STOICHIOMETRIC PRODUCER-GRAZER MODELS WITH VARYING NITROGEN POOLS AND AMMONIA TOXICITY

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Abstract. We formulate and analyze a stoichiometric model of producer-grazer systems with excess nutrient recycling (waste) that may inhibit grazer survival and growth. Specifically, we model the intoxication dynamics caused by accumulation of grazer waste and dead biomass decay. This system has a range of applications, but we focus on those in which the producers are microalgae and the limiting nutrient is nitrogen. High levels of ammonia (and to a lesser extent nitrite) have been observed to increase grazer death, especially in aquaculture systems. We assume that all nitrification is due to nitrogen uptake and assimilation by the producer; therefore, the model explores systems in which the producer serves the dual role of grazer food and water treatment. The model exhibits three equilibria corresponding to total extinction, grazer-only extinction, and coexistence. While a sufficient condition is found under which grazer extinction equilibrium is globally stable, we propose a conjecture for necessary and sufficient conditions, which remains an open mathematical problem. Local stability of grazer extinction equilibrium is ensured under a sharp necessary and sufficient condition. Local stability for the coexistence equilibrium is studied algebraically and numerically. Bifurcation diagrams with respect to total nitrogen and its implications are also presented.

1. Introduction. Ecosystem models of predator-prey and producer-grazer dynamics have always held an important status in the field of mathematical biology. Mathematical analysis of these models has been influential in the field of ecology, particularly for developing the general theory of ecological stoichiometry \cite{20}. The model (LKE model) in \cite{14} is probably the most mathematically tractable one to implement the idea that both producers and grazers are chemically heterogeneous organisms in a closed system. Indeed, its global dynamics have been thoroughly analyzed \cite{13}. The model is as follows

\[
\begin{align*}
\frac{dx}{dt} &= bx \left( 1 - \frac{x}{\min(K, (P_t - \theta y)/q)} \right) - f(x)y \\
\frac{dy}{dt} &= e \min \left( 1, \frac{(P_t - \theta y)/x}{\theta} \right) f(x)y - dy.
\end{align*}
\] (1)

where $x, y$ are densities of producer and grazer respectively, $P_t$ stands for total phosphorous (P) in the system, $\theta, q$ are fixed P:C ratio in grazer and minimum P:C ratio in producer, $b, e$ are producer maximum growth rate and grazing efficiency and...
$d$ is the death rate for grazer. Instead of using only nutrient quantities to model interactions between the two trophic levels, the LKE model takes into account the impact of food qualities on producer-grazer dynamics. To be specific, on the producer level the LKE model introduces phosphorous (P) to carbon (C) ratio into the growth rate by letting P:C ratio vary above a minimum value. On the other hand, on the grazer level, grazer growth would be reduced if producer P:C ratio is lower than the fixed P:C ratio of grazers. Consequently, the LKE model allows producer P:C ratio to vary and hence subjects the grazer growth rate to varying and sometimes low food qualities.

Recent empirical data \cite{2, 5} suggest that growth rate of grazers could decrease at excessively high levels of food P content. This phenomenon, dubbed the "stoichiometric knife edge", has been confirmed for a variety of organisms (daphnia, fish, snails) \cite{6, 5, 2}, and studied by Peace et. al. in the following model \cite{18},

$$
\begin{align*}
\frac{dx}{dt} &= bx \left( 1 - \frac{x}{\min(K, (P_t - \theta y)/q)} \right) - \min\left\{ f(x), \frac{\hat{f}_\theta}{Q} \right\} y \\
\frac{dy}{dt} &= \min\left\{ \hat{e} f(x), \frac{Q}{\theta} f(x), \hat{e} f(x) \frac{\theta}{Q} \right\} y - dy.
\end{align*}
$$

(2)

Where $\hat{e}$ is maximal production efficiency and $\hat{f} = \lim_{x \to \infty} f(x)$ is the limiting saturation value for grazing function $f$, while $q, \theta$ are respectively producer minimal P:C and grazer constant P:C. This model deals with an algae-daphnia producer-grazer system experiencing the influences of both deficiency and excess levels of producer P:C ratios on grazer growth rate. Here $Q$ is food P:C ratio. This model, using total nutrient ($P_t$) in the closed system as the bifurcation parameter, and the LKE model, with the carrying capacity ($K$) as the bifurcation parameter, generate similar bifurcation diagrams, in which grazers go extinct at both low and high values of bifurcation parameter, can coexist with producers in medium range of bifurcation parameter values. As the bifurcation parameter increases, grazer densities follow the positive equilibrium curve, subsequently burst into oscillations via Hopf bifurcation, and return to the state of a stable positive equilibrium.

While existing results on stoichiometric models for grazer-producer dynamics are exciting, most of them focus on the limiting nutrient P and its effects on grazer growth. However, recent studies find that efforts to maximize culture densities in aquaculture systems can inadvertently bring the risk of toxicity to the animals due to excessive waste concentrations. In particular, high levels of ammonia can decrease animal survival and growth \cite{8, 22, 19}. Empirical studies have shown that ammonia can be inhibitory even at low concentrations to animals such as Sea Bass \cite{12}. These findings motivate our study to investigate the role of limiting nutrient nitrogen has in a producer-grazer system and its toxicity effects on grazer dynamics.

The nitrogen cycle in these types of habitats, particularly those relevant to aquaculture, has been researched and modeled extensively \cite{15, 9, 10, 3}; however, most models either entirely focus on the nitrogen cycle or are too complicated for formal mathematical analysis. Some existing models explicitly consider the recirculation of water in the system, with physical separation of phytoplankton and animals. Others consider ponds and examine water exchange rates. The empirical model proposed in \cite{4}, for example, focuses in detail on nitrogen dynamics in an intensive shrimp pond. Modeling nitrogen dynamics is important for other industrial applications; for example, biofuel production \cite{17}.
The model in this paper builds on the structure of the model presented by Kuang et al [11].

\[
\begin{align*}
\frac{dx}{dt} &= \mu_m \left(1 - \frac{q}{Q}\right) - Dx - f(x)y \\
\frac{dy}{dt} &= e \min\left(1, \frac{Q}{\theta}\right) f(x)y - dy \\
\frac{dQ}{dt} &= \alpha P_f - \mu_m (Q - q).
\end{align*}
\]

where \(x, y, Q\) are density of plant, density of herbivore and plant’s cell quota for \(P, P_f\) is free \(P\) in the system, \(e, \theta, d\) are constant production efficiency, fixed P:C ratio and death rate for herbivore, \(\mu_m, q, D\) are maximum growth rate for plant, minimum P:C ratio for plant and death rate for plant. Here we add N-induced death rate and use N as the only limiting nutrient. Also we consider microalgae as producer and the death rate for producer to be negligible. We proceed to give more details of the model formulation, provide analytical and numerical results that obtain insights into the system dynamics.

2. Model. Since toxicity due to high levels of ammonia (and to a lesser extent nitrite) can lead to increased grazer death, our model explores the framework in which the producer serves the dual role of grazer food and water treatment. This model is largely built upon that proposed by Wang et al [25]. For simplicity, ammonia, nitrate, and other N-containing compounds are all considered with one explicit state variable \(N\), which can be derived from grazer waste and consumed by phytoplankton. In the model, \(N\) represents the total free nitrogen. It is assumed that \(N\) consists mostly of ammonia, for its accumulation is largely due to grazer waste and decay. The grazer death rate increases as \(N\) accumulates to high levels, consistent with the observation that ammonia and nitrite toxicity reduces survivability and increases death rate in farmed aquatic species.

\[
\begin{align*}
\frac{dx}{dt} &= m \left(1 - \frac{q}{Q}\right) x - f(x)y \\
\frac{dy}{dt} &= \min\left(1, \frac{Q}{\theta}\right) f(x)y - dy - c(N)y \\
\frac{dQ}{dt} &= \alpha P_f - \mu_m (Q - q). \\
\frac{dN}{dt} &= -v(N)x + (Q - r \min\{\theta, Q\}) f(x)y + (d + c(N)) \theta y
\end{align*}
\]

where for all \(x \geq 0, f(0) = 0, f'(x) > 0, f''(x) \leq 0\) and similarly for \(v\) and \(c\). A complete list of descriptions, units, and properties for the model parameters and state variables is given in Table 1. The system is closed under \(N\), which is reflected in the model by the fact that \(T'(t) = 0\), where \(T(t) = N(t) + Q(t)x(t) + \theta y(t)\) is defined to be the total \(N\). Since \(T\) is a constant and \(N(t) = T - Q(t)x(t) - \theta y(t)\), the model can be reduced to three dimensions.
Table 1. Parameter and variable descriptions.

<table>
<thead>
<tr>
<th>Name</th>
<th>Description</th>
<th>Units</th>
<th>Properties</th>
</tr>
</thead>
<tbody>
<tr>
<td>$x(t)$</td>
<td>producer biomass density</td>
<td>mg C/L</td>
<td>$0 &lt; x &lt; T/q$</td>
</tr>
<tr>
<td>$y(t)$</td>
<td>grazer biomass density</td>
<td>mg C/L</td>
<td>$0 &lt; y &lt; T/q$</td>
</tr>
<tr>
<td>$Q(t)$</td>
<td>producer N:C quota</td>
<td>mg N/(g C)</td>
<td>$q &lt; Q &lt; q + v(T)/m$</td>
</tr>
<tr>
<td>$N(t)$</td>
<td>free N concentration</td>
<td>mg N/L</td>
<td>$0 &lt; N &lt; T$</td>
</tr>
<tr>
<td>$n(t)$</td>
<td>producer N</td>
<td>mg N/L</td>
<td>$n = Qx, 0 &lt; n &lt; T$</td>
</tr>
<tr>
<td>$T$</td>
<td>total N in system</td>
<td>mg N/L</td>
<td>$T = N + Qx + \theta y$</td>
</tr>
<tr>
<td>$f(x)$</td>
<td>grazing/feeding rate</td>
<td>mg C/(mg C·d)</td>
<td>$f(0) = 0, f' &gt; 0, f'' \leq 0$</td>
</tr>
<tr>
<td>$v(N)$</td>
<td>N uptake rate</td>
<td>mg N/(mg C·d)</td>
<td>$v(0) = 0, v' &gt; 0, v'' \leq 0$</td>
</tr>
<tr>
<td>$c(N)$</td>
<td>N-induced death rate</td>
<td>d⁻¹</td>
<td>$c(0) = 0, c' &gt; 0, c'' \leq 0$</td>
</tr>
<tr>
<td>$q$</td>
<td>producer min N:C quota</td>
<td>mg N/(mg C)</td>
<td>$q \ll \theta$</td>
</tr>
<tr>
<td>$\theta$</td>
<td>grazer N:C quota</td>
<td>mg N/(mg C)</td>
<td>$\theta \gg q$</td>
</tr>
<tr>
<td>$r$</td>
<td>grazing effiency</td>
<td>unitless</td>
<td>$0 &lt; r &lt; 1$</td>
</tr>
<tr>
<td>$m$</td>
<td>producer max growth rate</td>
<td>d⁻¹</td>
<td></td>
</tr>
<tr>
<td>$d$</td>
<td>grazer natural death rate</td>
<td>d⁻¹</td>
<td></td>
</tr>
</tbody>
</table>

\[
\begin{bmatrix}
\frac{dx}{dt} \\
\frac{dy}{dt} \\
\frac{dQ}{dt}
\end{bmatrix} = \begin{bmatrix}
m \left(1 - \frac{q}{Q}\right)x - f(x)y \\
r \min \left\{1, \frac{Q}{\theta}\right\} f(x) - d - c(T - Qx - \theta y) y \\
v(T - Qx - \theta y) - m(Q - q)
\end{bmatrix}
\tag{5}
\]

3. Preliminary analysis. In this section we present a basic investigation of the model where boundedness and positive invariance of the solution are established. We also locate model equilibria and study local stabilities of total extinction and grazer-only extinction equilibria.

3.1. Positive invariance. The following theorem indicates that with natural initial positive values, solutions is confined in a biologically meaningful region.

**Theorem 3.1.** Solutions to system (5) with initial conditions in the set

$$\Omega = \{(x, y, Q) : 0 < x < T/q, 0 < y, q < Q < q + v(T)/m, Qx + \theta y < T\}$$

will remain there for all time.

**Proof.** Let $S(t) = (x(t), y(t), Q(t))$ be a solution of (5) with $S(0) \in \Omega$. Suppose there exists $t_1 > 0$ such that $\forall t < t_1, S(t) \in \Omega$ but $S(t_1)$ touches or crosses the boundary of $\Omega$. There are several cases to consider.

**Case I:** $Q(t_1) = q$.

Then $\forall t \in [0, t_1],$

$$Q' \geq -m(Q - q) \Rightarrow Q(t) \geq (Q(0) - q) \exp(-mt) + q > q,$$

a contradiction.

**Case II:** $x(t_1) = 0$.

Let $Y = \max_{t \in [0, t_1]}\{y(t)\}$. Then $\forall t \in [0, t_1]$, since $Q(t) > q$,

$$\begin{align*}
x'(t) &\geq -f'(0)Yx \\
\Rightarrow x(t) &\geq x(0) \exp(-f'(0)Y) > 0,
\end{align*}$$

and this contradicts the assumption that $x(t_1) = 0$.
To prove that $E^*$ is unstable, it suffices to show that the eigenvalues of the linearization of (5) at $E^*$ do not have strictly negative real parts. This follows from $\det J_0 = m^2 (1 - q/Q^*) (d + c(T)) > 0$, where

$$J_0 = \begin{pmatrix} m (1 - q/Q^*) & 0 & 0 \\ 0 & -d - c(T) & 0 \\ -v'(T)Q & -v'(T)\theta & -m \end{pmatrix}.$$
3.2.2. **Grazer only extinction.** Let $E_1 = (T/q, 0, q)$ be the steady state corresponding to grazer-only extinction. The Jacobian matrix takes the following form:

$$J_1 = \begin{pmatrix}
0 & -f(T/q) & mT/q^2 \\
0 & r(qf(T/q)/\theta - d) & 0 \\
-v'(0)q & -v'(0)/\theta & -v'(0)T/q - m
\end{pmatrix}.$$  

By Routh-Hurwitz criterion, all eigenvalues of $J_1$ have strictly negative real parts if the following conditions hold:

1. $\text{tr} J_1 < 0$,  
2. $\det J_1 < 0$,  
3. $\det J_1 - (\text{tr} J_1) \left( \sum_{k=1}^{3} A_{kk} \right) > 0$,

where $A_{kk}$ is the determinant of the $2 \times 2$ matrix obtained by removing the $k$-th row and $k$-th column from $J_1$.

The following theorem gives a sufficient condition for the local stability of $E_1$.

**Theorem 3.3.** $E_1$ is locally asymptotically stable if and only if $rf(T/q) < d\theta$.

**Proof.** The result follows from the Routh-Hurwitz criterion. Let $U = r(qf(T/q)/\theta - d)$, $V = v'(0)T/q + m$. Then, clearly, the following is true if and only if $U < 0$:

$$\text{tr} J_1 = U - V < 0, \quad \det J_1 = (v'(0)mT/q)U < 0,$$

and

$$\det J_1 - (\text{tr} J_1) \left( \sum_{k=1}^{3} A_{kk} \right) = V \left( U^2 - VU + v'(0)mT/q \right) > 0.$$

4. **Global stability of $E_1$.** In this section we propose a sufficient condition for globally asymptotical stability of grazer-only extinction equilibrium $E_1$ of (5). To prove this result, we use Bendixson criterion, Poincaré-Bendixson Theorem, and results obtained by [16, 21] on asymptotically autonomous differential systems. Also a conjecture is raised about necessary and sufficient conditions for globally asymptotic stability of $E_1$, which remains an open mathematical question.

**Theorem 4.1.** The grazer-only extinction equilibrium $E_1$ is globally asymptotically stable if

$$rf(T/q) < d.$$  

**Proof.** First we note that by Theorem 3.1, the set $\Omega$ is positively invariant under system (5). Hence here we only consider the open domain $\Omega \subset \mathbb{R}^3$. Also we see that, if $rf(T/q) < d$

$$\frac{y'}{y} = r \min \left\{ 1, \frac{Q}{\theta} \right\} f(x) - d - c(T - Qx - \theta y)$$

$$< r \min \left\{ 1, \frac{Q}{\theta} \right\} f(x) - d \quad \text{since } c(x) > c(0) = 0$$

$$\leq rf(x) - d \quad \text{by properties of min function}$$

$$< rf(T/q) - d \quad \text{since } f'(x) > 0$$

$$< 0.$$
Therefore
\[ y < y(0) e^{(r f(T/q) - d) t} \to 0 \quad \text{as } t \to \infty. \]
Since \( y > 0 \) by Theorem 3.1, we obtain that
\[ \lim_{t \to \infty} y(t) = 0. \]
So in the original autonomous system (5), the component \( y(t) \) converges to 0. Let us consider the behavior of system (5) on the plane \( y = 0 \), ie
\[
\begin{align*}
\frac{dx}{dt} &= m \left( 1 - \frac{q}{Q} \right) x \\
\frac{dQ}{dt} &= v(T - Qx) - m(Q - q).
\end{align*}
\]
(7) is the limit system of the asymptotically autonomous system (5) under the condition \( rf(T/q) < d \). It is from results of Markus [16] and Thieme [21] that bounded solutions of asymptotically autonomous systems, in our case (5), converge to its \( \omega \)-limit set, which is invariant under its limit autonomous system, here (7).
We also observe that since \( \lim_{t \to \infty} y(t) = 0 \) the \( \omega \)-limit set \( \omega \) of system (5) is of the following form
\[ \omega = \{(x, 0, Q) \mid 0 < x < T/q, q < Q < q + v(T)\}. \]
Let
\[ \Omega_1 = \{(x, Q) \mid 0 < x < T/q, q < Q < q + v(T)\} \]
be the domain where system (7) is defined. In the reduced limit system, there are two equilibriums
\[ \bar{E}_1 = (0, \frac{mq + v(T)}{m}) \quad \bar{E}_2 = \left( \frac{T}{q}, q \right). \]
Next we show that in the reduced limit system (7) the positive equilibrium \( \bar{E}_2 \) is globally asymptotically stable.
To show this is true, first we prove that periodic orbits or limit cycles don’t exist. Observe that
\[
\begin{align*}
\int_{\Omega_1} \left\{ \frac{\partial}{\partial x} \left( m \left( 1 - \frac{q}{Q} \right) x \right) + \frac{\partial}{\partial Q} \left( v(T - Qx) - m(Q - q) \right) \right\} \ dx \ dQ \\
&= \int_{\Omega_1} \left\{ m \left( 1 - \frac{q}{Q} \right) - x v'(T - Qx) - m \right\} \ dx \ dQ \\
&= \int_{\Omega_1} \left\{ -\frac{mq}{Q} - x v'(T - Qx) \right\} \ dx \ dQ \\
&< 0 \quad \text{since } (x, Q) \in \Omega_1 \text{ and } v' > 0.
\end{align*}
\]
Therefore by Bendixson criterion, no periodic orbits or limit cycles exist in \( \Omega_1 \).
On the other hand, Jacobian matrices at \( \bar{E}_1 \) and \( \bar{E}_2 \) are
\[
J(\bar{E}_1) = \begin{pmatrix} \frac{mv(T)}{v(T)+mq} & 0 \\ \frac{-mv(T)}{v(T)+mq} v'(T) & -m \end{pmatrix} \quad \text{and} \quad J(\bar{E}_2) = \begin{pmatrix} 0 & \frac{mv(T)}{m(T/q)} \frac{v'(T/q)}{v'(T)} \\ -q v'(0) & -m \end{pmatrix}.
\]
So \( \bar{E}_1 \) is an unstable saddle point since eigenvalues of \( J(\bar{E}_1) \) are
\[
\frac{mv(T)}{v(T) + mq} > 0 \quad \text{and} \quad -m < 0.
\]
However $\bar{E}_2$ is locally asymptotically stable since

$$\det(J(\bar{E}_2)) = \frac{mTv'(0)}{q} > 0 \quad \text{and} \quad \text{tr}(J(\bar{E}_2)) = -\frac{T}{q}v'(0) - m < 0.$$ 

Consequently, since in the simply connected region $\Omega_1$ there are no periodic orbits or limit cycles, by Poincaré-Bendixson Theorem, solutions of (7) starting in $\Omega_1$ all converge to $\bar{E}_2 = (T/q, q)$.

Markus [16] and Thieme [21] also show that if the $\omega$-limit set of the asymptotically autonomous system, in our case (5), has one point $u_0$ through which the solution of the limit autonomous system, in our case (7), converges to $e$, then the $\omega$-limit set $\omega$ of (5) $\omega = \{e\}$.

Hence, suppose there is a point in $\omega$ different from $E_1 = (T/q, 0, q)$. Let it be $u = (x_1, 0, Q_1)$.

where either $x_1 \neq T/q$ or $Q_1 \neq q$. Then in the limit system (7) solution starting from $(x_1, Q_1)$ will eventually converge to $\bar{E}_2 = (T/q, q)$ by the global stability of $\bar{E}_2$. Therefore it follows that

$$\omega = \{(T/q, 0, q)\}.$$ 

Therefore, suppose $\phi(t) = (x(t), y(t), Q(t))$ is a solution of system (5) with initial condition in the positively invariant domain $\Omega \subset \mathbb{R}^3$, provided $rf(T/q) < d$, we have

$$\text{dist}(\phi(t), \omega) \to 0 \quad \text{as} \quad t \to \infty$$

in other words the grazer-only extinction equilibrium is globally asymptotically stable

$$\lim_{t \to \infty} x(t) = \frac{T}{q}, \quad \lim_{t \to \infty} y(t) = 0, \quad \text{and} \quad \lim_{t \to \infty} Q(t) = q.$$ 

From Theorem 3.3 about necessary and sufficient conditions for local stability of $E_1$, we propose the following conjecture, which remains an open mathematical question.

**Conjecture 1.** The grazer-only extinction equilibrium $E_1$ is globally asymptotically stable if and only if

$$rqf(T/q) < d\theta.$$ 

5. Coexistence. For coexistence equilibriums we will resort to brute force computations and numerical simulations, since the amount of algebraic derivation involved is forbiddingly large and numerical simulations can present us with visually straightforward and interesting system dynamics.

Let $E^* = (x^*, y^*, Q^*)$ be a positive coexistence equilibrium. From (5) it has to satisfy the following equations:

$$\begin{cases} 
    m \left(1 - \frac{\theta}{Q^*}\right) x^* - f(x^*) y = 0 \\
    r \min \left\{1, \frac{Q^*}{T}\right\} f(x^*) - d - c (T - Q^* x^* - \theta y^*) = 0 \\
    v (T - Q^* x^* - \theta y^*) - m (Q^* - q) = 0
\end{cases} \quad (8)$$

Short of knowing specific expressions for $f, c, v$, we can nevertheless obtain from their properties, ie strictly increasing functions and continuous second derivatives, that all of them are bijective and have unique and continuously differentiable inverses.
From (8) we can obtain the following general expressions for $E^*$

$$A = \frac{1}{r} \left( d + c \left( v^{-1} (m (Q^* - q)) \right) \right)$$

$$x^* = \begin{cases} f^{-1} \left( \frac{\theta}{Q^*} A \right) & \text{if } Q^* \leq \theta \\ f^{-1} (A) & \text{if } Q^* > \theta \end{cases}$$

$$y^* = \frac{m}{f'(x^*)} \left( 1 - \frac{q}{Q^*} \right) x^*$$

$$v (T - Q^* x^* - \theta y^*) - m (Q^* - q) = 0.$$

The Jacobian of (5) at $E^*$ is, if $Q^* \leq \theta$

$$J(E^*) = \begin{pmatrix} m \left( 1 - \frac{q}{Q^*} \right) - f'(x^*) y & -f(x^*) & \frac{mq}{Q^*} x^* \\ r \frac{Q^*}{T} f'(x^*) + Q^* B & \theta B & r \frac{f(x^*)}{T} + x^* B \\ -Q^* C & -\theta C & -x^* C - m \end{pmatrix}$$

where

$$B = c'(T - Q^* x^* - \theta y^*), \quad C = v'(T - Q^* x^* - \theta y^*).$$

When $Q^* > \theta$ the Jacobian matrix at $E^*$ is the same except that the second row is replaced by

$$(r f'(x^*) + Q^* B \quad \theta B \quad x^* B).$$

All the above would be helpful if the expressions of $f, c, v$ are known and sufficiently simple. So next for simplicity we assume that $f, c, v$ are linear functions, with

$$f(x) = k_1 x, \quad c(x) = k_2 x, \quad v(x) = k_3 x$$

where $k_1, k_2, k_3 > 0$ are constant. Properties for functions $f, c, v$ listed in Table 1 are readily checked.

Next we will perform local stability analysis and numerical simulations on positive coexistence equilibrium(s) $E^*$ with linear $f, c, v$ as defined in (10).

From (9) we find that

$$A = \frac{1}{r} \left( d + \frac{k_2 m}{k_3} (Q^* - q) \right)$$

$$x^* = \begin{cases} \frac{\theta}{Q^* k_1} A & \text{if } Q^* \leq \theta \\ \frac{1}{k_1} A & \text{if } Q^* > \theta \end{cases}$$

$$y^* = \frac{m}{k_1} \left( 1 - \frac{q}{Q^*} \right)$$

$$k_3 \cdot (T - Q^* x^* - \theta y^*) - m (Q^* - q) = 0$$

It follows that $Q^*$ must satisfy the following equations

$$D_1(Q^*)^3 + D_2(Q^*)^2 + D_3 Q^* + D_4 = 0$$

where $D_i$'s satisfy conditions in Table 2.

Local stability analysis can now proceed by computing zeros of (11) and finding eigenvalues of corresponding Jacobian matrices. Equation (11) can be further simplified as in Table 3. We observe that

- if $Q^* \leq \theta$, $Q^*$ is at the intersection of an opening-up parabola and a straight line crossing the origin;
Table 2. Coefficients of Equation (11)

<table>
<thead>
<tr>
<th></th>
<th>$D_1$</th>
<th>$D_2$</th>
<th>$D_3$</th>
<th>$D_4$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$Q^* \leq \theta$</td>
<td>0</td>
<td>$\frac{m\theta k_2}{r k_1 k_3} + \frac{m}{k_3}$</td>
<td>$\frac{d\theta}{r k_1} + \frac{m\theta}{k_1} - T - \frac{mq\theta k_2}{r k_1 k_3} - \frac{mq}{k_3}$</td>
<td>$-\frac{\theta mq}{k_1}$</td>
</tr>
<tr>
<td>$Q^* &gt; \theta$</td>
<td>$\frac{k_3 m}{r k_1 k_3}$</td>
<td>$\frac{d}{r k_1} + \frac{m - mq k_2}{r k_1 k_3}$</td>
<td>$\frac{\theta m}{k_1} - \frac{mq}{k_3} - T$</td>
<td>$-\frac{\theta mq}{k_1}$</td>
</tr>
</tbody>
</table>

Table 3. Simplification of Equation (11)

<table>
<thead>
<tr>
<th></th>
<th>$m (Q^* - q) \left[ \left( \frac{\theta k_2}{r k_1 k_3} + \frac{1}{k_3} \right) Q^* + \frac{\theta}{k_1} \right] = \left( T - \frac{d\theta}{r k_1} \right) Q^*$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$Q^* \leq \theta$</td>
<td>$m (Q^* - q) \left( \frac{k_2}{r k_1 k_3} (Q^<em>)^2 + \frac{1}{k_3} Q^</em> + \frac{\theta}{k_1} \right) = -\frac{d}{r k_1} (Q^<em>)^2 + TQ^</em>$</td>
</tr>
</tbody>
</table>

- if $Q^* > \theta$, $Q^*$ is at the intersection of an opening-down parabola that crosses the origin and $\frac{r k_1 T}{d}$ with a cubic polynomial that has two negative roots and one positive root at $q$.

To find the exact analytical form for $Q^*$ in each case is algebraically demanding, albeit not impossible. So we instead use a concrete example with specific values assigned to parameter values and compute $Q^*$, its local stability, then we will use numerical simulations to verify our computations.

Example 5.1. Parameter values here we use are

$m = 2, \quad q = 0.005, \quad r = 0.5, \quad \theta = 0.1, \quad d = 1, \quad T = 10, \quad k_1 = k_2 = k_3 = 0.5$

Hence if $Q^* \leq \theta = 0.1$, we use the first equation in Table 3 to find that the corresponding quadratic equation is

$4.8(Q^*)^2 - 9.224Q^* - 0.002 = 0$

with zeros at

$1.9219 \quad \text{or} \quad -0.0002$.

Since we need a positive $Q^* \leq 0.1$, it implies that the case where $Q^* \leq \theta = 0.1$ is unlikely.

On the other hand, if $Q^* > \theta = 0.1$, we use the second equation in Table 3 to find that the corresponding cubic equation is

$8(Q^*)^3 + 7.96(Q^*)^2 - 9.62Q^* - 0.002 = 0$

with zeros at

$-1.7016, \quad 0.7068, \quad -0.0002$. 
Hence we have a positive value $Q^* = 0.7068 > \theta = 0.1$. Next we find the positive coexistence equilibrium $E^*$ and consider its local stability.

It follows that

$$A = 4.8072, \quad x^* = 9.6145, \quad y^* = 3.9717, \quad Q^* = 0.7068.$$  

Thus the Jacobian matrix at $E^* = (x^*, y^*, Q^*)$ is

$$J(E^*) = \begin{pmatrix} 0 & -4.8072 & 0.1925 \\ 2.1204 & 0.05 & 7.3072 \\ -0.3534 & -0.05 & -6.8072 \end{pmatrix}$$

with its eigenvalues being

$$-0.1185 + 2.9541i, \quad -0.1185 - 2.9541i, \quad -6.5202.$$  

Therefore eigenvalues for the Jacobian matrix at positive coexistence equilibrium $E^*$ all have negative real parts. It implies that the positive coexistence equilibrium is locally asymptotically stable. To show this result, we use numerical simulations. Results are shown in Figure 1.

![Figure 1](image)

**Figure 1.** Simulation results with parameter values are defined in Example 1. Numerical simulations confirm computation results and local stability analysis. The coexistence equilibrium $E^*$ is locally and globally asymptotically stable. Note that here $rqf(T/q) = 2.5 > d\theta = 0.1$. Hence both total extinction and grazer-only extinction equilibrium are unstable.

6. **Numerical experiments.** This section describes results of numerical simulations that use Holling type II functional responses for grazing rate function $f$, intoxication-induced death rate function $c$, and producer Nitrogen uptake rate function $\nu$.

$$f(x) = \frac{c_1x}{a_1 + x}, \quad c(x) = \frac{c_2x}{a_2 + x}, \quad \nu(x) = \frac{c_3x}{a_3 + x}.$$  

Parameter values are listed in Table 4 and mostly based on reliable estimation from literatures.
Table 4. Model parameters for numerical simulations

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Value</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T$</td>
<td>Total N in the system</td>
<td>0–0.6 (mg N)/L</td>
<td>ad hoc</td>
</tr>
<tr>
<td>$q$</td>
<td>Producer min N:C quota</td>
<td>0.1 (mg N)/(mg C)</td>
<td>[7]</td>
</tr>
<tr>
<td>$m$</td>
<td>Producer max growth rate</td>
<td>1.2 d$^{-1}$</td>
<td>[1, 14, 18, 24]</td>
</tr>
<tr>
<td>$\theta$</td>
<td>Grazer N:C quota</td>
<td>0.2 (mg N)/(mg C)</td>
<td>[1, 14, 18, 24]</td>
</tr>
<tr>
<td>$r$</td>
<td>Grazing max efficiency</td>
<td>0.8</td>
<td>[1, 14, 18, 24]</td>
</tr>
<tr>
<td>$d$</td>
<td>Grazer natural death rate</td>
<td>0.25 d$^{-1}$</td>
<td>[1, 14, 18, 24]</td>
</tr>
<tr>
<td>$c_1$</td>
<td>Max grazing rate</td>
<td>0.81 d$^{-1}$</td>
<td>[1, 14, 18, 24]</td>
</tr>
<tr>
<td>$a_1$</td>
<td>Half saturation for $f(x)$</td>
<td>0.25 (mg C)/L</td>
<td>[1, 14, 18, 24]</td>
</tr>
<tr>
<td>$c_2$</td>
<td>Max intoxication death rate</td>
<td>0.01 d$^{-1}$</td>
<td>ad hoc</td>
</tr>
<tr>
<td>$a_2$</td>
<td>Half saturation for $c(N)$</td>
<td>1 (mg N)/L</td>
<td>ad hoc</td>
</tr>
<tr>
<td>$c_3$</td>
<td>Max producer N uptake rate</td>
<td>0.8 d$^{-1}$</td>
<td>ad hoc</td>
</tr>
<tr>
<td>$a_3$</td>
<td>Half saturation for $\nu(N)$</td>
<td>1 (mg N)/L</td>
<td>ad hoc</td>
</tr>
</tbody>
</table>

Figure 2. Numerical simulations conducted using parameter values are listed in Table 4 and varying values for $T$, (a) low total nitrogen $T = 0.05$ mg N/L, (b) $T = 0.12$ mg N/L, (c) $T = 0.18$ mg N/L, (d) excess nitrogen $T = 0.5$ mg N/L. Panel (a) shows grazer extinction due to starvation, and panel (b) shows a positive grazer density where a stable coexistence equilibrium exists. Panel (c) depicts periodic oscillations around an unstable positive coexistence equilibrium while panel (d) also shows oscillations but with an extremely unstable grazer density, almost nearing extinction for prolonged a period of time and quickly recovering from it. Both panels (c) and (d) describe effects of intoxication-induced death rates on grazers despite high producer abundance.

The parameter $T$ represents the total nitrogen in the system. Since producers take up nitrogen, the level of $T$ influences N:C quota in producers. Low levels of $T$ lower N:C quota in producers and result in poor quality food for grazers, which in turn could cause grazers extinction due to starvation. However, high levels of $T$
will result in high abundance of N in both producers and system, causing grazer loss due to excess nitrogen induced intoxication.

In our numerical simulations we increase $T$ in the ecologically meaningful range 0 to 0.6 mg N/L. When $T = 0.05$ mg N/L population densities are at grazer-only extinction equilibrium (Figure 2(a)), with grazers extinct due to starvation. And at $T = 0.12$ mg N/L producers and grazers densities are eventually at a positive coexistence equilibrium (Figure 2(b)). However when $T = 0.18$ mg N/L population densities no longer converge to any specific values but oscillate around an unstable positive equilibrium (Figure 2(c)). Similarly as $T = 0.5$ mg N/L the system displays oscillations in population densities, but with both producer and grazer densities alternate to plummet and subsequently undergo prolonged near-extinction state (Figure 2(d)).

7. Discussion. Aquaculture research is a highly active field, with implications for not only commercialization but also environmental science and ecology. Here we have demonstrated how existing models in ecological stoichiometry can be extended to aquaculture systems. Such systems can be considered as individual ecosystems themselves, making such extensions natural and intuitive. They can also give rise to dynamics interesting for both formal analysis and numerical simulations.

Our model considers only mortality as an effect of nitrogen-induced toxicity. Since even acute toxicity at low ammonia concentrations can decrease animal growth [19, 8], future improvements could modify the growth rate function. Nonetheless, our toxicity term can be interpreted as one which encompasses both a decrease in
Figure 4. A bifurcation diagram of the grazer density with total nitrogen \( T \) being the bifurcation parameter. Parameter values are the same as listed in Table 4 with \( T \) values varying from 0 to 0.6 mg N/L. Initial conditions are controlled so that \( x = 0.2T/\theta \) mg C/L, \( y = 0.8T/\theta \) mg C/L, and \( Q = 0.4\theta \) with \( T - xQ - \theta y \geq 0 \). For \( T \) less than 0.084 mg N/L the grazer cannot survive and go extinct due to starvation. When \( T \) increases from 0.084 to 0.14 the grazer population experience improved food quality and can coexist with producers at a stable positive equilibrium. At \( T = 0.14 \) mg N/L this stable positive equilibrium loses stability via a Hopf bifurcation and gives rise to a stable limit cycle for grazer densities. Between \( T = 0.14 \) and \( T = 0.48 \) mg N/L this stable limit cycle continue to exist, but around \( T = 0.48 \) “collides” with manifolds of unstable total extinction equilibrium and unstable grazer-only extinction equilibrium, thus resulting in limit cycles quite resembling heteroclinic orbits on \( xy \)-plane. As \( T \) further increases, producer and grazer densities alternate to undergo prolonged near-extinction state and subsequent rapid recovery to high abundance level.

growth and an increase in mortality. Rather than modifying the previously used and examined functional growth response, \( c(N) \) can be constructed mechanistically for a particular application, i.e. pond system. A decrease in growth implies an increase in nitrogen waste, which justifies the inclusion of \( c(N) \) in \( N'(t) \) regardless if it represents mortality or growth inhibition.

Furthermore, we have considered a closed system analogous to a batch culture. Commercial aquaculture systems have not only harvesting, but also water recirculation or exchange. How the former would be implemented depends on the specific system; for example, it could be continuous or discrete. Existing models incorporate water recirculation; for example, in [3] a separate tank is considered in which both algae and bacteria help to filter waste from the water. We propose for future work that such processes be implemented through our modeling framework by means of modifying a chemostat system.

Although toxicity in aquaculture ponds can be often attributed to nitrogenous waste, other factors such as pH, CO\(_2\) concentration, and even salinity can have
a synergistic effect \[8, 12, 23\]. We have proposed a simple model in which only ammonia, abstracted as nitrogen, is considered. Future work can expand on this framework to include other such factors.

Also it remains as an open mathematical question if the grazer-only extinction equilibrium of system (5) is globally asymptotically stable under the same condition as that in Theorem 3.3. Some preliminary numerical experiment results, that in Figure 1 for example, certainly support this conjecture; however, numerical examples cannot be exhaustive and we propose as part of future work to prove this conjecture or its alternatives.

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REFERENCES


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