

Mathematical model of marine protected areas

L. BEREZANSKY

*Departments of Mathematics and Computer Science,
Ben-Gurion University of Negev, Beer-Sheva 84105, Israel*

L. IDELS*

*Department of Mathematics, Vancouver Island University,
900 Fifth Street, Nanaimo, British Columbia V9S5S5, Canada*

*Corresponding author: lidels@shaw.ca

AND

M. KIPNIS

*Department of Mathematics, Chelyabinsk State Pedagogical University,
69 Lenin Avenue, Chelyabinsk 454080, Russia*

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We consider two regions with a fish population that is dispersing between the two areas, and fishing takes place only in region 2, with region 1 established as no-fishing zone. Marine protected areas (MPAs) have been promoted as conservation and fishery management tools, and at present, there are over 1300 MPAs in the world. A new mathematical model of an MPA that reflects the complexity of the natural setting is presented. The resulting model of an age-structured fish population belongs to a class of non-linear systems of differential equations with delay. New easily verifiable sufficient conditions for the existence, boundedness, permanence and stability of the positive internal steady-state solutions are obtained. From the point of view of fishery managers, the existence of stable solutions is necessary for planning harvesting strategies and sustaining the fishing grounds. Numerical simulations illustrate qualitative behaviour of the model, including stability switches.

Keywords: marine protected areas; fishery models; harvesting models, system of non-linear delay differential equations; boundedness; stability; population dynamics.

1. Introduction

Marine protected and marine reserves areas have been promoted as conservation and fishery management tools to hedge marine life and sustain ecosystems. The following definitions have emerged as commonly used terms (Lubchenko *et al.*, 2003):

Marine reserves are defined as areas completely protected in perpetuity from all extractive and destructive activities. Marine reserves are also known as “no-take areas” or ‘no-take/no-harm areas’. A ‘no-take’ aquatic reserve means that people are not permitted to fish by any method, destroy marine life or collect dead or alive marine organisms, including empty shells. Reserves are a special category of marine protected areas (MPAs).

MPAs are defined as areas designated to enhance conservation of marine resources through legal protections from disturbance, harm and/or fishing.

According to recent studies, MPAs extend age structure of targeted species, sustain higher rate of reproduction, provide insurance against management failure, restrict fishing mortality and allow habitat to recover (Ami *et al.*, 2005; Gell & Roberts, 2003; Gerber *et al.*, 2002, 2003; Grafton *et al.*, 2005; Guenette & pitcher, 1999; Lockwood *et al.*, 2002; Nowlis & Roberts, 1999; Sumaila *et al.*, 2000). Recent interest in modelling MPA has largely been driven by hope to fill some of the knowledge gaps and predict effectiveness of the reserves (Armstrong, 2007; Pitchford *et al.*, 2007; Hauser *et al.*, 2006).

Two general approaches have been used to model MPA: mathematical models based on systems of ordinary differential equations (source–sink models) and empirical models based on the fitting programs. MPAs are modelled using logistic differential equations that are capable of generating trivial equilibrium dynamics and are unable to capture complex behaviour often observed in nature; do not incorporate age structure and selective harvesting (Dubey *et al.*, 2000; Doyen & Bene, 2003; Grafton *et al.*, 2005; Guenette & pitcher, 1999).

In the existing patchy models (see for example Xu, 2005), homogeneity of the patches is assumed and the latter undermined the actual MPA design.

The empirical models are based on the fitting programs such as spatially explicit Ecopath–Ecosim models and produce a deterministic appraisal of current fisheries (Christensen *et al.*, 2004). The equilibrium model for predicting the efficacy of an MPA is a step towards new ways to understand the benefits of MPA networks (Walters *et al.*, 2007). Note that the effects of specific larval dispersal patterns on MPAs have been addressed via integro-differential equations in Hastings & Botsford (2003).

We introduce an MPA-delayed model that incorporates age structure, explicit spatial characteristics such as diffusion and/or migration; management criteria, such as the number of reserves, areas allocated to the protected and fishing zones, and selective harvesting strategies. The resulting model of an age-structured fish population belongs to a class of non-linear systems of differential equations with delay and presents interesting, non-trivial and unexpected mathematical problems that we will study.

The paper is organized as follows. In Section 2, we present biological motivation and description of the model. Biologically motivated conditions for the existence of positive steady-state solutions are obtained in Section 3. The questions of the boundedness, interval bounds and persistence of positive solutions are studied in Section 4. By applying a new result, obtained by authors in Idels & Kipnis (2008) and the argument principle techniques, sufficient conditions for the global stability of the model are obtained in Section 5. In Section 6, we study local asymptotical stability of a non-trivial equilibrium, find the regions of local stability and instability and discuss stability switches.

2. Delay model of MPAs

To describe the ecological linkage between the reserve and the fishing ground, we will consider the two regions that have two areas A_1 and A_2 . Assume that fishing takes place only in region 2, with region 1 established as an MPA or no-fishing zone. It is well known (see, e.g. Doyen & Bene, 2003; Gerber *et al.*, 2002; Sobel & Dahlgren, 2004) that possible values of the system's control parameters are strongly related to biological and spatial characteristic, such as fish age and the size of the protected area. Let t denote a time and a is a chronological age. We define the following functions: $u_1 = u_1(t, a)$ is the age distribution of the fish population in the MPA; $u_2 = u_2(t, a)$ is the age distribution of the fish population in the fishing area; $M_1(a)$ is the natural mortality rate in the MPA and $M_2(a)$ is the natural mortality in the fishing area.

Firstly, assume that there is no migration between the two areas and the fish population in zone A_2 is unharvested. Based on the conservation law (see, e.g. Brauer & Castillo-Chavez, 2001), we introduce the following linear Foerster–McKendrick system:

$$\begin{aligned} \left(\frac{\partial}{\partial t} + \frac{\partial}{\partial a}\right) u_1(t, a) &= -M_1(a)u_1(t, a), \\ \left(\frac{\partial}{\partial t} + \frac{\partial}{\partial a}\right) u_2(t, a) &= -M_2(a)u_2(t, a) \end{aligned} \quad (2.1)$$

with

$$u_i(0, a) = \omega_i(a) \geq 0,$$

where $\omega_i(a)$ denotes initial conditions and

$$u_i(t, 0) = b_i(t),$$

where $b_i(t)$ is the birth function.

To tackle system (2.1), we used methods, developed by Smith & Thieme (1991) and presented in a recent paper by Gourley & Kuang (2009), that based on structured population models coupled with the technique of integration along characteristics. Clearly, for $t > \tau$

$$u_i(t, \tau) = b_i(t - \tau) \exp\left(-\int_0^\tau M_i(s) ds\right). \quad (2.2)$$

If $\tau \geq 0$ is the maturation time, then the total matured population $x_i(t)$ at time t is defined as

$$x_i(t) = \int_\tau^\infty u_i(t, a) da.$$

We also assume that $x_i(t)$ satisfies an equation of the form

$$\frac{dx_i(t)}{dt} = u_i(t, \tau) - m_i x_i(t), \quad (2.3)$$

where the term $m_i x_i(t)$ is the adult mortality function, whereas the first term is the maturation rate. Equations (2.2) and (2.3) yield the following form:

$$\frac{dx_i(t)}{dt} = \gamma_i(\tau) b_i(t - \tau) - m_i x_i(t), \quad (2.4)$$

where $\gamma_i(\tau) = \exp\left(-\int_0^\tau M_i(s) ds\right)$. It is biologically reasonable to assume that only mature fish (with $a > \tau$) can reproduce and the reproduction rate depends on the mature population. Therefore, we assume that $u_i(t, 0) = b_i(x_i(t))$. Hence, (2.4) moves to the equation

$$\frac{dx_i(t)}{dt} = \gamma_i(\tau) b_i(x_i(t - \tau)) - m_i x_i(t). \quad (2.5)$$

For a more complex model, we assume that the fish population is dispersing between the two areas, and area A_2 is open to fishing with the harvesting rate $h(t)$. Let d_1 be a net transfer rate, i.e. some net flow

of adult fishes from the reserve and d_2 is the immigration rate from the fishing area to the reserve, say larval dispersion. The resulting model for the matured population in the MPA becomes a system of two non-linear delay differential equations:

$$\begin{aligned} \frac{dx_1}{dt} &= \gamma_1(\tau)b_1(x_1(t - \tau)) - m_1x_1 - d_1x_1 + d_2x_2, \\ \frac{dx_2}{dt} &= \gamma_2(\tau)b_2(x_2(t - \tau)) - m_2x_2 - d_2x_2 + d_1x_1 - h(t)x_2, \end{aligned}$$

where $\gamma_i(\tau) = P_i e^{-\mu_i \tau}$, with non-negative constants μ_i and P_i ($i = 1, 2$). Denote for $i = 1, 2$

$$B_i = \gamma_i(\tau)b_i(x_i).$$

The functions $B_i(x)$ represent the growth rate, including a decreased survivorship $\gamma_i(\tau)$ over a longer incubation or maturation time. The general feature exhibited by the functions $B_i(x)$ is that the population growth rate is positive when the population size is small, then the birth rate function increases until it reaches the carrying capacity and then it decreases due to the crowding effect.

In this paper, we choose the Ricker's form of the birth function:

$$b_i(x_i) = x_i e^{-\alpha_i x_i}$$

with positive constants α_i ($i = 1, 2$) (see, e.g. Kuang, 1993).

Finally, the model under study has a form

$$\begin{aligned} \frac{dx_1}{dt} &= -m_1x_1 - d_1x_1 + d_2x_2 + \gamma_1x_{1\tau} e^{-\alpha_1x_{1\tau}}, \\ \frac{dx_2}{dt} &= -m_2x_2 - d_2x_2 + d_1x_1 + \gamma_2x_{2\tau} e^{-\alpha_2x_{2\tau}} - hx_2 \end{aligned} \tag{2.6}$$

and for $t \in [-\tau, 0]$

$$x_1(t) = \varphi_1(t) \geq 0, \quad x_2(t) = \varphi_2(t) \geq 0, \tag{2.7}$$

where $\gamma_i = \gamma_i(\tau)$, $x_i = x_i(t)$ and $x_{i\tau} = x_i(t - \tau)$.

3. Equilibrium analysis

To find all equilibria of system (2.6) and (2.7), we set

$$\begin{aligned} m_1x_1 + d_1x_1 - d_2x_2 - \gamma_1x_1 e^{-\alpha_1x_1} &= 0, \\ m_2x_2 - d_1x_1 + d_2x_2 + hx_2 - \gamma_2x_2 e^{-\alpha_2x_2} &= 0. \end{aligned} \tag{3.1}$$

From system (3.1), we have two curves:

$$\begin{aligned} L_1 : \quad x_2 &= \phi_1(x_1) = \frac{m_1 + d_1 - \gamma_1 e^{-\alpha_1x_1}}{d_2} x_1, \\ L_2 : \quad x_1 &= \phi_2(x_2) = \frac{m_2 + d_2 + h - \gamma_2 e^{-\alpha_2x_2}}{d_1} x_2. \end{aligned} \tag{3.2}$$

Apart from the zero solution, system (3.2) has a non-trivial positive solution (\bar{x}_1, \bar{x}_2) .

THEOREM 3.1 System (2.6) has a unique internal positive equilibrium if the following conditions hold:

$$(i) m_1 + d_1 \leq \gamma_1 \quad \text{and} \quad (ii) m_2 + d_2 + h \leq \gamma_2. \quad (3.3)$$

We would like to point out that the assumptions (3.3) are biologically motivated, i.e. the total rate of 'loss' in every region should be less than the corresponding rate of growth in the region.

Let

$$x_1^* = \frac{\gamma_1}{m_1 + d_1} \quad \text{and} \quad x_2^* = \frac{\gamma_2}{m_2 + d_2 + h}.$$

Then for curve L_1 : $0 \leq x_2 < 0$ for $0 \leq x_1 < x_1^*$, and $x_2 > 0$ for $x_1 \geq x_1^*$; and for curve L_2 : $0 \leq x_1 < 0$ for $0 \leq x_2 < x_2^*$, and $x_1 > 0$ for $x_2 \geq x_2^*$.

To prove the existence of a non-trivial equilibrium, firstly note that the curves L_1 and L_2 have asymptotes

$$x_2 = \frac{m_1 + d_1}{d_2} x_1$$

and

$$x_2 = \frac{d_1}{m_2 + d_2 + h} x_1$$

correspondingly. Clearly,

$$\frac{m_1 + d_1}{d_2} > \frac{d_1}{m_2 + d_2 + H},$$

thus, for sufficiently large x_1 , points on the curve L_1 lie above the corresponding points of the curve L_2 . On the other hand, in the neighbourhood of the origin, each of the conditions (i) and (ii) guarantees that points on the curve L_2 lie above points of the curve L_1 . Therefore, a positive internal equilibrium of system (2.6) and (2.7) exists.

To prove that this equilibrium is a unique point, firstly, we note that from system (3.2),

$$\begin{aligned} L_1 : \quad \frac{dx_2}{dx_1} &= \frac{x_2}{x_1} + \frac{\gamma_1}{d_2} \alpha_1 x_1 \exp(-\alpha_1 x_1) > \frac{x_2}{x_1}, \quad x_1 \geq x_1^*, \\ L_2 : \quad \frac{dx_1}{dx_2} &= \frac{x_1}{x_2} + \frac{\gamma_2}{d_1} \alpha_2 x_2 \exp(-\alpha_2 x_2) > \frac{x_1}{x_2}, \quad x_2 \geq x_2^*. \end{aligned} \quad (3.4)$$

Let θ be a polar angle of the point on the curve L_1 (with Ox_1 as a polar axis),

$$\theta = \arctan \frac{x_2}{x_1}.$$

If x_1 moves from x_1^* to ∞ , then

$$\frac{d\theta}{dx_1} = \frac{1}{1 + \left(\frac{x_2}{x_1}\right)^2} \frac{d}{dx_1} \left(\frac{x_2}{x_1}\right) = \frac{x_1}{x_1^2 + x_2^2} \left(\frac{dx_2}{dx_1} - \frac{x_2}{x_1}\right).$$

The latter equality and inequalities (3.4) guarantee $\frac{d\theta}{dx_1} > 0$, thus $\theta(x_1)$ is a monotone increasing function for $x_1 \geq x_1^*$. Similarly, let ϑ be a polar angle of the point on the curve L_2 with the same polar axis. If x_2 moves from x_2^* to ∞ , then $\vartheta(x_2)$ is a monotone decreasing function. At the equilibrium point $\theta = \vartheta$, increase of the function θ and decrease of the function ϑ guarantee the uniqueness of a non-trivial equilibrium. Thus, Theorem 3.1 is proved.

4. Boundedness of the solutions

Consider system (2.6) with initial conditions (2.7) in a vector form

$$\frac{dx}{dt} = Ax + f(x(t - \tau)), \quad (4.1)$$

where

$$A = \begin{bmatrix} -(m_1 + d_1) & d_2 \\ d_1 & -(m_2 + d_2 + h) \end{bmatrix},$$

$$x(t) = \begin{bmatrix} x_1(t) \\ x_2(t) \end{bmatrix}, \quad f = \begin{bmatrix} f_1 \\ f_2 \end{bmatrix}$$

with

$$f_i = \gamma_i x_i(t - \tau) \exp(-\alpha_i x_i(t - \tau)), \quad (i = 1, 2).$$

We denote

$$a = \frac{2 \max(\gamma_1, \gamma_2)}{\min(m_1, m_2) \min(\alpha_1, \alpha_2)}. \quad (4.2)$$

THEOREM 4.1 Any solution of system (4.1) with non-negative initial functions and positive initial conditions ultimately enters the square region

$$K = \{0 < x_1(t) \leq a, 0 < x_2(t) \leq a\},$$

where a is defined by (4.2) and remains in it.

Proof. Note that from standard differential equation theory (Bellman & Cooke, 1963), system (2.6) has solution $x_1(t) > 0$ and $x_2(t) > 0$ for $t > 0$, provided that $x_1(0) > 0$ and $x_2(0) > 0$ and

$$x_1(t) = \varphi_1(t) \geq 0, \quad x_2(t) = \varphi_2(t) \geq 0,$$

for $t \in [-\tau, 0)$.

Let $z = x_1 + x_2$, then from system (4.1), we have

$$\frac{dz}{dt} = -m_1 x_1 - m_2 x_2 - h x_2 + f_1(x_1(t - \tau)) + f_2(x_2(t - \tau)).$$

For $0 < \epsilon < \min(m_1, m_2)$, we have

$$\begin{aligned} \frac{dz}{dt} + \epsilon z &= -(m_1 - \epsilon)x_1 - (m_2 - \epsilon)x_2 - h x_2 + \\ &\quad f_1(x_1(t - \tau)) + f_2(x_2(t - \tau)) < \\ f_1(x_1(t - \tau)) + f_2(x_2(t - \tau)) &\leq \max\{f_1, f_2\} \leq \max\left\{\frac{\gamma_1}{\alpha_1}, \frac{\gamma_2}{\alpha_2}\right\} = W. \end{aligned}$$

Therefore,

$$\frac{dz}{dt} + \epsilon z < W$$

or

$$z(t) < \frac{W}{\epsilon} + \left(z(0) + \frac{W}{\epsilon} \right) e^{-\epsilon t}. \quad (4.3)$$

Thus, all solutions of system (2.6) along with system (4.1) are bounded.

We note that due to usual arguments (see, e.g. Hale & Lunel, 1993), the local solution is not a global solution if there exists $t_1 > 0$ such that $\limsup_{t \rightarrow t_1^-} |x(t)| = \infty$. But all solutions of system (4.1) are positive and bounded functions, hence, every local solution is also a global solution.

Since $x_1(t) > 0$ and $x_2(t) > 0$, it follows from inequality (4.3) that there exists t_0 , such that $x_i(t) < 2W/\epsilon < a$ ($i = 1, 2$) for $t_0 \leq t < \infty$. Thus, Theorem 4.1 is proved. \square

5. Stability analysis of the trivial solution

Consider a non-linear system

$$\begin{aligned} \frac{dx}{dt} &= Ax(t) + F(t, x(t - \tau_1), \dots, x(t - \tau_k)), \quad t > 0, \\ 0 < \tau_1 &\leq \tau_2 \leq \dots \leq \tau_k, \quad x(t) = \phi(t), \quad t \in [-\tau_k, 0], \end{aligned} \quad (5.1)$$

where $x : [-\tau_k, \infty] \rightarrow \mathbb{R}^n$, $A \in \mathbb{R}^{n \times n}$, here $F: \mathbb{R}_+ \times \mathbb{R}^{n \times k} \rightarrow \mathbb{R}^n$ non-linear and continuous vector function. We shall use $|\cdot|$ and $\|\cdot\|$ to denote norms in \mathbb{R}^n and $\mathbb{R}^{n \times n}$.

Let $\mu(A): \mathbb{R}^{n \times n} \rightarrow \mathbb{R}$ be a function such that

$$\|e^{At}\| \leq e^{\mu(A)t}.$$

Idels & Kipnis (2008) proved the following result.

THEOREM 5.1 Suppose that there exist the non-negative sequence ζ_i ($1 \leq i \leq k$), such that for every $u_i \in \mathbb{R}^n$ and $t \in \mathbb{R}$, the inequalities

$$|F(t, u_1, u_2, \dots, u_k)| \leq \sum_{i=1}^k \zeta_i |u_i|, \quad -\mu(A) > \sum_{i=1}^k \zeta_i$$

hold. Then there are positive constants σ and C such that every solution $x(t)$ of the system (5.1) satisfies the inequality

$$|x(t)| \leq C e^{-\sigma t} \max_{-\tau_k \leq t \leq 0} |\phi(t)|.$$

Based on this theorem, we also proved the following.

THEOREM 5.2 If

$$\min(m_1, m_2 + h) \geq \max(\gamma_1, \gamma_2), \quad (5.2)$$

then zero solution of the system (4.1) is globally asymptotically stable.

We would like to point out that the assumption (5.2) is biologically motivated to avoid population extinction under the excessive harvesting and the minimum ‘loss’ in every region should be less than the maximum ‘gain’ in the region.

For a scalar Nicholson delay differential equation

$$\frac{dx}{dt} = -mx(t) + \gamma x(t - \tau)e^{-x(t-\tau)}, \tag{5.3}$$

the delay-independent global asymptotic stability condition was obtained (see, e.g. Berezansky *et al.*, 2010).

LEMMA 5.1 If $\gamma < me^2$ then a non-trivial solution of (5.3) is the global attractor.

EXAMPLE 5.1 Without migration ($d_1 = d_2 = 0$), the delay differential model (2.6) is a direct extension of the well-known model of Nicholson’s–Bailey model (see, e.g. Brauer & Castillo-Chavez, 2001). Nonmigration system

$$\begin{aligned} \frac{dx_1}{dt} &= -m_1x_1 + \gamma_1x_1(t - \tau) \exp(-\alpha_1x_1(t - \tau)), \\ \frac{dx_2}{dt} &= -(m_2 + h)x_2 + \gamma_2x_2(t - \tau) \exp(-\alpha_2x_2(t - \tau)) \end{aligned} \tag{5.4}$$

has a positive equilibrium

$$\left(\frac{1}{\alpha_1} \ln \frac{\gamma_1}{m_1}, \frac{1}{\alpha_2} \ln \frac{\gamma_2}{m_2 + h} \right),$$

provided $m_1 < \gamma_1$ and $m_2 + h < \gamma_2$.

EXAMPLE 5.2 According to Ruan *et al.* (2003), the equilibrium point $\bar{x}_1 = \bar{x}_2 = \bar{x}$ is called a homogeneous equilibrium. In order to obtain the condition of existence of such an equilibrium for model (2.6), we shall use system (3.1).

PROPOSITION 5.1 If

$$\frac{\gamma_1}{m_1 + d_1 - d_2} = \left(\frac{\gamma_2}{m_2 + d_2 - d_1 + h} \right)^{\frac{\alpha_1}{\alpha_2}},$$

then a homogeneous equilibrium of system (2.6) exists and

$$\bar{x} = \frac{1}{\alpha_1} \ln \frac{\gamma_1}{m_1 + d_1}.$$

EXAMPLE 5.3 Consider the following symmetric non-migration model:

$$\begin{aligned} \frac{dx_1}{dt} &= -mx_1(t) + \gamma x_1(t - \tau) \exp(-x_1(t - \tau)), \\ \frac{dx_2}{dt} &= -mx_2(t) + \gamma x_2(t - \tau) \exp(-x_2(t - \tau)). \end{aligned} \tag{5.5}$$

PROPOSITION 5.2 For the decoupled system (5.5), if $\gamma < me^2$, then there exists a unique equilibrium $x_1^* = x_2^* = \ln \frac{\gamma}{m}$ such that it is the global attractor.

6. Local stability analysis of non-trivial equilibrium

Let

$$z(t) = \begin{bmatrix} x_1(t) - \bar{x}_1 \\ x_2(t) - \bar{x}_2 \end{bmatrix}.$$

Then a linearization of system (4.1) has the following vector form:

$$\frac{dz}{dt} = Az(t) - G(\tau)z(t - \tau), \quad (6.1)$$

where

$$G(\tau) = \begin{bmatrix} g_1(\tau) & 0 \\ 0 & g_2(\tau) \end{bmatrix}$$

with

$$g_i(\tau) = \gamma_i(\tau) \exp(-\alpha_i \bar{x}_i) (\alpha_i \bar{x}_i - 1), \quad (i = 1, 2). \quad (6.2)$$

The stability of a non-trivial equilibrium of system (6.1) is determined by the roots of the quasi-polynomial characteristic equation

$$\lambda^2 + q\lambda + s + [c(\tau)\lambda + d(\tau) + r(\tau)e^{-\lambda\tau}]e^{-\lambda\tau} = 0, \quad (6.3)$$

where

$$\begin{aligned} q &= m_1 + d_1 + m_2 + d_2 + h, \\ s &= (m_1 + d_1)(m_2 + d_2 + h) - d_1 d_2, \\ c(\tau) &= g_1(\tau) + g_2(\tau), \\ r(\tau) &= g_1(\tau)g_2(\tau), \\ d(\tau) &= (m_1 + d_1)g_2(\tau) + (m_2 + d_2 + h)g_1(\tau). \end{aligned}$$

Note that $q > 0$ and $s > 0$.

We assume that

$$\gamma_1(\tau) > (m_1 + d_1)e, \quad \gamma_2(\tau) > (m_2 + d_2 + h)e. \quad (6.4)$$

Clearly, conditions (6.4) imply the inequalities $\alpha_i \bar{x}_i > 1$ ($i = 1, 2$), thus all functions $c(\tau)$, $r(\tau)$ and $d(\tau)$ are positive functions.

Let $\eta_1 = m_1 + d_1$ and $\eta_2 = m_2 + d_2 + h$ be the ‘loss’ rates for the populations in the MPA. There is a critical value of the time delay that switches stability to of a limit-cycle type fluctuations, and the period of the cycles is set mainly by the delay τ and the ‘loss’ rates η_i (Li & Ma, 2004). High values of $\gamma_i \tau$ and $\eta_i \tau$ will give large amplitude cycles.

Denote

$$F(\lambda) = \lambda^2 + q\lambda + s + [c(\tau)\lambda + d(\tau) + r(\tau)e^{-\lambda\tau}]e^{-\lambda\tau}. \quad (6.5)$$

If for any root λ of (6.3), we have $\text{Re}(\lambda) < 0$, then system (6.1) is asymptotically stable. If there exists a root λ , such that $\text{Re}(\lambda) > 0$, then the system is unstable (Kuang, 1993).

To investigate stability of system (6.1), we shall use the argument principle (see, e.g. Knopp, 1996). Consider a contour K of a complex plane consisting of a segment $I_R: \lambda = -i\omega$ ($-R \leq \omega \leq R$) and semicircle $C_R: \lambda = Re^{i\omega}$ ($-\pi/2 \leq \omega \leq \pi/2$).

By the principle of argument, if λ moves along K , then $\Delta \text{Arg}F(\lambda) = 2\pi N$, where N is a number of roots of equation (6.3) inside the contour K .

Hence, the necessary and sufficient condition for asymptotic stability of system (6.1) is

$$\Delta \text{Arg}F(\lambda) = 0,$$

when λ moves along K with sufficiently large R . We call the curve $F(\lambda)$ a hodograph. Since λ^2 is the main term in $F(\lambda)$, we have $\Delta \text{Arg}F(\lambda) \rightarrow 2\pi$, while λ moves along the curve C_R with $R \rightarrow \infty$. Hence, for the asymptotic stability of system (6.1), it is necessary and sufficient to have the condition

$$\Delta \text{Arg}F(\lambda) = -2\pi,$$

where λ moves along I_R with $R \rightarrow \infty$. By symmetry, an equivalent form of the latter condition is written as

$$\Delta \text{Arg}F(-i\omega) = -\pi \quad (0 \leq \omega < \infty).$$

Denote $u(\omega) = \text{Re}F(-i\omega)$ and $v(\omega) = \text{Im}F(-i\omega)$. Then

$$\begin{aligned} u(\omega) &= -\omega^2 + s + c\omega \sin \omega\tau + d(\tau) \cos \omega\tau + r(\tau) \cos 2\omega\tau, \\ v(\omega) &= -q\omega - c\omega \cos \omega\tau + d(\tau) \sin \omega\tau + r(\tau) \sin 2\omega\tau. \end{aligned} \tag{6.6}$$

Finally, since $\text{Arg}F(0) = 0$, we have the following stability diagnosis procedure for system (6.1). Firstly, draw curve (6.6) for $0 \leq \omega < \infty$. If $\text{Arg}(u(\omega) + iv(\omega)) \rightarrow -\pi$ with $\omega \rightarrow \infty$, then system (6.1) is asymptotically stable, otherwise it is unstable. For the qualitative estimations of the stability domain, we shall provide the explicit sufficient stability conditions in the space of the parameters.

THEOREM 6.1 If

$$q > c + \tau d(\tau) + 2\tau r(\tau), \tag{6.7}$$

then $\text{Re}(\lambda) < 0$ for any root λ of quasi-polynomial (6.5). Thus, system (6.1) is asymptotically stable.

Proof. Condition (6.7) implies $v(\omega) < 0$ when $\omega > 0$. Hence, the value of $\text{Arg}F(-i\omega)$ varies continuously from 0 to $(-\pi)$ while ω moves from 0 to ∞ . Thus, Theorem 6.1 is proved. Thus, system (6.1) is asymptotically stable.

EXAMPLE 6.1 To illustrate trajectories of the non-linear system (2.6), we choose the following parameters:

$$\begin{aligned} m_1 &= 0.2, m_2 = 0.5, d_1 = d_2 = 1, h = 0.7, \\ \gamma_1(\tau) &= 14, \gamma_2(\tau) = 7, \alpha_1 = 0.16, \alpha_2 = 0.9. \end{aligned} \tag{6.8}$$

System (6.1) has a non-zero equilibrium $\bar{x}_1 = 18.337$ and $\bar{x}_2 = 8.349$. Data set (6.8) and equalities (6.2) and (6.4) yield

$$q = 3.400, s = 1.640, c = 1.465, r = 0.036, d = 1.783. \tag{6.9}$$

In Fig. 1(a), the delay $\tau = 1$ is sufficiently small to satisfy the inequality (6.7) of Theorem 6.1, thus, the non-zero equilibrium point is asymptotically stable. Figure 1(b) illustrates instability of the equilibrium point for the delay value $\tau = 3$. Trajectories in Fig. 1 were calculated by the MATLAB program DDE23.

‘Delay-independent’ stability condition is constructed in the following theorem.

THEOREM 6.2 If

$$s > 1 + c + d(\tau) + r(\tau) \quad \text{and} \quad q > c + d(\tau) + r(\tau), \tag{6.10}$$

then $\text{Re}(\lambda) < 0$ for any root λ of quasi-polynomial (6.5).

Proof. First condition of (6.10) implies $u(\omega) > 0$ when $0 \leq \omega \leq 1$. Second condition of (6.10) guaranteed the inequality $v(\omega) < 0$ when $\omega > 1$. Hence (see (6.6)), the hodograph $F(-i\omega)$ avoids the quarter $u < 0$ and $v > 0$ of the (u, v) plane. Therefore, $\Delta \text{Arg} F(-i\omega) = -\pi$, while ω moves from 0 to ∞ . Thus, Theorem 6.2 is proved.

Consider now instability condition for system (6.1).

THEOREM 6.3 If

$$\frac{\pi(q + c)}{2(d(\tau) + 2r(\tau))} < \tau < \frac{\pi}{4(c + \sqrt{d(\tau) + s + r(\tau)})}, \tag{6.11}$$

then system (6.1) is unstable.

Proof. Consider $\omega\tau \leq \frac{\pi}{4}$ in hodograph (6.6). The left-hand side of inequality (6.11) implies $\pi(q+c)\omega < 2\tau d(\tau)\omega + 4\tau r(\tau)\omega$, hence, system (6.6) with $\omega\tau \leq \frac{\pi}{4}$ yields

$$v(\omega) > -q\omega - c\omega + d(\tau)\frac{2}{\pi}\omega\tau + r(\tau)\frac{4}{\pi}\omega\tau > 0.$$

Let $\omega\tau > \frac{\pi}{4}$. The right-hand side of (6.11) implies

$$\omega > \frac{\pi}{4\tau} > c + \sqrt{d(\tau) + s + r(\tau)}.$$

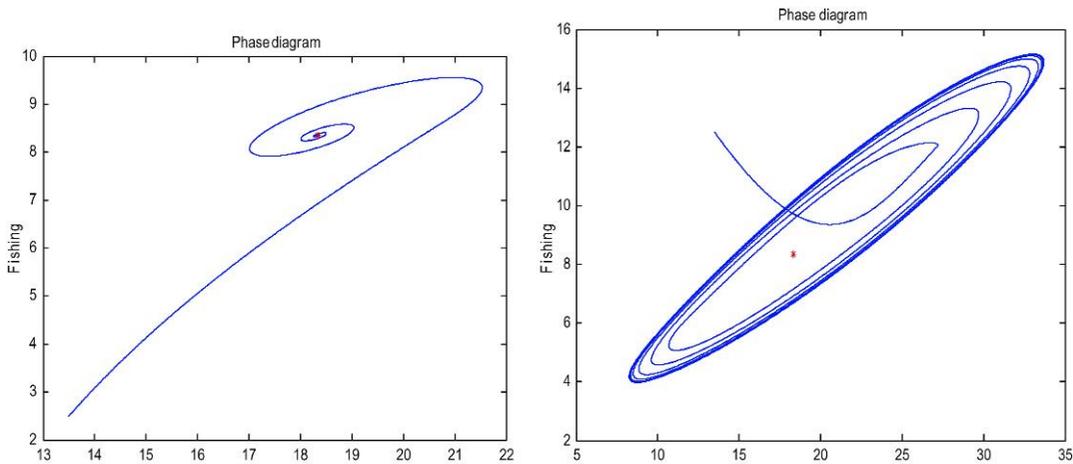


FIG. 1. Trajectories of non-linear system (2.6) with the parameters given by data set (6.8): a) $\tau = 1$ and b) $\tau = 3$.

Therefore,

$$\omega^2 - c\omega > \omega\sqrt{d(\tau) + s + r(\tau)} > c\sqrt{d(\tau) + s + r(\tau)} + d(\tau) + s + r(\tau),$$

hence (see (6.6)), $u(\omega) < 0$. Thus, with any value of $\omega \in (0, \infty)$, hodograph (6.6) avoids the domain $u > 0$ and $v < 0$.

Finally, $\Delta \text{Arg}F(-i\omega) = \text{Arg}F(-i\infty) - \text{Arg}F(0) = \pi$. Thus, Theorem 6.3 is proved.

REMARK 6.1 A gap between the left- and right-hand side of (6.11) is non-empty, when the value of $d(\tau)$ is sufficiently large compared with $q, c, r(\tau)$ and s . The latter is consistent with inequalities (6.10). For example, if $q = 0.3, c = 0.3, r(\tau) = 0.1, s = 0.1$ and $d = 3.8$, constraints (6.10) are satisfied, therefore, system (6.1) is unstable by Theorem 6.3.

7. Discussion

In this paper, we made an attempt towards modelling and analysing an MPAs model for a fish population. It is difficult to solve the MPA's problems empirically because they require population data of large spatial and temporal extent. One of the benefits of a theoretical modelling of MPAs is insight into the type of informative fisheries data that should be collected in order that the best design can be established. We introduced a new age-structured model of MPAs. The novel aspect of our model is the incorporation of age structure, migration and harvesting. The resulting model belongs to a class of non-linear delay differential equations. Compared to the canonical ODE's models, our model added more ecological complexity and demonstrated the influence of a reserve on the levels of stock biomass and catch. We obtained easily verifiable necessary and sufficient conditions for the existence of steady equilibrium points. We also proved that all solutions are non-negative and bounded for every set of the positive initial functions and initial conditions. We would like to point out that the assumptions of Theorem 3.1 are biologically motivated. To avoid population extinction under excessive harvesting, the 'loss' in every region should be less than the 'gain' in the region. For qualitative estimations of the stability domain in the space of parameters along with the stability diagnosis, explicit sufficient stability delay-dependent and delay-independent conditions are obtained. To find the regions of local stability or instability of the system, we used the argument principle for a direct analysis of the characteristic equation.

Our most interesting results are Theorems 6.1 and 6.3 and its implications, e.g. a critical value of the time delay exists such that it switches stability of a limit-cycle type fluctuations. This critical value depends on the 'loss' rates in both regions and the value of the delay. Although all theorems are established for model, most of its important biological implications should remain true for more advanced models of MPA, including diffusion models. Numerical simulations illustrate existence of stability switches in the model. It follows from our findings that introduction of protected areas could save a fish population even under excessive harvesting. There are many assumptions and simplifications in our model that are open to objections.

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