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Nonlinear dynamics of open marine population with space-limited recruitment

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1 Introduction

Let us consider populations of marine invertebrates that have sessile adults and pelagic larvae, such as *barnacles*, contained in a local area. They could change in their abundance and spatial distribution through time, but their population dynamics would be be very different from that of vertebrates. The main reason for this is that while the sessile adults can be viewed as living in a limited area, their larvae can freely move from one area to another, since each area (patch) is connected by the pelagic pool containing the larvae. That is, such a population system is essentially open, newly settled larvae are carried from outside from the region. Moreover it has been observed that for sessile marine populations, the space to be settled by the larvae is a principal limiting resource, and the number of settlements is approximately proportional to the free space available to larvae.

2 The linear model

Under such observations as mentioned above, Roughgarden et al. (1985) have proposed an age-structured population model for sessile invertebrates living in a local area as follows:

$$\begin{cases} \frac{\partial p(t,a)}{\partial t}+\frac{\partial p(t,a)}{\partial a}=-\mu(a)p(t,a), & t>0,\ 0<a<\omega, \\ p(t,0)=kF(t), & t>0 \\ F(t)=A-\int_0^\omega \beta(a)p(t,a)da, & t>0 \end{cases} \tag{2.1}$$

where $p(t,a)$ denotes the density of adults of age a at time t, A the total area of available substrate and $F(t)$ be the size of free space available by the larvae at time t, k the instantaneous settling rate per unit of free space, $\beta(a)$ the size of individual of age a, $\mu(a)$ the age-specific death rate and ω the upper bound of age of individuals. Here we modify the original model formulation by Roughgarden et al. such that the maximum attainable age of individuals is finite, since it is biologically more reasonable assumption.

Then it is natural to assume that $\beta\in L_+^\infty(0,\omega)$, $\mu(a)$ is positive for all $a\in[0,\omega]$, locally integrable on $[0,\omega)$ and it follows that $\int_0^\omega\mu(\sigma)d\sigma=\infty$. This condition is needed to make the maximum attainable age to be finite. In fact, the survival rate (the proportion of newly settled larvae who can survive to age a) is given by $\ell(a):=\exp\left(-\int_0^a\mu(\sigma)d\sigma\right)$. Under the above assumption, the natural state space of the age density function may be $\left\{p\in L_+^1(0,\omega):\int_0^\omega\mu(a)p(a)da<\infty, \int_0^\omega\beta(a)p(a)da\le A\right\}$.

Here we briefly summarize mathematical features of the basic linear model (2.1). For another kind of treatments for this system, the reader may refer to Roughgarden et al. (1985), Kuang and So (1995), Zhang and Freedman (1999) and Zhang et al. (1999).

First in order to avoid mathematical troubles about the singularity of μ, let us factor out the natural death rate in the basic model (2.1). Define a new function $q(t,a)$ by $p(t,a)=\ell(a)q(t,a)$. Then it is easy to see that the system (2.1) can be reduced to a simpler system for q as follows:

$$\begin{cases} \frac{\partial q(t,a)}{\partial t}+\frac{\partial q(t,a)}{\partial a}=0, & t>0,\ 0<a<\omega, \\ q(t,0)=k\left(A-\int_0^\omega\phi(a)q(t,a)da\right), & t>0 \\ q(0,a)=\frac{p_0(a)}{\ell(a)}\in L_+^1(0,\omega), \end{cases} \tag{2.2}$$

where $\phi(a):=\beta(a)\ell(a)$ is the expected space size occupied by the population at age a and we assume that $p_0/\ell\in L_+^1(0,\omega)$. For this new system, it is natural to assume that the age density function $t\to q(t,*)$ takes a value in $L_+^1(0,\omega)$.

Next it is easy to see that for the model (2.2), there always exists a unique positive steady state as $q^*(a)=\frac{kA}{1+k\int_0^\omega\phi(a)da}$. In order to rewrite the basic model so as to have a homogeneous boundary condition, let us introduce a new variable $u(t,a)$ as $u(t,a) = q(t,a) - q^*(a)$. Then the system (2.8)-(2.10) can be written into the following homogeneous system:

$$\begin{cases} \frac{\partial u(t,a)}{\partial t} + \frac{\partial u(t,a)}{\partial a} = 0, & t > 0,\ 0 < a < \omega, \\ u(t,0) = -k \int_0^\omega \phi(a) u(t,a) da, & t > 0, \\ u(0,a) = q_0(a) - q^*(a), & a \geq 0. \end{cases} \tag{2.3}$$

Therefore we know that Roughgarden et al.'s model is reduced to a linear homogeneous age-dependent population system in L^1 , and that the well known argument for Lotka's stable population model can be applied to this new system.

Integrating the McKendrick equation in (2.3) along the characteristic line, we obtain the following expression:

$$u(t,a) = \begin{cases} b(t-a), & t-a > 0 \\ u_0(a-t), & t-a < 0 \end{cases} \tag{2.4}$$

where $b(t) := u(t,0)$. Inserting (2.4) into the boundary condition in (2.3), we have a renewal integral equation as

$$b(t) = -g(t) - k \int_0^t \phi(a) b(t-a) da, \tag{2.5}$$

where $g(t)$ is defined by

$$g(t) = \begin{cases} k \int_t^\omega \phi(a) u_0(a-t) da, & t < \omega \\ 0, & t > \omega \end{cases} \tag{2.6}$$

and we extend the domain of $\phi(a)$ such that $\phi(a) = 0$ for $a > \omega$.

Let Λ be the set of characteristic roots as $\Lambda := \{\lambda \in \mathbf{C} : 1 + k\hat{\phi}(\lambda) = 0\}$ where $\hat{\phi}$ denotes the Laplace transform of ϕ, that is, $\hat{\phi}(\lambda) := \int_0^\infty e^{-\lambda a} \phi(a) da$.

In the similar manner as in the traditional stable population theory (see Iannelli 1995), we can prove the following proposition, for its proof the reader may refer to Huang (1990) and Zhang et al. (1999):

Proposition 2. 1 *$\Lambda \cap \mathbf{R} = \emptyset$ and Λ are composed of countable infinite number of discrete, complex conjugate pairs. For any real number α, there is at most finitely many roots in the right half plane $\Re\lambda > \alpha$, then there is a dominant pair whose real part is grater than real part of any other characteristic root.*

On the other hand the solution of (2.5) can be obtained by the inverse Laplace transformation:

$$b(t) = -\frac{1}{2\pi i} \int_{\sigma - i\infty}^{\sigma + i\infty} \frac{\hat{g}(\lambda) e^{\lambda t}}{1 + k\hat{\phi}(\lambda)} d\lambda, \tag{2.7}$$

where σ is a real number such that $\sigma > \max\{\Re\lambda : \lambda \in \Lambda\}$. Let λ_0 and $\bar{\lambda}_0$ be the dominant pair. Then it follows that

$$\begin{aligned} b(t) &= b_0 e^{\lambda_0 t} + \bar{b}_0 e^{\bar{\lambda}_0 t} + O(e^{(\Re\lambda_0 - \epsilon)t}) \\ &= e^{\Re\lambda_0 t} [\Re b_0 \cos(\Im\lambda_0 t) - \Im b_0 \sin(\Im\lambda_0 t)] + O(e^{(\Re\lambda_0 - \epsilon)t}), \end{aligned} \tag{2.8}$$

where $\epsilon > 0$ is a small number such that $\{\lambda : \lambda \in \Lambda \setminus \{\lambda_0, \bar{\lambda}_0\}\} \subset \{\lambda : \Re\lambda \leq \Re\lambda_0 - \epsilon\}$ and b_0 is given by

$$b_0 := \frac{\int_0^\omega e^{-\lambda_0 t} g(t) dt}{k \int_0^\omega a e^{-\lambda_0 a} \phi(a) da}. \tag{2.9}$$

For the proof of the above statements, the reader may refer to Iannelli (1995).

Hence asymptotically the dominant part of the solution of the basic model (2.1) is given as

$$\ell(a) q^*(a) + e^{\Re\lambda_0 (t-a)} \ell(a) [\Re b_0 \cos(\Im\lambda_0 (t-a)) - \Im b_0 \sin(\Im\lambda_0 (t-a))], \tag{2.10}$$

then there is no Malthusian solution, and the steady state is globally asymptotically stable if $\Re\lambda_0 < 0$, it is unstable if $\Re\lambda_0 > 0$. Moreover the following *fifty percent free space rule* for stability holds (Roughgarden et al. 1985):

Proposition 2. 2 *Let π be the proportion of free space at the steady state:*

$$\pi := \frac{F^*}{A} = \frac{1}{1 + k\int_0^\omega \phi(a)da}. \tag{2.11}$$

Then if $\pi > 1/2$, the steady state is globally asymptotically stable.

Proof. Suppose that $\pi > 1/2$ and there exists a characteristic root $\lambda = x + iy$ with $x \geq 0$. Then it follows that

$$1 = k\left|\int_0^\omega e^{-\lambda a}\phi(a)da\right| \leq k\int_0^\omega e^{-xa}\phi(a)da \leq k\int_0^\omega \phi(a)da = \frac{1}{\pi} - 1.$$

This contradicts to our assumption. □

Note that the condition $\pi > 1/2$ can be rewritten as follows

$$R_0 := k\int_0^\omega \phi(a)da < 1. \tag{2.12}$$

The number R_0 denotes the basic reproduction number of free space, that is, the expected total area ever occupied by settled larvae per unit free space. As is already known in human demography (Frauenthal 1975), there is the possibility that the characteristic equation has a pair of characteristic root with positive real part if k is large enough. Wachter (1991) has pointed out that for the Lotka type characteristic equation, the existence of a span of ages before the onset of reproduction is sufficient to show the existence of characteristic root with nonnegative real part. For our model, we can prove the following destability result, while its proof is given in Appendix:

Proposition 2. 3 *Suppose that there is a number $0 < \alpha < \omega$ such that $\phi(a) = 0$ for $a \in [0, \alpha]$ and ϕ is a nonnegative, bounded and integrable function on $[0, \omega]$. Then the characteristic equation*

$$k\int_\alpha^\omega e^{-\lambda a}\phi(a)da = -1, \tag{2.13}$$

has a complex root with positive real part for sufficiently large $k > 0$.

Therefore if the growth of occupied area of settled larvae can be neglected in a age span $[0, \alpha]$, the linear system will be destabilized when the settling rate becomes larger. If there exists a characteristic root with positive real part, the amplitude of the oscillatory solution of (2.1) will grow infinitely, and the physical constraint $0 \leq F(t) \leq A$ will be destroyed and the linear model no longer work.

As was pointed out by Roughgarden et al., the above shortcoming will be overcome if we assume more realistically that the mortality of adult population increases as the free space decreases. Moreover, by numerical simulation, Roughgarden et al. found that the destabilization of the steady state of the density dependent model could lead a limit cycle as the free space become exhausted. Hence in the following we introduce the density dependent mortality into the model and examine its behavior.

3 The nonlinear model

First we extend the basic model such that it has the density dependent mortality. Let $\mu(a)$ be the natural death rate at age a and $\delta(a, S(t))$ be the extra death rate of settled population with free space $A - S$ and age a, where $S(t)$ denote the size of occupied space:

$$S(t) := \int_0^\omega \beta(a)p(t, a)da. \tag{3.1}$$

Then the basic model is formulated by the following system:

$$\begin{cases} \frac{\partial p(t,a)}{\partial t} + \frac{\partial p(t,a)}{\partial a} = -(\mu(a) + \delta(a, S(t)))p(t,a), & t > 0, \ a \in [0, \omega] \\ p(t,0) = k(A - S(t)), & t > 0 \\ p(0,a) = p_0(a), & a \in [0, \omega], \end{cases} \tag{3.2}$$

where p_0 is a given initial data.

Observe that if we define formally the size-dependent age-specific birth rate $m(a, S)$ by

$$m(a, S) := \frac{k(A - S)}{S}\beta(a), \tag{3.3}$$

then, as was pointed out by Roughgarden et al. (1985), the system (3.2) can be formally rewritten as the Gurtin's and MacCamy's nonlinear age-dependent population model (Gurtin and MacCamy 1974):

$$\begin{cases} \frac{\partial p(t,a)}{\partial t} + \frac{\partial p(t,a)}{\partial a} = -(\mu(a) + \delta(a, S(t)))p(t,a), \\ p(t,0) = \int_0^\omega m(a, S(t))p(t,a)da, \\ S(t) = \int_0^\omega \beta(a)p(t,a)da. \end{cases} \tag{3.4}$$

Then the demographic basic reproduction number corresponding to the weighted population size S, denoted by $R_0(S)$, is given as follows:

$$R_0(S) = \int_0^\omega m(a, S)e^{-\int_0^a (\mu(\sigma)+\delta(\sigma,S))d\sigma}da. \tag{3.5}$$

Due to the singularity of the size-dependent birth rate m at $S = 0$, the population with size zero has an infinitely large reproductivity, which reflects the fact that newly settled larvae are recruited from the environment. Hence we can not apply the general theory of nonlinear age-dependent population dynamics to our open marine population model.

Next note that it will be intuitively clear that if the growth rate of the size of individual is high enough, the positivity of the birth rate will be lost in the model. To avoid this inappropriate nature of the basic model, we adopt the following reasonable assumption:

Assumption 3. 1

(1) For any fixed $x \in [0, A]$, $\delta(a, x)$ is positive and bounded on $[0, \omega]$ and $\delta(a, x)$ is differentiable with respect to x and there exist numbers $\bar{\delta}$ and $M > 0$ such that

$$0 \le \delta(a, x) \le \bar{\delta}, \quad 0 \le \frac{\partial \delta(a, x)}{\partial x} \le M, \tag{3.6}$$

for almost all $(a, x) \in [0, \omega] \times [0, A]$.

(2) β is differentiable, positive and bounded function on $[0, \omega]$ and

$$(\mu(a) + \delta(a, 0))\beta(a) \le \beta'(a) \le (\mu(a) + \delta(a, A))\beta(a), \tag{3.7}$$

for almost all $a \in [0, \omega]$ and $\beta(0) = 0$.

Just the same as the linear case, in order to make mathematical treatment easier, let us factor out the natural death rate in the basic model (3.2). Define a new function $q(t, a)$ by $p(t, a) = \ell(a)q(t, a)$ where $\ell(a)$ is the survival function given by $\ell(a) := \exp(-\int_0^a \mu(\sigma)d\sigma)$. Then it is easy to see that the system (3.2) can be reduced to a simpler one as follows:

$$\begin{cases} \frac{\partial q(t,a)}{\partial t} + \frac{\partial q(t,a)}{\partial a} = -\delta(a, S(t))q(t,a), & t > 0, \ a \in [0, \omega] \\ q(t,0) = k(A - S(t)), & t > 0 \\ S(t) = \int_0^\omega \phi(a)q(t,a)da, & t > 0 \\ q(0,a) = \frac{p_0(a)}{\ell(a)} \in L^1_+(0, \omega), \end{cases} \tag{3.8}$$

where $\phi(a) := \beta(a)\ell(a)$ is the expected space size occupied by the population at age a. Naturally we can define the state space of the new system (3.9) as

$$\Omega := \left\{ q \in L^1_+(0,\omega) : \int_0^\omega \phi(a)q(a)da \le A \right\}. \tag{3.9}$$

In order to be a biologically meaningful model, the solution of the system (3.9) must be in the state space Ω if $q_0 \in \Omega$. Under the Assumption 3.1, if $q_0 \in \Omega$, the nonnegative solution of the system (3.9), as long as it exist, will stay in the state space Ω. In fact if we integrate by parts, we obtain that

$$\begin{aligned}\frac{dS(t)}{dt} &= \int_0^\omega \beta(a)\ell(a)\left(-\frac{\partial}{\partial a} - \delta(a, S(t))\right) q(t,a)da \\ &= \int_0^\omega (\beta'(a) - (\mu(a) + \delta(a, S(t)))\beta(a))\ell(a)q(t,a)da.\end{aligned}$$

Then it follows from Assumption 3.1, $S(t)$ is bounded in the interval $[0, A]$ for all $t \ge 0$, because $S' \le 0$ at the neighborhood of $S = A$ and $S' \ge 0$ at the neighborhood of $S = 0$.

4 The semigroup solution

In the following we mainly consider the new system (3.9). First observe that the system (3.9) has a unique positive steady state. Let $q^*(a)$ be a steady state solution for the system (3.9) and let S^* be the corresponding size of occupied space. Then we have

$$\begin{cases} q^*(a) = q^*(0)e^{-\int_0^a \delta(\sigma, S^*)d\sigma}, \\ q^*(0) = k(A - S^*) = k\left(A - \int_0^\omega \phi(a)q^*(a)da\right) \end{cases} \tag{4.1}$$

Then it is easy to see that

$$R_0(S^*) = 1, \tag{4.2}$$

$$q^*(a) = \frac{S^* e^{-\int_0^a \delta(\sigma,S^*)d\sigma}}{\int_0^\omega \phi(a)e^{-\int_0^a \delta(\sigma,S^*)d\sigma}da} = k(A - S^*)e^{-\int_0^a \delta(\sigma,S^*)d\sigma}. \tag{4.3}$$

That is, if the equation (4.2) has a positive root $S^* > 0$, the corresponding steady state is given by (4.3). Since $R_0(S)$ is a monotone decreasing function and it decreases from infinity to zero when S moves from zero to infinity, hence we can conclude that (4.2) has a unique positive root, which provides the steady space size occupied by the steady population q^*.

By using the steady state solution, we can rewrite the basic system (3.9) as a semilinear Cauchy problem. Let us define a new variable $u(t,a)$ as $u(t,a) := q(t,a) - q^*(a)$ where $p^*(a)$ is a stationary solution of (3.9). Then the system (3.9) can be written as the following new system of $u(t,a)$:

$$\begin{cases} \frac{\partial u(t,a)}{\partial t} + \frac{\partial u(t,a)}{\partial a} = -\delta(a, q^* + G(u))(q^*(a) + u(a)) - q^*_a(a), \\ u(t,0) = -kG(u), \\ u(0,a) = u_0(a) := q_0(a) - q^*(a), \end{cases} \tag{4.4}$$

where $G(u)$ is given by

$$G(u) := \int_0^\omega \phi(a)u(a)da, \tag{4.5}$$

and we formally extend the domain of $\delta(a,x)$ as

$$\delta(a,x) = \begin{cases} \delta(a,A), & \text{for } x > A, \\ \delta(a,0), & \text{for } x < 0. \end{cases} \tag{4.6}$$

Therefore we can formulate the basic model as a semilinear Cauchy problem in L^1 as follows:

$$u'(t) = Au(t) + F(u(t)), \tag{4.7}$$

where the differential operator A and the nonlinear operator F are defined by

$$\begin{cases} (Au)(a) := -\frac{du(a)}{da}, \\ \mathcal{D}(A) := \{f \in W^{1,1}(0,\omega) : f(0) = -kG(f)\} \\ (Ff)(a) := -\delta(a, q^* + G(f))(q^*(a) + f(a)) - q^*_a(a), \end{cases} \tag{4.8}$$

where $\mathcal{D}(A)$ denotes the domain of differential operator A. It is well known that the linear operator A generates a strongly continuous semigroup $T_0(t) = e^{tA}$ and it has a compact resolvent (Webb 1984, 1985).

Moreover under the Assumption 3.1, the bounded nonlinear operator F is locally Lipschitz continuous, so a weak local solution of (4.7) is given by a continuous solution of the variation of constants formula as

$$u(t) = T_0(t)u_0 + \int_0^t T_0(t-s)F(u(s))ds. \tag{4.9}$$

Then we can define the semiflow $T(t)$ by $T(t)u_0 = u(t)$. If $q_0 \in \mathcal{D}(A)$, then the weak solution given by (4.9) becomes a classical solution (Pazy 1983). Let ω_0 be the growth bound of the linear semigroup e^{tA} such that

$$\|T_0(t)\| \le e^{\omega_0 t}. \tag{4.10}$$

It follows from (4.9) that

$$\|u(t)\| \le e^{\omega_0 t}\|u_0\| + \int_0^t e^{\omega_0(t-s)}[\bar{\delta}(\|q^*\| + \|u(s)\|) + \|q^*_a\|]ds. \tag{4.11}$$

Then it is easy to see that

$$\|u(t)\| \le (\|u_0\| + \omega^{-1}(\bar{\delta}\|q^*\| + \|q^*_a\|))e^{(\omega_0+\bar{\delta})t}. \tag{4.12}$$

Therefore the norm of the weak solution grows at most exponentially, so we know that the local solution can be extended to the global solution defined for all $t \in [0,\infty)$. Then the solution of the system (3.9) can be obtained by $q(t,a) = q^*(a) + u(t,a)$, which stays in Ω if $q_0 \in \Omega$ as we have shown in the last of section 3. Thus we obtain the following result:

Proposition 4. 1 *Suppose that there exists $q_0 \in \Omega$ such that the initial data for the original system (3.1) is given as $p_0(a) = \ell(a)q_0(a)$. Then if $q_0 \in \mathcal{D}(A)$, then the unique global solution for (3.1) is given by*

$$p(t,a) = \ell(a)(q^*(a) + (T(t)u_0)(a)), \tag{4.13}$$

where $T(t)$ is the semiflow defined by (4.9) and $u_0 := q_0 - q^*$.

5 Stability of equilibria

In this section we mainly consider conditions for stability and instability of the steady state of (3.9). The linearized system of (4.7) is given as

$$u'(t) = (A + F'[0])u, \tag{5.1}$$

$$(F'[0]u)(a) := -\delta(a, S^*)u(a) - \delta_x(a, S^*)q^*(a)G(u). \tag{5.2}$$

In order to investigate the stability of the equilibrium, let us consider the resolvent equation for $A + F'[0]$:

$$(\lambda - (A + F'[0]))u = f, \quad u \in \mathcal{D}(A), \ f \in L^1, \ \lambda \in \mathbf{C}. \tag{5.3}$$

Then we obtain

$$u'(a) + (\lambda + \delta(a, S^*))u(a) + \delta_x(a, S^*)q^*(a)G(u) = f(a), \tag{5.4}$$

$$u(0) = -kG(u). \tag{5.5}$$

By formal integration, we have the following expression:

$$u(a) = -kG(u)e^{-\lambda a - \int_0^a \delta(\sigma,S^*)d\sigma} \tag{5.6}$$

$$- \int_0^a e^{-\lambda(a-s) - \int_s^a \delta(\sigma,S^*)d\sigma}[f(s) + \delta_x(s,S^*)q^*(s)G(u)]ds.$$

From the above expression, we can calculate $G(u)$ as

$$G(u) = -(1-\Delta(\lambda))^{-1}\int_0^\omega \phi(a)\int_0^a e^{-\lambda(a-s)-\int_s^a \delta(\sigma,S^*)d\sigma} f(s)dsda, \tag{5.7}$$

where the complex function $\Delta(\lambda)$ is given by

$$\Delta(\lambda) := -k\int_0^\omega \phi(a)e^{-\lambda a - \int_0^a \delta(\sigma,S^*)d\sigma}da \tag{5.8}$$

$$- \int_0^\omega \phi(a)\int_0^a e^{-\lambda(a-s)-\int_s^a \delta(\sigma,S^*)d\sigma}\delta_x(s,S^*)q^*(s)dsda.$$

Here we note that integrals in (5.8) can be rewritten as follows:

$$\int_0^\omega \phi(a)\int_0^a e^{-\lambda(a-s)-\int_s^a \delta(\sigma,S^*)d\sigma}\delta_x(s,S^*)q^*(s)dsda$$

$$= \int_0^\omega \phi(a)\int_0^a e^{-\lambda z - \int_{a-z}^a \delta(\sigma,S^*)d\sigma}\delta_x(a-z,S^*)q^*(a-z)dzda$$

$$= \int_0^\omega e^{-\lambda z}dz\int_z^\omega \phi(a)e^{-\int_{a-z}^a \delta(\sigma,S^*)d\sigma}\delta_x(a-z,S^*)q^*(a-z)da$$

$$= \int_0^\omega e^{-\lambda z}dz\int_z^\omega \phi(a)q^*(a)\delta_x(a-z,S^*)da,$$

$$k\int_0^\omega \phi(a)e^{-\lambda a - \int_0^a \delta(\sigma,S^*)d\sigma}da = \int_0^\omega \phi(a)e^{-\lambda a}\frac{q^*(a)}{A-S^*}da,$$

where we use the expression (4.1). Then we obtain an expression of the characteristic equation as follows:

$$\Delta(\lambda) = -\int_0^\omega e^{-\lambda a}q^*(a)\Phi(a)da = 1, \tag{5.9}$$

where $\Phi(a)$ is defined by

$$\Phi(a) := \frac{\phi(a)}{A-S^*} + \int_a^\omega \frac{q^*(s)}{q^*(a)}\phi(s)\delta_x(s-a,S^*)ds. \tag{5.10}$$

Then we can easily conclude that

Proposition 5. 1 *If $\Delta(0) > -1$, then the steady state is locally asymptotically stable.*

Proof. It is sufficient to show that under the condition, all characteristic roots have negative real parts. If there is a characteristic root λ with $\Re\lambda \geq 0$, it follows that

$$1 = |\Delta(\lambda)| \leq \int_0^\omega q^*(a)\Phi(a)da = -\Delta(0),$$

which contradicts our assumption. Then there is no characteristic root with nonnegative real part if $\Delta(0) > -1$. □

Observe that

$$-\Delta(0) = \int_0^\omega q^*(a)\Phi(a)da = \frac{S^*}{A - S^*} + \int_0^\omega da \int_a^\omega q^*(s)\phi(s)\delta_x(s-a, S^*)ds$$

$$= \frac{S^*}{A - S^*} + \int_0^\omega q^*(s)\phi(s)\int_0^a \delta_x(s, S^*)dsda.$$

Therefore the condition $\Delta(0) > -1$ is equivalent to the following condition

$$\frac{S^*}{A - S^*} + \int_0^\omega q^*(a)\phi(a)\int_0^a \delta_x(s, S^*)dsda < 1. \tag{5.11}$$

For example, it follows from the Assumption 3.1. that

$$\int_0^\omega q^*(s)\phi(s)\int_0^a \delta_x(s, S^*)dsda \le S^* M\omega. \tag{5.12}$$

Therefore if

$$\frac{S^*}{A - S^*} + M\omega S^* < 1, \tag{5.13}$$

then the steady state is locally asymptotically stable. By solving the quadratic inequality (5.13), we know that the steady state is locally asymptotically stable if the occupied area satisfies the following:

$$0 < S^* < \frac{1}{M\omega} + \frac{A}{2} - \sqrt{\frac{1}{(M\omega)^2} + \frac{A^2}{4}}. \tag{5.14}$$

Note that the above condition is consistent with the 50 percent free space rule, since if $M \to 0$ the right hand side of (5.14) approaches to $A/2$. On the other hand, if M is large, S^* must be very small to satisfy (5.14). Roughly speaking, we can conclude that the steady state is locally asymptotically stable as long as its free space is large enough.

We have already known that if there is no density dependence in mortality, the linear system can be destabilized if the settling rate becomes large enough. Hence if the extra death rate is small enough, we can conjecture that the steady state of the nonlinear system could also become unstable.

6 Discussion

In this paper, we have mainly considered the Roughgarden et al.'s model with density dependent mortality and analyse its mathematical properties. In the nonlinear model (3.2)-(3.4), some aspects are still neglected for simplification of the model. In more realistic models, $\beta(a)$ may depend on $F(t)$ and k also may depend on the abundance of larvae in the pool, which are reproduced by adult populations. Moreover, it is so far implicitly assumed that the abundance of larvae in the pool is not affected by the settlements of larvae in the local area. Roughgarden and Iwasa (1986) have formulated a metapopulation model for sessile marine populations which takes into account the dynamics of the abundance of larvae in the pool. We will take up the Roughgarden-Iwasa model and the model with density-dependent growth rate in a separate paper.

7 Appendix

Proof of Proposition 2.3 Let us define real functions $u(x,y)$ and $v(x,y)$, $x,y\in\mathbf{R}$ as follows:

$$u(x,y)=\int_\alpha^\omega e^{-xa}\cos(ya)\phi(a)da,\quad v(x,y)=\int_\alpha^\omega e^{-xa}\sin(ya)\phi(a)da. \tag{7.1}$$

If we let $\lambda=x+iy$, then the characteristic equation can be written as

$$u(x,y)-iv(x,y)=-\frac{1}{k}. \tag{7.2}$$

Hence if there exist $x_0\geq 0$ and $y_0\in\mathbf{R}$ such that $v(x_0,y_0)=0$ and $u(x_0,y_0)<0$, then (2.13) has a root x_0+iy_0 for $k=-1/u(x_0,y_0)>0$. Let us choose real numbers β_1, β_2 and γ such that $\alpha<\beta_1<\beta_2$ and $\beta_2/\alpha<\gamma<3/2$. Next we fix an interval $I:=[\pi/\beta_2,\gamma\pi/\beta_2]$. First we prove that there exists $x_0\geq 0$ and y_0 such that $v(x_0,y_0)=0$. For any $x\geq 0$, observe that $v(x,y)=v_1(a,y)+v_2(x,y)+v_3(x,y)$ where

$$v_1(x,y):=\int_\alpha^{\beta_1} e^{-xa}\sin(ya)\phi(a)da,\quad v_2(x,y):=\int_{\beta_1}^{\beta_2} e^{-xa}\sin(ya)\phi(a)da,$$

$$v_3(x,y):=\int_{\beta_2}^{\omega} e^{-xa}\sin(ya)\phi(a)da.$$

If $a\in[\alpha,\beta_1]$, then we have $\frac{\pi}{\beta_2}a\in[\frac{\alpha\pi}{\beta_2},\frac{\pi\beta_1}{\beta_2}]\subset(\frac{2\pi}{3},\pi)$, $\frac{\gamma\pi}{\beta_2}a\in[\frac{\gamma\alpha\pi}{\beta_2},\frac{\gamma\pi\beta_1}{\beta_2}]\subset(\pi,\frac{3\pi}{2})$. Therefore it follows that $v_1(x,\frac{\pi}{\beta_2})>0$ and $v_1(x,\frac{\gamma\pi}{\beta_2})<0$. Next if $a\in[\beta_1,\beta_2]$, we obtain that $\frac{\pi}{\beta_2}a\in[\frac{\beta_1\pi}{\beta_2},\pi]$, $\frac{\gamma\pi}{\beta_2}a\in[\frac{\gamma\beta_1\pi}{\beta_2},\gamma\pi]\subset(\pi,\frac{3\pi}{2})$. Therefore it follows that $v_2(x,\frac{\pi}{\beta_2})>0$ and $v_2(x,\frac{\gamma\pi}{\beta_2})<0$. Finally it is easily seen that $|v_3(x,y)|\leq e^{-\beta_2 x}\|\phi\|_{L^1}$. From the above inequalities, we have

$$v(x,\frac{\pi}{\beta_2})>v_1(x,\frac{\pi}{\beta_2})-|v_3(x,\frac{\pi}{\beta_2})|\geq e^{-\beta_1 x}\int_\alpha^{\beta_1}\phi(a)\sin(\frac{\pi a}{\beta_2})da-e^{-\beta_2 x}\|\phi\|_{L^1}$$

$$=e^{-\beta_1 x}\left(\int_\alpha^{\beta_1}\phi(a)\sin(\frac{\pi a}{\beta_2})da-e^{-(\beta_2-\beta_1)x}\|\phi\|_{L^1}\right).$$

$$v(x,\frac{\gamma\pi}{\beta_2})<v_1(x,\frac{\gamma\pi}{\beta_2})+|v_3(x,\frac{\gamma\pi}{\beta_2})|\leq e^{-\beta_1 x}\int_\alpha^{\beta_1}\phi(a)\sin(\frac{\gamma\pi a}{\beta_2})da+e^{-\beta_2 x}\|\phi\|_{L^1}$$

$$=e^{-\beta_1 x}\left(\int_\alpha^{\beta_1}\phi(a)\sin(\frac{\gamma\pi a}{\beta_2})da+e^{-(\beta_2-\beta_1)x}\|\phi\|_{L^1}\right).$$

Therefore we can choose a very large $x_0>0$ such that $v(x_0,\frac{\pi}{\beta_2})>0$ and $v(x_0,\frac{\gamma\pi}{\beta_2})<0$, since

$$\int_\alpha^{\beta_1}\phi(a)\sin(\frac{\pi a}{\beta_2})da>0,\ \int_\alpha^{\beta_1}\phi(a)\sin(\frac{\gamma\pi a}{\beta_2})da<0.$$

It follows from the mean value theorem that there exists $y_0\in I$ such that $v(x_0,y_0)=0$.

Next we show that if we take x_0 so large, $u(x_0,y_0)<0$. Again we divide the integral of u into three parts: $u(x,y)=u_1(a,y)+u_2(x,y)+u_3(x,y)$, where

$$u_1(x,y):=\int_\alpha^{\beta_1} e^{-xa}\cos(ya)\phi(a)da,\quad u_2(x,y):=\int_{\beta_1}^{\beta_2} e^{-xa}\cos(ya)\phi(a)da,$$

$$u_3(x,y):=\int_{\beta_2}^{\omega} e^{-xa}\cos(ya)\phi(a)da.$$

If $a \in [\alpha, \beta_1]$ and $y \in I$, then we have $ya \in [\frac{\alpha\pi}{\beta_2}, \frac{\gamma\pi\beta_1}{\beta_2}] \subset (\frac{2\pi}{3}, \frac{3}{2}\pi)$. Therefore it follows that $u_1(x,y) < 0$. Next if $a \in [\beta_1, \beta_2]$ and $y \in I$, we obtain that $ya \in [\frac{\beta_1\pi}{\beta_2}, \gamma\pi] \subset (\frac{2\pi}{3}, \frac{3\pi}{2})$. Then it follows that $u_2(x,y) < 0$. Finally we have $|u_3(x,y)| \le e^{-\beta_2 x}\|\phi\|_{L^1}$. From the above inequalities, we have

$$u(x,y) < u_1(x,y) + |u_3(x,y)| \le e^{-\beta_1 x}\int_\alpha^{\beta_1} \phi(a)\cos(ya)da + e^{-\beta_2 x}\|\phi\|_{L^1}$$

$$= e^{-\beta_1 x}\left(\int_\alpha^{\beta_1} \phi(a)\cos(ya)da + e^{-(\beta_2-\beta_1)x}\|\phi\|_{L^1}\right).$$

Therefore we conclude that for sufficiently large $x > 0$, $u(x,y) < 0$. Note that

$$\frac{\partial v}{\partial y} = \int_\alpha^\omega ae^{-xa}\phi(a)\cos(ya)da.$$

In the same manner as above, we can prove that for large $x > 0$, $\partial v/\partial y < 0$ for $y \in I$. Thus we know that for sufficiently large $x_0 > 0$, v is monotone decreasing with respect to $y \in I$ and there exists a unique $y_0 \in I$ such that $v(x_0, y_0) = 0$ and $u(x_0, y_0) < 0$. This completes our proof. □

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