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STABILITY ANALYSIS OF 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 when there is a constant inflow of newborns Daphnia from an external source. We determine the steady states and study their stability. We also give examples that illustrate the stability results.

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1. Introduction

In this paper, we study a size-structured population dynamics model for Daphnia together with the dynamics of algae as a source of food for Daphnia. Also, we assume that there is a constant inflow of newborns Daphnia, C, from an external source. The model takes the following form:

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$$\begin{cases} \dfrac{\partial p(a,t)}{\partial t} + \dfrac{\partial}{\partial a}(V(a,F)p(a,t)) + \mu(a,F)p(a,t) = 0, \\ \qquad\qquad\qquad\qquad a \in [0,l), \quad l \leq +\infty, \quad t > 0, \\ V(0,F)p(0,t) = C + \displaystyle\int_0^l \beta(a,F)p(a,t)da, \quad t \geq 0, \\ p(a,0) = p_0(a), \quad a \in [0,l), \\ \dfrac{dF(t)}{dt} = \phi(F) - \displaystyle\int_0^l I(a,F,P)p(a,t)da, \quad t \geq 0, \\ F(0) = F_0, \\ P(t) = \displaystyle\int_0^l p(a,t)da, \quad t \geq 0, \end{cases} \tag{1}$$

where $p(a,t)$ is the density of Daphnia with respect to size $a \in [0,l)$ at time $t \geq 0$, where, $l \leq +\infty$, is the maximum size 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 algae concentration in the absence of Daphnia; $I(a,F,P) \geq 0$ 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, $C \geq 0$, is a constant that represents the inflow of newborns Daphnia from an external source.

We study problem (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 $F \in C^0(\mathbb{R}^+ : L_\infty([0,l)))$; $I(a,I,P) \in C^0([0,l) \times \mathbb{R}^{+2})$; $\phi(F) \in C^1(\mathbb{R}^+)$; $I_F(a,F,P), I_P(a,F,P)$, 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 $F, P \in C^0(\mathbb{R}^{+2} : L_\infty([0,l)))$.

In recent years size-structured and age-size-structured population dynamics models for Daphnia coupled with the dynamics of its source of food, algae, has received considerable attention, for example, Metz, et al (1986), started their models from the basic ingredients to model analysis and numerical results. Thieme (1988), considered the well possedness of Daphnia magna models. De Roos, et al (1992), derived methods for numerical integration. De Roos, et al (1990), derived a characteristic equation and obtained analytical as well as numerical results. Diekmann, et al (2010), reformulated the age-size-structured models, obtained characteristic equations and analyzed them both analytically and numerically; furthermore, the principle of linearized stability as well as the Hopf bifurcation Theorem are deduced. Farkas, et al (2007), studied problem (1) when $l < +\infty$, i.e., they assumed finite maximum size for Daphnids, and obtained conditions for the (in)stability of a nontrivial steady state. El-Doma (Preprint -2), studied problem (1) and proved the principle of linearized stability.

We note that problem (1) is different from the classical model of Daphnia in that the feeding rate of Daphnia $I(a, F, P)$ depends on the total population size of Daphnids P; also classical models did not consider the inflow of newborns from an external source. Models of Daphnia are considered by many other authors, for example, see the references cited in the above mentioned papers and a book.

Our motivation for this work is to extend the work in Farkas, et al (2007), in several directions; on one hand, to show that other important results can be obtained without assuming finite maximum size for Daphnids, and on the other hand, to improve both the (in)stability results given therein. We note that the stability results given in Farkas, et al (2007), does not give results when the feeding rate of Daphnia $I(a, F, P)$ takes the classical form: $I(a, F)$, for example, those in Metz, et al (1986), De Roos, et al (1992), De Roos, et al (1990), and Diekmann, et al (2010). Also, the instability condition for a nontrivial steady state can be rewritten concisely and that render it handy for biological and ecological interpretation.

In this paper, we study problem (1) and determine its steady states and examine their stability. We prove that if $C = 0$, then a trivial steady state as well as a nontrivial steady state exist. Whereas if $C > 0$, then the only possible steady state is the nontrivial one. We give conditions for (in)stability of the trivial steady state. We also show that if $C > 0$, then there are as many nontrivial steady states as the solutions of the two equations: $R(F_\infty, P_\infty) = 1, R^\phi(F_\infty, P_\infty) = 0$, provided that $P_\infty > 0, F_\infty \geq 0$, see Section 2 for the definitions of $R(J, P), R^\phi(F, P)$. We also show that these steady states remain unchanged if each of the vital rates i.e., the birth rate, the death rate and the growth rate as well as the inflow rate is multiplied by any positive continuous function $f(J, A)$. Furthermore, we give sufficient conditions for their existence and uniqueness.

We also determine sufficient conditions for the local asymptotic stability of a nontrivial steady state, $P_\infty = J_\infty + A_\infty$, for the general model, when $C > 0$, and then we give several corollaries for special cases, and we also give a condition for the instability of a nontrivial steady state.

In addition, we show that the characteristic equation for problem (1) remains unchanged if each of the vital rates as well as the inflow rate is multiplied by any positive function $f(J, A) \in C^1(\mathbb{R}^{+2})$. Accordingly, all the (in)stability results that have been proved are also true for this case. Finally, we also give examples that illustrate our theorems.

The organization of this paper as follows: in Section 2 we determine the steady states; in Section 3 we study the stability of the steady states; in Section 4 we give examples that illustrate some of our theorems; in Section 5 we conclude our results; in Section 6 we give an Appendix.

2. The Steady States

In this section, we determine the steady states of problem (1). A steady state of problem (1) satisfies the following:

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

From (2), by solving the differential equation, we obtain that

$$p_\infty(a) = p_\infty(0)V(0, F_\infty)\frac{\pi(a, F_\infty)}{V(a, F_\infty)}, \tag{3}$$

where $\pi(a, F_\infty)$ is defined as

$$\pi(a, F_\infty) = e^{-\int_0^a \frac{\mu(\tau, F_\infty)}{V(\tau, F_\infty)}d\tau}.$$

We note that we similarly define $\pi(a)$ by the same formula, i.e., $\pi(a) = e^{-\int_0^a \frac{\mu(\tau)}{V(\tau)}d\tau}$.

Also, from (2) and (3), we obtain that $p_\infty(0)$ satisfies the following:

$$p_\infty(0) = \frac{C}{V(0, F_\infty)} + p_\infty(0)\int_0^l \frac{\beta(a, F_\infty)}{V(a, F_\infty)}\pi(a, F_\infty)da. \tag{4}$$

Accordingly, from (4), we conclude that $p_\infty(a) \equiv 0$ is not a steady state when $C > 0$, and the pair F_∞, P_∞ satisfies the following:

$$1 = \int_0^l \frac{\beta(a, F_\infty)}{V(a, F_\infty)} \pi(a, F_\infty) da + \frac{C}{P_\infty} \int_0^l \frac{\pi(a, F_\infty)}{V(a, F_\infty)} da. \tag{5}$$

Also, from (2), we obtain that

$$\phi(F_\infty) = \frac{P_\infty}{\int_0^l \frac{\pi(a,F_\infty)}{V(a,F_\infty)} da} \int_0^l \frac{I(a, F_\infty, P_\infty)\pi(a, F_\infty)}{V(a, F_\infty)} da. \tag{6}$$

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

$$R(F, P) = \int_0^l \frac{\beta(a, F)}{V(a, F)} \pi(a, F) da + \frac{C}{P} \int_0^l \frac{\pi(a, F)}{V(a, F)} da, \tag{7}$$

which when, $C \equiv 0$, is interpreted as the number of children expected to be born to an individual Daphnia, in a life time, when the population size is P,

$$R^\phi(F, P) = \int_0^l \frac{I(a, F, P)\pi(a, F)}{V(a, F)} da - \frac{\phi(F)}{P} \int_0^l \frac{\pi(a, F)}{V(a, F)} da, \tag{8}$$

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

We note that from equation (3), $p_\infty(0) = \dfrac{P_\infty}{V(0, F_\infty) \displaystyle\int_0^l \frac{\pi(a, F_\infty)}{V(a, F_\infty)} da}$, and accordingly, $p_\infty(a)$ is completely determined.

In the following theorem, we describe the steady states of problem (1).

Theorem 1. (1) *If $C = 0$, then Problem (1) has the trivial steady state, $P_\infty = 0$, as well as nontrivial steady states given by $R(F_\infty, P_\infty) = 1 = \displaystyle\int_0^l \frac{\beta(a, F_\infty)}{V(a, F_\infty)} \pi(a, F_\infty) da, P_\infty > 0, F_\infty \geq 0$.*

(2) *If $C > 0$, then Problem (1) has no trivial steady state, $P_\infty = 0$.*

(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).*

Proof. We note that the first part of (1) and (2) are easy to prove, and the second part of (1) is proved in (3). To prove (3), suppose that we have a nontrivial steady state, then we know that it is easy to show that it satisfies the conditions of the theorem. On the other hand, suppose that the pair, $(F_\infty, P_\infty), F_\infty \geq 0, P_\infty > 0$, satisfies $R(F_\infty, P_\infty) = 1$, and, $R^\phi(F_\infty, P_\infty) = 0$. Then use P_∞ to determine $p_\infty(a)$ by setting $P_\infty = \displaystyle\int_0^l p_\infty(a)da$ and using equation (3) to obtain that $p_\infty(a) = \dfrac{P_\infty}{\int_0^l \frac{\pi(a,F_\infty)}{V(a,F_\infty)}da} \dfrac{\pi(a, F_\infty)}{V(a, F_\infty)}$. Then this $p_\infty(a)$ satisfies equations $(2)_1, (2)_2$, because $R(F_\infty, P_\infty) = 1$. Also, equation $(2)_3$ is satisfied, because $R^\phi(F_\infty, P_\infty) = 0$. This completes the proof of the theorem. □

We note that if $\displaystyle\int_0^l I(a, F_\infty, P_\infty)\frac{\pi(a, F_\infty)}{V(a, F_\infty)}da \neq 0$, then from (2) and for a nontrivial steady state, we obtain that $p_\infty(0)$ satisfies

$$p_\infty(0) = \frac{\phi(F_\infty)}{V(0, F_\infty)\int_0^l I(a, F_\infty, P_\infty)\frac{\pi(a,F_\infty)}{V(a,F_\infty)}da} > 0. \tag{9}$$

Accordingly, $\phi(F_\infty) > 0$, and therefore, $F_\infty < F_\infty^T$, where F_∞^T corresponds to the trivial steady state, and hence $\phi(F_\infty^T) = 0$, for example, see Metz, et al (1986), for a discussion in this direction.

In the next result, we determine conditions for the existence and uniqueness of a nontrivial steady state when, $R^\phi(F, P)$, given by equation (8), takes the special form: $R^\phi(F_\infty, P_\infty) = G(F_\infty)$. In this case, $F_\infty \geq 0$, is the only unknown and is given as the solutions of the equation, $G(F_\infty) = R^\phi(F_\infty, P_\infty) = 0$, provided that we use the equation $R(F_\infty, P_\infty) = 1$, to determine $P_\infty > 0$ first.

Theorem 2. *A nontrivial steady state exists and is unique in each of the following cases:*

1. $G'(x) < 0 \forall x \geq 0, G(0) > 0$, *and,* $\exists x^* > 0$ *such that* $G(x^*) < 0$, *where* $G(F_\infty) = R^\phi(F_\infty, P_\infty)$ *when* $P_\infty > 0$ *is substituted for from the equation* $R(F_\infty, P_\infty) = 1$.

2. $G'(x) > 0 \forall x \geq 0, G(0) < 0$, *and,* $\exists x^* > 0$ *such that* $G(x^*) > 0$, *where* G *is defined in 1.*

Proof. The proof of the theorem follows immediately from the monotonicity of $G(x)$ and the conditions on $G(0)$. Therefore, we omit the details of the proof. This completes the proof of the theorem. □

We note that a similar result to (2) in Theorem 2 is given in Diekmann, et al (2008). Also see Calsina, et al (2003), for an equivalent result.

In the following result, we show that the steady states of problem (1) remain unchanged if we multiply all the vital rates as well as the inflow rate by any positive continuous function of the pair (F, P).

Theorem 3. *Suppose that,* $\beta = \beta(a, F)f(F, P), \mu = \mu(a, F) \times f(F, P), V = V(a, F)f(F, P)$, *where,* f, *is a positive continuous function, and the inflow rate,* C, *is replaced by,* $Cf(F, P)$. *Then the steady states of problem (1) is the same as when,* $\beta = \beta(a, F), \mu = \mu(a, F), V = V(a, F)$, *and the inflow rate is,* C.

Proof. The proof is by using Theorem 1. We first note that it is easy to see that equation (5) remains unchanged i.e., equation (5) is satisfied in the case, $\beta = \beta(a, F)f(F, P), \mu = \mu(a, F)f(F, P), V = V(a, F)f(F, P)$, when C is replaced by $Cf(J, A)$. Also, similarly, equation (6) remains unchanged. Therefore, by Theorem 1, we obtain the same steady state as in the case, $\beta = \beta(a, F), \mu = \mu(a, F), V = V(a, F)$, and the inflow rate is C. This completes the proof of the theorem. □

In the next result, we use Theorems 2-3 to extend the result given in Theorem 2.

Corollary 4. *A nontrivial steady state for the special case,* $\beta = \beta(a, F)f(F, P), \mu = \mu(a, F)f(F, P), V = V(a, F)f(F, P)$, *where,* f, *is a positive continuous function, and the inflow rate is,* $Cf(F, P)$, *exists and is unique in each of the cases given in Theorem 2.*

Proof. The result follows directly from Theorems 2-3. This completes the proof of the corollary. □

Remark 2.1. We note that the results of Theorem 3 and Corollary 4 hold when $C \equiv 0$.

3. Stability of the Steady States

In this section, we study the stability of the steady states for problem (1) as given by Theorem 1.

To study the stability of a steady state $p_\infty(a)$, which is a solution of (2) and is given by equation (3), we linearize problem (1) at $p_\infty(a)$ in order to obtain a characteristic equation, which in turn will determine conditions for the stability. To that end, we consider a perturbation $\omega(a,t)$ defined by $\omega(a,t) = p(a,t) - p_\infty(a)$, where $p(a,t)$ is a solution of problem (1). Accordingly, we obtain that $\omega(a,t)$ satisfies the following:

$$\begin{cases} \dfrac{\partial\omega(a,t)}{\partial t} + [V_a(a,F_\infty) + \mu(a,F_\infty)]\omega(a,t) + V(a,F_\infty)\omega(a,t)_a + \\ [V_{Fa}(a,F_\infty)p_\infty(a) + V_F(a,F_\infty)p'_\infty(a) + \mu_F(a,F_\infty)p_\infty(a)]\hat{\omega}(t) = 0, \\ \\ \omega(0,t)V(0,F_\infty) = \hat{\omega}(t)\Big[\displaystyle\int_0^l \beta_F(a,F_\infty)p_\infty(a)da - p_\infty(0)V_F(0,F_\infty)\Big] \\ \\ + \displaystyle\int_0^l \beta(a,F_\infty)\omega(a,t)da \\ \dfrac{d\hat{\omega}(t)}{dt} = \Big[\phi_F(F_\infty) - \displaystyle\int_0^l I_F(a,F_\infty,P_\infty)p_\infty(a)da\Big]\hat{\omega}(t) - \\ \displaystyle\int_0^l I(a,F_\infty,P_\infty)\omega(a,t)da - \Big(\int_0^l I_P(a,F_\infty,P_\infty)p_\infty(a)da\Big)\times \\ \Big(\displaystyle\int_0^l \omega(a,t)da\Big). \end{cases} \tag{10}$$

By substituting $\omega(a,t) = N(a)e^{\xi t}, \hat{\omega}(t) = de^{\xi t}$, in (10), where ξ is a complex number, d is a constant, and straightforward but tedious calculations, we obtain the following characteristic equation:

$$\begin{aligned} &\left[1 - \frac{1}{V(0,F_\infty)}\int_0^l e^{-\int_0^a E(\tau)d\tau}\beta(a,F_\infty)da\right]\times \qquad (11)\\ &\Big\{\xi + D_2 - \int_0^l\int_0^a e^{-\int_\sigma^a E(\tau)d\tau} g(\sigma,F_\infty)h(a,F_\infty,P_\infty)d\sigma da\Big\} \\ &+ \frac{1}{V(0,F_\infty)}\Big\{D_1 - \int_0^l\int_0^a e^{-\int_\sigma^a E(\tau)d\tau}\beta(a,F_\infty)g(\sigma,F_\infty)d\sigma da\Big\} \\ &\times \int_0^l e^{-\int_0^a E(\tau)d\tau} h(a,F_\infty,P_\infty)da = 0, \end{aligned}$$

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

$$D_1 = \int_0^l \beta_F(a,F_\infty)p_\infty(a)da - p_\infty(0)V_F(0,F_\infty), \tag{12}$$

$$D_2 = \int_0^l I_F(a,F_\infty,P_\infty)p_\infty(a)da - \phi_F(F_\infty), \tag{13}$$

$$E(\sigma) = \frac{\xi + V_\sigma(\sigma, F_\infty) + \mu(\sigma, F_\infty)}{V(\sigma, F_\infty)}, \tag{14}$$

$$g(\sigma, F_\infty) = \frac{\frac{\partial}{\partial\sigma}\Big(V_F(\sigma, F_\infty)p_\infty(\sigma)\Big) + p_\infty(\sigma)\mu_F(\sigma, F_\infty)}{V(\sigma, F_\infty)}, \tag{15}$$

$$h(a, F_\infty, P_\infty) = \Big[I(a, F_\infty, P_\infty) + \int_0^l I_P(a', F_\infty, P_\infty)p_\infty(a')da'\Big]. \tag{16}$$

In the next theorem, we give a condition for the instability of a nontrivial steady state. In order to facilitate our writing, we define Ξ by

$$\Xi = [\phi(F_\infty) + P_\infty \int_0^l I_P(a, F_\infty, P_\infty)p_\infty(a)da]R_F(F_\infty, P_\infty) + CR_F^\phi(F_\infty, P_\infty). \tag{17}$$

Theorem 5. *A nontrivial steady state is unstable if* $\Xi < 0$.

Proof. We suppose that ξ is real and denote the left-hand side of the characteristic equation (11) by $H(\xi)$, and also suppose that $\Xi < 0$. We first show that $H(0) = \Xi$, the proof of this fact is relegated to an Appendix.

Also, since ξ is real, $H(\xi) \longrightarrow +\infty$ as $\xi \longrightarrow +\infty$. Accordingly, $\exists \xi^* > 0$ such that $H(\xi^*) = 0$, and hence a nontrivial steady state is unstable. This completes the proof of the theorem. □

In the next theorem, we prove that, $\xi = 0$, is a root of the characteristic equation (11) iff $\Xi = 0$, where Ξ is given by equation (17).

Theorem 6. $\xi = 0$, *is a root of the characteristic equation (11) iff* $\Xi = 0$.

Proof. We note that if $\xi = 0$, then using equation (5), the characteristic equation (11) becomes,

$$[\phi(F_\infty) + P_\infty \int_0^l I_P(a, F_\infty, P_\infty)p_\infty(a)da]R_F(F_\infty, P_\infty) + CR_F^\phi(F_\infty, P_\infty) = \Xi = 0. \tag{18}$$

This completes the proof of the theorem. □

We note that according to Theorem 5 a nontrivial steady state is unstable i.e., ξ with $\Re\xi > 0$, is a root of the characteristic equation (11) if, $\Xi < 0$. Also, by Theorem 6 if, $\Xi = 0$, then, $\xi = 0$, is a root of the characteristic equation (11). And therefore, a necessary condition for a nontrivial steady state to be locally asymptotically stable is, $\Xi > 0$.

In the following theorem, we describe the stability of the trivial steady state, $p_\infty(a) \equiv 0$.

Theorem 7. *The trivial steady state, $p_\infty(a) \equiv 0$, is locally asymptotically stable if the following two conditions are satisfied:*

1. $R(F_\infty, 0) < 1$,
2. $\phi'(F_\infty) < 0$.

   The trivial steady state, $p_\infty(a) \equiv 0$, is unstable if one of the following conditions is satisfied:

3. $R(F_\infty, 0) > 1$,
4. $\phi'(F_\infty) > 0$.

Proof. We note that for the trivial steady state, $p_\infty(a) \equiv 0$, $P_\infty = 0$, and therefore, from the characteristic equation (11), we obtain the following characteristic equation:

$$\left[1 - \int_0^l e^{-\xi \int_0^a \frac{d\tau}{V(\tau, F_\infty)}} \frac{\beta(a, F_\infty)}{V(a, F_\infty)} \pi(a, F_\infty) da\right] \left[\xi - \phi'(F_\infty)\right] = 0. \tag{19}$$

To prove the local asymptotic stability of the trivial steady state, we note that the roots of the characteristic equation (19) are the union of the roots of the equation

$$1 = \int_0^l e^{-\xi \int_0^a \frac{d\tau}{V(\tau, F_\infty)}} \frac{\beta(a, F_\infty)}{V(a, F_\infty)} \pi(a, F_\infty) da, \tag{20}$$

and the single root $\xi = \phi'(F_\infty) < 0$, and latter is negative and therefore, it suffices to show that the roots of the former also have negative real parts. To that end, we assume that $R(F_\infty, 0) < 1$, then equation (20) can not be satisfied for any ξ with, $\Re\xi \geq 0$, because

$$\Big| \int_0^l e^{-\xi \int_0^a \frac{d\tau}{V(\tau, F_\infty)}} \frac{\beta(a, F_\infty)}{V(a, F_\infty)} \pi(a, F_\infty) da \Big| \leq$$

$$\int_0^l e^{-\Re\xi \int_0^a \frac{d\tau}{V(\tau,F_\infty)}} \frac{\beta(a,F_\infty)}{V(a,F_\infty)} \pi(a,F_\infty)da \le R(F_\infty,0) < 1.$$

This proves the stability part.

To show the instability of the trivial steady state when $R(F_\infty, 0) > 1$, or $\phi'(F_\infty) > 0$, we note the latter condition gives instability immediately, whereas equation (20) gives instability if $R(F_\infty, 0) > 1$, because if we define a function $M(\xi)$ by

$$M(\xi) = \int_0^l e^{-\xi \int_0^a \frac{d\tau}{V(\tau,F_\infty)}} \frac{\beta(a,F_\infty)}{V(a,0,0)} \pi(a,F_\infty)da,$$

and suppose that ξ is real, then we can easily see that $M(\xi)$ is a decreasing function if $\xi > 0$, $M(\xi) \longrightarrow 0$ as $\xi \longrightarrow +\infty$, and $M(0) = R(F_\infty, 0)$. Therefore, if $R(F_\infty, 0) > 1$, then there exists $\xi^* > 0$ such that $M(\xi^*) = 1$, and hence the trivial steady state is unstable. This completes the proof of the theorem. □

Theorem 5 is ecologically intuitive since $R(F_\infty, 0)$ represents the number of children expected to be born to an individual, in a life time, when the population size is zero and the algae concentration is F_∞. So, it is clear that if $R(F_\infty, 0) < 1$, then the population of Daphnia will not grow; and if simultaneously $\phi'(F_\infty) < 0$, i.e., the algal food concentration is decreasing, then the trivial steady state is locally asymptotically stable. Whereas if $R(F_\infty, 0) > 1$, then the population will eventually grow and accordingly, instability occurs; or if $\phi'(F_\infty) > 0$, then the algal food concentration is increasing, and that leads to instability.

In the following lemma, we prove a useful result that we shall need in our future development.

Lemma 8. *Suppose that* $\Re\xi \ge 0$, *then we obtain*

$$\left|1 - \frac{1}{V(0,F_\infty)} \int_0^l e^{-\int_0^a E(\tau)d\tau} \beta(a,F_\infty)da\right| \ge \frac{C}{p_\infty(0)V(0,F_\infty)}.$$

Proof. Note that for $\Re\xi \ge 0$, and using equation (5), we obtain

$$\left|\frac{1}{V(0,F_\infty)} \int_0^l e^{-\int_0^a E(\tau)d\tau} \beta(a,F_\infty)da\right| \le \int_0^l \frac{\beta(a,F_\infty)}{V(a,F_\infty)} \pi(a,F_\infty)da$$
$$= 1 - \frac{C}{p_\infty(0)V(0,F_\infty)}.$$

Therefore,

$$\left|1 - \frac{1}{V(0,F_\infty)} \int_0^l e^{-\int_0^a E(\tau)d\tau} \beta(a,F_\infty)da\right| \ge \frac{C}{p_\infty(0)V(0,F_\infty)}.$$

This completes the proof of the lemma. □

In the next theorem, we give sufficient conditions for the local asymptotic stability of a nontrivial steady state. We note that this result is for the general problem (1), and in the sequel we give other conditions which are for special cases of problem (1). We also note that these results also hold if the vital rates and the inflow rate are all multiplied by a positive function $f(F,P) \in C^1(\mathbb{R}^{+2})$, and this fact will be proved in Corollary 13 below.

Theorem 9. *Suppose that $C > 0$, and the following holds:*

$$D_2 > \int_0^l \int_0^a \frac{\pi(a,F_\infty)}{V(a,F_\infty)} V(\sigma,F_\infty) \Big| g(\sigma,F_\infty) h(a,F_\infty,P_\infty) \Big| d\sigma da \tag{21}$$
$$+ \Big\{ |D_1| + \int_0^l \int_0^a \frac{\pi(a,F_\infty)}{V(a,F_\infty)} V(\sigma,F_\infty) \beta(a,F_\infty) \Big| g(\sigma,F_\infty) \Big| d\sigma da \Big\}$$
$$\times \frac{1}{C} \Big\{ \phi(F_\infty) + P_\infty \Big| \int_0^l I_P(b,F_\infty,P_\infty) p_\infty(b) db \Big| \Big\}.$$

Then a nontrivial steady state is locally asymptotically stable.

Proof. Suppose that $\Re\xi \geq 0$, then by Lemma 8, we can divide by the first bracketed term of the characteristic equation (11), which is estimated in Lemma 8. Also, for $C > 0$, we observe that since D_2 is real, and $\Re\xi \geq 0$, then the equation $H(\xi) = 0$ will not be satisfied if D_2 is greater than the sum of the absolute values of the remaining two terms after the division as in inequality (21). This completes the proof of the theorem. □

We note that apparently condition (21) shows that the effect of the inflow of newborns from an external source is stabilizing since if C is large, then condition (21) is more likely to be satisfied.

We note that D_2, given by equation (13), can be interpreted as the change in the difference between the feeding rate by Daphnids and the rate of change of algae concentration, at the steady state, due to change in algae concentration.

The following corollaries follow directly from Theorem 9, and therefore, the details of the proofs are omitted.

Corollary 10. *Suppose that, $\mu(a,F) = \mu(a), V(a,F) = V(a)$. Then a nontrivial steady state is locally asymptotically stable if the following holds:*

$$D_2 > \frac{1}{C} \Big| \int_0^l \beta_F(a,F_\infty) p_\infty(a) da \Big| \Big\{ \phi(F_\infty) + \tag{22}$$

$$P_\infty\Big|\int_0^l I_P(b,F_\infty,P_\infty)p_\infty(b)db\Big|\Big\}.$$

In the next corollary, we give stability result for the feeding rate of the classical Daphnia model, for example, those in De Roos, et al (1992), Metz, et al (1986), De Roos, et al (1990) and Diekmann (2010).

Corollary 11. *Suppose that, $I(a,F,P) = I(a,F)$. Then a nontrivial steady state is locally asymptotically stable if the following holds:*

$$D_2 > \int_0^l \int_0^a \frac{\pi(a,F_\infty)}{V(a,F_\infty)} V(\sigma,F_\infty)\Big|g(\sigma,F_\infty)\Big| I(a,F_\infty)d\sigma da + \frac{\phi(F_\infty)}{C}\Big\{|D_1| + \int_0^l\int_0^a V(\sigma,F_\infty)\beta(a,F_\infty)\Big|g(\sigma,F_\infty)\Big|d\sigma da\Big\}. \tag{23}$$

In the following result, we prove that the characteristic equation (11) remains unchanged if each of the vital rates as well as the inflow rate is multiplied by any positive function, $f(F,P)\in C^1(\mathbb{R}^{+2})$.

Theorem 12. *Suppose that, $\beta = \beta(a,F)f(F,P), \mu = \mu(a,F) \times f(F,P), V = V(a,F)f(F,P)$, where, $f(F,P)\in C^1(\mathbb{R}^{+2})$, is a positive function. And also suppose that the inflow rate, C, is replaced by, $Cf(F,P)$. Then the characteristic equation for problem (1), in this case, is the same as when, $\beta = \beta(a,F), \mu = \mu(a,F), V = V(a,F)$, and, the inflow rate is given by, C, i.e., it satisfies (11) too.*

Proof. By Theorem 3, the steady states are the same. So, we linearize problem (1) at $p_\infty(a)$, as before, but this time we use the new vital rates, $\beta = \beta(a,F)f(F,P), \mu = \mu(a,F)f(F,P), V = V(a,F)f(F,P)$, as well as the new inflow rate, $Cf(F,P)$. Then we obtain (10) again after simple manipulations and using (2). This completes the proof of the theorem. □

In the next result, we generalize the (in)stability results obtained so far to the general case when the vital rates and the inflow rate, respectively, assume $\beta = \beta(a,F)f(F,P), \mu = \mu(a,F)f(F,P), V = V(a,F)f(F,P), Cf(F,P)$.

Corollary 13. *Suppose that, $\beta = \beta(a,F)f(F,P), \mu = \mu(a,F) \times f(F,P), V = V(a,F)f(F,P)$, where, $f(F,P)\in C^1(\mathbb{R}^{+2})$, is a positive function. And also suppose that the inflow rate, C, is replaced by, $Cf(F,P)$. Then the (in)stability results for problem (1), in this case, is the same as when, $\beta = \beta(a,F); \mu = \mu(a,F); V = V(a,F)$, and, the inflow rate is given by, C.*

Proof. We note the instability result given in Theorem 5 follows in this case because by Theorem 12, we use the same characteristic equation (11). A similar reasoning as above holds for Theorem 6 and Theorem 7. We also note that Theorem 9 and all its corollaries are obtained from the characteristic equation (11), and therefore if $C > 0$, the result follows in this case too. This completes the proof of the corollary. □

Remark 3.1. We note that the results of Theorem 12 and Corollary 13 hold if $C \equiv 0$.

4. Examples

Example 1. In this example, we consider the case when, $l = +\infty, V = V(F), \mu = \mu(F), I = I(F)$. Then the characteristic equation becomes

$$\Big[1 - \int_0^\infty \frac{\beta(a,F_\infty)}{V(F_\infty)} e^{-\frac{a}{V(F_\infty)}(\xi+\mu(F_\infty))} da\Big]\Big[\xi - \phi'(F_\infty) + I'(F_\infty)P_\infty - \frac{I(F_\infty)p_\infty(0)}{\xi\mu(F_\infty)}\Big(\mu'(F_\infty)V(F_\infty) - \mu(F_\infty)V'(F_\infty)\Big)\Big] + \frac{I(F_\infty)}{(\mu(F_\infty)+\xi)}\Big[D_1 + \frac{C}{\xi V(F_\infty)}\Big(\mu'(F_\infty)V(F_\infty) - \mu(F_\infty)V'(F_\infty)\Big)\Big] = 0. \tag{24}$$

Now, if we assume that $C = 0, \xi = yi \neq 0, I(F_\infty)p_\infty(0)\Big(\mu'(F_\infty)V(F_\infty) - \mu(F_\infty)V'(F_\infty)\Big) > 0$, we obtain

$$1 - \int_0^\infty \frac{\beta(a,F_\infty)}{V(F_\infty)}\pi(a,F_\infty)\cos\frac{ya}{V(F_\infty)} da = \frac{I(F_\infty)D_1y^2}{\Delta_0}\Big\{y^2 + \mu(F_\infty)\Big(\phi'(F_\infty) - I'(F_\infty)P_\infty\Big) + \frac{I(F_\infty)p_\infty(0)}{\mu(F_\infty)}\Big(\mu'(F_\infty)V(F_\infty) - \mu(F_\infty)V'(F_\infty)\Big)\Big\}, \tag{25}$$

where Δ_0 is defined as follows

$$\Delta_0 = [\mu^2(F_\infty) + y^2]\Big\{\Big[y^2 + \frac{I(F_\infty)p_\infty(0)}{\mu(F_\infty)}\Big(\mu'(F_\infty)V(F_\infty) - \mu(F_\infty)V'(F_\infty)\Big)\Big]^2 + y^2\Big[I(F_\infty)P_\infty - \phi'(F_\infty)\Big]^2\Big\}. \tag{26}$$

In equation (25), if we assume that

$$\frac{I(F_\infty)p_\infty(0)}{\mu(F_\infty)}\Big(\mu'(F_\infty)V(F_\infty)-\mu(F_\infty)V'(F_\infty)\Big)+\mu(F_\infty)\Big(\phi'(F_\infty)-I'(F_\infty)P_\infty\Big) \geq 0, \quad D_1<0,$$

then we notice that the left-hand side of equation (25) is positive, whereas the right-hand side is negative, i.e., $\xi = yi \neq 0$ is not a root of the characteristic equation and therefore, crossing the imaginary axis is not possible in this case.

We also note that $y = 0$ is not a root of the characteristic equation because from equation (9), we have $\phi(F_\infty) > 0$, for a nontrivial steady state, and also since

$$R_F(F_\infty, P_\infty) = \frac{1}{p_\infty(0)V(F_\infty)} \left\{D_1 - \frac{\Big(\mu'(F_\infty)V(F_\infty) - \mu(F_\infty)V'(F_\infty)\Big)\int_0^\infty a\beta(a, F_\infty)p_\infty(a)da}{V^2(F_\infty)}\right\} < 0,$$

we have $\Xi \neq 0$, accordingly, Theorem 6 gives that we can assume that $D_1 \leq 0$ and obtain the non existence of solutions $\xi = yi$ for the characteristic equation (11).

We also note that since $\xi = yi$ is not a root of the characteristic equation in this case, we do not expect a destabilization of the nontrivial steady state via a Hopf bifurcation, for example, see Diekmann, et al (2010), (2007a), (2007b), (2008).

Furthermore, since our calculation has shown that $\Xi < 0$, the nontrivial steady state is unstable by Theorem 5. Alternatively, we can alter our conditions so that we can obtain roots of the form $\xi = yi$, such a program is carried out in Diekmann, et al (2010) for the case when β does not depend on size.

Example 2. In this example, we consider the case when, $l = +\infty, V = V(a), \displaystyle\int_0^\infty \frac{d\tau}{V(\tau)} = +\infty, \mu = \mu(F), I = I(F)$. Then the characteristic equation becomes

$$\Big[1 - \int_0^\infty \frac{\beta(a, F_\infty)}{V(a)}\pi(a, F_\infty)e^{-\xi\int_0^a \frac{d\tau}{V(\tau)}}da\Big]\Big[\xi - \phi'(F_\infty) + I'(F_\infty)P_\infty - \frac{I(F_\infty)p_\infty(0)V(0)\mu'(F_\infty)}{\xi\mu(F_\infty)}\Big] + \frac{I(F_\infty)}{(\mu(F_\infty)+\xi)}\Big[D_1 + \frac{C\mu'(F_\infty)}{\xi}\Big] = 0. \tag{27}$$

Now, if we assume that $C = 0, \xi = yi \neq 0, I(F_\infty)p_\infty(0)\mu'(F_\infty)V(0) > 0$, we obtain

$$1 - \int_0^\infty \frac{\beta(a, F_\infty)}{V(F_\infty)} \pi(a, F_\infty) \cos y \int_0^a \frac{d\tau}{V(\tau)} da = \tag{28}$$

$$\frac{I(F_\infty)D_1 y^2}{\Delta_0^*} \Big\{ y^2 + \frac{I(F_\infty)p_\infty(0)V(0)\mu'(F_\infty)}{\mu(F_\infty)} + \mu(F_\infty)\Big(\phi'(F_\infty) - I'(F_\infty)P_\infty\Big) \Big\},$$

where Δ_0^* is defined as follows

$$\Delta_0^* = [\mu^2(F_\infty) + y^2] \Big\{ \Big[y^2 + \frac{I(F_\infty)p_\infty(0)\mu'(F_\infty)V(0)}{\mu(F_\infty)} \Big]^2 + y^2 \Big[I'(F_\infty)P_\infty - \phi'(F_\infty) \Big]^2 \Big\}. \tag{29}$$

In equation (28), if we assume that

$$I'(F_\infty)P_\infty - \phi'(F_\infty) \leq 0, \quad D_1 < 0,$$

$$\frac{I(F_\infty)p_\infty(0)\mu'(F_\infty)V(0)}{\mu(F_\infty)} + \mu(F_\infty)\Big(\phi'(F_\infty) - I'(F_\infty)P_\infty\Big) \geq 0,$$

then we notice that the left-hand side of equation (28) is positive whereas the right-hand side is negative, i.e., $\xi = yi \neq 0$ is not a root of the characteristic equation and therefore, crossing the imaginary axis is not possible in this case.

We also note that $y = 0$ is not a root of the characteristic equation because for a nontrivial steady state we have $\phi(F_\infty) > 0$, and because $R_F(F_\infty, P_\infty) = \frac{1}{p_\infty(0)V(0)} \Big\{ D_1 - \mu'(F_\infty) \int_0^\infty \int_0^a \beta(a, F_\infty) \frac{p_\infty(a)}{V(\sigma)} d\sigma da \Big\} < 0.$

We also note that since $\xi = yi$ is not a root of the characteristic equation in this case, we do not expect a destabilization of the nontrivial steady state via a Hopf bifurcation, for example, see Diekmann, et al (2010), (2007a), (2007b), (2008).

Moreover, since our calculation has shown that $\Xi < 0$, the nontrivial steady state is unstable by Theorem 5. Alternatively, we can alter our conditions so that we can obtain roots of the form $\xi = yi \neq 0$, such a program is carried out in Diekmann, et al (2010) for the case when β does not depend on size.

Example 3. In this example we consider the case considered in Example 1, and further we assume that μ, V are constants, $\beta = \beta(F)$, and accordingly, we obtain the following characteristic equation:

$$\Big[1 - \frac{\beta(F_\infty)}{\xi + \mu}\Big]\Big[\xi - \phi'(F_\infty) + \frac{I'(F_\infty)p_\infty(0)V}{\mu}\Big] + \frac{I(F_\infty)D_1}{\xi + \mu} = 0. \tag{30}$$

We note that following the method given Diekmann, et al (2010), we can rewrite equation (30) in the following form:

$$1 = \frac{\beta(F_\infty)}{\xi + \mu} \frac{\Big[\xi - \phi'(F_\infty) + \frac{I'(F_\infty)p_\infty(0)V}{\mu} - \frac{I(F_\infty)D_1}{\beta(F_\infty)}\Big]}{\Big[\xi - \phi'(F_\infty) + \frac{I'(F_\infty)p_\infty(0)V}{\mu}\Big]}. \tag{31}$$

We also note that from equation (5), we obtain

$$\beta(F_\infty) = \mu\Big[1 - \frac{C}{p_\infty(0)V}\Big]. \tag{32}$$

Accordingly, we obtain the following condition for the non existence of roots $\xi = yi$ for the characteristic equation:

$$\Big[1 - \frac{C}{p_\infty(0)V}\Big]\Big| - \phi'(F_\infty) + \frac{I'(F_\infty)p_\infty(0)V}{\mu} - \frac{I(F_\infty)D_1}{\beta(F_\infty)}\Big| \tag{33}$$
$$< \Big| - \phi'(F_\infty) + \frac{I'(F_\infty)p_\infty(0)V}{\mu}\Big|.$$

From (33), we notice the effect of the inflow of newborns from an external source on the condition.

We note that it is clear that we can use equation (31) to obtain condition under which the characteristic equation have roots $\xi = yi$, for such results see Diekmann, et al (2010).

Example 4. In this example, we consider the case when, $\beta = \beta(a), \mu = \mu(a), V = V(a)$. In such case we can easily see that equation (5) gives the following unique steady state for problem (1), provided that $C > 0$:

$$P_\infty = \frac{C\int_0^\infty \frac{\pi(a)}{V(a)}da}{[1 - \int_0^\infty \frac{\beta(a)}{V(a)}\pi(a)da]}. \tag{34}$$

We also note that in El-Doma (Preprint -1), it is shown that this steady state is globally stable, under suitable conditions. Apparently in this case the food resource has no effect on the dynamics of the Daphnia, and the inflow from an external source maintains the population of Daphnia.

5. Conclusion

In this paper, we studied a size-structured population dynamics model for Daphnia coupled with an unstructured model for its algal food. The maximum size for Daphnia is either finite or infinite, and there is an inflow of newborns Daphnia from an external source.

We determined the steady states of the model and examined their stability. We proved that if $C = 0$, then a trivial steady state as well as a nontrivial steady state may exist, whereas if $C > 0$, then a trivial steady state does not exist, and there are as many nontrivial steady states as the solutions of the two equations: $R(F_\infty, P_\infty) = 1, R^\phi(F_\infty, P_\infty) = 0$, provided that $P_\infty > 0, F_\infty \geq 0$, where $R(J, A), R^\phi(F, P)$ are given, respectively, by equations (7), (8).

We also showed that these steady states remain unchanged if each of the vital rates i.e., the birth rate, the death rate, and the growth rate as well as the inflow rate, is multiplied by any positive continuous function $f(F, P)$. Furthermore, we gave sufficient conditions for their existence and uniqueness.

Moreover, we determine conditions for the (in)stability of the trivial steady state, we also determined sufficient conditions for the local asymptotic stability of a nontrivial steady state, when $C > 0$, for the general model, and then we gave several corollaries for this result, and we also gave a condition for the instability of a nontrivial steady state, when $C \geq 0$.

In addition, we showed that the characteristic equation (11) remains unchanged if each of the vital rates as well as the inflow rate, is multiplied by any positive function, $f(F, P) \in C^1(\mathbb{R}^{+2})$. And accordingly, all the (in)stability results obtained with the original vital rates and the inflow rate are also true when these rates are multiplied by $f(F, P)$. Finally, we also gave examples that illustrated our theorems.

We note the effect of the inflow of newborns from external source is stabilizing, for example, see Theorem 9.

We note that the model studied in this paper is studied previously in Farkas, et al (2007), where an instability result is obtained via similar methods, albeit not in a concise form as in this paper, this result works for the current model as well as for the classical model which has a feeding rate that does not depend on the total size of Daphnia and $C \equiv 0$. However, for the local asymptotic stability of the nontrivial steady state, they used semgroups and obtained conditions for the positivity of the semigroup, but then these conditions imply that for, the classical Daphnia model, the feeding rate must be zero, and therefore, is absurd, and, in fact, the result given therein is not a general one. In this case our result, given in Theorem 9, gives conditions for the local asymptotic stability of a nontrivial steady state of the classical model of Daphnia when $C > 0, l \geq +\infty$ and therefore, we improved the result therein. In addition, we also obtained other results which are not developed therein, for example, those in Theorem 2, Theorem 3, Corollary 4, Theorem 6, Theorem 7, Theorem 12, and Corollary 13.

We finally note that Theorem 9 is not applicable when $C \equiv 0$, this fact is also true for the corresponding theorem in Farkas, et al (2007), and hence, the local asymptotic stability of a nontrivial steady state for the classical Daphnia model is unresolved yet.

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References

[1] A.M. De Roos, J.A.J. Metz, E. Evers, A. Leipoldt, A size dependent predator-prey interaction: who pursues whom?, *J. Math. Biol.,* **28** (1990), 609-643.

[2] A.M. De Roos, O. Diekmann, J. A. J. Metz, Studying the dynamics of structured population models: a versatile technique and its application to Daphnia, *Amer. Nat.,* **139**, No. 1 (1992), 123-147.

[3] O. Diekmann, P. Getto, M. Gylenberg, Stability and bifurcation analysis of Volterra functional equations in the light of suns and stars, *SIAM J. MATH. ANAL.,* **39** (2007), 1023-1069.

[4] O. Diekmann, M. Gylenberg, J. A. J. Metz, S. Nakaoka, A. M. De Roos, Daphnia revisited: Local stability and bifurcation theory for physiologically structured population models explained by way of an example, *J. Math. Biol.,* **61** (2010), 277-318.

[5] O. Diekmann, M. Gylenberg, Abstract delay equations inspired by population dynamics, In: *Functional Analysis and Evolution Equations, The Günter Lumer Volume*, Birkhäuser Verlag Basel, Switzerland (2007), 187-200.

[6] O. Diekmann, M. Gylenberg, The second half-with a quarter of century delay, *Math. Model. Nat. Phenom.,* **3** (2008), 36-48.

[7] M. El-Doma, Size-Structured Population Models with Constant Inflow of Newborns, *Preprint*.

[8] M. El-Doma, The principle of linearized stability for a size-structured population dynamics model for Daphnia, *Preprint*.

[9] J. Z. Farkas, T. Hagen, Linear stability and positivity results for a generalized size-structured Daphnia model with inflow. *Appl. Anal.,* **86** (2007), 1087-1103.

[10] J.A.J. Metz, O. Diekmann, *The Dynamics of Physiologically Structured Populations,* Springer-Verlag, Lecture Notes in Biomathematics, **68** (1986).

[11] H.R. Thieme, Well-posedness of physiologically structured population models for Daphnia magna, *J. Math. Biol.,* **26**, (1988), 299-317.

Appendix

In this Appendix, we outline a prove for the part of Theorem 5 which we relegated to this Appendix, viz. we show that $H(0) = \Xi$. We start by noting that, in our current calculation, we assume that $\xi = 0$. Accordingly, we observe that

$$D_1 - \int_0^l \int_0^a e^{-\int_\sigma^a E(\tau)d\tau} \beta(a, F_\infty) g(\sigma, F_\infty) d\sigma da = \tag{35}$$
$$R_F(F_\infty, P_\infty) p_\infty(0) V(0, F_\infty) - C \frac{V_F(0, F_\infty)}{V(0, F_\infty)}$$
$$- \frac{C p_\infty(0) V(0, F_\infty)}{P_\infty} \int_0^l \frac{\partial}{\partial F} \Big[\frac{\pi(a, F_\infty)}{V(a, F_\infty)} \Big] da.$$

Also, similarly, we note that

$$\frac{C}{p_\infty(0) V(0, F_\infty)} \Big\{ D_2 - \tag{36}$$
$$\int_0^l \int_0^a e^{-\int_\sigma^a E(\tau)d\tau} I(a, F_\infty, P_\infty) g(\sigma, F_\infty) d\sigma da -$$

$$\Big(\int_0^l I_P(b,F_\infty,P_\infty)p_\infty(b)db\Big)\int_0^l\int_0^a e^{-\int_\sigma^a E(\tau)d\tau}g(\sigma,F_\infty)d\sigma da\Big\}$$

$$=\frac{C}{p_\infty(0)V(0,F_\infty)}\Big\{D_2+\frac{\phi(F_\infty)V_F(0,F_\infty)}{V(0,F_\infty)}+\frac{P_\infty V_F(0,F_\infty)}{V(0,F_\infty)}\times$$

$$\int_0^l I_P(a,F_\infty,P_\infty)p_\infty(a)da\Big\}+$$

$$C\int_0^l h(a,F_\infty,P_\infty)\frac{\partial}{\partial F}\Big[\frac{\pi(a,F_\infty)}{V(a,F_\infty)}\Big]da.$$

Also, we note that

$$\frac{1}{V(0,F_\infty)}\int_0^l e^{-\int_0^a E(\tau)d\tau}I(a,F_\infty,P_\infty)da+ \tag{37}$$

$$\Big(\int_0^l I_P(b,F_\infty,P_\infty)p_\infty(b)db\Big)\int_0^l e^{-\int_0^a E(\tau)d\tau}da$$

$$=\frac{1}{p_\infty(0)V(0,F_\infty)}\Big[\phi(F_\infty)+P_\infty\int_0^l I_P(a,F_\infty,P_\infty)p_\infty(a)da\Big].$$

Now, using the characteristic equation (11), and equations (35) - (37), we obtain the result. This completes the Appendix.

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