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WELL-POSEDNESS ANALYSIS FOR A SIZE-STRUCTURED MODEL OF SPECIES IN A SPACE-LIMITED HABITAT*

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Abstract We present a size-structured population model to describe marine invertebrates whose life stage is composed of sessile adults and pelagic larvae. The model is a nonlinear coupled system of size distribution of adults and the abundance of larvae. The existence and uniqueness of non-negative solutions to the model are proved by means of the theory of non-densely defined operators, which lays a solid foundation for the investigation of other problems such as stability and control.

Keywords Space-limitation, size-structure, non-densely defined operator, basic reproduction number.

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1. Introduction

Understanding the dynamics of marine invertebrates (e.g. Corals and Barnacles) is quite significant in ecology (see Knowlton etc. [10], Hughes [7] and the Ref.s therein). The life history of such kind of populations consists of two phases: sessile adults and pelagic larvae. Adults occupy hard space of the free area in reefs and produce larvae when they reach maturity, while larvae move freely from one area to another. Roughgarden etc. [14] proposed an age-structured model for populations living in a local area, obtained conditions for the local stability of the unique steady state, and suggested by numerical examples that the steady state could be destabilized if the settlement rate is sufficiently high and oscillations should be possible. Their model should be thought as an open system since the larvae may not be released by the adults in the same pool. This model has been further developed or extended by Bence [2], Kuang [11], Zhang etc. [18] and Inaba [8]. In 2005, Kamioka [9] developed a rigorous mathematical approach to a closed age-structured population model with space-limited recruitment, which can be seen as a non-linear extension of the Roughgarden-Iwasa model.

Field researches during the last fifty years show that, for many populations such as wild animals, plants and marine invertebrates, demographic and life history processes (e.g. growth, reproduction and death) depend on the size of individuals rather than age. Individual's size is better than age to estimate the ecological and commercial values in ecology and resources economy. For these reasons, there have

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been many attempts to construct size-structured models (see e.g. Sinko etc. [15] and Artzy-Randruo etc. [1]). Although several discrete size-time models have been formulated for populations in space-limited habitats (see e.g. Pascual etc. [13]), there are only few attempts, however, to analyze continuous time size-structured model with space-limited recruitment, since a rigorous mathematical analysis of continuous size-structured models usually involves some considerable complexities. Artzy-Randrup et al. proposed a continuous size-time model in [1], and concentrated on the local stability analysis of the steady state, based on several different forms of growth rate functions.

In the present paper, we formulate a size-structured model for marine invertebrates, and study its dynamical behaviors by means of operator theoretical methods. The paper is organized as follows. In section 2, we propose the basic nonlinear model, which is an initial-boundary problem of an integro-differential equations system. Section 3 is devoted to the treatment of existence and uniqueness of non-negative solutions to the model via a non-densely defined operator theory, the final section contains some remarks.

2. The population model

In this paper, we propose the following size-structured model to describe the evolution of the target population:

$$p_t(s,t) + (g(s)p(s,t))_s = -\mu(s)p(s,t) - \delta(s,Q(t))p(s,t),\ t>0,\ 0<s<m, \tag{2.1}$$

$$g(0)p(0,t) = c(M-Q(t))L(t),\ t>0, \tag{2.2}$$

$$\frac{\mathrm{d}}{\mathrm{d}t}L(t) = -(v + c(M-Q(t)))L(t) + \int_0^m \beta(s)p(s,t)\mathrm{d}s,\ t>0, \tag{2.3}$$

$$p(s,0) = p_0(s),\ L(0) = L_0,\ 0 \le s < m, \tag{2.4}$$

$$Q(t) = \int_0^m \gamma(s)p(s,t)\mathrm{d}s,\ t>0, \tag{2.5}$$

where $p(s,t)$ denotes the density of adults of size $s \in (0,m)$ at time $t \in (0,\infty)$, $m > 0$ is the (finite) maximum size of any individual in the population. M denotes the total area of available space and $Q(t)$ the area of occupied space. The vital rates $\mu(s)$, $\beta(s)$ and $g(s)$ denote natural mortality, fertility and growth rate, respectively; $\delta(s, Q(t))$ represents the extra death rate, which depends on the area of occupied space $Q(t)$. The quantity $\gamma(s)$ denotes the area occupied by one individual of size s, $L(t)$ denotes the abundance of larvae in the pelagic pool at time t. v stands for the natural death rate of larvae and c the settlement rate per unit area of free space. L_0 and $p_0(s)$ provide the initial data of larvae and adults.

Based on the consideration of biological background and mathematical treatment, the following assumptions will be used throughout this paper:

Assumptions:

(i) $c,\ v,\ M,\ m$ are positive constants and L_0 is non-negative;

(ii) $g(s),\ \beta(s),\ p_0(s)$ are positive and bounded functions on $(0,m)$, and $g(s)$ is differentiable and $g(m) = 0$. Moreover, $\int_0^m \beta(s)p_0(s)\mathrm{d}s > 0$.

(iii) $\mu(s)$ is positive for all $s \in [0,m]$, locally integrable on $[0,m]$ and meets the requirement that $\int_0^m \frac{\mu(s)}{g(s)}\mathrm{d}s = +\infty$, which makes the maximum attainable size to be finite;

(iv) $\delta(s,Q)$ is non-negative and uniformly bounded for $(s,Q)\in[0,m]\times[0,M]$, has the bounded derivative with respect to Q and satisfies $\delta_Q(s,Q):=\frac{\partial\delta(s,Q)}{\partial Q}\geq 0$;

(v) $\gamma(s)$ is differentiable, positive and bounded function on $[0,m]$ with $\gamma(0)>0$ and $\gamma'(s)\leq\frac{\gamma(s)}{g(s)}(\mu(s)+\delta(s,M))$ for almost all $s\in[0,m)$.

Without loss of generality, we assume that the initial size of adult individuals is zero.

The survival rate, i.e., the proportion of newly settled larvae who can survive to size s, is given by

$$l(s):=\exp\left\{-\int_0^s\frac{\mu(r)}{g(r)}\mathrm{d}r\right\}. \tag{2.6}$$

Then, from assumption (iii), we have $l(m)=0,\ l'(s)=-l(s)\frac{\mu(s)}{g(s)}$.

In order to avoid mathematical troubles due to the singularity of the mortality rate μ, let us factor out the natural death rate $\mu(s)$ in the model (2.1)-(2.5). Define a new function $q(s,t)$ by $p(s,t):=q(s,t)l(s)$. Then it is not difficult to see that the system (2.1)-(2.5) can be reduced to a simpler system for $(q(s,t),L(t))$ as follows:

$$q_t(s,t)+(g(s)q(s,t))_s=-\delta(s,Q(t))q(s,t),\ t>0,\ 0<s<m, \tag{2.7}$$

$$g(0)q(0,t)=c(M-Q(t))L(t),\ t>0, \tag{2.8}$$

$$\frac{\mathrm{d}}{\mathrm{d}t}L(t)=-(v+c(M-Q(t)))L(t)+\int_0^m\phi(s)q(s,t)\mathrm{d}s,\ t>0, \tag{2.9}$$

$$q(s,0)=q_0(s):=\frac{p_0(s)}{l(s)},\ L(0)=L_0,\ 0\leq s<m, \tag{2.10}$$

$$Q(t)=\int_0^m\psi(s)q(s,t)\mathrm{d}s,\ t>0, \tag{2.11}$$

where $\phi(s):=\beta(s)l(s)$ is the net reproduction function of the adult population of size s, $\psi(s):=\gamma(s)l(s)$ is the expected space area occupied by an individual.

3. Existence and uniqueness of solutions to the model

In this section we mainly consider the initial-boundary value problem (2.7)-(2.11), and show the existence and uniqueness of solutions for the problem by operator theoretical approach.

Since the problem has the non-linear boundary condition (2.8), it is difficult to analyze directly. We apply the method of Thieme [16] which removes the non-linearity from the domain and incorporates it into the Lipschitz perturbation. Firstly, we define the state space and related operators.

Definition 3.1. Let us introduce a state space $Z:=\mathbb{R}\times L^1(0,m)\times\mathbb{R}$, endowed with the norm $\|z\|_Z=|z_1|+\|z_2\|_{L^1}+|z_3|$ for $z=(z_1,z_2,z_3)^{\mathrm{T}}\in Z$, hereafter α^{T}

denotes the transpose of vector α. We define the following sets:

$$Z_0 := \{(z_1, z_2, z_3)^{\mathrm{T}} \in Z : z_1 = 0\},$$
$$Z_+ := \{(z_1, z_2, z_3)^{\mathrm{T}} \in Z : z_i \geq 0, i = 1, 2, 3\},$$
$$Z_{0+} := Z_0 \cap Z_+,$$
$$\Omega := \{(z_1, z_2, z_3)^{\mathrm{T}} \in Z_+ : \langle \psi, z_2 \rangle \leq M\}, \text{ where } \langle \psi, z_2 \rangle = \int_0^m \psi(s) z_2(s) \mathrm{d}s,$$
$$\Omega_0 := \Omega \cap Z_0 = \{(z_1, z_2, z_3)^{\mathrm{T}} \in Z_{0+} : \langle \psi, z_2 \rangle \leq M\}.$$

We define the linear operator $A : D(A) \subset Z_0 \to Z$,

$$(Au)(s) := \left(-g(0)q(0), \quad -\tfrac{\mathrm{d}}{\mathrm{d}s}(g(s)q(s)) - \delta(s, M)q(s), \quad -(v + cM)L \right), \tag{3.1}$$

where $u = (0, q(s), L)^{\mathrm{T}} \in D(A) := \{(0, q(s), L)^{\mathrm{T}} \in Z_0 : q \in W^{1,1}(0, m)\}$.

Define the non-linear operator $B : Z_0 \to Z$, for $u = (0, q(s), L)^{\mathrm{T}} \in Z_0$,

$$(Bu)(s) := \begin{pmatrix} c(M - Q)L \\ (\delta(s, M) - \delta(s, Q))q(s) \\ cQL + \langle \phi, q \rangle \end{pmatrix}, \ Q = \int_0^m \psi(s) q(s) \mathrm{d}s. \tag{3.2}$$

In order to prove the following Lemma 3.1, we have inserted $\pm\delta(s, M)q(s)$ into the operators A and B.

Based on the above notations, the problem (2.7)-(2.11) can be rewritten as the following abstract semi-linear Cauchy problem with non-densely defined operator A on Z:

$$\frac{\mathrm{d}}{\mathrm{d}t} u(t) = Au(t) + B(u)(t), \ t > 0, \tag{3.3}$$
$$u(0) = u_0 := (0, q_0, L_0)^{\mathrm{T}} \in \Omega_0. \tag{3.4}$$

Since $D(A)$ is non-dense in the whole space Z, we cannot directly apply the Hille-Yosida theory to solve the problem (3.3)-(3.4). Then we consider the weak solution of the following form:

Definition 3.2. A function $u \in C(0, \infty : Z_0)$ is called a weak solution of (3.3)-(3.4), if $\int_0^t u(r)\mathrm{d}r \in D(A)$ for all $t > 0$ and $u(t)$ satisfies

$$u(t) = u_0 + A \int_0^t u(r)\mathrm{d}r + \int_0^t B(u)(r)\mathrm{d}r. \tag{3.5}$$

In order to look for a density of population, we will consider solutions which lie in Ω_0. Hereafter by solution we always mean weak one. Let $\vartheta(Z)$ be the set of all bounded linear operators on Z and $\| \cdot \|_{\vartheta(Z)}$ denote its operator norm.

To prove the existence and uniqueness of solutions to the abstract initial value problem (3.3)-(3.4), we need the following lemma:

Lemma 3.1. *Under the assumptions (i)-(v), operators A and B have the following properties:*

(1) A is closed and $\|(\lambda - A)^{-1}\|_{\vartheta(Z)} \leq \frac{1}{\lambda}$, for all $\lambda > 0$.

(2) $\lambda(\lambda - A)^{-1}$ maps Ω_0 into itself for $\lambda > 0$.

(3) The non-linear operator B is locally Lipschitz continuous on Z_0.

(4) The tangential condition holds: $\lim_{h\to 0^+}\frac{1}{h}\mathrm{dist}(u+hB(u);\Omega)=0$, *for all* $u\in\Omega_0$,

where $\mathrm{dist}(y;\Omega):=\inf_{z\in\Omega}\|y-z\|_Z$.

Proof. (1) It is not difficult to see that A is closed. Then we consider the resolvent equation: $(\lambda-A)u=z,\ \lambda>0$. From (3.1) and Definition 3.1, we get that

$$\begin{pmatrix} g(0)q(0) \\ \lambda q(s)+\frac{\mathrm{d}}{\mathrm{d}s}(g(s)q(s))+\delta(s,M)q(s) \\ \lambda L+(v+cM)L \end{pmatrix} = \begin{pmatrix} z_1 \\ z_2(s) \\ z_3 \end{pmatrix}.$$

It is easy to obtain

$$\begin{aligned} z_1 &= g(0)q(0), \\ q(s) &= \frac{g(0)q(0)}{g(s)}e^{-\lambda\Gamma(s)}\pi(s,M) \\ &\quad + \int_0^s \frac{g(0)z_2(r)}{g(s)g(r)}e^{-\lambda\Gamma(s)}\pi(s,M)\left(\frac{g(0)}{g(r)}e^{-\lambda\Gamma(r)}\pi(r,M)\right)^{-1}\mathrm{d}r \quad (3.6) \\ &= \frac{z_1}{g(s)}e^{-\lambda\Gamma(s)}\pi(s,M)+\int_0^s \frac{z_2(r)}{g(s)}e^{-\lambda(\Gamma(s)-\Gamma(r))}\frac{\pi(s,M)}{\pi(r,M)}\mathrm{d}r, \\ L &= \frac{z_3}{\lambda+v+cM}, \quad (3.7) \end{aligned}$$

where $\Gamma(s)=\int_0^s\frac{1}{g(r)}\mathrm{d}r,\ \pi(s,M)=\exp\left\{-\int_0^s\frac{\delta(r,M)}{g(r)}\mathrm{d}r\right\}$. Thus $(\lambda-A)^{-1}$ is well defined.

Integrating by parts and changing the order of integrals, from (3.6) and (3.7) we get that

$$\begin{aligned} \|q\|_{L^1} &= \int_0^m q(s)\mathrm{d}s \\ &\le |z_1|\int_0^m\frac{e^{-\lambda\Gamma(s)}}{g(s)}\mathrm{d}s+\int_0^m\int_0^s\frac{z_2(r)}{g(s)}e^{-\lambda(\Gamma(s)-\Gamma(r))}\mathrm{d}r\mathrm{d}s \\ &= |z_1|\left(-\frac{1}{\lambda}e^{-\lambda\Gamma(s)}\Big|_0^m\right)+\int_0^m\int_r^m\frac{z_2(r)}{g(s)}e^{-\lambda(\Gamma(s)-\Gamma(r))}\mathrm{d}s\mathrm{d}r \quad (3.8) \\ &\le \frac{|z_1|}{\lambda}+\int_0^m z_2(r)e^{\lambda\Gamma(r)}\left(-\frac{1}{\lambda}e^{-\lambda\Gamma(s)}\Big|_r^m\right)\mathrm{d}r \\ &= \frac{1}{\lambda}(|z_1|+\|z_2\|_{L^1}), \\ |L| &= |\frac{z_3}{\lambda+v+cM}|\le\frac{|z_3|}{\lambda}. \quad (3.9) \end{aligned}$$

Using (3.8) and (3.9), we see $\|(\lambda-A)^{-1}z\|_Z\le\|z\|_Z/\lambda$, and property (1) is proved.

(2) Next let $z=(0,z_2,z_3)^{\mathrm{T}}\in\Omega_0$ and $\lambda>0$. From (3.6) and (3.7), we obtain

$$(\lambda(\lambda-A)^{-1}z)(s)=\begin{pmatrix} 0 \\ \lambda\int_0^s\frac{z_2(r)}{g(s)}e^{-\lambda(\Gamma(s)-\Gamma(r))}\frac{\pi(s,M)}{\pi(r,M)}\mathrm{d}r \\ \frac{\lambda z_3}{\lambda+v+cM}\end{pmatrix}=:\begin{pmatrix} 0 \\ x(s) \\ y\end{pmatrix}\in Z_{0+}.$$

From assumption (iii) and (v), we have $\lim\limits_{s\to m^-}\psi(s)=0,\ \frac{\mathrm{d}}{\mathrm{d}s}(\psi(s)\pi(s,M))\le 0$. By changing the order of integrals and integrating by parts, we obtain that

$$\begin{aligned}\langle\psi,x\rangle &= \int_0^m \lambda\psi(s)\int_0^s \frac{z_2(r)}{g(s)}e^{-\lambda(\Gamma(s)-\Gamma(r))}\frac{\pi(s,M)}{\pi(r,M)}\mathrm{d}r\mathrm{d}s\\ &= \int_0^m \mathrm{d}r\int_r^m \lambda\psi(s)\frac{z_2(r)}{g(s)}e^{-\lambda(\Gamma(s)-\Gamma(r))}\frac{\pi(s,M)}{\pi(r,M)}\mathrm{d}s\\ &= \langle\psi,z_2\rangle+\int_0^m \frac{z_2(r)}{\pi(r,M)}e^{\lambda\Gamma(r)}\mathrm{d}r\int_r^m \frac{\mathrm{d}}{\mathrm{d}s}(\psi(s)\pi(s,M))e^{-\lambda\Gamma(s)}\mathrm{d}s\\ &\le M.\end{aligned} \tag{3.10}$$

Therefore $\lambda(\lambda-A)^{-1}z\in\Omega_0$, and (2) is shown.

(3) For any $u_i=(0,q_i(s),L_i)\in\Omega_0,\ i=1,2$, such that $\|u_i\|_Z\le\eta$, by assumptions (ii)-(iv) we have

$$\begin{aligned}\|B(u_1)-B(u_2)\|_Z = &\ |c(M-Q_1)L_1-c(M-Q_2)L_2|\\ &+\|(\delta(s,M)-\delta(s,Q_1))q_1(s)-(\delta(s,M)-\delta(s,Q_2))q_2(s)\|_{L^1}\\ &+|cQ_1L_1-cQ_2L_2+\langle\phi,q_1\rangle-\langle\phi,q_2\rangle|,\end{aligned}$$

where $Q_i=\int_0^m\psi(s)q_i(s)\mathrm{d}s,\ i=1,2$. Since

$$\begin{aligned}&|c(M-Q_1)L_1-c(M-Q_2)L_2|\\ \le\ &(cM+cQ_1)|L_1-L_2|+cL_2|Q_1-Q_2|,\end{aligned}\tag{3.11}$$

$$\begin{aligned}&\|(\delta(s,M)-\delta(s,Q_1))q_1(s)-(\delta(s,M)-\delta(s,Q_2))q_2(s)\|_{L^1}\\ \le\ &(\delta(s,M)+\delta(s,Q_1))\|q_1-q_2\|_{L^1}+\|q_2\|_{L^1}\delta_Q(s,\zeta)|Q_1-Q_2|,\\ &\zeta\in(Q_1,Q_2),\end{aligned}\tag{3.12}$$

$$\begin{aligned}&|cQ_1L_1-cQ_2L_2+\langle\phi,q_1\rangle-\langle\phi,q_2\rangle|\\ \le\ &cQ_1|L_1-L_2|+cL_2|Q_1-Q_2|+\langle\phi,|q_1-q_2|\rangle,\end{aligned}\tag{3.13}$$

it follows from (3.11)-(3.13) that

$$\begin{aligned}\|B(u_1)-B(u_2)\|_Z\le\ &(cM+2cQ_1)|L_1-L_2|+(2cL_2+\|q_2\|_{L^1}\delta_Q(s,\zeta))|Q_1-Q_2|\\ &+\langle\phi,|q_1-q_2|\rangle+(\delta(s,M)+\delta(s,Q_1))\|q_1-q_2\|_{L^1}.\end{aligned}$$

Then it is not difficult to get

$$\begin{aligned}&\langle\phi,|q_1-q_2|\rangle\le\phi(r)\|q_1-q_2\|_{L^1},\ |Q_1-Q_2|\le\psi(r)\|q_1-q_2\|_{L^1},\ r\in(0,m),\\ &\|B(u_1)-B(u_2)\|_Z\le\ (cM+2cQ_1)|L_1-L_2|+\{\phi(r)+\psi(r)(2cL_2\\ &\qquad+\|q_2\|_{L^1}\delta_Q(s,\zeta))+\delta(s,M)+\delta(s,Q_1)\}\|q_1-q_2\|_{L^1}.\end{aligned}$$

From assumptions (ii)-(iv) and $\|u_i\|_Z\le\eta$, if we denote the constant

$$C_L=\max\{3cM,\bar\beta+\bar\gamma(2c\eta+\eta\bar\delta_Q)+2\bar\delta\},$$

where $\bar\beta,\bar\gamma,\bar\delta_Q,\bar\delta$ are upper bounds for $\beta(s),\gamma(s),\delta_Q(s,Q)$ and $\delta(s,Q)$, respectively, then we have $\|B(u_1)-B(u_2)\|\le C_L\|u_1-u_2\|$. Hence B is locally Lipschitz continuous, (3) is verified.

(4) Equation (3.2) leads to

$$u + hB(u) = \begin{pmatrix} hc(M-Q)L \\ \{1 + h[\delta(\cdot, M) - \delta(\cdot, Q)]\}q \\ (1 + chQ)L + h\langle\phi, q\rangle \end{pmatrix}, \ u = (0, q, L)^{\mathrm{T}}, \tag{3.14}$$

where $Q = \langle\psi, q\rangle \le M$. The assumption (iv) implies that $u + hB(u) \in Z_+$. If $M = Q$, then (3.14) reduces to

$$u + hB(u) = \begin{pmatrix} 0 \\ q \\ (1 + chQ)L + h\langle\phi, q\rangle \end{pmatrix} \in \Omega_0,$$

which satisfies the tangential condition in (4). Otherwise $0 < Q < M$, the assumption (iv) tells us that

$$\langle\psi, \{1 + h[\delta(s, M) - \delta(s, Q)]\}q\rangle \le \langle\psi, q + 2qh\bar{\delta}\rangle = (1 + 2h\bar{\delta})Q,$$

which implies $u + hB(u) \in \Omega$ if $0 < h < (M - Q)/2Q\bar{\delta}$. Hence (4) is true. □

Theorem 3.1. *Under the assumptions (i)-(v), there exists a unique continuous non-negative solution* $u(t) \in \Omega_0, \ t > 0$ *for initial-valued problem (3.3) and (3.4).*

Proof. By assumption (v) and Lemma 3.1, we can see that the problem (3.3) and (3.4) meets all the conditions of Theorem 2.3 in [18]. Therefore the initial-valued problem (3.3) and (3.4) has a unique continuous solution $u(t) = (0, q(s, t), L(t))$. Besides, it follows from the system (2.7)-(2.11) that $u(t) \ge 0, \ t > 0$. □

4. Concluding remarks

In this paper, we have rigorously treated the well-posedness for a size-structured population model of a marine species, the model is a realistic extension of that in [14] and [9]. Due to the model complexities, the key of the method is theory of non-densely defined operators. The results obtained provide a solid foundation for the investigation of topics such as stability of steady states, bifurcation, and related control problems, which will be pursued in our coming exploration.

As far as the possible generalizations of current model are concerned, we may consider its time-varying version; that is, the vital parameters in the model depends explicitly on time. This extension is meaningful since the real habitats do vary in time. As a special situation, models with periodic parameters should be paid attention.

On the other hand, we could make a more thorough investigation in population behaviors when a group of concrete parameters were focused, such as Sigmoidal growth rates, mortalities of U form, fertilities of normal distribution, and so on. Besides, what conditions are needed for the settlement rate c and the maximum space area M to survive the population with some prescribed lower bound of individuals? What kind of situations would happen with the changes of constant parameters? Problems like that are significant and interesting to explore.

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