Riv. Mat. Univ. Parma, Vol. **4** (2013), 123-133

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Study of a mathematical model of a marine invertebrates population

Abstract. The model we study deals with a structured population of marine invertebrates whose life stage is composed of adults and pelagic larvae such as barnacles contained in a local habitat. We prove existence and uniqueness of a continuous positive global mild solution and we give an estimate of the solution.

Keywords. Age-structured population dynamics, semigroup theory, affine semigroup, mild solution.

Mathematics Subject Classification (2010): 92D25, 47D06, 47B65.

1 - Introduction

If you walk along the sea shore, you can find barnacles on almost any solid surfaces that gets covered by water. On rocks, dock pilings, boats, even mussels, you can find cluster of these hard, cone-like houses.

Barnacles have two larval stages: the first (nauplius) spends its time as part of the zooplankton, floating wherever the wind, waves, currents, and tides may take it.

In this period, wich lasts for about two weeks, it can eat and moult; hence the second stage is reached.

At this point the nauplius metamorphoses into a non-feeding, more strongly swimming, cyprid larva.

Received: July 16, 2012; accepted in revised form: January 9, 2013.

This research was partially supported by Par 2006-Research Project of the University of Siena funds as well as by G.M.F.M. and M.U.R.S.T. research funds.

When an appropriate place is found, the cyprid larva cements itself headfirst to the surface and then undergoes metamorphosis into a juvenile barnacle.

Typical barnacles develop six hard plates to surround and protect their bodies. For the rest of their lives they are cemented to the ground, using their feathery legs to capture plankton and gametes when spawning. They are usually found in the intertidal zone. Once metamorphosis is over and they have reached their adult form, barnacles will continue to grow, but not moult. Instead, they grow by adding new material to the ends of their heavily calcified plates.

The model we study deals with a structured population of marine invertebrates whose life stage is composed of adults and pelagic larvae such as barnacles contained in a local habitat.

Roughgarden et al., [**6**]-[**10**] and [**13**], have first proposed an age-structured space-limited model to describe the cicle of life of barnacles, but the reproduction process of the larvae have been neglected and their density has beeen assumed constant. Even if this kind of models have been analyzed by several authors, they have the drawback of the occurrence of a negative population density.

In this paper, following Kamioka, [**10**], a couple of equations are given: the first one models the density of adults, whereas the second one involves larval evolution.

The equation are connected by means of the boundary conditions of the evolution of the adults, which takes into account the larval evolution.

The direct semigroup approach is technically quite difficult compared with the integral approach, so in [**10**] the integral solution is constructed by using the perturbation method of non densely defined operators.

The approach we propose here is different from that of Kamioka, since we shall prove the existence of a "mild" solution globai in time, by using affine semigroup techniques ([**1**], [**3**]).

On the other hand, we think that the existence of a "mild" solution is quite important from a biological point of view, because, it can be found by using a successive approximation procedure.

In fact, from [**4**], we know that if an evolution problem has an integral solution, it has also a "mild" solution: we shall just find it.

We get also estimates of the solution to prove that the local solution is global.

The paper is organized as follows: we consider, first, that the boundary value of the adults density $\chi(t)$ is known and has some suitable properties.

In this way, we find the mild solution of the evolution problem for the adults density, by means of affine semigroup techniques (see [**1**]) and successive approximation procedures.

Then, by using another successive approximation procedure, we find the function $\chi(t)$ in a suitable Banach space which ensures that $\chi(t)$ has the requested properties.

We think that our method is more convenient than that of Kamioka and we think that by applying it, one could prove also some other properties of the solution of the present model or study the existence and the regularity of the solutions of other similar age-structured population models.

2 - The model

The model under consideration reads as follows, [10]:

$$\begin{cases} \dfrac{\partial A}{\partial t} + \dfrac{\partial A}{\partial a} = -(\mu + \delta)A, \\ \dfrac{dL}{dt} = -\mu_L L - \rho(Q - S)L + \int\limits_0^\omega \beta A da, \end{cases} \tag{1}$$

where $A = A(a, t)$ represents the age-density function of sessile adults living in a local habitat, depending on the age-variable $a \in (0, \omega)$ (ω is the maximum attainable age) and time $t > 0$, whereas $L = L(t)$ gives the abundance of larvae in the pelagic pool.

Moreover, $\mu = \mu(a)$ is the natural death rate at age a, μ_L is the natural death rate of larvae and $\delta = \delta(a, S(t))$ represents the density-dependent death rate, where

$$S = S(t) = \int\limits_0^\omega \gamma(a) A(a, t) da \, ,$$

is the size of occupied space ($\gamma(a)$ is the area occupied by one individual of age a, $0 < \gamma < \bar{\gamma}$) with respect to the total available area Q.

Finally, ρ is the settlement rate for unit area and $\beta = \beta(a)$, $0 < \beta < \bar{\beta}$, is the age-specific birth rate.

The boundary and initial conditions associated to system (1) are:

$$A(0, t) = \rho(Q - S)L, \quad A(a, 0) = A_0(a), \quad L(0) = L_0, \tag{2}$$

where A_0 and L_0 are given non-negative initial data of adult and larval populations.

From a mathematical point of view, the following assumptions are made:

1. $\mu_L, \bar{\gamma}, \bar{\beta}, \rho, Q$ are positive constants;
2. μ is a locally integrable non-negative function, such that: $\int\limits_0^\omega \mu(a) da = +\infty$;
3. δ is such that $0 < \delta \leq \bar{\delta}$, with $\bar{\delta}$ a suitable positive constant;
4. a positive constant M exists such that $0 < \dfrac{\partial \delta}{\partial S} \leq M$.

Note that the preceeding assumptions are physically meaningful; in particular assumption 2. is necessary to make the maximum attainable age finite.

As we said in the introduction, in the first part of the paper, we study the system of equations by means of the semigroup theory.

Under suitable assumptions, we prove the existence and uniqueness of a continuous global positive mild solution, i.e., we prove that, given $T > 0$, the mild solution exists on the whole interval $[0, T]$ (see [**2**, p. 206], [**3**, p. 112]).

In the second part of the paper, we prove that the assumptions we made are consistent.

3 - Analysis of the model

To simplify the formulation of the problem in L^1 framework, define the so called "survival function", [**10**], $\widetilde{A} = \dfrac{A}{l}$, with $l = l(a) = \exp\left[-\int_0^a \mu(\sigma)d\sigma\right]$ and the function

$$\chi = \chi(t) = \rho(Q - S)L, \tag{3}$$

with S written in the form:

$$S = \int_0^{\omega} \psi(a)\widetilde{A}(a,t)da, \tag{4}$$

where $\psi = \gamma l$ is the expected space size occupied by the adult population, at age a.

Hence, we can naturally assume that $\widetilde{A}$ takes a value in $L^1(0,\omega)$, at each time t.

System (1) reduces to:

$$\begin{cases} \dfrac{\partial \widetilde{A}}{\partial t} + \dfrac{\partial \widetilde{A}}{\partial a} = -\delta \widetilde{A}, \\[2ex] \dfrac{dL}{dt} = -\mu_L L - \chi + \displaystyle\int_0^{\omega} \phi \widetilde{A} da, \end{cases} \tag{5}$$

where $\phi = \phi(a) = \beta(a)l(a)$ represents the net reproduction function of the adult population $(0 < \phi < \overline{\beta})$.

The boundary and the initial conditions (2) associated to system (5) becomes:

$$\widetilde{A}(0,t) = \chi(t), \quad \widetilde{A}(a,0) = \widetilde{A}_0(a), \quad L(0) = L_0, \tag{6}$$

where $\widetilde{A}_0 = lA_0$ is assumed belonging to the positive cone $L^1_+(0,\omega) = \{f(a) \in L^1(0,\omega), f(a) \geq 0, \text{ a.e. in } (0,\omega)\}$.

Define the Banach space $X = L^1(0, \omega)$, with its usual norm $\|f\|_X = \int_0^\omega |f(a)| da$, and denote by X^+ its positive cone $X^+ = \{f(a) \in L^1(0, \omega), f(a) \geq 0, \text{ a.e. in } (0, \omega)\}$. By defining the operator:

$$Nf = -\frac{df}{da}, \qquad D(N) = \left\{f \in X, \frac{df}{da} \in X, f(0) = 0\right\},$$

where $\frac{df}{da}$ is a distributional derivative, it is possible to prove the following lemma.

Lemma 3.1. *The operator N satisfies the following properties:*

1. $(\lambda I - N)^{-1}$ *exists for any* $\lambda > 0$*,*
2. N *is a closed operator,*
3. $D(N)$ *is dense in* X*.*

Proof. Since $D(N) \supset C_0^\infty(0, \omega)$, then $D(N)$ is dense in X and point 3. immediately follows.

Moreover, since, for $g \in X, \lambda > 0$,

$$\|(\lambda I - N)^{-1} g\|_X \leq \frac{1}{\lambda} \int_0^\omega da' |g(a')| [1 - e^{-\lambda(\omega - a')}] \leq \frac{1}{\lambda} \|g\|_X,$$

the operator $(\lambda I - N)^{-1}$ is defined for any $\lambda > 0$. Hence property 1. is proved.

Property 2. follows from the fact that $N = -\{(\lambda I - N)^{-1}\}^{-1} + \lambda I, \lambda > 0$. □

Thus, the operator N generates a strongly continuous C_0-semigroup of translation $\{exp(tN), t \geq 0\}$:

$$[\exp(Nt)f](a) = \begin{cases} f(a - t), & \text{if } 0 < a - t < \omega, \\ 0, & \text{otherwise.} \end{cases}$$

Assume, now, that χ is a given positive function which belongs to the Banach space ([**5**, Ch. VII, Thm VII.3])

$$W = \{f \in C((0, \infty), X) : \sup\{e^{-kt} \|f(t)\|_X\} < \infty\}, \tag{7}$$

with the norm $\|f\|_W = \sup\{e^{-kt} \|f(t)\|_X\}$, where k will be fixed later on.

Obviously, the function χ is bounded in any interval $[0, t_0]$, with $t_0 < \infty$, that is, if $t_0 > 0$ is fixed, a suitable $\bar{\chi} = \bar{\chi}(t_0) > 0$ exists such that $0 < \chi \leq \bar{\chi}$, for any $t \in [0, t_0]$.

We shall write, for semplicity $\bar{\chi}$ instead of $\bar{\chi}(t_0)$.

In the sequel, we shall prove that χ really satisfies all these properties.

We want to formulate an integral equation, whose solution is the analogous of the "mild" solution of the linear problem.

In particular, from system (5)-(6), we have the following equation for the adults:

$$\widetilde{A}(t) = e^{tN}\widetilde{A}_0 + \chi(t-a) - \int_0^t e^{(t-s)N}\delta\widetilde{A}ds. \tag{8}$$

Note that if the solution of (8) is differentiable, it will be the strong solution of system (5)-(6): this is the reason why it is called a "mild" solution.

To prove that $\widetilde{A}(t) \in X^+$, we add and subtract $\bar{\delta}\widetilde{A}$ in the first equation of (5), hence by passing to the mild form (see [**2**], [**12**]), we obtain:

$$\widetilde{A}(t) = \begin{cases} e^{tN}e^{-\bar{\delta}t}\widetilde{A}_0 + \displaystyle\int_0^t e^{-\bar{\delta}(t-s)}e^{[(t-s)N]}(\bar{\delta}-\delta)\widetilde{A}(s)ds, & t \le a, \\ \chi(t-a)e^{-\bar{\delta}t}\widetilde{A}_0 + \displaystyle\int_0^t e^{-\bar{\delta}(t-s)}e^{[(t-s)N]}(\bar{\delta}-\delta)\widetilde{A}(s)ds, & t > a. \end{cases} \tag{9}$$

Remark 3.1. Note that by adding and subtracting $\bar{\delta}\widetilde{A}$ in the first equation of (5), we obtain a differential equation that is obviuously equivalent to the first equation of (5).

It is possible to prove that also the mild versions (8), (9) are equivalent (see [**12,** § 3]) for details), hence from now on, we consider the mild solution in form (8) or (9) according to what it useful for the proof of the results we need.

Define the Banach space $Y = C([0, \bar{t}\,], X)$, with the norm

$$\|f\|_Y = \sup\{\|f(t)\|_X, t \in [0, \bar{t}\,]\}, \tag{10}$$

where $\bar{t}$ will be chosen later and consider the positive cone Y^+ of Y.

Define also the operator K $(D(K) = Y, R(K) \subset Y)$:

$$[K(\widetilde{A})(t)](a) = \begin{cases} K_1(a,t), & t \le a, \\ K_2(a,t), & t > a, \end{cases} \tag{11}$$

where

$$K_1(a,t) = e^{tN}e^{-\bar{\delta}t}\widetilde{A}_0 + \int_0^t e^{-\bar{\delta}(t-s)}e^{[(t-s)N]}(\bar{\delta}-\delta)\widetilde{A}(s)ds,\ t \le a, \tag{12}$$

$$K_2(a,t) = \chi(t-a)e^{-\bar{\delta}t}\widetilde{A}_0 + \int_0^t e^{-\bar{\delta}(t-s)}e^{[(t-s)N]}(\bar{\delta}-\delta)\widetilde{A}(s)ds,\ t > a. \tag{13}$$

Hence, (9) can be written as:

$$\widetilde{A} = K\widetilde{A}. \tag{14}$$

Lemma 3.2. *The operator K is locally Lipschitz on Y and:*

$$\|K\widetilde{A}_1 - K\widetilde{A}_2\|_Y \leq \left(2 + \frac{M\|\widetilde{A}_2\|_Y}{\bar{\delta}}\right)(1 - e^{-\bar{\delta}\bar{t}})\|\widetilde{A}_1 - \widetilde{A}_2\|_Y.$$

Moreover, the operator K maps the positive cone Y^+ into itself.

Proof. The inequality follows from (10), (11) and the Lagrange Theorem. Finally, K maps Y^+ into itself by definition. □

Remark 3.2. Let $r > 0$ be fixed, the set $D_r = \{f \in X : \|f\|_X \leq r\}$, $C_r = \{f \in Y : f(t) \in D_r, t \in [0, \bar{t}\,]\}$ are closed sets of X and Y repectively.

It is easy to prove that, for any $\widetilde{A} \in C_r$:

$$\|K\widetilde{A}\|_Y \leq \left[\frac{\|\widetilde{A}_0\|_X + \bar{\chi}\omega}{r} + 2(1 - e^{-\bar{\delta}\bar{t}})\right] r,$$

moreover for $\widetilde{A}_1, \widetilde{A}_2$ in C_r the inequality proved in Lemma 3.2 become

$$\|K\widetilde{A}_1 - K\widetilde{A}_2\|_Y \leq \left(2 + \frac{Mr}{\bar{\delta}}\right)(1 - e^{-\bar{\delta}\bar{t}})\|\widetilde{A}_1 - \widetilde{A}_2\|_Y.$$

Hence, the following Lemma follows.

Lemma 3.3. *The operator K is a contraction on C_r, for a small enough time $\bar{t}$.*

Proof. The quantity $(1 - e^{-\bar{\delta}t})$ vanishes as t goes to zero. Moreover, we can find a suitable r such that:

$$\frac{\bar{\chi}\omega + \|\widetilde{A}_0\|_X}{r} < 1. \tag{15}$$

Condition (15) is certainly fulfilled if we assume that $\varepsilon > 0$ exists such that $\|\widetilde{A}_0\|_X \leq \dfrac{r}{1 + \varepsilon}$.

In this way, the operator K maps C_r into itself and it is a contraction in C_r if $\bar{t}$ is small enough and r satisfies (15).

The proof follows directly from Lemma 3.2 and Remark 3.3. □

By using the Fixed Point Theorem, the following theorem can be proved:

Theorem 3.1. *Equation* (14) *has a unique positive solution* $\widetilde{A} \in [0, \bar{t}\,]$, *for* $\bar{t}$ *small enough.*

Note that $\bar{t}$ has to make the quantity $(1 - e^{-\bar{\delta}t})$ suitably small and $\bar{\chi} = \bar{\chi}(\bar{t})$. Note also that the constant r is only used to make a contraction in a bounded closed set of Y. In the sequel we prove a better estimate for the norm of the mild solution.

In fact, Theorem 3.1 gives a "local" solution of equation (14).

To prove that it is a solution defined in any interval $[0, T]$, $T > 0$, we have to find some a-priori estimates.

Thus, let $T > 0$ be fixed, from (8), by taking into account the nonnegativity of $\widetilde{A}(t)$ and Remark 3.1, we have:

$$\|\widetilde{A}(t)\|_X \leq \|\widetilde{A}_0\|_X + \omega\bar{\chi}.$$

Hence, we have just proved the following theorem.

Theorem 3.2. *The integral equation* (9) *has a unique continuous nonnegative solution $\widetilde{A}$, defined for $t \in [0, T]$ where $T > 0$ is fixed a priori and such that $\|\widetilde{A}(t)\|_X \leq R$, where $R = \{\|\widetilde{A}_0\|_X + \omega\bar{\chi}\} \leq \omega\{\|\widetilde{A}_0\|_\infty, +\bar{\chi}\}$.*

Obviously, $\bar{\chi} = \bar{\chi}(T)$ and $\| \bullet \|_\infty$ is the norm in $L^\infty(0, \omega)$.

Note that with similar techniques, it is possible to prove that (9) has a unique continuous nonnegative solution, defined for any $t \geq 0$, belonging to the closed set of X:

$$\Sigma(\bar{r}) = \{f \in X \cap L^\infty(0, \omega), \|f\|_\infty \leq \bar{r}\},$$

where $\bar{r}$ is fixed.

Moreover,

$$\|\widetilde{A}(t)\|_\infty \leq \Big\{\|\widetilde{A}_0\|_\infty + \bar{\chi}\Big\}. \tag{16}$$

Finally, by using the above estimate for $\|\widetilde{A}(t)\|_\infty$ we can conclude that the solution of (9) is a global solution ([**2**], [**3**], [**11**]).

The inequality of Theorem 3.2 can be proved also by using $\| \bullet \|_\infty$ norm.

In fact, since

$$\|\widetilde{A}(t)\|_X \leq \omega\|\widetilde{A}(t)\|_\infty, \tag{17}$$

it follows

$$\|\widetilde{A}(t)\|_X \leq \omega\{\|\widetilde{A}_0\|_\infty + \bar{\chi}\}. \tag{18}$$

As far as the larval equation of system (5) is concerned, we have that:

$$L(t) = L_0 e^{-\mu_L t} - \int_0^t e^{-\mu_L(t-s)}\chi(s)ds + \int_0^t e^{-\mu_L(t-s)} \int_0^\omega \phi(a)\widetilde{A}(a, s)da\, ds. \tag{19}$$

By substituting the espression of χ given by (3), we can prove that

$$L(t) \leq L_0 + \frac{\bar{\beta} Q}{\mu_L \bar{\gamma}}\,. \tag{20}$$

To get (20), note that $Q \geq S(t)$ (see definition (4)), if $Q \geq \bar{\gamma}\omega \max\{\bar{\chi}, \|A_0\|_\infty\}$.

Moreover, if $\dfrac{Q}{\bar{\gamma}} \geq \omega \max\{\bar{\chi}, \|A_0\|_\infty\}$, we have that $\|\widetilde{A}(t)\|_X \leq \dfrac{Q}{\bar{\gamma}}$ (see (18)).

4 - The function χ

In this section, by applying again the Fixed Point Theorem, we find the function $\chi(t)$.

Define the operator $(\Lambda\chi)(t) = \rho(Q - S)L(t)$, with $D(\Lambda) = W, R(\Lambda) \subset W$ (for the definition of W see (7)) .

Note that the function χ depends both on S and L, which depend on χ itself.

Let $T > 0$ be fixed, we have to evaluate:

$$|\Lambda\chi_1(t) - \Lambda\chi_2(t)| \leq \rho Q|L_{\chi_1}(t) - L_{\chi_2}(t)| + \rho|S_{\chi_1}(t)L_{\chi_1}(t) - S_{\chi_2}(t)L_{\chi_2}(t)|.$$

From (19), we have:

$$\begin{aligned}
|L_{\chi_1} - L_{\chi_2}| &\leq \int_0^t e^{-\mu_L t} e^{\mu_L s} \left\{ |\chi_1(s) - \chi_2(s)| + \left[\int_0^\omega \phi(a) |\widetilde{A}_1(s,a) - \widetilde{A}_2(s,a)| da \right] \right\} ds \\
&\leq \|\chi_1 - \chi_2\|_W e^{-\mu_L t} \int_0^t e^{(\mu_L + k)s} ds + \bar{\phi} \|\widetilde{A}_1 - \widetilde{A}_2\|_W e^{-\mu_L t} \int_0^t e^{(\mu_L + k)s} ds \\
&\leq \frac{e^{kt}}{\mu_L + k} \left[\|\chi_1 - \chi_2\|_W + \bar{\phi} \|\widetilde{A}_1 - \widetilde{A}_2\|_W \right].
\end{aligned}$$

Multiplying each side by e^{-kt} and taking the sup, we have:

$$\|L_{\chi_1} - L_{\chi_2}\|_W \leq \frac{1}{\mu_L + k} \left[\|\chi_1 - \chi_2\|_W + \bar{\phi} \|\widetilde{A}_1 - \widetilde{A}_2\|_W \right].$$

In a similar way, we can find an estimate for $\|\widetilde{A}_1 - \widetilde{A}_2\|_W$.

By using the Lagrange Theorem and the Gronwall Lemma, we obtain:

$$\|\widetilde{A}_1 - \widetilde{A}_2\|_W \leq \frac{1}{k - H} \|\chi_1 - \chi_2\|_W,$$

where

$$H = 2\bar{\delta} + MQ.$$

Finally, after many computations, we get the following estimate:

$$\|\Lambda\chi_1 - \Lambda\chi_2\|_W \leq \left[\frac{2\rho Q}{\mu_L + k} \left(1 + \frac{\bar{\beta}}{k - H} \right) + \frac{\rho}{k - H} \left(L_0 \bar{\gamma} + \frac{\bar{\beta} Q}{\mu_L} \right) \right] \|\chi_1 - \chi_2\|_W.$$

If $k > H$ is chosen great enough, the operator Λ is a contraction.

Hence, it has a unique fixed point and thus a unique function $\chi \in W$ exists as solution of $\chi = \Lambda\chi$.

It is easy to see that χ is bounded in $[0, T]$, with $T < \infty$ and from definition (3), it can be easily proved that χ is a non-negative function, if $Q \geq S(t)$.

Remark 4.1. We have transformed system (1) and hence (5) in the“mild” form (8) and (9).

When (8) and (9) are solved by using as χ the fixed point of the mapping Λ defined at the beginning of this section, then the solution $\widetilde{A}, L$ are the sought mild solution of the complete problem.

Acknowledgments. The authors acknowledge support by Par 2006-Research Project “Metodi e modelli matematici per le applicazioni” of the University of Siena funds as well as by G.M.F.M. and M.U.R.S.T. research funds.

The authors want to dedicate this paper to the memory of Prof. Aldo Belleni Morante, who showed them the way of modeling and studying evolution problems by means of semigroup theory.

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