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Stability analysis and traveling wave solution of a reaction–diffusion model for fish population incorporating time-dependent recruitment intensity

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Abstract

From the standpoint of fishery management, an essential component of the basic information upon which policy can be based consists of intelligence from field data and computations. In certain situations, these studies can provide quite a great deal of the necessary information. However, in other situations they have not been able to give unequivocal answers to important questions, especially where several influential factors are involved in the whole jigsaw of the complex fishery system, in which their relative abundance may vary with the intensity of the recruitment effort or with spatial migration. Here, we propose and analyze a reaction–diffusion model for the fish population incorporating time-dependent fishery intensity. Using the traveling wave coordinate, we derive analytical solutions to the model system. Conditions on the system parameters are derived which ensure stability of the system under study. Phase portrait and traveling wave solution are plotted and discussed in order to gain better insights into the spatial movement of the fish population in time.

Keywords: Reaction-diffusion equations; Time-dependent recruitment intensity; Traveling wave coordinate; Stability analysis

1 Introduction

The movement of fish populations in space has often been neglected in dynamic models of fisheries. However, this striking feature of spatial heterogeneity due to fish mobility is essential from the point of view of fish management and exploitation. Undoubtedly, fish population dynamics models play a crucial role in providing assessment of the fish abundance and information on fishery exploitation level, since they form the scientific basis for advised decision making on fisheries managements. Especially since the fishing industry is facing increasing pressure due to the effects of climate changes, it is more pressing than ever to carry out more detailed dynamical studies by proposing and analyzing more complex models dealing more accurately with population distributions and spatial heterogeneity [1].

According to Sibert *et al.* [2], an important aspect of fisheries is their highly heterogeneous nature in space and time. This feature significantly effects their functioning, so that fish mobility and distribution have to be accurately described using spatialized models.

In 2007, Birnir and Maury [3] derived a system of ordinary differential equations from a discrete system of Vicsek, Czirok *et al.* (1999) to describe the motion of a school of fish. Equivariant bifurcation theory was utilized to derive linear and stationary solutions of the model system as well as explore their stability. The author also showed that periodic and toroidal solutions exist under deterministic perturbations and structurally stable heteroclinic connections. The model was applied to model the migration of the capelin which is a pelagic fish that migrates extensively in the North Atlantic [3].

More recently, Boonrangsiman *et al.* [4] considered a stage-structure model applied to fisheries. They incorporate a time delay into their model in which there is a single prey population and a predator population that can be separated by reproduction ability into an immature and a mature stage. Both predators in their model are allowed to hunt the same prey. Their model system admits three nonnegative steady states, namely, a washout steady state, a predator-free steady state, and a steady state at which all three populations coexist. The coexistence steady state is shown to be stable for all time delays under certain conditions on the system parameters. It is shown that instability and a Hopf bifurcation may take place at a critical time delay, with a possibility of transition to chaotic behavior.

It has lately been more acceptable to represent movement with a diffusion process. Although spatial advection-diffusion models have a long history in ecology [5–7], they have only recently been applied to model fish movement [2, 8, 9].

In 2001, an advection-diffusion reaction equation was utilized to predict the movement and tag attrition parameters from skipjack tuna tagging data that have been collected off the Maldives, based on two sets of field data collected during two periods of the early 1990s [10]. When their results of the analysis and previous analyses were compared in terms of management of skipjack fisheries in the Maldives and in the Indian Ocean, it was found that the movements were highly variable in space and time, and it was not possible to observe many consistent patterns between the two data sets.

In 2005, an advection-diffusion size-structured fish population model was proposed and applied to simulate the skipjack tuna population in the Indian Ocean [1]. Their model is fully spatialized, while movements are parameterized using a combination of oceanographical and biological data in order to naturally react to variations in the environment. An initial-boundary value problem was constructed then a unique positive solution was shown to exist. A numerical scheme was chosen for the model simulation. The model parameters were estimated and the exact gradient of a Bayesian cost function was computed measuring the distance between the outputs of the model and catch and length frequency data. A sensitivity analysis was carried out which interestingly shows that not all parameters can be estimated from the data.

In terms of traveling wave solutions in a fishery model, [11] introduced a simple model, in which organisms prefer to move in the direction they are sensing. They found that the model supports a one parameter family of compact traveling waves or "swarms". Moreover, the model has traveling front solutions, by which a population migrates from a region of higher population density to that of a lower density. According to these authors, their model reproduces features of realistic organism aggregations which have been observed in fish schools whose speed increases with the density of the school. Their model is a simple one-dimensional one-way system of the form

$$\rho_t + \bigl(\rho u(\rho)\bigr)_x = 0,$$

where the density of organisms $\rho\ (x,\ t) \geq 0$, and u is the speed of the moving organism such as fish population.

To the best of our knowledge, none of the previous works have captured the effect of recruitment intensity on the fish population dynamics, which could significantly impact the functioning and management of the fishing industry. Here, we therefore propose a reaction–diffusion model to describe fish movement, incorporating the factor of intensity of recruitment which is assumed to vary with the fish population density, or count, at that point in space and time. The key aspects of our model which make it different from previous ones are that our model makes the explicit connection between the recruitment intensity and the fish abundance, while taking into account the spatial dimension. Moreover, previous modeling studies mostly provided numerical solutions of the model, not analytical ones, so that the relationship among different physical parameters and their impacts on the important variables we need to track, namely fish population density and recruitment intensity, are not very clear. The impacts of the two dependent variables on one another can be discerned more distinctly by analysis of analytical solutions derived in this study. Introducing a traveling wave coordinate, our model is found to be equivalent to a system of ordinary differential equations which is analyzed in terms of its stability. The analytical solution of the model is found, whose plots illustrate how waves of fish population dynamically travel in the spatial direction as time progresses. More specifically, in this study recruitment intensity is derived as a function of space and time, not taken to be constant or modeled by simple terms as in many previous models. The effect, on the fishing effort, of the amount of fish being caught, is modeled by a Monod-like catchability rate function which is more realistic, so that the variations in the fishing effort for commercial purposes can be better deduced and identified for more efficient management and exploitation.

2 Model system

Here, we shall consider a fish population whose density $X(r,t)$, in counts per unit area, at the time t depends on the position in space, r, measured in the radial direction from a point of reference at the center of the region of interest. It is assumed that the school of fish spreads out in the radial direction, homogeneously in the angular direction, so that X does not depend on the polar angle.

We let $Y(r,t)$ be the recruitment intensity, or fishing effort, whose rate of change varies directly as the rate of change of the population density at (r,t). Also incorporating fish movement with a diffusion term, we arrive at the following equation for the rate of change of $X(r,t)$:

$$\frac{\partial Y}{\partial t} = \sigma \frac{\partial X}{\partial t} - \omega \frac{\partial^2 X}{\partial r^2}, \tag{1}$$

where the second term on the right represents the movement of the school of fish with the diffusion constant ω, ω and σ being positive constants.

With the expansion of fisheries around the world, it has become necessary to be able to accurately quantify fishing effort that the increase of which has threatened many fish stocks and non-target species with collapse. According to McCluskey and Lewison [12], deciding on the "best" method ultimately depends on the intended application of the quantity. They suggested, however, that the quantification methods that best represent fishing effort on a broad scale are based on information on gear used and spatial distribution. Spatial structuring of fish stocks also can arise from regional variations in the dynamics of the fishery fleet, such as variation in fishing effort or gear use [13, 14].

According to Birnir and Maury [3], the intrinsic dynamics of a school of fish and its migration present us with a perplexing and fascinating problem which leads to many complications in our optimization attempts. This is in part due to the observation that, as mentioned by [13], the individual fish has the tendency to adjust their speed and movement direction to those of the school to which they belong while, to make matters worse, the internal structure of the school can be very complex. How fish organize and maintain schools from a basic mechanism to function as their predator avoidance and survival tactics is still being actively investigated. The exceptional speed at which individual fish reacts collectively to predatory attacks has been hypothesized to be owed to quick transfer of information locally between school members. These groups turn together in unison and produce "escape waves" [14]. The diffusion term is added to (2) in the attempt to capture this phenomenon.

The recruitment intensity $Y(r,t)$, on the other hand, increases more quickly if there appears to be more fish in the fishing area. If the population is observed to decrease, fishing effort would naturally be curtailed. Thus, the rate of fishing may be described as in the following equation:

$$\frac{\partial Y}{\partial t} = \tau X^{\gamma}(k - X) - \frac{\rho XY}{mY + X}, \tag{2}$$

where the logistic model is assumed for the first term on the right, which represents the perceived abundance of quarry as sensed by the hunting party, with the carrying capacity of k so that if X exceeds the carrying capacity, the fishing intensity will decrease. The parameters m, τ and γ are positive constants to be determined in the solution of the model using the traveling wave coordinate.

The second term on the right of (2) represents the effect, on the fishing effort, of the amount of fish being caught, or catchability rate. If ρ is positive, as more fish are caught the less intense fishing effort will become. If ρ is negative, the more fish are caught the more intense fishing effort will become, since it is perceived by the fishermen that there is an abundance of fish to be caught. If ρ is zero, there is no feedback on the fishing intensity from current catchability. Here, we use a saturating function, with m a positive constant, to account for the fact that at a certain level of X or Y, fishing cannot result in a higher yield any more. To the best of our knowledge, such an expression has not been used in modeling fish movements with recruitment. We base this term on the well-known Monod function often utilized to model bio-reactors or predator-prey systems. In this term, if the fishing intensity is kept constant, the amount caught will start to decrease when fish abundance is high due to saturating demand. It may be observed that this term saturates to ρY in the event that there is an abundance of fish ($X \to \infty$), so that the rate of change of fishing intensity Y then varies directly with Y. On the other hand, the term mY is included in the denominator to reflect the fact that when fishing effort increases to a certain level, the amount caught will become independent of the effort. There is a limit to how much it could be caught.

In terms of the units, many factors can give rise to biases on attempts to measure fishing effort [12]. For example, changes in regulation, number of fishing crew, length of trip or time spent actively fishing, or actual amount of gear utilized in the water, can all lead to different and confounding interpretation of the unit "trip" of fishing effort. Thus, it is suggested that multiple units of effort are used in order to minimize such biases of effort measurements [12]. To overcome this problem, we carry out a non-dimensionalization of the variables by letting

$$X = \chi X^*, \qquad Y = \eta Y^*, \qquad t = Tt^*, \qquad r = Lr^*, \qquad c = Cc^*,$$
$$\tau = \theta\tau^*, \qquad k = Kk^*, \qquad \rho = R\rho^*, \qquad m = Mm^*,$$

where $\sigma c = 1$. Substituting these into Eq. (1), and then dropping the stars, we arrive at the following equations:

$$\frac{\chi}{T}\frac{\partial X}{\partial t} = \frac{c\chi\omega}{L^2}\frac{\partial^2 X}{\partial r^2} + \frac{\eta C}{T}c\frac{\partial Y}{\partial t}$$

and

$$\frac{\eta}{T}\frac{\partial Y}{\partial t} = \chi^\gamma K\theta\tau kX^\gamma - \chi^{\gamma+1}\theta\tau X^{\gamma+1} - \frac{\chi\eta R\rho XY}{\eta MmY + \chi X}.$$

Letting

$$C = \frac{\chi}{\eta}, \qquad w = \frac{cT\omega}{L^2}, \qquad \theta = \frac{\eta}{T\chi^{\gamma+1}}, \qquad K = \frac{\eta}{\chi^\gamma T\theta}, \qquad M = \frac{\chi}{\eta}, \qquad R = \frac{1}{T},$$

we may then write (1) for future use as

$$\frac{\partial X}{\partial t} = w\frac{\partial^2 X}{\partial r^2} + c\frac{\partial Y}{\partial t} \tag{3}$$

and (2) remains the same, in which X and Y are now dimensionless.

Traveling wave coordinate.

We now introduce the traveling wave coordinate

$$z = r + vt,$$

assuming that the wave of fish movement is traveling at a constant speed v. Letting $x(z) = X(r,t)$, and $y(z) = Y(r,t)$, Eq. (3) becomes

$$vx' = wx'' + cvy' \tag{4}$$

and (2) becomes

$$vy' = \tau x^r(k - x) - \rho xy/(my + x), \tag{5}$$

where $(\cdot)'$ denotes the derivative with respect to z. Integrating (4), we find that an equation that x and y satisfy is

$$vx = wx' + cvy$$

or

$$y = \frac{x}{c} - \frac{wx'}{cv}.$$

Substituting this into (5), we arrive at

$$vy' = \tau x^{\gamma}(k - x) - \rho x\left(\frac{x}{c} - \frac{wx'}{cv}\right) \Big/ (my + x).$$

We now substitute the above into the term vy' in Eq. (4) which now becomes

$$vx' = wx'' + c\left(\tau x^{r}(k - x) - \rho x\left(\frac{x}{c} - \frac{wx'}{cv}\right) \Big/ (my + x)\right).$$

Multiplying the above equation by the factor $my + x$, we clear the equation of the denominator:

$$vx'(my + x) = wx''(my + x) + c\left(\tau x^{r}(k - x)(my + x) - \rho x\left(\frac{x}{c} - \frac{wx'}{cv}\right)\right)$$

or, upon re-arranging,

$$\left(wx'' - vx' + c\tau x^{r}(k - x)\right)(my + x) - c\rho x\left(\frac{x}{c} - \frac{wx'}{cv}\right) = 0.$$

We remove the dependence on y by substituting $y = \frac{x}{c} - \frac{wx'}{cv}$ to obtain the following second order ordinary differential equation on x which is equivalent to the model system of partial differential equations (2)–(3):

$$\left(wx'' - vx' + c\tau x^{r}(k - x)\right)\left(m\left(\frac{x}{c} - \frac{wx'}{cv}\right) + x\right) - c\rho x\left(\frac{x}{c} - \frac{wx'}{cv}\right) = 0. \tag{6}$$

In the next section, we shall derive analytical solutions of our model as functions of traveling wave coordinate z.

3 Analytical solutions

We seek a traveling wave solution in the form

$$x' = ax - bx^{n} \tag{7}$$

so that

$$x'' = \left(a - nbx^{n-1}\right)x'. \tag{8}$$

Substituting (7)–(8) into (6), one obtains

$$\begin{aligned}&\left(a - nbx^{n-1}\right)\left(ax - bx^{n}\right)\left[-mw^{2}\left(ax - bx^{n}\right) + (mvw + cvw)x\right] + mvw\left(ax - bx^{n}\right)^{2}\\&\quad - \left(mv^{2} + cv^{2}\right)x\left(ax - bx^{n}\right) + \left(ck\tau x^{\gamma} - c\tau x^{\gamma+1}\right)\left[-mw\left(ax - bx^{n}\right) + (mv + cv)x\right]\end{aligned}$$

$$+ c\rho w\left(ax^2 - bx^{n+1}\right) - c\rho v x^2 = 0. \tag{9}$$

Traveling wave solution for the case $n = \frac{3}{2}$, $\gamma = 1$.

Upon closer inspection, we can see that the traveling wave solution will exist if $n = \frac{3}{2}$, and $\gamma = 1$. Using these values of n and γ, re-arranging (9) and equating coefficients of like terms, we obtain the following set of equations which relate the model parameters together. From the coefficients of x^2:

$$\left(a^2 w + ck\tau\right)\delta + mvwa^2 - a\left(mv^2 + cv^2\right) + ac\rho w - c\rho v = 0. \tag{10}$$

From the coefficients of $x^{5/2}$,

$$2a^2bmw^2 - 5abw\delta - 4abmvw + 2b\left(mv^2 + cv^2\right) + 2ck\tau bmw - 2bc\rho w = 0. \tag{11}$$

From the coefficients of x^3,

$$\left(3b^2 w - 2c\tau\right)\delta + 2mvwb^2 - 5ab^2mw^2 = 0. \tag{12}$$

Finally, from the coefficients of $x^{7/2}$

$$3b^3mw^2 - 2c\tau bmw = 0, \tag{13}$$

where

$$\delta = mv + cv - amw.$$

Equations (10)–(13) can be re-arranged and combined to arrive at the following more simplified equations relating the system parameters:

$$a = \frac{2v}{w}, \tag{14}$$

$$b = \sqrt{\frac{2c\tau}{3w}}, \tag{15}$$

$$\rho = -\frac{2av(m-c)^2}{c^2}, \tag{16}$$

$$k = \frac{av(c-2m)}{c^2\tau}. \tag{17}$$

With the parameters that satisfy the conditions (14)–(17), we now derive the traveling wave solution, by re-arranging Eq. (7) and integrating, with $n = \frac{3}{2}$, yielding

$$\int \frac{dx}{ax - bx^{3/2}} = \int dz.$$

Letting $s = x^{1/2}$, the above integral may be written as

$$\int \frac{2s\,ds}{(bs^3 - as^2)} = \int \frac{2\,ds}{s(bs-a)} = -\int dz.$$

Upon using partial fraction decomposition, we can carry out the integral to obtain

$$\ln\left|\frac{bx^{1/2}-a}{bx^{1/2}}\right| = -\frac{a}{2}(z-z_0) \tag{18}$$

or

$$\frac{|a-bx^{1/2}|}{x^{1/2}} = \kappa e^{-az/2},$$

where

$$\kappa = \frac{|a-bx_0^{1/2}|}{x_0^{1/2}},$$

with $x_0 = x(z=0) = X(r=0,t=0)$. The wave front solution is then

$$x = \frac{a^2 e^{az}}{(\kappa + be^{az/2})^2}. \tag{19}$$

Since

$$y = \frac{x}{c} - \frac{wx'}{cv} = \frac{x}{c} - \frac{w(ax-bx^n)}{cv},$$

we are led to

$$y = \frac{(v-wa)a^2e^{az}}{cv(\kappa + be^{az/2})^2} + \frac{bwa^3e^{3az/2}}{cv(\kappa + be^{az/2})^3}. \tag{20}$$

In the space and time variables, the solution may be expressed as

$$X(r,t) = \frac{a^2e^{a(r+vt)}}{(\kappa + be^{a(r+vt)/2})^2}, \tag{21}$$

$$Y(r,t) = \frac{(v-wa)a^2e^{a(r+vt)}}{cv(\kappa + be^{a(r+vt)/2})^2} + \frac{bwa^3e^{3a(r+vt)/2}}{cv(\kappa + be^{a(r+vt)/2})^3}. \tag{22}$$

Traveling wave solution for the case $n = \gamma = 2$.

Upon further inspection, we can see that the traveling wave solution will also exist if $n = \gamma = 2$. Thus, re-arranging (7) and equating coefficients of like terms, we obtain the following set of equations which relate the model parameters together:

From the coefficients of x^2,

$$-a^3mw^2 + 2a^2mvw + a^2cvw - a(mv^2 + cv^2) + acdw - c\rho v = 0. \tag{23}$$

From the coefficients of x^3,

$$a^2bmw^2 - 3ab(-amw^2 + mvw + cvw) - 2abmvw + b(mv^2 + cv^2) + ck\tau(-amw + mv + cv) - bc\rho w = 0. \tag{24}$$

From the coefficients of x^4,

$$-3ab^2mw^2 + 2b^2\left(-amw^2 + mvw + cvw\right) + b^2mvw$$
$$+ bckm\tau w - c\tau(-amw + mv + cv) = 0. \tag{25}$$

From the coefficients of x^5,

$$2b^3mw^2 - bc\tau mw = 0. \tag{26}$$

Equations (23)–(26) can be used to arrive at the following simpler relationships among the system parameters.

We are now in the position to derive the analytical solution with the parameters that satisfy the conditions (23)–(26). To now derive the traveling wave solution, we re-arrange Eq. (7) and integrating to obtain

$$\int \frac{dx}{ax - bx^2} = z + C,$$

which yields, upon integrating and using partial fraction decompositions,

$$\ln\left|\frac{x}{a - bx}\right| = az + aC_0$$

or

$$\frac{x}{a - bx} = e^{az}/C,$$

where

$$C = \frac{a - bx_0}{x_0}, \qquad x_0 = x.$$

Since

$$y = \frac{x}{c} - \frac{wx'}{cv},$$

we are led to the analytical solution

$$x = \frac{a\sqrt{2w}e^{az}}{C\sqrt{2w} + \sqrt{c\tau}e^{az}}, \tag{27}$$

$$y = \frac{x}{c} - \frac{w}{cv}\left(ax - bx^2\right)$$
$$= \left(\frac{v - aw}{cv}\right)\frac{a\sqrt{2w}e^{az}}{C\sqrt{2w} + \sqrt{c\tau}e^{az}} + \frac{a^2bw}{cv}\left(\frac{\sqrt{2w}e^{az}}{C\sqrt{2w} + \sqrt{c\tau}e^{az}}\right)^2. \tag{28}$$

In the space and time variables, the solution may be expressed as

$$X(r,t) = \frac{a\sqrt{2w}e^{a(r+vt)}}{C\sqrt{2w} + \sqrt{c\tau}e^{a(r+vt)}}, \tag{29}$$

$$Y(r,t) = \left(\frac{\nu - aw}{c\nu}\right)\frac{a\sqrt{2w}e^{a(r+\nu t)}}{C\sqrt{2w} + \sqrt{c\tau}e^{a(r+\nu t)}} + \frac{a^2bw}{c\nu}\left(\frac{\sqrt{2w}e^{a(r+\nu t)}}{C\sqrt{2w} + \sqrt{c\tau}e^{a(r+\nu t)}}\right)^2. \tag{30}$$

We next carry out a stability analysis of the model system in this case where $\gamma = 2$. The analysis for other values of γ will be less tractable but is expected to follow qualitatively in a similar fashion.

4 Stability analyses

To investigate the stability of (6) in the case that $\gamma = 2$, we introduce in (6) the new variables: $u = x(z)$, and $\upsilon = x'(z)$, which leads us to the following system of first order nonlinear equations in u and υ:

$$u' = \upsilon \equiv F(u,\upsilon), \tag{31}$$

$$w\upsilon' = -c\tau u^2(k-u) + c\rho\frac{(\nu u - w\upsilon)u}{(m\nu u - mw\upsilon + c\nu u)} + \nu\upsilon \equiv wG(u,\upsilon). \tag{32}$$

The steady states of (31)–(32) are found by equating $F(u,\upsilon)$ and $G(u,\upsilon)$ to zero. They are $(u,\upsilon) = (u_1,0)$ and $(u,\upsilon) = (u_2,0)$ with

$$\tau u^2 - k\tau u + \frac{\rho}{(c+m)} = 0. \tag{33}$$

Thus,

$$u_{1,2} = \frac{k\tau \pm \sqrt{k^2\tau^2 - \frac{4\rho\tau}{c+m}}}{2\tau}. \tag{34}$$

We note that $u_{1,2}$ are real only if

$$k^2\tau^2 - \frac{4\rho\tau}{c+m} \geq 0. \tag{35}$$

In what follows, we let

$$a_1 \equiv \frac{c^2\rho}{\nu(c+m)^2} - \frac{\nu}{w}, \tag{36}$$

$$a_2 \equiv \frac{2c\rho}{w(c+m)} - \frac{ck^2\tau}{2w} - \frac{ck\sqrt{k^2\tau^2 - \frac{4\rho\tau}{c+m}}}{2w}. \tag{37}$$

We can then prove the following theorem on the stability of the model system (31)–(32).

Theorem 1 *If* (35) *holds the steady state* $(u_1,0)$ *is unstable for all parametric values, while the steady state* $(u_2,0)$ *will be stable provided*

$$a_1 > 0 \tag{38}$$

and

$$k^2\tau - k\sqrt{k^2\tau^2 - \frac{4\rho\tau}{c+m}} - \frac{4\rho}{(c+m)} < 0. \tag{39}$$

Proof The Jacobian matrix of (31)–(32) at the steady state $(u_1, 0)$ is

$$J(u_1,0) = \begin{pmatrix} 0 & 1 \\ \frac{ck^2\tau}{2w} + \frac{ck\sqrt{k^2\tau^2 - \frac{4\rho\tau}{c+m}}}{2w} - \frac{2c\rho}{w(c+m)} & \frac{v}{w} - \frac{c^2\rho}{v(c+m)^2} \end{pmatrix}.$$

The characteristic equation of (31)–(32) at $(u_1, 0)$ is then

$$\lambda^2 + a_1\lambda + a_2 = 0 \tag{40}$$

with a_1 and a_2 as defined in (36) and (37), respectively. For stability, we need the coefficients in (40) to be both positive. That is, we need $a_1 > 0$ and $a_2 > 0$.

However, we need (35) to hold for this steady state to exist. On multiplying (35) through by $\frac{c}{2w}$, one sees that

$$\frac{2c\rho}{w(c+m)} - \frac{ck^2\tau}{2w} \le 0$$

and hence, $a_2 \le 0$ which means $(u_1, 0)$ is an unstable saddle point.

For the steady state$(u_2, 0)$, the Jacobian can be written as

$$J(u_2,0) = \begin{pmatrix} 0 & 1 \\ \beta & \frac{v}{w} - \frac{c^2\rho}{v(c+m)^2} \end{pmatrix},$$

where

$$\beta = -\frac{2ck\tau}{w}u_2 + \frac{3c\tau}{w}u_2^2 + \frac{c\rho}{w(c+m)}.$$

Thus, for stability, we need (38) to hold, and $\beta < 0$. Using (33), β becomes

$$\beta = k\tau u_2 - \frac{2\rho}{(c+m)}.$$

Using (34) to substitute into u_2, we find that $\beta < 0$ if

$$\frac{k^2\tau - k\sqrt{k^2\tau^2 - \frac{4\rho\tau}{c+m}}}{2} - \frac{2\rho}{(c+m)} < 0,$$

which is satisfied since condition (39) in the hypothesis of the theorem holds. This completes the proof. □

In Fig. 1, we show a phase portrait of the model system (31)–(32) in the case where (35), (38) and (39) hold. The solution trajectories are seen as expected to tend towards the steady state $(u_2, 0)$ which is a stable focus in Fig. 1(a). Some trajectories tend towards $(u_1, 0)$ a little as z increases, but eventually get pushed away from the saddle point. We also show in Fig. 1(b) a graph of $u(z) = x(r, t)$ in this case, plotted as a function of the traveling wave coordinate z. The fish population is seen here to travel in waves with ripples of higher density alternating with low density that dampen as we look further into the distance $(z \to \infty)$.

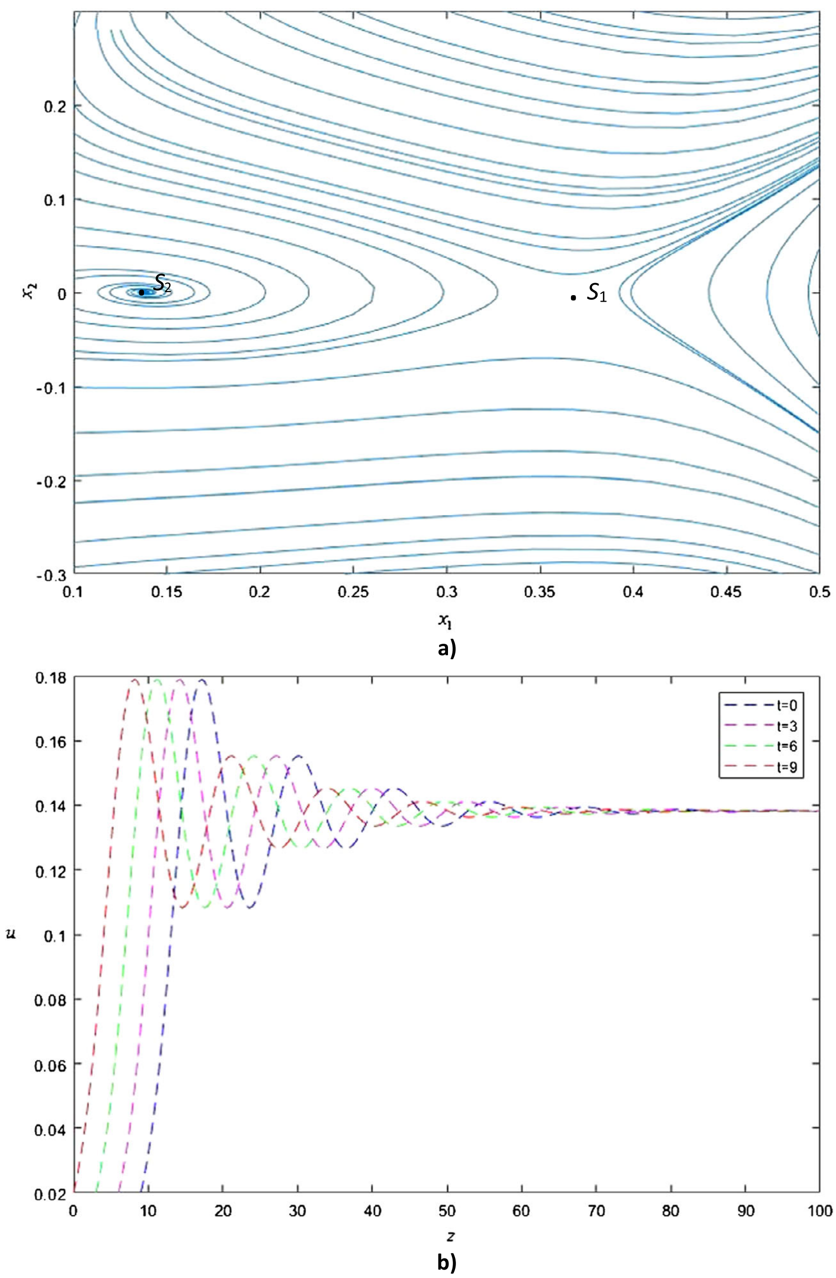

Figure 1 Phase portrait. (**a**) Plot of the phase portrait of the model system (7)–(8) showing solution trajectories in the vicinity of the two steady states, one of which is a saddle point and the other a stable focus as predicted by Theorem 1. Here, S_1 is the steady state $(u_1, 0)$ and S_2 is $(u_2, 0)$. (**b**) Plot of fish population density u as a function of traveling wave coordinate for t between 0 and 9. Here, $a = \frac{1}{2}$, $b = 2$, $c = 4$, $\rho = \frac{1}{2}$, $k = \frac{1}{2}$, $m = 1$, $\tau = 2$, $v = \frac{1}{2}$, and $w = 1$

5 Discussion and interpretation

In order to plot the traveling wave solutions to illustrate how a school of fish moves in space and time, as well as compare the impacts of different efforts on the population abundancy and pattern of mobility, we must find parametric values that satisfy the conditions (24)–(27), or (33)–(36), together with the stability conditions (11) and (14)–(15).

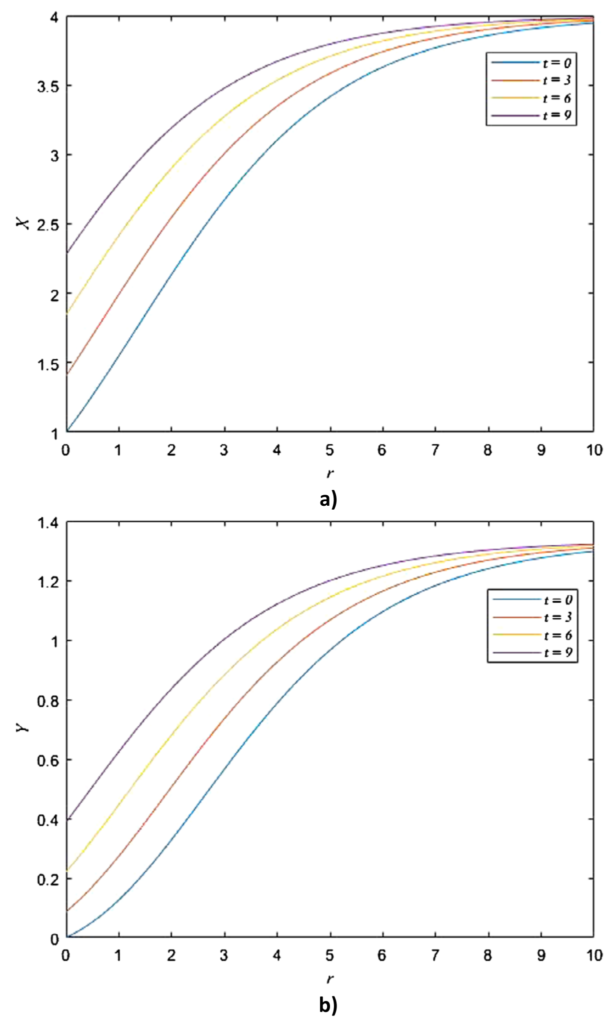

Figure 2 Traveling wave solution. Traveling waves of (**a**) fish density x, and (**b**) recruitment intensity y, as functions of spatial position r for t from 0 (furthest left) to 9 (furthest right), given by (31)–(32). The waves are seen moving from right to left. Here, $a = 1, b = \frac{1}{2}, c = 3, \rho = -\frac{2}{9}, k = \frac{4}{9}, \kappa = 0.5, m = 1, \tau = \frac{1}{16}, v = \frac{1}{4}$, and $w = \frac{1}{2}$

With the parameter values chosen in such a manner, we are able to plot the analytical solution given by (31)–(32), seen as a wave of movement of fish population from right to left along the spatial direction r as time progresses in Fig. 2. Here, $a = 1$, $b = \frac{1}{2}$, $c = 3$, $\rho = -\frac{2}{9}$, $k = \frac{4}{9}$, $\kappa = 0.5$, $m = 1$, $\tau = \frac{1}{16}$, $v = \frac{1}{4}$, and $w = \frac{1}{2}$. We observe x and y to tend, in an increasing fashion, toward their respective values at the stable steady state $(u_2, 0)$ as r tends to infinity. If we focus on a single position, fixing r, then we see that the fish density x increases as time increases, and similarly to the fishing intensity y. This is the case where $\rho < 0$, in which the increase in fishing yield at each moment in time will increase the fishing effort even more.

Figure 3 shows the analytical solution given by (39)–(40), seen as a wave of movement of fish population from right to left along the spatial direction r as time progresses. Here, $a = \frac{1}{2}$, $b = 2, c = 4$, $\rho = 0$, $k = \frac{1}{4}$, $\tau = 2, v = \frac{1}{2}, w = 1$ and $C = 1$, chosen to satisfy (33)–(36). This is the case that $\rho = 0$, which is when the current fishing yield does not have any impact on the decision to increase or decrease the fishing effort.

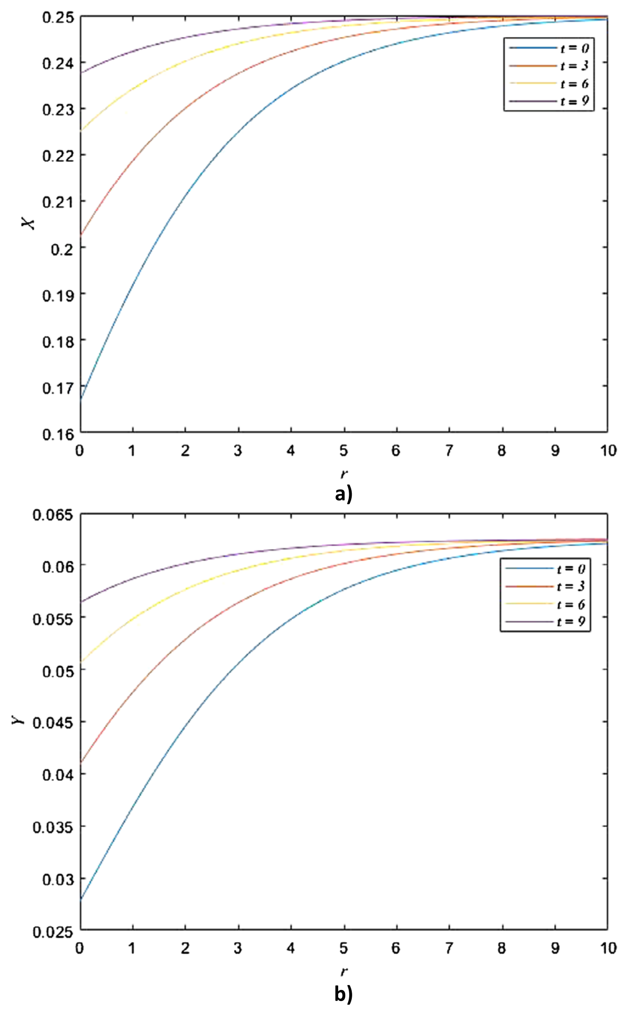

Figure 3 Traveling wave solution. Traveling waves of (**a**) fish density x, and (**b**) recruitment intensity y, as functions of spatial position r for t from 0 (furthest left) to 9 (furthest right), given by (39)–(40). The waves are seen moving from right to left. Here, $a = \frac{1}{2}, b = 2, c = 4, \rho = 0, k = \frac{1}{4}, \tau = 2, v = \frac{1}{2}, w = 1$ and $C = 1$

In both cases in which we are able to identify the traveling wave solutions, the current catch yield does not impose a curb on the fishing effort ($\rho \leq 0$). In the case where $n = \frac{3}{2}, \gamma = 1$, it even encourages more intense fishing ($\rho < 0$). The traveling waves travel from right to left along which, at a fixed time, the number of fish increases as we travel downstream further from the point of reference ($r \to \infty$), and the fishing intensity follows suit. On the other hand, at a fixed location r, the number of fish increases as time progresses ($t \to \infty$), and the fishing intensity follows suit.

The stability of the steady state $(u_2, 0)$ where the fish population is not wiped out, which is the desirable situation, is contingent on the condition (15) to hold. Considering (15), we see that if k is large enough, the non-wipeout stability will be ensured, and the fish population will tend towards a positive steady level as time progresses. The parameter k may be seen as the carrying capacity of the environment, and high value of k means that the environment is favorable in support of high levels of aquatic species.

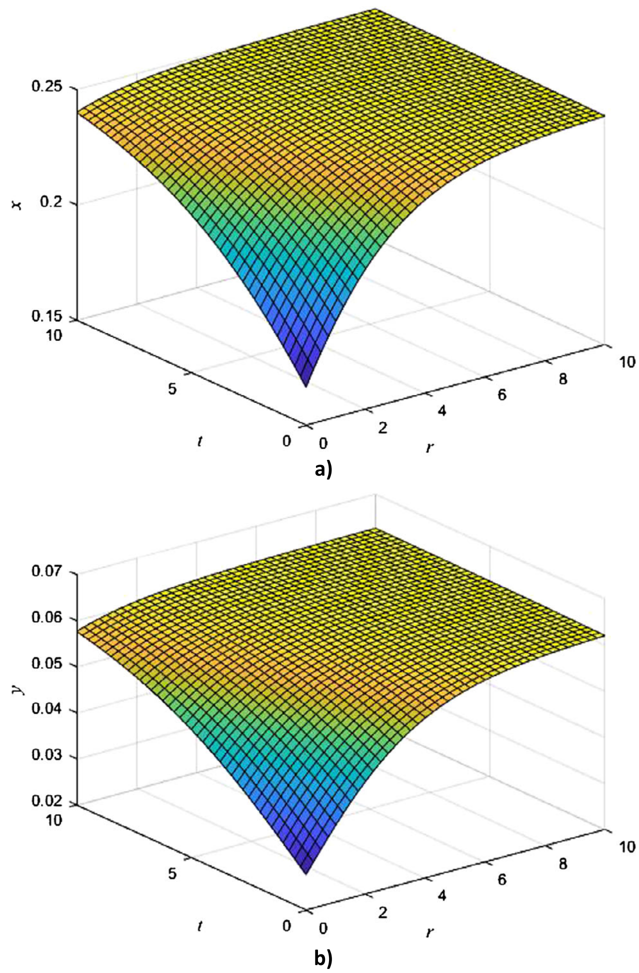

Figure 4 Three-dimensional illustrations. Three-dimensional plots of traveling wave solutions of (**a**) fish density x, and (**b**) recruitment intensity y, as functions of spatial position r for t. Here, $a = \frac{1}{2}, b = 2, c = 4, \rho = 0, k = \frac{1}{4}, \tau = 2, v = \frac{1}{2}, w = 1$ and $C = 1$

Finally, in Fig. 4, we show a three-dimensional plot of X and Y as functions of r and t. The variations in population density and fishing intensity can be traced easily as we vary the observation location or time.

Considering the plots in the above figures, we note that our model is able to exhibit realistic physical behavior, essentially due to our choice to incorporate impacts of recruitment intensity on the model dynamics. If a simpler term were used for the impact of catchability on the fishing intensity, specifically, if $m = 0$ in the catchability rate term in Eq. (2), reducing the term to a simpler linear form, the graphs of the levels of population density and recruitment intensity will be different, since m influences the choice of a in the equations relating all the system parameters, and hence impacts on the solution given in (21)–(22) and (29)–(30). It would also be harder to fit our model to physical data if this parameter is missing, limiting the degree of freedom. The conditions that ensure the system's stability also depend on m, for example in (39). The presence of this parameter ensures better accuracy of the result.

Now, if the factor $mY + X$ is removed from the second term on the right of (2) altogether, so that the term reduces to ρXY, the system will lose its stability. There would not be the terms in (36) and (37) that allow a_1 and a_2 to be positive, thereby ensuring the system's stability. What this means is that, whatever the physical conditions, the levels of X or Y eventually become unbounded unless they start from their respective steady state values. This, apart from being less than realistic, would defeat the purpose of our modeling effort to try to find the best way to manage and control the system.

As far as we can ascertain, articles that provide data which can be used in relation to our model results are extremely rare, since most articles mainly reported on data that related population density and fishing effort to ages or lengths of the fish species of interest. Limited data can be found that give time series of the fish population but the measurements were done for very long time intervals, in years not in days or weeks that could be used to calibrate our model. The studies cited in the introduction section [1–11] constructed their models based on general observations and not on any rigorous physical data measurements and relatively crude data was used in their model simulations. In fact, for this reason, our modeling should be a valuable springboard and provide an impetus for researchers to collect physical data that are more relevant to the effort at fisheries management. To be able to fit the model to the data and estimate the system's parametric values, the data need to be collected with the appropriate units of time and space. The finer these measurements are made, the more accurate the model's solutions will be.

According to Cornejo-Donoso *et al.* [15], the use of Marine Protected Areas (MPA) has become recognized as a viable management approach. However, if the goal is to manage species that are relatively not as active, MPAs have been shown to be quite successful. On the other hand, this type of spatial protection is not very successful in meeting this goal if the organisms are highly mobile, moving frequently outside the protected area. A larger MPA has been proposed to compensate for such extensive movements [15]. Since our model describes the distribution of fish populations over time and space, it offers an ideal tool that can provide valuable insights into MPA designs, and predict potential outcomes of MPA utilization and management, in terms of to the appropriate sizes and boundaries of MPAs as well as optimum recruitment scheduling and locations that protect marine lives, maintain biomass, as well as increase fisheries productivity at the same time. In particular, we have shown that conditions on the physical conditions exist that ensure that the population density will tend towards a bounded homogeneous value as time passes, in certain situation in an oscillatory fashion in space (Fig. 1), or monotonic in fashion in other circumstances (Figs. 3–4). If these conditions are not satisfied, then the desirable trends in fish population may not be relied upon. We also can tell how the parameter a, which is twice the ratio of the speed of the traveling wave v and the diffusion coefficient w, significantly effects the trends in the fish population.

Concerning model limitations, some investigators may argue that predictions from our model are subject to simplified movement assumptions and neglect of other important factors that possibly influence the outcomes. Yet, we need to explore the limitations of our model and the value of increasing the detail of the movement assumptions leading to an increased behavioral complexity and mathematical intractability of the resulting model. For example, our model assumes deterministic dynamics when a random, diffusive movement could be more realistic. Stochastic simulations can easily be carried out to check whether this will add significantly to the accuracy of the result or not. Another effect to which we have not paid attention in this paper is that of aggregations, which may be aggregations in response to forces of the environment such as the surface temperature, and other environmental factors that may be transported by ocean currents, as investigated by Cornejo-Donoso *et al.* in [15]. Future research can involve weakly nonlinear stability analysis to derive conditions under which aggregation may lead to the emergence of Turing patterns or other interesting spatial distributions that have been observed and reported in some literature [16].

6 Conclusion

Highly mobile aquatic species make tracking and management efforts to protect marine lives, restore biomass, and increase fisheries yields extremely difficult. While Marine Protected Areas (MPAs) have been proposed and experimented upon to meet these goals for many relatively sluggish marine species, their benefits to highly mobile species are doubtful still due to their frequent movement outside the protected area, posing many limitations in the testing and verification. Mathematical models can help to overcome these limitations by identifying designs and predict potential outcomes. According to Cornejo-Donoso *et al.* [15], large scaled protected areas can be effective in overfished stocks recovery, pelagic fish protection ensuring significant rises in fisheries yields.

Numerous reports have been published in which simulations of individual movements dynamics are carried out on heterogeneous spatial regions [17]. The main assumption in these studies is that each fish individuals imitate the movement of nearby fishes, leading to the formation and movements in aggregations [17]. A few researchers have argued that predictions from these models are subject to simplified movement assumptions [15] in assuming diffusive movement. However, by incorporating the influences of fishing intensities that depends on space and time as well as the abundance of resources, our model was shown to simulate different patterns of fish movements, depending upon different values of the physical parameters, in the form of traveling wave fronts shown in Figs. 3–4, or waves of fish migration with ripple effects as seen in Fig. 1. Our model is, therefore, expected to expand our understanding of how more insightful knowledge about fish movement dynamics, and how they vary with the physical parameters, can affect the design of effective alternatives to managing highly mobile stocks in the open waters.

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Competing interests
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Authors' contributions
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References

1. Faugeras, B., Maury, O.: An advection-diffusion-reaction size-structured fish population dynamics model combined with a statistical parameter estimation procedure: application to the Indian Ocean skipjack tuna fishery. Math. Biosci. Eng. **2**, 1–23 (2005)
2. Sibert, J.R., Hampton, J., Fournier, D.A., Bills, P.J.: An advection-diffusion-reaction model for the estimation of fish movement parameters from tagging data, with application to skipjack tuna (Katsuwonus pelamis). Can. J. Fish. Aquat. Sci. **56**, 925–938 (1999)
3. Birnir, B., Maury, O.: An ODE model of the motion of pelagic fish. J. Stat. Phys. **128**, 1–34 (2007)
4. Boonrangsimana, S., Bunwonga, K., Moore, E.J.: A bifurcation path to chaos in a time-delay fisheries predator–prey model with prey consumption by immature and mature predators. Math. Comput. Simul. **124**, 16–29 (2016)
5. Skellam, J.G.: Random dispersal in theoretical populations. Biometrika **38**, 196–218 (1951)
6. Okubo, A.: Diffusion and Ecological Problems: Mathematical Models. Biomathematics, vol. 10. Springer, Berlin (1980)
7. Holmes, E.E., Lewis, M.A., Banks, J.E., Veit, R.R.: Partial differential equations in ecology: spatial interactions and population dynamics. Ecology **75**, 17–29 (1994)
8. Bertignac, M., Lehodey, P., Hampton, J.: A spatial population dynamics simulation model of tropical tunas using a habitat index based on environmental parameters. Fish. Oceanogr. **7**, 326–334 (1998)
9. Maury, O., Gascuel, D.: SHADIS (Simulateur HAlieutique de DYnamiques Spatiales), a GIS based numerical model of fisheries. Example application: the study of a marine protected area. Aquatic Living Resour. **12**, 77–88 (1999)
10. Shiham Adam, M., Sibert, J.R.: Population dynamics and movements of skipjack tuna (*Katsuwonus pelamis*) in the Maldivian fishery: analysis of tagging data from an advection-diffusion-reaction model. Aquatic Living Resour. **15**, 13–23 (2002)
11. Milewski, P.A., Yang, X.: A simple model for biological aggregation with symmetric sensing. Commun. Math. Sci. **6**, 397–416 (2008)
12. McCluskey, S.M., Lewison, R.L.: Quantifying fishing effort: a synthesis of current methods and their applications. Fish Fish. **9**, 188–200 (2009)
13. Booth, A.J.: Incorporating the spatial component of fisheries data into stock assessment models. ICES J. Mar. Sci. **57**, 858–865 (2000)
14. Guan, W., Cao, J., Chen, Y., Cieri, M.: Impacts of population and fishery spatial structures on fishery stock assessment. Can. J. Fish. Aquat. Sci. **70**, 1178–1189 (2013)
15. Cornejo-Donoso, J., Einarsson, B., Birnir, B., Gaines, S.D.: Effects of fish movement assumptions on the design of a marine protected area to protect an overfished stock. PLoS ONE (2017). https://doi.org/10.1371/journal.pone.0186309
16. Adam, M.S., Sibert, J.R.: Population dynamics and movements of skipjack tuna (Katsuwonuspelamis) in the Maldivian fishery: analysis of tagging data from an advection-diffusion-reaction model. Aquatic Living Resour. **15**, 13–23 (2002)
17. Hubbard, S., Babak, P., Sigurdsson, S.T., Magnússon, K.G.: A model of the formation of fish schools and migrations of fish. Ecol. Model. **174**, 359–374 (2004)