A size-structured population dynamics model of Daphnia

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ABSTRACT

The stability of a size-structured population dynamics model of Daphnia coupled with the dynamics of an unstructured algal food source is investigated for the case where there is also an inflow of newborns from an external source. We determine the steady states and study the stability of the nontrivial steady states. We also identify a demographic-algae parameter that determines a condition for the stability.

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1. Introduction

Recently, papers [1,2] have studied the following size-structured population dynamics model for Daphnia coupled with the dynamics of algae as a source of food for Daphnia:

$$\begin{cases} \dfrac{\partial p(a, t)}{\partial t} + \dfrac{\partial}{\partial a}(V(a, F)p(a, t)) + \mu(a, F)p(a, t) = 0, & a \in [0, l),\ l \le +\infty,\ t > 0, \\[2mm] V(0, F)p(0, t) = C + \displaystyle\int_0^l \beta(a, F)p(a, t)da, & t \ge 0,\ p(a, 0) = p_0(a),\ a \in [0, l), \\[2mm] \dfrac{dF(t)}{dt} = \phi(F) - \displaystyle\int_0^l I(a, F, P)p(a, t)da, & t > 0,\ F(0) = F_0, \end{cases} \qquad (1.1)$$

where $p(a, t)$ is the density of Daphnia with respect to size $a \in [0, l)$ at time $t \ge 0$, where $l \le +\infty$ is the maximum size that an individual in the population can attain; $P(t) = \int_0^l p(a, t)da$ is the total population size of Daphnia at time t; F is the concentration of algae; $\phi(F)$ is the autonomous rate of change of the concentration of algae in the absence of Daphnia; $I(a, F, P) \ge 0$ is the feeding rate of an individual Daphnia of size a when the population size is P and the concentration of algae is F; $\beta(a, F), \mu(a, F)$ are, respectively, the birth rate, i.e. the average number of offspring, per unit time, produced by an individual of size a when the concentration of algae is F and the mortality rate, i.e. the death rate at size a, per unit population, when the concentration of algae is F; $0 < V(a, F)$ is the growth rate of an individual Daphnia of size a when the concentration of algae is F; and $C \ge 0$ is a constant that represents the inflow of Daphnia newborns from an external source.

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We note that several recent papers have studied similar models for Daphnia albeit with feeding rate $I = I(a, F)$ and an inflow rate from an external source $C \equiv 0$, for example, those in [3–6], and the references therein. We also note that in contrast to our approach in this work, the approach to the problem in the above mentioned papers was via numerical studies and simulations.

From our study in [2], we noted that the case $C \equiv 0$ cannot be handled by the methods in [1], or those in [2]. Accordingly, we decided to devote effort to studying this problem separately here.

We study problem (1.1) under the following general assumptions:

$0 \leq p_0(a) \in L^1([0, l)) \cap L_\infty[0, l), \mathbb{R}^+ = [0, \infty); V(a, F), \beta(a, F)$ and $\mu(a, F) \in C^0([0, l) \times \mathbb{R}^+)$ and are nonnegative functions; $V_P(a, F), V_{Fa}(a, F), \beta_F(a, F), \mu_F(a, F)$ exist $\forall a \geq 0, F \geq 0; V_F(., F), V_{Fa}(., F), \beta(., F), \beta_F(., F), \mu(., F), \mu_F(., F)$ as functions of $F \in C^0(\mathbb{R}^+ : L_\infty([0, l))); I(a, I, P) \in C^0([0, l) \times \mathbb{R}^{+2}); F, \phi \in C^1(\mathbb{R}^+); I_F(a, F, P), I_P(a, F, P)$ exist $\forall a \geq 0, F \geq 0, P \geq 0; I(a, I, P), I_F(a, F, P), I_P(a, F, P)$ as functions of $F, P \in C^0(\mathbb{R}^{+2} : L_\infty([0, l)))$.

2. The steady states

In this section, we determine the steady states of problem (1.1). A steady state of problem (1.1) satisfies the following:

$$
\begin{cases}
\dfrac{d}{da}[V(a, F_\infty)p_\infty(a)] + \mu(a, F_\infty)p_\infty(a) = 0, & a \in [0, l), \\[2mm]
V(0, F_\infty)p_\infty(0) = C + \displaystyle\int_0^l \beta(a, F_\infty)p_\infty(a)da, \\[2mm]
0 = \phi(F_\infty) - \displaystyle\int_0^l I(a, F_\infty, P_\infty)p_\infty(a)da.
\end{cases}
\tag{2.1}
$$

In order to facilitate our exposition, we define two threshold parameters $R(F, P), R^\phi(F, P)$ by

$$
R(F, P) = \int_0^l \frac{\beta(a, F)}{V(a, F)}\pi(a, F)da + \frac{C}{P}\int_0^l \frac{\pi(a, F)}{V(a, F)}da, \quad \pi(a, F) = e^{-\int_0^a \frac{\mu(\tau, F)}{V(\tau, F)}d\tau},
\tag{2.2}
$$

which when $C \equiv 0$ is interpreted as the number of offspring expected to be born to an individual Daphnia, in a lifetime, when the population size is P, and the algae concentration is F,

$$
R^\phi(F, P) = \int_0^l \frac{I(a, F, P)\pi(a, F)}{V(a, F)}da - \frac{\phi(F)}{P}\int_0^l \frac{\pi(a, F)}{V(a, F)}da,
\tag{2.3}
$$

which can be interpreted as the difference between the average feeding rate of an individual Daphnia, in a lifetime, and the average of the autonomous rate of change of algae concentration in the absence of Daphnia.

In the following theorem, we describe the steady states of problem (1.1). We note that the proof of this theorem is given in [2].

Theorem 2.1. (1) *If $C = 0$, then Problem (1.1) has the trivial steady state, $P_\infty = \phi(F_\infty) = 0$, as well as nontrivial steady states given by*

$$
R(F_\infty, P_\infty) = 1 = \int_0^l \frac{\beta(a, F_\infty)}{V(a, F_\infty)}\pi(a, F_\infty)da, \qquad R^\phi(F_\infty, P_\infty) = 0, \quad P_\infty > 0, \; F_\infty \geq 0.
$$

(2) *If $C > 0$, then Problem (1.1) has no trivial steady state $P_\infty = \phi(F_\infty) = 0$.*

(3) *All pairs (F_∞, P_∞) satisfying $F_\infty \geq 0, P_\infty > 0, R(F_\infty, P_\infty) = 1$, and $R^\phi(F_\infty, P_\infty) = 0$ are nontrivial steady states of problem (1.1).*

3. The stability of the steady states

In this section, we study the stability of the steady states for problem (1.1) as given by Theorem 2.1.

We note that in [2], we obtained the following characteristic equation for problem (1.1):

$$
\left[1 - \frac{1}{V(0, F_\infty)}\int_0^l e^{-\int_0^a E(\tau)d\tau}\beta(a, F_\infty)da\right]\left\{\xi + D_2 - \int_0^l \int_0^a e^{-\int_\sigma^a E(\tau)d\tau}g(\sigma, F_\infty)h(a, F_\infty, P_\infty)d\sigma\, da\right\}
$$

$$
+ \frac{1}{V(0, F_\infty)}\left\{D_1 - \int_0^l \int_0^a e^{-\int_\sigma^a E(\tau)d\tau}\beta(a, F_\infty)g(\sigma, F_\infty)d\sigma\, da\right\}\int_0^l e^{-\int_0^a E(\tau)d\tau}h(a, F_\infty, P_\infty)da = 0,
\tag{3.1}
$$

where $D_1, D_2, E(\sigma), g(\sigma, F_\infty), h(a, F_\infty, P_\infty)$ are given, respectively, by

$$D_1 = \int_0^l \beta_F(a, F_\infty) p_\infty(a) da - p_\infty(0) V_F(0, F_\infty), \tag{3.2}$$

$$D_2 = \int_0^l I_F(a, F_\infty, P_\infty) p_\infty(a) da - \phi_F(F_\infty), \tag{3.3}$$

$$E(\sigma) = \frac{\xi + V_\sigma(\sigma, F_\infty) + \mu(\sigma, F_\infty)}{V(\sigma, F_\infty)}, \tag{3.4}$$

$$g(\sigma, F_\infty) = \frac{\frac{\partial}{\partial \sigma} (V_F(\sigma, F_\infty) p_\infty(\sigma)) + p_\infty(\sigma) \mu_F(\sigma, F_\infty)}{V(\sigma, F_\infty)}, \tag{3.5}$$

$$h(a, F_\infty, P_\infty) = \left[I(a, F_\infty, P_\infty) + \int_0^l I_P(a', F_\infty, P_\infty) p_\infty(a') da' \right]. \tag{3.6}$$

In order to facilitate our exposition, we define the following:

$$M_0(\beta, \cos y) = \int_0^l \frac{\beta(a, F_\infty)}{V(a, F_\infty)} \pi(a, F_\infty) e^{-x \int_0^a \frac{ds}{V(s, F_\infty)}} \cos y \int_0^a \frac{d\sigma}{V(\sigma, F_\infty)} da, \tag{3.7}$$

$$M_0(\beta, \sin y) = \int_0^l \frac{\beta(a, F_\infty)}{V(a, F_\infty)} \pi(a, F_\infty) e^{-x \int_0^a \frac{ds}{V(s, F_\infty)}} \sin y \int_0^a \frac{d\sigma}{V(\sigma, F_\infty)} da, \tag{3.8}$$

$$M_1(\beta, \cos y) = \int_0^l \int_0^a \frac{\beta(a, F_\infty)}{V(a, F_\infty)} \frac{D(\sigma)}{\pi(\sigma, F_\infty)} \pi(a, F_\infty) e^{-x \int_\sigma^a \frac{ds}{V(s, F_\infty)}} \cos y \int_\sigma^a \frac{d\tau}{V(\tau, F_\infty)} d\sigma da, \tag{3.9}$$

$$M_1(\beta, \sin y) = \int_0^l \int_0^a \frac{\beta(a, F_\infty)}{V(a, F_\infty)} \frac{D(\sigma)}{\pi(\sigma, F_\infty)} \pi(a, F_\infty) e^{-x \int_\sigma^a \frac{ds}{V(s, F_\infty)}} \sin y \int_\sigma^a \frac{d\tau}{V(\tau, F_\infty)} d\sigma da, \tag{3.10}$$

where $D(\sigma) = g(\sigma, F_\infty) V(\sigma, F_\infty)$, and $M_0(I, \cos y), M_0(I, \sin y), M_1(I, \cos y), M_1(I, \sin y)$ are defined similarly.

Now, if we let $\xi = x + iy$, $I = I(a, F_\infty)$, $I_P(a, F_\infty, P_\infty) \equiv 0$ in the characteristic equation (3.1) and use Eqs. (3.7)–(3.10), we obtain the following pair of equations for the real part and imaginary part of the characteristic equation (3.1):

$$[1 - M_0(\beta, \cos y)] \{x + D_2 - M_1(I, \cos y)\} - M_0(\beta, \sin y) \{y + M_1(I, \sin y)\}$$
$$+ M_0(I, \cos y) \{D_1 - M_1(\beta, \cos y)\} + M_0(I, \sin y) M_1(\beta, \sin y) = 0, \tag{3.11}$$

$$[1 - M_0(\beta, \cos y)] \{y + M_1(I, \sin y)\} + M_0(\beta, \sin y) \{x + D_2 - M_1(I, \cos y)\}$$
$$+ M_0(I, \cos y) M_1(\beta, \sin y) - M_0(I, \sin y) \{D_1 - M_1(\beta, \cos y)\} = 0. \tag{3.12}$$

From Eq. (3.12), and for $y \neq 0$, we obtain

$$y = -\frac{1}{[1 - M_0(\beta, \cos y)]} \{M_0(\beta, \sin y) [x + D_2 - M_1(I, \cos y)] + M_0(I, \cos y) M_1(\beta, \sin y)$$
$$- M_0(I, \sin y) [D_1 - M_1(\beta, \cos y)]\} - M_1(I, \sin y). \tag{3.13}$$

Now, using (3.13) in (3.11), we obtain

$$[x + D_2 - M_1(I, \cos y)] \{[1 - M_0(\beta, \cos y)]^2 + M_0(\beta, \sin y)^2\}$$
$$+ [D_1 - M_1(\beta, \cos y)] \{M_0(I, \cos y) [1 - M_0(\beta, \cos y)] - M_0(\beta, \sin y) M_0(I, \sin y)\}$$
$$+ M_1(\beta, \sin y) [M_0(\beta, \sin y) M_0(I, \cos y) + M_0(I, \sin y)[1 - M_0(\beta, \cos y)]] = 0. \tag{3.14}$$

In the next result, we prove the local asymptotic stability of a nontrivial steady state in the special case where the feeding rate I takes the classical form $I = I(a, F)$. Also note that the method in [1] fails to give a condition for the stability in this case, except in the trivial case when $I = I(a, F) \equiv 0$. We also note that the general case can be deduced from this special case.

We note that in work which is under review, we proved that the principle of linearized stability for problem (1.1) holds if $\alpha = \int_0^l \frac{d\sigma}{V(\sigma, F_\infty)} = +\infty$. Accordingly, we assume that $\alpha = +\infty$ throughout the remaining part of this work.

Theorem 3.1. *Suppose that the following hold:* (1) $0 < \int_0^l \frac{I(a, F_\infty)}{V(a, F_\infty)} \pi(a, F_\infty) da < +\infty$, (2) $\int_0^l \int_0^a \frac{I(a, F_\infty)}{V(a, F_\infty)} \frac{|D(\sigma)|}{\pi(\sigma, F_\infty)} \pi(a, F_\infty) d\sigma da < +\infty$, (3) $\int_0^l \int_0^a \frac{\beta(a, F_\infty)}{V(a, F_\infty)} \frac{|D(\sigma)|}{\pi(\sigma, F_\infty)} \times \pi(a, F_\infty) d\sigma da < +\infty$, (4) $D_1 - \int_0^l \int_0^a \frac{\beta(a, F_\infty)}{V(a, F_\infty)} \frac{D(\sigma)}{\pi(\sigma, F_\infty)} \pi(a, F_\infty) d\sigma da \neq 0$. *Then a nontrivial steady state is locally asymptotically stable if* D_2 *is a sufficiently large positive number.*

Proof. We note that by assumption (4), $x = y = 0$ is not a root for Eq. (3.11). Also note that since if $y \neq 0, x \geq 0$, then from (2.2), we obtain $1 - M_0(\beta, .) > 0$, and accordingly, Eq. (3.14) will not be satisfied if D_2 is a sufficiently large positive number, because of assumptions (1)–(3) and the Riemann–Lebesgue Lemma. Similarly, if $x > 0, y = 0$, then from (2.2), we obtain $1 - M_0(\beta, .) > 0$, and accordingly, Eq. (3.11) will not be satisfied for D_2 a sufficiently large positive number, because of assumptions (1)–(3) and the Riemann–Lebesgue Lemma. This completes the proof of the theorem. $\square$

The next result follows directly from Theorem 3.1; therefore, we omit the proof.

Corollary 3.2. *Suppose that $V = V(a)$, $\mu = \mu(a)$. Then a nontrivial steady state is locally asymptotically stable if the following hold:* (1) D_2 *is a sufficiently large positive number,* (2) $0 < \int_0^l \frac{I(a, F_\infty)}{V(a)} \pi(a) da < +\infty$, $\pi(a) = e^{-\int_0^a \frac{\mu(\tau)}{V(\tau)} d\tau}$, (3) $D_1 \neq 0$.

We note that D_2, given by Eq. (3.3), can be interpreted as the change in the difference between the feeding rate of Daphnids and the autonomous rate of change of algae concentration in the absence of Daphnids, at the steady state, due to a change in algae concentration.

We also note that for the general case when $I = I(a, F_\infty, P_\infty)$, and $I_P(a, F_\infty, P_\infty)$ is not identically zero, we can obtain results similar to those in Theorem 3.1 and Corollary 3.2 if we replace I by h in Eqs. (3.9)–(3.14), and make the appropriate changes by considering the absolute values.

We note that conditions for the (in)stability of the trivial steady state, $P_\infty \equiv 0$, are given in [2]. Also, conditions for the instability of a nontrivial steady state are given in [1,2].

Example. In this example, we would like to illustrate the fact that D_2, given by Eq. (3.3), is indeed sufficiently large and positive under realistic assumptions. To that end, we have chosen $\phi(F) = \alpha(F_{max} - F)$, $I(a, F) = \frac{\nu \lambda F a^2}{1 + \lambda F}$ (a Holling type II functional response), $p_\infty(0) = 2.0$, and then obtained values for the parameters from [3] as follows: $\lambda = 7.0 \times 10^{-6}$, $\nu = 1.8 \times 10^6$, $\alpha = 0.5$, $\mu = 0.055$, $V = 0.5$, $l = 6.0$. Accordingly, we obtained that $D_2 \approx 89.0267$. We note that if we increase the value of $p_\infty(0)$, assumed to be equal to 2.0 in this calculation, then the value of D_2 will also increase.

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