modeling possibilities such as size-dependent parameters and coupling with external factors like fluid dynamics or higher predation. To strike a balance, it may be useful to start with a simple model that focuses on one factor affecting the ecosystem, and use it to obtain analytical results and study general trends. For an introduction to the construction of NPZ models, see [9].

We will focus on the role of maturity in the juvenile zooplankton population within an ecosystem while keeping all other factors as simple as possible. In this vein, a simple NPZ model is coupled with a standard linear first-order PDE that describes the spectrum of the juvenile zooplankton population as a function of time and maturity. It is a known result that this type of PDE is closely related to delay equations. Examples of population models where time delay is a consequence of age structure can be found in [4, 5, 14, 31]. We will be considering size structure where the rate of growth of the juvenile zooplankton is permitted to depend on the concentration of the phytoplankton. With this assumption, the delay in the related delay equation is not

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explicitly defined, but rather defined implicitly through a threshold-type condition. Consequently, systems with this type of delay are known as threshold delay differential equations. They have been studied in the case of ecological models with a single population split into a juvenile and a mature class [23, 27, 28, 29, 30], for example. These models operate under the assumption that maturation occurs when an immature individual accumulates enough of some quantity, such as size or weight. Other applications include blood cell production [2, 3, 19, 21] and immunology [25, 34].

Our model is formulated in such a way that biomass is conserved. In other words, we are considering a closed ecosystem with no mass being added to or subtracted from the system. NPZ models with this property have been studied, for example, in [10] and [35]. A typical property of these systems is that the amount of biomass, which is determined by initial conditions, plays a crucial role in determining the types of dynamics that can and do occur. Most notably, an insufficient amount of biomass leads to the extinction of plankton—either the zooplankton only, or both the phytoplankton and zooplankton.

The plan for our article is as follows. In section 2 we consider the model with stage structure and discuss the main assumption on the parameters and nonlinearities in the model. In section 3 we use an approach due to Smith [27, 28, 28, 30] to show how this model can be reduced to a threshold delay differential equation model and which in turn can be transformed to a delay differential equation model with fixed delay. In section 4 we discuss existence and uniqueness of solutions of the delay differential equations. In section 5 we determine the nontrivial equilibria of the models and find the characteristic equation of the linearization of the model about them. In section 6 we derive stability results for the equilibria. In section 7 we use numerical simulations to verify and supplement our analytical results. In section 8 we summarize our results and discuss their implications.

2. Structured model.

We consider a nutrient-phytoplankton-zooplankton (NPZ) model in which the zooplankton population is split into a mature class and a juvenile class. We will consider the quantity of juvenile phytoplankton as a function of time and maturity, denoted $\rho(t,s)$. Maturity is considered to be an abstract quantity, and the juvenile zooplankton must accumulate a sufficient amount to enter adulthood. The total concentration of immature zooplankton with maturity levels between s_1 and s_2 at time t is then $\int_{s_1}^{s_2} \rho(t,s)\,ds$. We restrict s to the interval $[0,m]$, where m is the required level of maturity for adulthood. The nutrient, phytoplankton, and mature zooplankton variables will therefore depend only on time.

Since the zooplankton feed on phytoplankton, we will assume that the maturation rate, R, of the juvenile zooplankton depends on the quantity of phytoplankton. We will denote this dependence as $R(P)$.

The following equations model the ecosystem for $t \geq 0$ and $s \in [0,m]$. We will refer to it as the PDE1 model.

$$\frac{dN(t)}{dt} = -\mu P(t)f(N(t)) + \lambda P(t) + \delta Z(t) + (1-\gamma)gZ(t)h(P(t)) + \int_0^m \delta_0 \rho(t,s)\,ds, \tag{2.1a}$$

$$\frac{dP(t)}{dt} = \mu P(t)f(N(t)) - \lambda P(t) - gZ(t)h(P(t)), \tag{2.1b}$$

$$\frac{dZ(t)}{dt} = R(P(t))\rho(t,m) - \delta Z(t), \tag{2.1c}$$

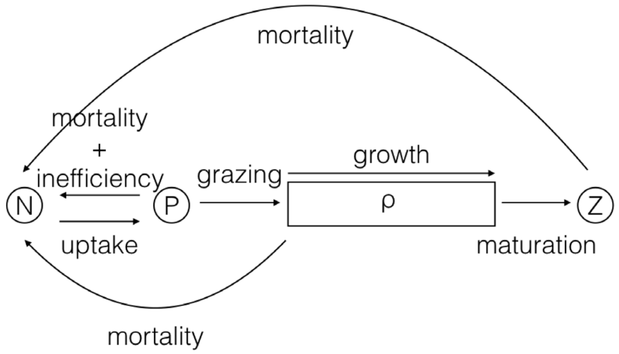


FIG. 1. *Schematic of the PDE*1 *model* (2.1).

$$\frac{\partial\rho}{\partial t}(t,s)+R(P(t))\frac{\partial\rho}{\partial s}(t,s)=-\delta_0\rho(t,s), \tag{2.1d}$$

$$R(P(t))\rho(t,0)=\gamma g Z(t)h(P(t)). \tag{2.1e}$$

Appropriate initial conditions for these equations are

$$N(0)=N_0,\quad P(0)=P_0,\quad Z(0)=Z_0,\quad \rho(0,s)=\rho_0(s), \tag{2.2}$$

where N_0, P_0, and Z_0 are nonnegative real numbers and ρ_0 is a nonnegative, continuous function on the interval $[0,m]$.

A few basic ecological processes govern the system; see Figure 1. Phytoplankton, P, uptake nutrient, N, at a rate that is proportional to the quantity of phytoplankton and a function of the dissolved nutrient, $f(N)$. Zooplankton, Z, graze on phytoplankton at a rate that is proportional to the quantity of zooplankton and a function of phytoplankton, $h(P)$. This is marked by a grazing efficiency factor, $\gamma\in(0,1]$. Phytoplankton mortality is proportional to the amount of phytoplankton present at time t. Zooplankton mortality is similarly proportional to the amount of zooplankton in the system. Nutrient recycling transforms dead biomass and fecal matter back to the dissolved nutrient variable. Equation (2.1d) is a standard transport equation [21] with a decay term due to natural mortality. The boundary condition, given in (2.1e), says that the birth rate of the immature zooplankton is equal to some fraction of the biomass obtained by the zooplankton through grazing.

The model parameters are defined in Table 1. The parameters are all positive, but other than γ the values vary tremendously depending on the particular species and ecosystem involved. See [32] for a thorough discussion of parameter ranges for plankton models.

Biologically appropriate forms for the nonlinear functions f and h have been studied in [10]. For our theoretical work we will pose a minimum set of assumptions on these functions which are consistent with [10], as we now describe. For the phytoplankton nutrient uptake response, we assume $f\in\mathcal{C}^1$ and

$$f(0)=0,\qquad f'(N)>0,\qquad \lim_{N\to\infty}f(N)=1. \tag{2.3}$$

Similarly, for the zooplankton functional response for grazing on phytoplankton, we assume $h\in\mathcal{C}^1$ and

$$h(0)=0,\qquad h'(P)\geq 0,\qquad \lim_{P\to\infty}h(P)=1. \tag{2.4}$$

TABLE 1
Model parameters and functions.

Parameter	Meaning
μ	phytoplankton maximum birth rate
λ	phytoplankton death rate
g	zooplankton maximum grazing rate
γ	zooplankton assimilation efficiency
δ	zooplankton grazing rate
Function	**Meaning**
$f(N(t))$	phytoplankton nutrient uptake function
$g(P(t))$	zooplankton grazing function
$R(P(t))$	zooplankton maturation rate function

These assumptions on h encompass both type II (concave down) and type III (sigmoidal shaped) responses, as described in [17].

We will also assume throughout that all parameter values are positive (although we will allow δ_0 to be zero) and that

$$\mu > \lambda, \qquad \gamma g > \delta,$$

so that $f^{-1}(\lambda/\mu)$ and $h^{-1}(\delta/(\gamma g))$ exist. Biologically, these conditions correspond to the maximum birth rate exceeding the death rate.

It will be assumed that $R \in \mathcal{C}^1$ and that it satisfies the following properties:

$$R(P) \geq 0,\ R \in \mathcal{C}^1,\ R'(P) \geq 0,\ R'(0) > 0 \text{ if } R(0) = 0,\ \lim_{P\to\infty} R(P) = R_\infty < \infty. \tag{2.5}$$

These assumptions can be justified by laboratory experiments in [20], where they measured the development rate of the zooplankter *Daphnia* as a function of F, the amount of available food. They found that the development rate was proportional to $F/(F + F_{\text{half}})$.

The assumptions on h in (2.4) and the third assumption on R in (2.5) imply that

$$\lim_{P\to 0} \frac{h(P)}{R(P)} < \infty. \tag{2.6}$$

This puts a bound on $\rho(t, 0)$ as the phytoplankton population approaches zero, as seen in (2.1e).

As previously stated, there is no biomass lost from the PDE1 model (2.1). We can confirm this by noting that (2.1) satisfies the following conservation law:

$$N_T = N(t) + P(t) + Z(t) + \int_0^m \rho(t, s)\, ds, \tag{2.7}$$

where N_T is the total biomass in the system. Given this conservation law, the total amount of juvenile zooplankton can be determined from the total biomass and the quantity of the dissolved nutrient, phytoplankton, and zooplankton. Making the appropriate substitution of (2.7) into the PDE1 model (2.1) yields the following system:

$$\begin{aligned}\frac{dN(t)}{dt} &= -\mu P(t) f(N(t)) + \lambda P(t) + \delta Z(t) + (1-\gamma) g Z(t) h(P(t)) \\ &\quad + \delta_0 (N_T - N(t) - P(t) - Z(t)),\end{aligned} \tag{2.8a}$$

$$\frac{dP(t)}{dt} = \mu P(t) f(N(t)) - \lambda P(t) - gZ(t)h(P(t)), \tag{2.8b}$$

$$\frac{dZ(t)}{dt} = R(P(t))\rho(t,m) - \delta Z(t), \tag{2.8c}$$

$$\frac{\partial \rho}{\partial t}(t,s) + R(P(t))\frac{\partial \rho}{\partial s}(t,s) = -\delta_0 \rho(t,s), \tag{2.8d}$$

$$R(P(t))\rho(t,0) = \gamma g Z(t) h(P(t)). \tag{2.8e}$$

We will refer to this system as the PDE2 model. While the substitution is straightforward, it is important to note that we have now fixed N_T. Thus, in order for a solution of the PDE1 model (2.8) to be the same as a solution to the PDE1 model (2.1), we must choose initial conditions in (2.2) that satisfy

$$N_T = N(0) + P(0) + Z(0) + \int_0^m \rho_0(s)\,ds. \tag{2.9}$$

In other words, the total biomass, N_T, is set by the initial conditions for the PDE1 model (2.1), so if we treat it as a parameter in the PDE2 model (2.8), then we have to restrict the possible initial conditions by the relation (2.9). If we fix N_T in the PDE2 model (2.8) and then choose initial conditions that do not satisfy (2.9), then the resulting solution is not a solution of the PDE1 model. We can show, however, that a solution to system PDE2 will asymptotically approach a solution to PDE1, assuming that both solutions exist for all time. Due to the simpler nature of the PDE2 model, we will study it instead of the original system and assume that initial conditions satisfy (2.9).

3. Reduction to a delay differential equation.

In a series of papers, Smith [27, 28, 29, 30] studies models in a form similar to the PDE2 model (2.8), although the models are for a single species which is split into a juvenile and a mature class. The model closest to ours is in [28], where the maturation rate of the immature class depends on the amount of nutrient available. In his work, Smith reduced the equations so that they became a threshold delay equation. This type of equation has a state-dependent delay where a newly born individual must first reach maturity before entering into the adult population. Smith then uses a clever change of variables to transform the system to a functional differential equation where the delay no longer depends on the state. Due to the similar form of the PDE2 model (2.8) to Smith's model, we will use the same methods to reduce our model to a threshold delay equation and then to a delay differential equation with a bounded and state-independent delay.

As in [27, 28], we solve (2.8d) and (2.8e) for ρ as a function of P and Z using the method of characteristics, and then substitute this solution into (2.8c). It can be verified that the solution for ρ is

$$\rho(t,s) = \begin{cases} e^{-\delta_0 t}\rho_0\left(s - \int_0^t R(P(u))\,du\right) & \text{for } (t,s) \in S_1, \\ e^{-\delta_0 \tau(s,P_t)} \frac{\gamma g Z(t-\tau(s,P_t)) h(P(t-\tau(s,P_t)))}{R(P(t-\tau(s,P_t)))} & \text{for } (t,s) \in S_2, \end{cases} \tag{3.1}$$

where $P_t(u) = P(t+u)$,

$$S_1 = \left\{ (t,s) : 0 \le s \le m, \int_0^t R(P(v))\,dv < s \right\},$$

$$S_2 = \left\{ (t,s) : 0 \le s \le m, \int_0^t R(P(v))\,dv \ge s \right\},$$

and $\tau(s,P_t)$ is defined implicitly by

$$\int_{-\tau(s,\phi)}^{0} R(\phi(u))\,du = s. \tag{3.2}$$

Biologically, this is the time is takes for the immature zooplankton to grow to maturity level s as a function of the history of phytoplankton. For example, if the phytoplankton is at an equilibrium value $P(t)=P^*$ for all t, then $\tau(s,P_t)=\frac{s}{R(P^*)}$.

Substituting $\rho(t,m)$, defined by (3.1), into (2.8c) gives a nonautonomous equation. Using an approach similar to that found in [28], one can analyze this equation to show that if P_0 is sufficiently large or $N_T > f^{-1}(\lambda/\mu)$, then there exists a time t_0 such that the solution of the model PDE2 exists on $[0,t_0]$ and $\int_0^{t_0} R(P(v))\,dv = m$. The time t_0 is when all of the immature zooplankton initially present at $t=0$ have reached maturity. Then for $t>t_0$, $(t,s)\in S_2$, and solutions of the model PDE2 will satisfy the autonomous system

$$\begin{aligned}\frac{dN(t)}{dt} =& -\mu P(t)f(N(t)) + \lambda P(t) + \delta Z(t) + (1-\gamma)gZ(t)h(P(t))\\ &+ \delta_0(N_T - N(t) - P(t) - Z(t)),\end{aligned} \tag{3.3a}$$

$$\frac{dP(t)}{dt} = \mu P(t)f(N(t)) - \lambda P(t) - gZ(t)h(P(t)), \tag{3.3b}$$

$$\frac{dZ(t)}{dt} = R(P(t))e^{-\delta_0\tau(m,P_t)}\frac{\gamma g Z(t-\tau(m,P_t))h(P(t-\tau(m,P_t)))}{R(P(t-\tau(m,P_t)))} - \delta Z(t). \tag{3.3c}$$

We will refer to this system as the TDE model, as systems in this form are known as threshold delay equations. Note that the delay is defined via the integral

$$\int_{-\tau(m,P_t)}^{0} R(P_t(u))\,du = m. \tag{3.4}$$

Thus $\tau(m,P_t)$ is a differentiable function of P_t and t and satisfies

$$\frac{\partial\tau}{\partial t} = 1 - \frac{R(P(t))}{R(P(t-\tau(m,P_t)))}. \tag{3.5}$$

Considered as a state-dependent delay equation, appropriate initial conditions for the TDE model (3.3) are

$$N_{t_0}(u)=\phi_1(u),\ P_{t_0}(u)=\phi_2(u),\ Z_{t_0}(u)=\phi_3(u),\ -t_0\le u\le 0 \text{ with } \tau(m,\phi_2)=t_0. \tag{3.6}$$

We can connect the TDE model to the PDE2 model by taking the initial data $(\phi_1(u),\phi_2(u),\phi_3(u))$ to correspond to the solution for $(N(t),P(t),Z(t))$ of the PDE2 model on $[0,t_0]$, i.e., $u=t-t_0$. Note that the condition that defines t_0 guarantees that the condition on $\tau(m,\phi_2)$ is satisfied in this case.

Alternatively, we can connect the two models with the conservation law. It can be verified that if the initial conditions for the TDE model (3.3) satisfy

$$N_T = \phi_1(0)+\phi_2(0)+\phi_3(0)+\int_0^m e^{-\delta_0\tau(s,\phi_2)}\frac{\gamma g\phi_3(-\tau(s,\phi_2))h(\phi_2(-\tau(s,\phi_2)))}{R(\phi_2(-\tau(s,\phi_2)))}\,ds, \tag{3.7}$$

then we have

$$N_T = N(t) + P(t) + Z(t) + \int_0^m e^{-\delta_0 \tau(s,P_t)} \frac{\gamma g Z(t-\tau(s,P_t))h(P(t-\tau(s,P_t)))}{R(P(t-\tau(s,P_t)))}\, ds \tag{3.8}$$

for $t \geq t_0$. Since initial conditions satisfying (3.7) are the only ones that relate to the PDE2 model (2.1), we will restrict our attention to this particular choice. For later use we define the set

$$\begin{aligned} D_{N_T} = \{&(\phi_1,\phi_2,\phi_3)^T \in \mathcal{C}([-t_0,0],\mathbb{R}^3) : \phi_i(t) > 0, i=1,2,3, t\in[-t_0,0], \\ &\tau(m,\phi_2) = t_0, \text{ and (3.7) is satisfied}\}. \end{aligned}$$

This is the set of initial conditions which we will consider. That is, we will not study cases where N, P, or Z have initial values equal to zero as we are interested in studying the dynamics when all three trophic levels are initially present.

We note that TDE model (3.3) is a differential equation with locally bounded delay. Since $R(0) = 0$, it is possible that the delay becomes arbitrarily large if the phytoplankton population approaches zero. However, for any given state, the delay is bounded for all states in a neighborhood. Results for differential equations with locally bounded delay can be found in [33]. However, our system is in a form that may be transformed into a simpler system, as we describe below. We will therefore use that approach.

It is possible to remove the state dependence on the delay through a clever change in variable, as given in [26, 27, 28, 29, 30]. Since the details are similar to those papers, we only present some highlights. The transformation is a state-dependent change of the time variable

$$\hat{t} = \int_0^t \frac{R(P(u))}{R^*}\, du, \tag{3.9a}$$

$$\hat{N}(\hat{t}) = N(t), \quad \hat{P}(\hat{t}) = P(t), \quad \hat{Z}(\hat{t}) = Z(t) \tag{3.9b}$$

for $t > 0$, where R^* is a typical value of $R(P)$. With this change of variables, the TDE model (3.3) is transformed into the following delay differential equation:

$$\begin{aligned} \frac{d\hat{N}(\hat{t})}{d\hat{t}} = \frac{R^*}{R(\hat{P}(\hat{t}))}[&-\mu\hat{P}(\hat{t})f(\hat{N}(\hat{t})) + \lambda\hat{P}(\hat{t}) + \delta\hat{Z}(\hat{t}) + (1-\gamma)g\hat{Z}(\hat{t})h(\hat{P}(\hat{t})) \\ &+ \delta_0(N_T - \hat{N}(\hat{t}) - \hat{P}(\hat{t}) - \hat{Z}(\hat{t}))], \end{aligned} \tag{3.10a}$$

$$\frac{d\hat{P}(\hat{t})}{d\hat{t}} = \frac{R^*}{R(\hat{P}(\hat{t}))}[\mu\hat{P}(\hat{t})f(\hat{N}(\hat{t})) - \lambda\hat{P}(\hat{t}) - g\hat{Z}(\hat{t})h(\hat{P}(\hat{t}))], \tag{3.10b}$$

$$\frac{d\hat{Z}(\hat{t})}{d\hat{t}} = \gamma g e^{-\delta_0\hat{\tau}(m,\hat{P}_t)} \frac{R^*}{R(\hat{P}(\hat{t}-\mathcal{T}))}\hat{Z}(\hat{t}-\mathcal{T})h(\hat{P}(\hat{t}-\mathcal{T})) - \frac{R^*}{R(\hat{P}(\hat{t}))}\delta\hat{Z}(\hat{t}) \tag{3.10c}$$

for $\hat{t} \geq \mathcal{T}$, where $\mathcal{T} = m/R^*$ and $\hat{\tau}(m,\hat{P}_t)$ is defined by

$$\hat{\tau}(s,\hat{P}_{\hat{t}}) = \tau(s,P_t) = \int_{t-\tau(s,P_t)}^{t} du = \int_{\hat{t}-s/R^*}^{\hat{t}} \frac{R^*}{R(\hat{P}(r))}\, dr. \tag{3.11}$$

We will refer to this system as the DDE model. The corresponding initial conditions are

$$\hat{N}(\mathcal{T}+t) = \hat{\phi}_1(\hat{t}), \qquad \hat{P}(\mathcal{T}+t) = \hat{\phi}_2(\hat{t}), \qquad \hat{Z}(\mathcal{T}+t) = \hat{\phi}_3(\hat{t}) \tag{3.12}$$

for $t \in [-\mathcal{T}, 0]$, where $\hat{\phi}_1, \hat{\phi}_2, \hat{\phi}_3 \in \mathcal{C}[-\mathcal{T}, 0]$. Again, solutions corresponding to the PDE1 model (2.1) should satisfy

$$N_T = \hat{\phi}_1(0) + \hat{\phi}_2(0) + \hat{\phi}_3(0) + \int_0^m e^{-\delta_0 \hat{\tau}(s,\hat{\phi}_2)} \frac{\gamma g \hat{\phi}_3(-\frac{s}{R^*}) h(\hat{\phi}_2(-\frac{s}{R^*}))}{R(\hat{\phi}_2(-\frac{s}{R^*}))} \, ds. \tag{3.13}$$

For an initial condition that satisfies (3.13), the solution to DDE model (3.10) satisfies

$$N_T = \hat{N}(\hat{t}) + \hat{P}(\hat{t}) + \hat{Z}(\hat{t}) + \int_0^m e^{-\delta_0 \hat{\tau}(s,\hat{P}_{\hat{t}})} \frac{\gamma g \hat{Z}(\hat{t} - \frac{s}{R^*}) h(\hat{P}(\hat{t} - \frac{s}{R^*}))}{R(\hat{P}(\hat{t} - \frac{s}{R^*}))} \, ds \tag{3.14}$$

for all $\hat{t} \geq \mathcal{T}$ for which the solution exists.

If we were to apply the time transformation in (3.9a) directly to the PDE2 model (2.8) and then proceed with the method of characteristics, we would arrive at the DDE model (3.10). In essence, the time transformation removes the dependency of the characteristic curves on $P(t)$ and instead places this dependence on the solutions along the curves. In [29] and [30], Smith applies an analogous time transform to a system coupling a single adult population coupled with its corresponding maturity-structured juvenile population.

Since the delay in the DDE model (3.10) is bounded and state independent, the standard theory for functional differential equations [15] may be applied.

4. Existence and uniqueness of solutions.

In this section, we will develop conditions whereby a unique solution to the initial value problem for the TDE model (3.6)–(3.3) can exist for all time. This will be done by matching it to a corresponding initial value problem for the DDE model (3.10)–(3.12). First, define the open set

$$\hat{\Omega} = \{(\hat{\psi}_1, \hat{\psi}_2, \hat{\psi}_3)^T \in \mathcal{C}[-\mathcal{T}, 0] : \hat{\psi}_2(\theta) \neq 0 \text{ for } \theta \in [-\mathcal{T}, 0]\}. \tag{4.1}$$

From the properties of f, h, and R given in (2.3)–(2.5), the right-hand side of the DDE model (3.10) is Lipschitz on $\hat{\Omega}$. Thus standard results on functional differential equations with bounded delay (for example, see [15]) give us that for $(\hat{\phi}_1, \hat{\phi}_2, \hat{\phi}_3) \in \hat{\Omega}$, the DDE initial value problem (3.10)–(3.12) has a unique maximal solution defined on $[0, \hat{w})$ for some $\hat{w} > 0$. We can then deduce the following result.

PROPOSITION 4.1. *If $\hat{\phi}_1, \hat{\phi}_2, \hat{\phi}_3$ are positive functions that satisfy* (3.13)*, then the unique maximal solution to the DDE initial value problem* (3.10)–(3.12)*, denoted as $(\hat{N}, \hat{P}, \hat{Z})^T : [0, \hat{w}) \to \mathbb{R}^3$, satisfies $\hat{N}(\hat{t}), \hat{P}(\hat{t}), \hat{Z}(\hat{t}) \in (0, N_T)$ for all $\hat{t} \in [0, \hat{w})$.*

Proof. Since $\hat{\phi}_1, \hat{\phi}_2, \hat{\phi}_3$ are positive functions, the result is clearly true for $\hat{t} \in [0, \mathcal{T}]$. By the properties of R in (2.5) and the definition of the phase space $\hat{\Omega}$ in (4.1), we find that $\hat{P}(\hat{t}) > 0$ for all $\hat{t} \in [0, \hat{w})$. Suppose there exists $\beta_1 > \mathcal{T}$ such that $\hat{Z}(\beta_1) = 0$ and $\hat{Z}(\hat{t}) > 0$ for $\hat{t} < \beta_1$. Then for $\hat{t} \in [\mathcal{T}, \beta_1]$ we have that $\frac{d\hat{Z}(\hat{t})}{d\hat{t}} \geq -\delta \hat{Z}(\hat{t})$, which implies that $\hat{Z}(\hat{t}) > 0$ since $\hat{Z}(\mathcal{T}) > 0$. In particular, $\hat{Z}(\beta_1) > 0$, which is a contradiction, so it must be true that $\hat{Z}(\hat{t}) > 0$ for all $\hat{t} \in [0, \hat{w})$. Equation (3.14) then implies that $\hat{N}(\hat{t}) + \hat{P}(\hat{t}) + \hat{Z}(\hat{t}) < N_T$, which implies that $\hat{N}$ is increasing at sufficiently small and positive values of $\hat{N}(\hat{t})$. Therefore, $\hat{N}(\hat{t}) > 0$ for all $\hat{t} \in [0, \hat{w})$. From (3.14), $\hat{N}(\hat{t}), \hat{P}(\hat{t}), \hat{Z}(\hat{t}) > 0$ implies also that $\hat{N}(\hat{t}), \hat{P}(\hat{t}), \hat{Z}(\hat{t}) < N_T$. ☐

It follows from this proposition that solutions are bounded. From the definition of the phase space $\hat{\Omega}$ in (4.1), standard results for functional differential equations

[15] imply that it must be true that each solution to the DDE initial value problem (3.10)–(3.12) either exists for all time or satisfies

$$\lim_{\hat{t}\to\hat{w}^-} R(\hat{P}(\hat{t})) = 0.$$

That is, solutions either exist for all time or approach $\partial\hat{\Omega}$.

Proposition 4.2. *If* $(\phi_1, \phi_2, \phi_3)^T \in D_{N_T}$*, then the solution to the TDE initial value problem* (3.6)–(3.3) *exists for all time and satisfies* $N(t), P(t), Z(t) \in (0, N_T)$ *for all* $t \in [0, \infty)$.

Proof. Consider the corresponding DDE initial value problem (3.10)–(3.12) with $\hat{\phi}_i(\hat{t}) = \phi_i(t)$ for $i = 1, 2, 3$ with $\hat{t}$ and t related through (3.9a). There exists a unique maximal solution $(\hat{N}, \hat{P}, \hat{Z})^T : [0, \hat{w}) \to \mathbb{R}^3$, where $\hat{w} > \mathcal{T}$ may be finite or infinite. Using the results in [26], $(N, P, Z)^T : [0, w) \to \mathbb{R}^3$ defined by $(N(t), P(t), Z(t))^T = (\hat{N}(\hat{t}), \hat{P}(\hat{t}), \hat{Z}(\hat{t}))^T$ is the unique maximal solution to the initial value problem (3.6)–(3.3) with $w = \lim_{\hat{t}\to\hat{w}^-} \int_0^{\hat{t}} R^*(R(\hat{P}(r)))^{-1}\, dr$.

If $\hat{w} = \infty$, then

$$w = \lim_{\hat{t}\to\infty} \int_0^{\hat{t}} \frac{R^*}{R(\hat{P}(r))}\, dr = \infty$$

since $R^*/R(\hat{P}(r)) > R^*/R(N_T) > 0$.

If $\hat{w} < \infty$, then we have that $\lim_{\hat{t}\to\hat{b}^-} (\hat{N}(\hat{t}), \hat{P}(\hat{t}), \hat{Z}(\hat{t}))^T \in \partial\hat{\Omega}$ [15]. Since $(\hat{N}(\hat{t}), \hat{P}(\hat{t}), \hat{Z}(\hat{t}))^T$ is bounded by Proposition 4.1, in order for the solution to approach $\partial\hat{\Omega}$ we must have that

$$\lim_{\hat{t}\to\hat{w}^-} R(\hat{P}(\hat{t})) = 0.$$

This implies that $\lim_{\hat{t}\to\hat{w}^-} \hat{P}(\hat{t}) = 0$. From (3.10b) and the properties of h and R in (2.4) and (2.5), there exists a positive A such that

$$\frac{d}{dt} R(\hat{P}(\hat{t})) > -A$$

for $t \in (\hat{w} - \mathcal{T}, \hat{w})$. It then follows that $R(\hat{P}(\hat{t})) < A(\hat{w} - \hat{t})$ for $\hat{t} \in (\hat{w} - \mathcal{T}, \hat{w})$, which implies that

$$w = \lim_{\hat{t}\to\hat{w}^-} \int_0^{\hat{t}} \frac{R^*}{R(\hat{P}(r))}\, dr > \lim_{\hat{t}\to\hat{w}^-} \int_{\hat{t}-\mathcal{T}}^{\hat{t}} \frac{R^*}{A(\hat{w} - r)}\, dr = \infty.$$

The last part, $N(t), P(t), Z(t) \in (0, N_T)$ for all $t \in [0, \infty)$, follows directly from Proposition 4.1 and the fact that $(N(t), P(t), Z(t))^T = (\hat{N}(\hat{t}), \hat{P}(\hat{t}), \hat{Z}(\hat{t}))^T$. ∎

5. Equilibrium solutions and linearization.

To begin, note that $(N^*, P^*, Z^*)^T$ is an equilibrium solution of the DDE model (3.10) if and only if $(N^*, P^*, Z^*)^T$ with $R(P^*) \neq 0$ is an equilibrium solution of the TDE model (3.3). For a fixed value of N_T, the DDE model (3.10) has an equilibrium solution $(\hat{N}(\hat{t}), \hat{P}(\hat{t}), \hat{Z}(\hat{t}))^T = (N^*, P^*, Z^*)^T$ for $t \geq 0$ if N^*, P^*, Z^* are constants that satisfy

(5.1a)
$$\frac{R^*}{R(P^*)}[-\mu P^* f(N^*) + \lambda P^* + \delta Z^* + (1 - \gamma) g Z^* h(P^*) + \delta_0(N_T - N^* - P^* - Z^*)] = 0,$$

$$\frac{R^*}{R(P^*)}[\mu P^* f(N^*) - \lambda P^* - gZ^* h(P^*)] = 0, \tag{5.1b}$$

$$\frac{R^*}{R(P^*)}[\gamma g e^{-\delta_0 m/R(P^*)} Z^* h(P^*) - \delta Z^*] = 0. \tag{5.1c}$$

where $m/R(P^*) \overset{\text{def}}{=} \tau^*$ is the equilibrium value of the delay. If $\delta_0 = 0$, then these three equations are redundant in the sense that if two are satisfied, then the third is also satisfied. To avoid this problem, we use the conservation law (3.8) in place of (5.1a). For $P^* \neq 0$, equilibrium solutions should satisfy

$$N^* + P^* + Z^* + \gamma g Z^* h(P^*) \frac{1 - e^{-\delta_0 m/R(P^*)}}{\delta_0} - N_T = 0, \tag{5.2a}$$

$$\mu P^* f(N^*) - \lambda P^* - gZ^* h(P^*) = 0, \tag{5.2b}$$

$$\gamma g e^{-\delta_0 m/R(P^*)} Z^* h(P^*) - \delta Z^* = 0, \tag{5.2c}$$

where we have used $\tau(s, P^*) = s/R(P^*))$ and assumed $\delta_0 \neq 0$. When $\delta_0 = 0$, the term $\frac{1-e^{-\delta_0 m/R(P^*)}}{\delta_0}$ is replaced by $m/R(P^*)$. If $\delta_0 \neq 0$ and $P^* \neq 0$, then (5.1a)–(5.1c) are satisfied if and only if (5.2a)–(5.2c) are satisfied. However, when $\delta_0 = 0$, (5.2a)–(5.2c) give the equilibrium solution corresponding to the value of total biomass, N_T, in which we are interested, whereas (5.1a)–(5.1c) do not.

There are two types of equilibrium solutions that can exist: $E_1 = (N_1^*, P_1^*, 0)^T$ and $E_2 = (N_2^*, P_2^*, Z_2^*)^T$. We will say that an equilibrium point exists if all its components are nonnegative, as these represent physical quantities. We will only consider $Z_2^* > 0$ to distinguish between the two types.

Note that any equilibrium solution $(N^*, P^*, Z^*)^T$ of the DDE or TDE model corresponds to an equilibrium solution $(N^*, P^*, Z^*, \rho^*(s))^T$ of the PDE1 or PDE2 model, with

$$\rho^*(s) = \frac{\gamma g Z^* h(P^*)}{R(P^*)} e^{\frac{-\delta_0 s}{R(P^*)}}.$$

5.1. The phytoplankton-only equilibrium E_1.

Considering E_1, we see that $Z^* = 0$ implies that (5.2c) is satisfied. Then, for positive P_1^*, (5.2b) is satisfied if and only if $N_1^* = f^{-1}(\lambda/\mu)$. Consequently, (5.2a) is satisfied if and only if $P_1^* = N_T - N_1^*$. Therefore, E_1 exists if and only if

$$N_T > N_{T1},$$

where

$$N_{T1} = f^{-1}\left(\frac{\lambda}{\mu}\right). \tag{5.3}$$

Note that as N_T increases, P_1 increases linearly while N_1 remains fixed. That is, while E_1 is a stable equilibrium, increasing the total biomass in the ecosystem increases the phytoplankton population while the dissolved nutrient remains fixed.

5.2. The phytoplankton-zooplankton equilibrium E_2.

For the equilibrium E_2, we have that $Z_2^* > 0$, so it is required that

$$\gamma g e^{-\delta_0 m/R(P_2^*)} h(P_2^*) - \delta = 0$$

in order for (5.2c) to be satisfied. This is true if and only if

$$m = \frac{R(P_2^*)}{\delta_0} \ln\left(\frac{\gamma g h(P_2^*)}{\delta}\right). \tag{5.4}$$

Given m, P_2^* is defined implicitly through this equation. Under the assumption that R and h are both increasing and saturating functions, we can see that P_2^* increases with m, $P_2^* = h^{-1}(\delta/\gamma g)$ when $m = 0$, and $P_2^* \to \infty$ as $m \nearrow R_\infty \ln(\gamma g/\delta)/\delta_0$. There is no solution for m larger than this value. However, if $m \in [0, R_\infty \ln(\gamma g/\delta)/\delta_0)$, then there is a unique positive value P_2^* that satisfies (5.4).

Assuming that $m \in [0, R_\infty \ln(\gamma g/\delta)/\delta_0)$, we get that (5.2b) is satisfied if and only if

$$Z_2^* = (\mu f(N_2^*) - \lambda)\frac{P_2^*}{gh(P_2^*)}.$$

Assuming $Z_2^* > 0$, we require $N_2^* > N_{T1}$. Then (5.2a) is satisfied if N_2^* satisfies

$$N_2^* + P_2^* + (\mu f(N_2^*) - \lambda)\frac{P_2^*}{gh(P_2^*)}\left(1 + \gamma g h(P_2^*)\frac{1 - e^{-\delta_0 m/R(P_2^*)}}{\delta_0}\right) - N_T = 0,$$

with P_2^* fixed and given by (5.4). We can see that N_2^* increases with increasing N_T and that $N_2^* = N_{T1}$ when $N_T = N_{T1} + P_2^*$. Therefore, E_2 exists and is unique if and only if $m \in [0, R_\infty \ln(\gamma g/\delta)/\delta_0)$ and $N_T > N_{T2}$ where

$$N_{T2} = f^{-1}\left(\frac{\lambda}{\mu}\right) + P_2^*,$$

with P_2^* defined through (5.4). Since $N_{T2} > N_{T1}$, the existence of E_2 implies the existence of E_1. As N_T is increased, P_2 is fixed while N_2 and Z_2 increase.

Figure 2 shows how the dominant equilibrium solutions change as the total biomass increases, for several values of m and two choices of δ_0. We use the parameter values given in Table 2, which were taken from [24]. We consider the case where $R(P) = P/(P + 0.159)$ and various values of m. Note that if $m = 0$, then the zooplankton are considered mature immediately at birth. In this case there is no delay and the TDE model (3.3) and DDE model (3.10) reduce to systems of ordinary differential equations. Plots (a), (c), (e) are for $\delta_0 = 0$, while (b), (d), (f) are for $\delta_0 = \delta$. The former case represents the situation where the immature zooplankton have a zero death rate. That is, we ignore the possibility of them dying before reaching maturity. In the latter case the immature zooplankton have the same death rate as the mature zooplankton. We see that $N^* = N_T$ and $P^* = Z^* = 0$ for $N_T < N_{T1}$ (e_0 is plotted). Then for $N_{T1} < N_T < N_{T2}$ (E_1 is plotted), P^* increases linearly with N_T while N^* is fixed at N_{T1} and Z^* is fixed at 0. Then for $N_T > N_{T2}$ (E_2 is plotted), P^* is fixed and N^* and Z^* increase with N_T, though Z^* saturates and N^* increases indefinitely. Note that N_{T2} depends on m when $\delta_0 \neq 0$, but not when $\delta_0 = 0$. Also, P^* is independent of m when $\delta_0 = 0$, but changes for $N_T > N_{T2}$ when $\delta_0 \neq 0$. The value to which Z^* saturates does not change with m when $\delta_0 = 0$, but increases with m when $\delta_0 \neq 0$.

We can interpret these observations biologically as follows. As might be expected, the presence of the juvenile zooplankton stage affects only the zooplankton-phytoplankton equilibrium point E_2. Increasing the maturity level for adulthood, m, corresponds to increasing the maturation delay, so zooplankton spend more time in

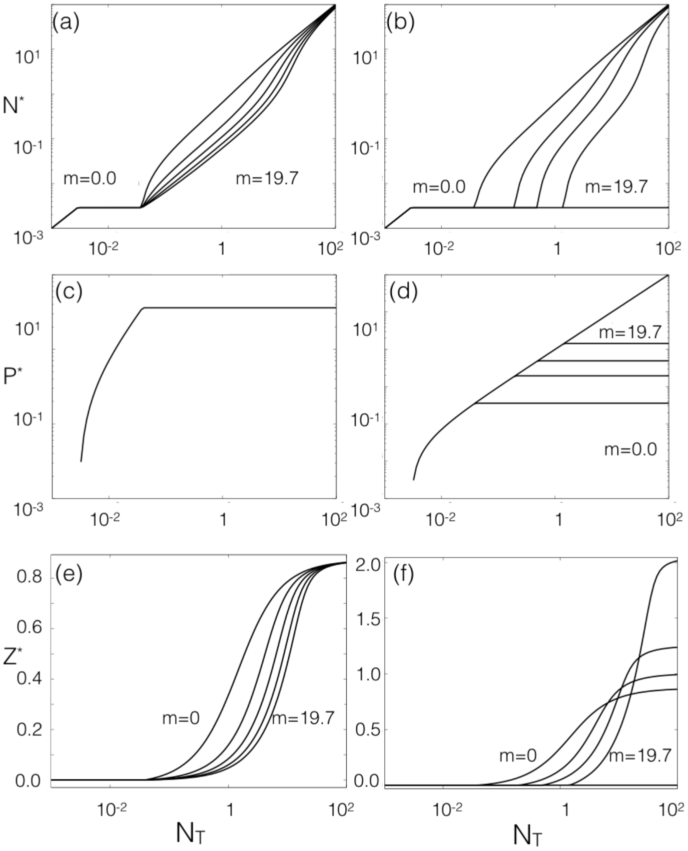


FIG. 2. *Equilibrium solutions as a function of total biomass for* $m = 0, 5, 10, 15, 19.7$ *and* $R(P) = P/(P + 0.159)$. *Plots* (a), (c), (e) *are for* $\delta_0 = 0$ *and* (b), (d), (f) *are for* $\delta_0 = \delta$. *If* E_2 *exists, it is the solution plotted. If* E_2 *does not exist, but* E_1 *does, then* E_1 *is plotted. If neither exist, the limit point* $(N_T, 0, 0)^T$ *is plotted.*

TABLE 2
Parameter values used for all computations.

Parameter	Value
μ	5.9 day^{-1}
λ	0.017 day^{-1}
g	7 day^{-1}
γ	0.7
δ	0.17 day^{-1}
$f(N)$	$\frac{N}{N+k}$
$h(P)$	$\frac{P}{P+K}$
k	1.0μM
K	1.0μM

the juvenile stage. In the case that juveniles do not die ($\delta_0 = 0$), the effect of the maturation delay is mild. This is primarily because the equilibrium distribution of the juvenile zooplankton is constant, ρ_0^*, determined by (2.1e). Thus the main effect is that there is more biomass in a juvenile zooplankton compartment at equilibrium, which leads (through the conservation law) to lower equilibrium values for the nutrient and zooplankton. The equilibrium values for the phytoplankton and the minimum total nutrient needed to support zooplankton (N_{T2}) are unaffected by the presence of the juvenile stage. If the juveniles die ($\delta_0 > 0$), the equilibrium distribution of juveniles is a decaying exponential $\rho^*(s) = \rho_0^* e^{-\delta_0 s/R(P^*)}$, and the effect of the juvenile stage is more complex. For low amounts of total nutrient (N_T small) the effect is similar to that when the juveniles don't die, except that there is more phytoplankton at equilibrium and more total nutrient is needed to support zooplankton. However, when there is a large enough amount of total nutrient available, the amount of zooplankton at equilibrium increases as the maturation delay increases.

5.3. Linearization and characteristic equation. We now derive the linearization about the equilibrium points described above and the corresponding characteristic equation. As linearization results exist for equations with bounded state-dependent delays [7, 16] and for equations with constant delay [15], we could work with either the TDE model (3.3) or the DDE model (3.10). We have carried out the computations for both models, and they yield the same results. Below we present the results for the TDE model (3.3). Although our state-dependent delay becomes unbounded as $P \to 0$, we focus here on the linearization about E_1 and E_2. Thus we can restrict our work to neighborhoods of these points where P is bounded away from zero, and hence the delay is bounded.

Consider the threshold delay equation in the general form

$$\frac{dx(t)}{dt} = f(x(t), x(t-\tau(x_t)), \tau(x_t)), \qquad \int_{-\tau(x_t)}^{0} K(x_t(u))\, du = m, \tag{5.5}$$

where f and K are $\mathcal{C}^1$.

Let x^* be an equilibrium solution of equations (5.5), that is, a constant function such that $f(x^*, x^*, \tau(x^*)) = 0$, where $\tau^* = m/K(x^*) = \tau(x^*)$. Let $y(t) = x(t) - x^*$. By setting the state-dependent delay to its equilibrium value, and linearizing (5.5) as in [7, 16], we obtain

$$\frac{dy(t)}{dt} = D_1 f(x^*, x^*, \tau^*) y(t) + D_2 f(x^*, x^*, \tau^*) y(t-\tau^*) + D_3 f(x^*, x^*, \tau^*) D\tau(x^*) y_t, \tag{5.6}$$

where $D_i f$ is the derivative of f with respect to its ith argument, and

$$D\tau(x^*) y_t = -\frac{DK(x^*)}{K(x^*)} \int_{-\tau^*}^{0} y_t(u)\, du, \tag{5.7}$$

where D denotes the Fréchet derivative.

We can check that (5.7) is correct by verifying that

$$\lim_{\eta \to 0} \frac{\left| \tau(x^* + \eta) - \tau(x^*) + \frac{DK(x^*)}{K(x^*)} \int_{-\tau^*}^{0} \eta(u)\, du \right|}{||\eta||} = 0, \tag{5.8}$$

where $\eta \in \mathcal{C}[-r, 0]$ for some $r > \tau(\phi)$ for all ϕ in a neighborhood of x^*. Here, $||.||$ is the usual sup norm. We proceed as follows:

$$\begin{aligned}&\left|\tau(x^*+\eta)-\tau(x^*)+\frac{DK(x^*)}{K(x^*)}\int_{-\tau^*}^{0}\eta(u)\,du\right|\\&=\frac{1}{K(x^*)}\left|\int_{-\tau(x^*+\eta)}^{0}K(x^*)\,du-\int_{-\tau^*}^{0}K(x^*)\,du+DK(x^*)\int_{-\tau^*}^{0}\eta(u)\,du\right|.\end{aligned}$$

Under the assumption that $K\in\mathcal{C}^1$, it is true that $K(x^*)=K(x^*+x)-DK(x^*)x+G(x)$, with G satisfying

$$\lim_{x\to 0}\frac{|G(x)|}{||x||_E}=0,$$

where $||.||_E$ is the Euclidean norm on $\mathbb{R}^n$. Then

$$\begin{aligned}&\int_{-\tau(x^*+\eta)}^{0}K(x^*)\,du\\&=\int_{-\tau(x^*+\eta)}^{0}K(x^*+\eta(u))\,du-DK(x^*)\int_{-\tau(x^*+\eta)}^{0}\eta(u)\,du+\int_{-\tau(x^*+\eta)}^{0}G(\eta(u))\,du.\end{aligned}$$

Then by the definition of τ,

$$\int_{-\tau(x^*+\eta)}^{0}K(x^*+\eta(u))\,du=\int_{-\tau(x^*)}^{0}K(x^*)\,du=m.$$

So it can then be seen that

$$\begin{aligned}&\lim_{\eta\to 0}\frac{\left|\tau(x^*+\eta)-\tau(x^*)+\frac{DK(x^*)}{K(x^*)}\int_{-\tau(x^*)}^{0}\eta(u)\,du\right|}{\|\eta\|}\\&=\lim_{\eta\to 0}\frac{\left|DK(x^*)\int_{-\tau^*}^{-\tau(x^*+\eta)}\eta(u)\,du+\int_{-\tau(x^*+\eta)}^{0}G(\eta(u))\,du\right|}{K(x^*)\|\eta\|}\\&=0\end{aligned}$$

from the properties of G.

In particular, the linearization of the TDE model (3.3) about an equilibrium solution $(N^*,P^*,Z^*)^T$ with R^* taken to be $R(P^*)$ is

$$\frac{dy(t)}{dt}=A_1y(t)+A_2y(t-\mathcal{T})+A_3\int_{-\mathcal{T}}^{0}y(t+u)\,du, \tag{5.9}$$

where

$$A_1=\begin{pmatrix}-\mu P^*a-\delta_0 & -\mu c+\lambda+(1-\gamma)gZ^*b-\delta_0 & \delta-\delta_0+(1-\gamma)gd\\ \mu P^*a & \mu c-\lambda-gZ^*b & -gd\\ 0 & e^{-\delta_0\mathcal{T}}\gamma gZ^*d\frac{R'(P^*)}{R(P^*)} & -\delta\end{pmatrix},$$

$$A_2=\begin{pmatrix}0&0&0\\0&0&0\\0& e^{-\delta_0\mathcal{T}}\gamma gZ^*(b-\frac{R'(P^*)}{R(P^*)}d) & e^{-\delta_0\mathcal{T}}\gamma gd\end{pmatrix},$$

$$A_3 = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & \delta_0 e^{-\delta_0 \mathcal{T}} \gamma g Z^* d \frac{R'(P^*)}{R(P^*)} & 0 \end{pmatrix},$$

and $a = f'(N^*)$, $b = h'(P^*)$, $c = f(N^*)$, $d = h(P^*)$, and $\mathcal{T} = m/R(P^*) = \tau(m, P^*) = \hat{\tau}(m, P^*)$.

Substituting $y(t) = ve^{st}$ into (5.9), with $v \in \mathbb{R}^3$, we can obtain the characteristic equation

$$\det\left(sI - A_1 - A_2 e^{-s\mathcal{T}} + A_3 \frac{(1 - e^{-s\mathcal{T}})}{s}\right) = 0. \tag{5.10}$$

If all values of s that satisfy (5.10) have a negative real part, then $(N^*, P^*, Z^*)^T$ is an asymptotically stable equilibrium solution of the TDE model (3.3) [16].

6. Stability and extinction.

6.1. Conditions for the extinction of plankton. It is possible for the solutions to the TDE model (3.3) to approach the point $e_0 = (N_T, 0, 0)^T$. To show this, we will use the following lemma.

Lemma 6.1. *If* $(N(t), P(t), Z(t))^T$ *is a solution of the TDE model* (3.3) *such that* $\lim_{t\to\infty} P(t) = 0$, *then* $\lim_{t\to\infty}(N(t), P(t), Z(t))^T = (N_T, 0, 0)^T$.

Proof. Assume that $\lim_{t\to\infty} P(t) = 0$. The term $e^{-\delta_0 \tau(m, P_t)}$ is clearly bounded. Also, by Proposition 4.2, $Z(t - \tau(m, P_t)) < N_T$, so this term is also bounded. Recall that the properties of h and R in (2.4) and (2.5) imply (2.6). It follows that there is a function, w, such that $\lim_{t\to\infty} w(t) = 0$ and $\frac{dZ(t)}{dt} < w(t) - \delta Z(t)$ for $t \geq t_0$. Integrating this inequality, we obtain

$$Z(t) < e^{-\delta(t-t_0)} Z(t_0) + e^{-\delta t} \int_{t_0}^{t} e^{\delta u} w(u)\, du.$$

In the case where $\int_{t_0}^{\infty} e^{\delta u} w(u)\, du < \infty$ it is obvious the final term approaches zero as $t \to \infty$. Otherwise, we can apply l'Hôpital's rule and get the same result. Since $Z(t) > 0$ by Proposition 4.2, we have that $\lim_{t\to\infty} Z(t) = 0$.

The result then follows from conservation law (3.8) if it is true that

$$\lim_{t\to\infty} \int_0^m e^{-\delta_0 \tau(s, P_t)} \frac{\gamma g Z(t - \tau(s, P_t)) h(P(t - \tau(s, P_t)))}{R(P(t - \tau(s, P_t)))}\, ds = 0.$$

If $\lim_{t\to\infty} \tau(s, P_t) < \infty$, then $Z(t - \tau(s, P_t)) \to 0$ and the result immediately follows. If $\lim_{t\to\infty} \tau(s, P_t) = \infty$, then $e^{-\delta_0 \tau(s, P_t)} \to 0$ and the result follows. ◻

This also implies that if $\hat{P}(\hat{t})$ in the solution to the DDE model (3.10) reaches zero in finite time, then $\hat{Z}(\hat{t})$ reaches zero at the same finite moment in time. This is because the transformation maps $t = \infty$ to $\hat{t} = \hat{w} < \infty$.

Consider the following proposition.

Proposition 6.2. *If* $0 < N_T < N_{T1}$, *where* N_{T1} *is given in* (5.3), *and* $(\phi_1, \phi_2, \phi_3)^T \in D_{N_T}$, *then the solution to the TDE initial value problem* (3.6)–(3.3) *asymptotically approaches* $(N_T, 0, 0)^T$.

Proof. From (3.3b), we have that $\frac{dP}{dt} < \mu f(N_T) P(t) - \lambda P(t)$. Then $N_T < N_{T1}$ implies that $\mu f(N_T) - \lambda < 0$, which implies that $P(t) < P(t_0) e^{(\mu f(N_T) - \lambda)(t - t_0)}$. Since $P(t) > 0$ from Proposition 4.2, $\lim_{t\to\infty} P(t) = 0$. The result then follows from Lemma 6.1. ◻

6.2. Global stability of E_1. Here we will show conditions for the global stability of E_1. Consider the following lemma.

LEMMA 6.3. *Let* $(\phi_1, \phi_2, \phi_3)^T \in D_{N_T}$ *and denote* $(N, P, Z)^T : [0, \infty) \to \mathbb{R}^3$ *as the solution to the TDE initial value problem* (3.6)–(3.3). *If* $N_T > N_{T1}$, *then for any constant* $\beta > N_T - N_{T1}$, *there exists a* $t_1 \geq t_0$ *such that* $P(t) < \beta$ *for all* $t \geq t_1$.

Proof. Fix $\beta < N_T - N_{T1}$. From the conservation law (3.8) and Proposition 4.2, $N(t) < N_T - P(t)$. Then for $P(t) \geq \beta$ we have

$$\begin{aligned}\frac{dP(t)}{dt} &< [\mu f(N(t)) - \lambda]P(t),\\ &< [\mu f(N_T - P(t)) - \lambda]P(t),\\ &< [\mu f(N_T - \beta) - \lambda]P(t).\end{aligned}$$

Since $\mu f(N_T - \beta) - \lambda < \mu f(N_{T1}) - \lambda = 0$, we have

$$\frac{dP(t)}{dt} < [\mu f(N_T - \beta) - \lambda]\beta$$

for $P(t) \geq \beta$. Therefore there exists $t_1 \geq t_0$ such that $P(t) < \beta$ for all $t \geq t_1$. □

PROPOSITION 6.4. *Let* $(\phi_1, \phi_2, \phi_3)^T \in D_{N_T}$ *and denote* $(N, P, Z)^T : [0, \infty) \to \mathbb{R}^3$ *as the solution to the TDE initial value problem* (3.6)–(3.3). *If* $N_{T1} < N_T < N_{T2}$, *then* $\lim_{t\to\infty}(N(t), P(t), Z(t))^T = (N_1^*, P_1^*, 0)^T$.

Proof. Note that $\mu f(N_1^*) - \lambda = 0$ and $P_1^* = N_T - N_1^* < P_2^*$ for $N_T < N_{T2}$. Consider the function

$$V_1(t) = \int_{N_1^*}^{N(t)} [\mu f(x) - \lambda]\, dx + \delta_0 \int_{N_T - N_1^*}^{P(t)} \frac{x + N_1^* - N_T}{x}\, dx.$$

We have that $V_1(t) \geq 0$ for $P(t) > 0$. Taking the derivative along solutions to the TDE model (3.3), we obtain

$$\begin{aligned}\frac{d}{dt}V_1(t) = {}& [\mu f(N(t)) - \lambda][-\mu P(t) f(N(t)) + \lambda P(t) + \delta Z(t) + (1-\gamma) g Z(t) h(P(t))\\ &+ \delta_0(N_T - N(t) - P(t) - Z(t))]\\ &+ \delta_0 \frac{P(t) + N_1^* - N_T}{P(t)}[\mu P(t) f(N(t)) - \lambda P(t) - g Z(t) h(P(t))]\\ \leq {}& -P(t)[\mu f(N(t)) - \lambda]^2 - \delta_0[N(t) - N_1^*][\mu f(N(t)) - \lambda] + M Z(t)\end{aligned}$$

for some positive constant M. This M exists because $N(t)$ and $P(t)$ are bounded and because of the properties of h in (2.4). Then consider the function

$$V_2(t) = Z(t) + \int_{t-\tau(m,P_t)}^{t} \gamma g e^{-\delta_0 \tau(m,\beta)} Z(u) h(P(u))\, du.$$

We have that $V_2(t) \geq 0$. Choose $\beta \in (N_T - N_{T1}, P_2^*)$. Then by Lemma 6.3 there exists $t_1 \geq t_0$ such that $P(t) < \beta$ for $t \geq t_1$. This implies that

$$\gamma g e^{-\delta_0 \tau(m,P_t)} h(P(t)) < \gamma g e^{-\delta_0 \tau(m,\beta)} h(\beta) < \gamma g e^{-\delta_0 \tau(m,P_2^*)} h(P_2^*) = \delta$$

for $t \geq t_1$. Define the positive constant $\alpha = \delta - \gamma g e^{-\delta_0 \tau(m,\beta)} h(\beta)$. Differentiating, we have that

$$\begin{aligned} \frac{d}{dt} V_2(t) = {} & R(P(t)) e^{-\delta_0 \tau(m,P_t)} \frac{\gamma g Z(t-\tau(m,P_t)) h(P(t-\tau(m,P_t)))}{R(P(t-\tau(m,P_t)))} - \delta Z(t) \\ & + \gamma g e^{-\delta_0 \tau(m,\beta)} Z(t) h(P(t)) \\ & - \gamma g e^{-\delta_0 \tau(m,\beta)} Z(t-\tau(m,P_t)) h(P(t-\tau(m,P_t))) \left(1 - \frac{\partial \tau}{\partial t}\right), \\ \leq {} & - \alpha Z(t), \end{aligned}$$

where we have used (3.5), $h(P(t)) < h(\beta)$, and $e^{-\delta_0 \tau(m,P_t)} < e^{-\delta_0 \tau(m,\beta)}$ for $t \geq t_1$. Setting $V(t) = V_1(t) + \frac{M+M_1}{\alpha} V_2(t)$, where $M_1 > 0$, we have that $V(t) \geq 0$ and that

$$\frac{d}{dt} V(t) \leq -\delta_0 [N(t) - N_1^*][\mu f(N(t)) - \lambda] - M_1 Z(t)$$

for $t \geq t_1$. Integrating, we obtain that

$$V(t) + \int_{t_0}^{t} [\delta_0 (N(u) - N_1^*)(\mu f(N(u)) - \lambda) + M_1 Z(u)]\, du \leq V(t_1). \tag{6.1}$$

Since $V(t)$ and the above integrand are nonnegative, and since inequality (6.1) must be true for all time, it must also be true that

$$\int_{t_0}^{\infty} [\delta_0 (N(u) - N_1^*)(\mu f(N(u)) - \lambda) + M_1 Z(u)]\, du < \infty.$$

By Barbălat's lemma [11], it must be true that $N(t) \to N_1^*$ and $Z(t) \to 0$. By the conservation law (3.8) it then follows that $P(t) \to P_1^*$. ◻

The attractivity of E_1 has thus been shown. However, Proposition 6.4 does not address its stability. Let $(N,P,Z)^T : [0,\infty) \to \mathbb{R}^3$ denote the solution to the TDE initial value problem (3.6)–(3.3). We will consider an equilibrium point E to be asymptotically stable if for any $\varepsilon > 0$, there exists a neighborhood N_ε around E such that if $(\phi_1, \phi_2, \phi_3) \in D_{N_T} \cap N_\varepsilon$, then $||(N(t), P(t), Z(t))^T - E|| < \varepsilon$ for $t \geq t_0$ and $\lim_{t \to \infty} (N(t), P(t), Z(t))^T = E$.

We will use the linearization of the TDE model (3.3) to prove the following proposition.

PROPOSITION 6.5. *If $N_{T1} < N_T < N_{T2}$, then E_1 is asymptotically stable.*

Proof. The condition $N_{T1} < N_T$ ensures that $E_1 = (N_1^*, P_1^*, 0)^T$ exists. The characteristic equation of the corresponding linear system is

$$\begin{aligned} & \det \begin{pmatrix} s + \mu P_1^* a + \delta_0 & \delta_0 & -\delta + \delta_0 - (1-\gamma) g d \\ -\mu P_1^* a & s & g d \\ 0 & 0 & s + \delta - \gamma g d e^{-(\delta_0 + s)\mathcal{T}} \end{pmatrix} \\ & = (s + \mu P_1^* a)(s + \delta_0)(s + \delta - \gamma g d e^{-(\delta_0 + s)\mathcal{T}}). \end{aligned}$$

The first two factors give two negative real eigenvalues. Since $N_T < N_{T2}$, it is true that $\gamma g d e^{-\delta_0 \mathcal{T}} < \delta$. Set $s = \alpha + i\omega$ for real α and ω and assume that $\alpha \geq 0$. We have that $s + \delta - \gamma g d e^{-(\delta_0 + s)\mathcal{T}} = 0$ if and only if $\alpha + i\omega + \delta = \gamma g d e^{-(\delta_0 + \alpha + i\omega)\mathcal{T}}$. Squaring the modulus of both sides we obtain

$$(\alpha + \delta)^2 + \omega^2 = (\gamma g d)^2 e^{-2(\delta_0 + \alpha)\mathcal{T}} < \delta^2,$$

which implies $\alpha < 0$. This contradiction shows that there are no solutions with nonnegative real part. Since all the eigenvalues have negative real parts, E_1 is asymptotically stable. ∎

The global attractivity together with the local stability of E_1 for $N_{T1} < N_T < N_{T2}$ shows that E_1 is globally asymptotically stable on D_{N_T}.

6.3. Stability of E_2: No delay. Recall that if $m = 0$, then the zooplankton are considered mature immediately at birth. In this case there is no delay and the TDE model (3.3) is just a system of ordinary differential equations. In [18], we showed that in the case of no delay, E_2 is always asymptotically stable if h has a negative second derivative (a type II response) and f has a negative second derivative, which is the case we will consider in the following sections. There is a unique $N_{T3} > N_{T2}$ such that E_2 is asymptotically stable if $N_{T2} < N_T < N_{T3}$ and unstable if $N_T > N_{T3}$. This value of N_{T3} is independent of δ_0 and the functional form of $R(P)$, since $m = 0$ implies that δ_0 and $R(P)$ do not play a role in the TDE model (3.3) under the assumption that $(\phi_1, \phi_2, \phi_3) \in D_{N_T}$.

6.4. Stability of E_2: State-independent delay. Consider the case where $R(P)$ is constant. That is, the maturation rate of zooplankton is independent of the phytoplankton population. Without loss of generality, we will assume m has been scaled so that $R(P) = 1$. In this sense, m has dimensions of time and represents the age at which zooplankton reach maturity. In this case, the delay is no longer state dependent and is fixed at $\tau = m$.

Due to the complicated nature of the resulting characteristic equation, we use numerical methods to study the stability of E_2, both here in the state-independent delay case and in the following section, which deals with the state-dependent delay problem. We use the parameter values in Table 2.

By setting $s = i\omega$ in the characteristic equation (5.10) and allowing the m and N_T parameters to vary, we can find solutions where the eigenvalues have zero real part. These represent critical points where stability might switch. Since the characteristic equation is complex valued, it gives us two equations that need to be satisfied. The equilibrium equations change with changing m and N_T, so (5.2) gives us three more equations to solve. We then have six unknowns: $N^*, P^*, Z^*, m, N_T, \omega$. We can then find one-dimension curves where the five equations are satisfied, using pseudo-arclength continuation [12]. Note that if $(N^*, P^*, Z^*, m, N_T, \omega)$ solves the five equations, then ω represents the frequency for solutions to the TDE model (3.3) near the corresponding equilibrium solution (N^*, P^*, Z^*) when the size at which the immature zooplankton reach maturity is m and the total biomass is N_T.

Figure 3 shows regions in the $m - N_T$ plane where the equilibrium solutions exhibit different behavior. Two cases were considered: $\delta_0 = 0$ (Figure 3(a)) and $\delta_0 = \delta$ (Figure 3(b)). In region 1 we have that E_1 and E_2 do not exist. This region is the same, regardless of the value of δ_0. In region 2, E_1 exists, but E_2 does not. This region does depend on the value of δ_0, as a larger δ_0 requires more biomass for the E_2 equilibrium to exist. Region 3 shows where E_1 and E_2 exist. We note that $R_\infty \ln(\gamma g/\delta)/\delta_0 \approx 19.77$, which is an upper limit for m when $\delta_0 > 0$. The solid curves show the values of m and N_T where the linearized system has an eigenvalue with zero real part. The subset of region 3 below the solid curves represents values of m and N_T where the E_2 equilibrium is asymptotically stable. This follows from the continuity of the eigenvalues with respect to parameter values and the fact that there are no eigenvalues with nonnegative real parts when $m = 0$ and $N_{T2} < N_T < N_{T3}$ (between

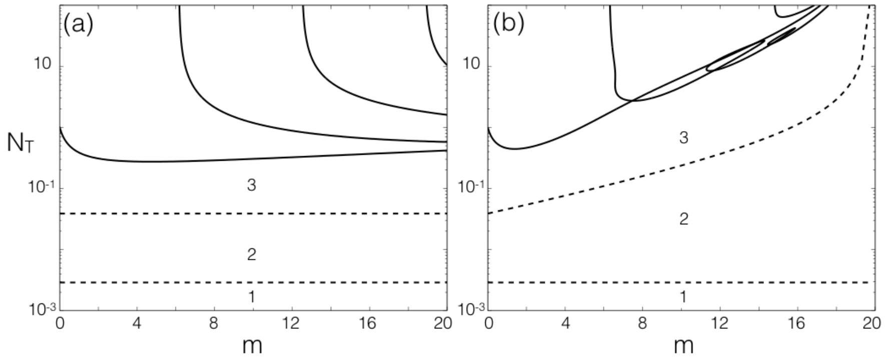


FIG. 3. *The solid curves are where the linearized system has an eigenvalue with zero real part for* $R(P) = 1$ *and* (a) $\delta_0 = 0$; (b) $\delta_0 = \delta$. *Region* 1 *is where* E_1 *and* E_2 *do not exist. Region* 2 *is where* E_1 *exists, but* E_2 *does not. Region* 3 *is where* E_1 *and* E_2 *exist. The subset of region* 3 *under the solid curves is where* E_2 *is asymptotically stable.*

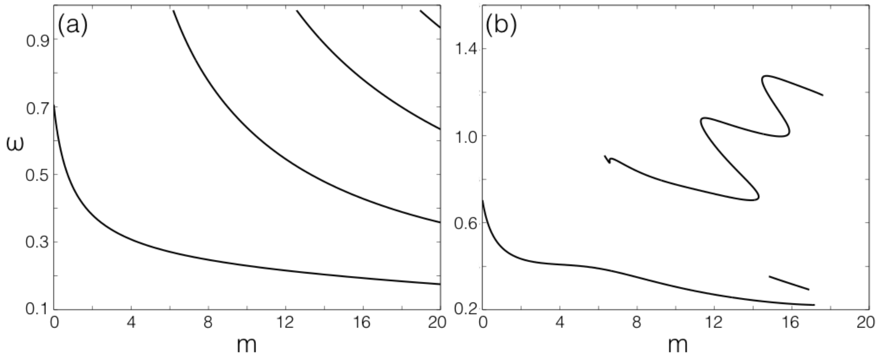


FIG. 4. *The corresponding frequencies to the curves in Figure* 3. *The value of* ω *is the imaginary part of the eigenvalue with zero real part along these curves.*

where the upper dotted curve intersects the vertical axis and where the solid curve intersects the vertical axis).

These regions are all fairly independent of m when $\delta_0 = 0$. That is, if the juvenile zooplankton have a zero death rate, then the level of maturity required for adulthood has little effect on the stability of the equilibrium solutions. However, when there is a positive death rate for the immature zooplankton, the required level of maturity plays a more important role. We see that critical values of total biomass increase with increasing m.

Figure 4 shows the frequencies that correspond to the curves in Figure 3. These are the imaginary parts of the eigenvalues with zero real parts along the curves. For values of m and N_T near the solid curves in Figure 3, we would expect a slow growth or decay rate in the solution to the TDE model (3.3) when it is near the equilibrium solution, and for it to have a frequency close to the corresponding value of ω in Figure 4.

6.5. Stability of E_2: State-dependent delay. Here we consider the case where $R(P) = \frac{P}{P+l}$ for various values of l. Using the same numerical technique as in the previous section, we compute curves in the $m - N_T$ plane where there is an eigenvalue with zero real part. This tells us parameter values where stability can change.

The parameter l is important as it determines how strongly the maturation rate and hence maturation delay, through (3.4), of the juvenile zooplankton depend on the amount of phytoplankton available. The larger l is, the more we would expect the dynamics of the phytoplankton to affect that of the immature zooplankton. We will see this in the results below.

Figure 5 shows regions in the $m - N_T$ plane that have different behavior. We varied both δ_0 and l: $\delta_0 = 0$ (plots (a), (c), (e)) and $\delta_0 = \delta$ (plots (b), (d), (f)); $l = 0.01$ (plots (a), (b)), $l = 0.159$ (plots (c), (d)), $l = 1.00$ (plots (e), (f)). As before, region 1 is where neither E_1 nor E_2 exists. Region 2 is where E_1 exists, but E_2 does not. Region 3 is where both E_1 and E_2 exist. The solid curves are where there is an eigenvalue with zero real part for the system linearized about E_2. Hence, the subset of region 3 beneath the solid curves represents the values of m and N_T where the equilibrium solution E_2 is asymptotically stable.

We can see that the case where $l = 0.01$ is very similar to the case $R(P) = 1$, shown in Figure 3. This is due to the fact that l in this case is small enough relative to P so that $R(P)$ is approximately constant.

When l is increased to 0.159, its value is no longer small relative to typical values of P (see Figure 2). In this case, the delay has a stronger dependence on the quantity of the phytoplankton.

We see many more curves in the case of $\delta_0 = 0$. The minimum values of N_T for these curves increase slightly as m is increased. For $l = 1.00$ there are about an order of magnitude more curves. The minimum values of N_T for these curves increase more as m is increased, which creates an overall larger region of stability than when $l = 0.159$.

For $l = 0.159$ and $\delta_0 = \delta$ there is a single curve that loops three times. In fact, it was observed that $l = 0.01$ is a single curve with three loops as well, but we would have to continue it for N_T values much larger than 100 in order to see this. As we vary l from 0.01 to 0.159, we see this loop become tighter. As l increases to 1.00, the loops either vanish or become smaller than what can be detected at this scale. Either way, we get a much simpler region of stability, even though a larger value of l means that the delay has a stronger dependence on the quantity of phytoplankton.

Figure 6 shows the corresponding frequencies to the curves in Figure 5. In this figure, ω is the imaginary part of the eigenvalues with zero real parts. In the case where $\delta_0 = 0$, the characteristic equation is periodic in m in the sense that if the characteristic equation is zero when $m = m_0$, then it is also zero when $m = m_0 + 2n\pi R(P^*)/\omega$. This is because m only appears in the characteristic equation in the form $e^{im\omega/R(P^*)}$. This periodicity can be easily seen in Figure 6 when $\delta_0 = 0$. Since changing l by an order of magnitude changes $R(P^*)$ by an order of magnitude, we get an order of magnitude more curves for the same range of m.

7. Numerical simulations.

In order to verify some of the results from the previous section, we perform a series of numerical simulations. Rather than simulating the TDE model (3.3) directly, we simulated the DDE model (3.10) and then transformed the resulting time series using equations (3.9b) and the inverse transform of (3.9a). The DDE model (3.10) was simulated using a second-order method for differential equations with fixed delay provided in MATLAB. The integral (3.11) was discretized using a trapezoidal rule. The simulations allowed us to verify the regions

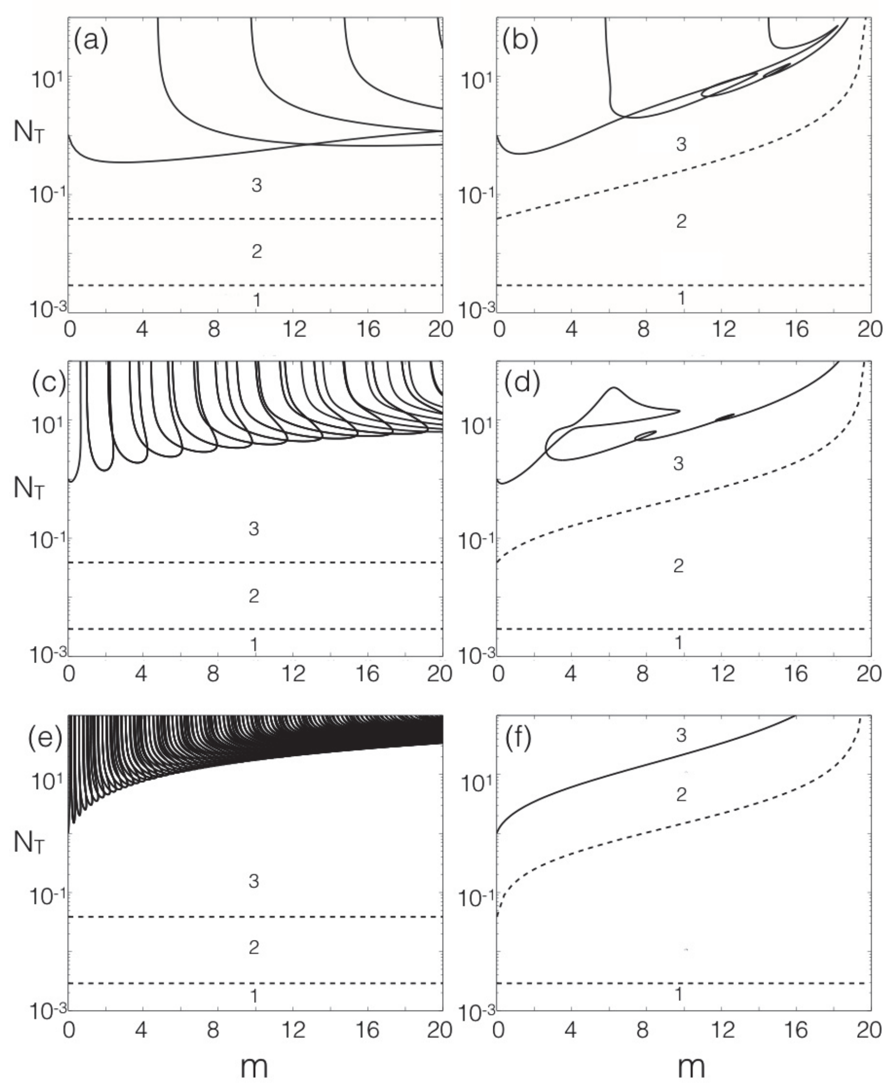


FIG. 5. *The solid curves are where the linearized system has an eigenvalue with zero real part for* $R(P) = \frac{P}{P+l}$ *for various values of* l *and* $\delta_0 = 0$ (plots (a), (c), (e)) *and* $\delta_0 = \delta$ (plots (b), (d), (f)). *Region* 1 *is where* E_1 *and* E_2 *do not exist. Region* 2 *is where* E_1 *exists, but* E_2 *does not. Region* 3 *is where* E_1 *and* E_2 *exist. The subset of region* 3 *under the solid curves is where* E_2 *is asymptotically stable.*

of stability for E_2 that were computed numerically. For instance, we varied values of m and N_T near the solid curves in Figure 5. The initial conditions for the simulation were chosen close to the equilibrium solution E_2. For values of m and N_T that were in a stable region, we verified that the time series of the simulation decayed in time. For values of m and N_T that were in an unstable region, we verified that the time series of the simulation grew in time. Many tests were done for various values of l and for $\delta_0 = 0$ and $\delta_0 = \delta$, and no inconsistencies were found. That is, the simulations always agreed with the numerical stability analysis.

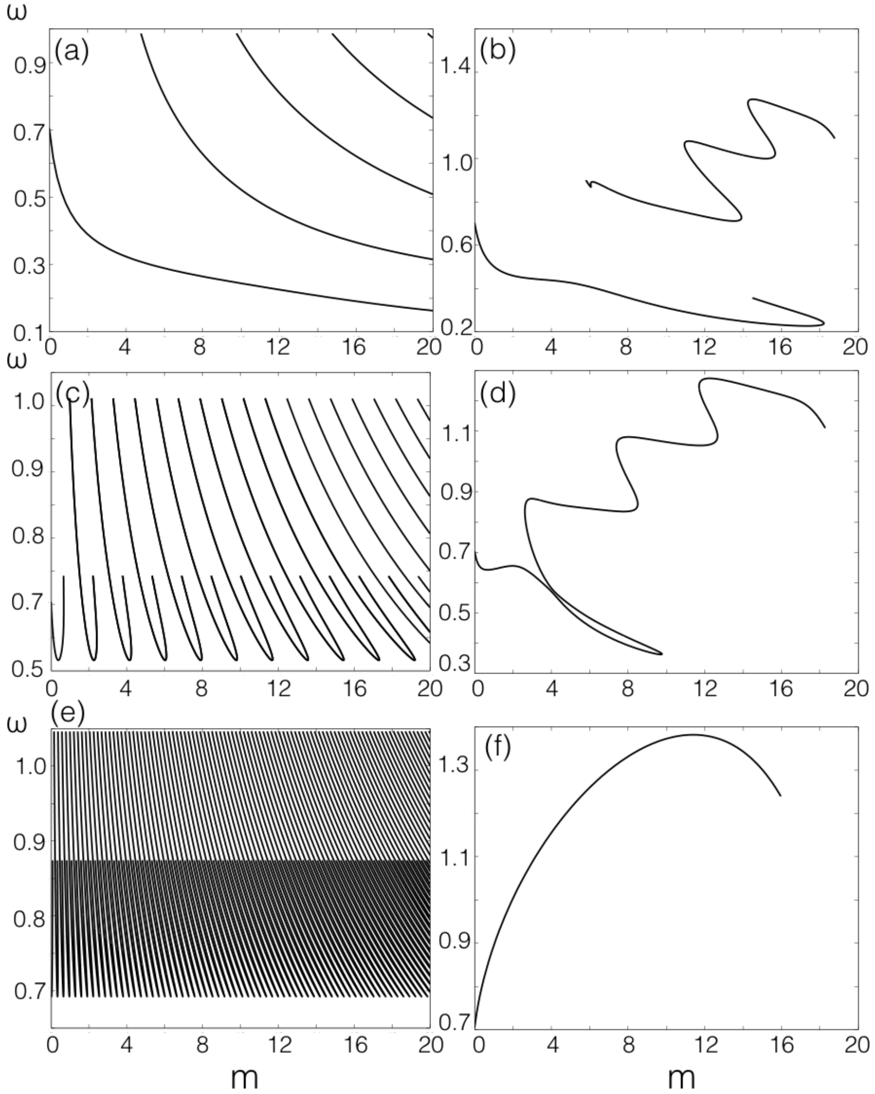
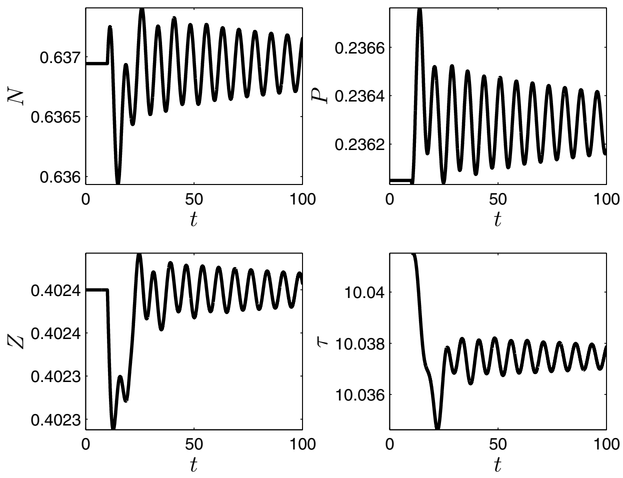


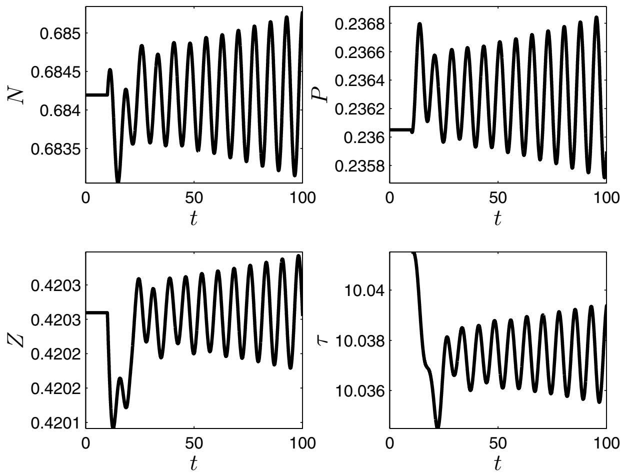
FIG. 6. *The corresponding frequencies to the curves in Figure* 5*. The value of* ω *is the imaginary part of the eigenvalue with zero real part along these curves.*

Figure 7 shows one such verification. For $l = 0.159$, $\delta_0 = \delta$, and $m = 6$, Figure 5 predicts that E_2 should be stable for $N_T = 10^{0.49}$ and unstable for $N_T = 10^{0.51}$. In Figure 7(a), the simulation for $N_T = 10^{0.49}$ indeed suggests that the equilibrium solution is stable. In Figure 7(b), the simulation for $N_T = 10^{0.51}$ suggests that the equilibrium is unstable. While such simulations are by no means proof of stability, it is still reassuring that they agree with the predictions from the numerical stability analysis.

Figure 5 shows the existence of the intersection of the lines where the characteristic equation has a pair of pure imaginary eigenvalues. Assuming that the equation satisfies appropriate nondegeneracy and nonresonance conditions, such points corre-



(a) $N_T = 10^{0.49}$



(b) $N_T = 10^{0.51}$

FIG. 7. *The time series of simulations for* $R = \frac{P}{P+0.159}$, $\delta_0 = \delta$, $m = 6$, *and two values of* N_T. *The initial conditions were chosen near the equilibrium solution.* (a) *For* $N_T = 10^{0.49}$, *the simulation suggests that the equilibrium solution is stable.* (b) *For* $N_T = 10^{0.51}$, *the simulation suggests that the equilibrium solution is unstable. This agrees with Figure* 5(d), *which indicated that there is a zero eigenvalue at* $m = 6$ *and* $N_T = 10^{0.50}$. *Also plotted is the time series of the* $\tau(m, P_T)$, *which is the state-dependent delay.*

spond to points of double Hopf bifurcation [1, 15] and can lead to complex dynamics such as bistability between different limit cycles or the presence of a two-torus [13]. In fact this figure shows that multiple intersection points can occur close together, which points to the possibility of even more complex behavior. When $\delta_0 = \delta$, the intersection points are fairly isolated, and thus we would not expect the complex behavior to persist in large regions of the N_T, m parameter space. In the case that $\delta_0 = 0$,

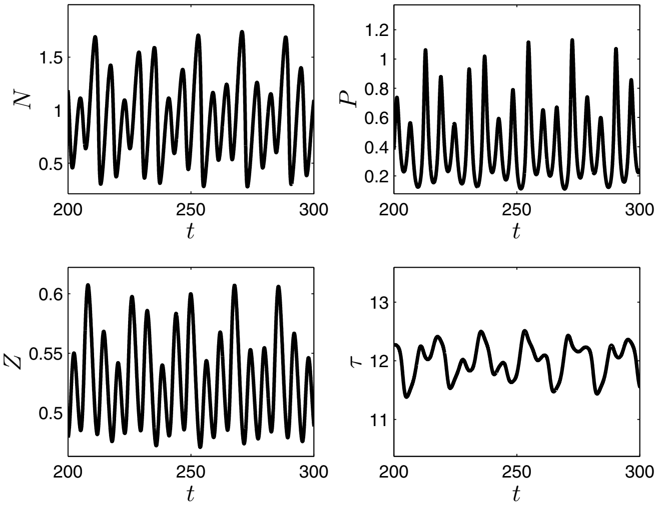


FIG. 8. *A subinterval of the time series of a simulation for* $R = \frac{P}{P+0.159}$, $\delta_0 = \delta$, $m = 8$, *and* $N_T = 10^{0.73}$. *The state-dependent delay,* $\tau(m, P_t)$ *is also shown. This simulation shows the possibility of very irregular and possibly chaotic solutions to the TDE model* (3.3).

however, there are intersection points in a large region of the N_T, m parameter space, and we may expect the complex behavior to be more widespread.

Figure 8 gives an example of the complex behavior induced by such intersection points. It shows a portion of a time series of a simulation for $l = 0.159$, $\delta_0 = \delta$, $m = 8$, and $N_T = 10^{0.73}$. For these values, Figures 5 and 6 together show that there are about five pairs of eigenvalues with real parts close to zero. Thus, we might expect the solution to exhibit up to five frequencies. In Figure 8 we see that the solution is very irregular, which is not surprising given the predicted spectrum in 6. This behavior appears to be stable as it persisted in much longer simulations (not shown).

8. Discussion.

We have looked at a model of a closed planktonic ecosystem that depends on the maturity structure of the immature zooplankton. Using techniques in [26] and [27], we were able to transform the model into a delay differential equation with a state-dependent threshold-type delay or a delay differential equation with a state-independent delay. Such transformations allowed us to use results readily available from the theory of delay differential equations to study the qualitative features of the model, such as existence and uniqueness of solutions, boundedness, persistence, and stability. For instance, we showed that solutions of the TDE model exist for all time, remain positive, and are bounded, which are desirable features for an ecological model to have.

Being able to represent a system in a variety of ways is very beneficial from a mathematical perspective, as we are able to choose the framework that is most convenient for the situation at hand. For instance, the state-independent delay differential equation was useful for applying well-established theory for functional differential equations with fixed delay, as well as performing numerical simulations. The state-dependent threshold differential equation was convenient for computing the linearization and for arguing qualitative results. The PDE was useful since it represents the model in its most intuitive form, and therefore offers the best framework for interpreting results.

Furthermore, in a practical sense, the different models offer flexibility in what initial data is required for numerical simulations. For instance, in some situations it may be convenient to measure the spectrum of the juvenile zooplankton at a given time, while in other situations it may be more convenient to measure the histories of the phytoplankton and mature zooplankton over a sufficiently long time interval. Since it is possible to transform between the PDE and TDE models, the type of data obtained for the initial conditions does not necessarily dictate which equations we need to use to simulate the ecosystem.

A key parameter in the study of closed ecosystems is the amount of biomass, which is fixed by the initial conditions. General results include the existence of two critical values of the total biomass. The first is the minimum amount needed to sustain the phytoplankton population, which we have called N_{T1}. If the biomass is less than N_{T1}, then the phytoplankton and zooplankton both become extinct, as there is not enough biomass to sustain their populations. Conversely, if the biomass is greater than N_{T1}, then the phytoplankton do not become extinct. The second critical value of the total biomass, which we have called N_{T2}, is the minimum amount needed to sustain the zooplankton population. If the total biomass is less than N_{T2}, then the zooplankton population becomes extinct, but it does not if the biomass is greater than N_{T2}. We have shown that if the total biomass is greater than N_{T1}, but less than N_{T2}, then the system globally approaches a unique, phytoplankton-only equilibrium solution that depends on the total biomass. Future work might include further study of the system when the biomass is greater than N_{T2}, including a formal study of weak/strong (uniform) persistence [6] and possibly global behavior of solutions. Here, for $N_T > N_{T2}$, we mainly focused on local stability of the unique equilibrium solution with numerical techniques for a chosen set of parameter values.

In the case when the juvenile zooplankton have a zero mortality rate ($\delta_0 = 0$), the stability results have a strong dependence on the total biomass (N_T), while the required level of maturity (m) is less significant. In essence, it seems that the time to maturity does not matter if juvenile zooplankton are not being lost due to mortality. However, when we allow them to have a positive mortality rate ($\delta_0 > 0$), the required level of maturity becomes more important with regards to stability. In this case, Figure 5 suggests that m must increase with N_T in order to maintain stability of the phytoplankton-zooplankton equilibrium. As well as stable behavior, the model ecosystem can simply exhibit periodic solutions as well as more complicated dynamics. We saw complicated orbits in many cases where parameters were such that the characteristic equation had multiple pairs of eigenvalues that had real parts close to zero.

Further work may include adding structure to the immature phytoplankton population in a way similar to what was done for the immature zooplankton. In [18], we have included a delay in nutrient recycling while ignoring the structure of the immature zooplankton, but a more complete model would include both of these effects. It may also be worthwhile to see how nonlinear closure terms affect the overall behavior of the system when the zooplankton size structure is present. An investigation into the role of this closure term in models without such size structure is given in [8] and is generally considered to be very significant in determining the dynamics that can occur. Spatial structure can also be added, but similar transformations between PDEs and delay differential equations may not be possible in this case.

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