TWO-SPECIES COMPETITION MODEL WITH DIFFUSION AND HARVESTING: A NUMERICAL STUDY

A Thesis

by

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This thesis meets the standards for scope and quality of Texas A&M University-Corpus Christi and is hereby approved.

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ABSTRACT

Predicting well observed states in ecology such as co-existence, competitive exclusion of one competitor, and bi-stability is vital during multi-species competitions. Models that examine these aspects of living systems have extensive applications in the overlapping areas of applied mathematics, population ecology, invasion science, evolutionary biology, and economics. The present study investigated a twin-species Lotka-Volterra competition system accommodating diffusion and harvesting environments - a scenario widely anticipated in mathematical ecology. Our mathematical setup converts the diffusion and harvesting incorporated physical model into a system of second order nonlinear partial differential equations (PDES) describing the competition of the two species in closed domains. A finite difference numerical scheme is developed to solve the nonlinear boundary value problem (BVP) with Neumann boundary conditions. We applied our model results to the case of Brown and Pink shrimp in southeastern Gulf of Campeche that compete for resources in Marine Protected Areas (MPAs). For this specific example, we computed theoretical results for the sustainable biomass yield due to the competition and the mobility in the presence of multiple fishing zones. Our numerical solutions reveal that the speed or mobility of species is critical for the design of MPAs to attain a maximum sustainable biomass yield. Additionally, the results indicate that harvesting rate is adjustable for larger number of MPAs along the coastal line for efficient fishing. Further, it is observed that a sustainable biomass can be achieved for low mobile species such as the brown and pink shrimps by having smaller MPAs and both the species can co-exist in Gulf of Campeche.

DEDICATION

For my parents, Jose Angel Caro and Linda Reyes Caro, who, despite not completing their own education, always supported and encouraged me to pursue mine.

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1: INTRODUCTION

Ecology is a branch of biology. In particular, Ecology is a study of interaction of living organisms and its environment. It is a subject that has peaked the interest of both mathematicians and scientists alike. It uses mathematical models to answer questions about how a species interaction with its environment affects said species. Examples of this include SIR models, population dynamics, competition models, etc. There are several ways to model population dynamics using differential equations, difference equations, and partial differential equations. PDEs are widely used in ecology due to their ability to model physical phenomena.

A multi-species model is a system of equations that contain information about more than one species. Multispecies models are used to develop an understanding of how different species together affect a system. We see applications of these models in forestry management, rangeland management, fishery management, and epidemiology (Arino et al., 2005; Hanson et al., 1988; Karp et al., 2023; Kohyama, 1992). Since the 1980's, the use of multispecies models in place of single species models has increased (Karp et al., 2023; Hollowed et al., 2000). There are several advantages to using a multi-species model as opposed to a single species model. A multi-species model provides a more realistic representation of a population's dynamics by including outside influences that can impact the a population. In comparison, single species models are limited in their long term predictions of population fluctuations as they are not able to take into account outside influences on the population such as predation, competition, or mutualism; all of which can have a substantial effect on a population (Karp et al., 2023; Hollowed et al., 2000). In addition, modelling with a secondary, or even tertiary, species of interest can help uncover or further our understanding of the ecological connections between species in a system. This is necessary due to the fact that many population studies concern an ecosystem rather than a single species of interest.

One of the most well known multispecies model is the Lotka-Volterra Model (LVM), developed by Alfred J. Lotka and Vito Volterra in the 1920's. Today, the LVM is considered a building block of population ecology. Although initially developed for chemistry and mathematical biology applications (Anisiu, 2014), the LVM has also found applications in economics, chemical systems and others (Gatabazi et al., 2019; Hering, 1990). To be more precise, the LVM is a multispecies interaction model commonly referred to as the Lotka-Volterra Predator-Prey model, though it can also be used to model competition and mutualism as well. The system describes the instantaneous growth of two species as a result of their populations, growth rates, and interactions. Whether the model displays predation, competition, or mutualism depends on each population's response to the interaction. If the intent is to model predation, one population benefits from the interaction and the other population incurs a negative effect. For the purpose of this study, our concern is competition. In a competition model both species experience a negative effect as a result of an interaction, though the magnitude of the effect can be different depending on the species. As previously mentioned, the Lotka-Volterra model has many applications. One such application is in the management of systems with the intent to maintain a healthy population of any species of interest. These modelling applications provide us with information of how a systems works. The information gained from modelling these systems can be very useful when applied to ecosystems in nature particularly, as it pertains to this study, marine ecosystems.



Figure 1.1 Alfred James Lotka (Alfred James Lotka, 2023)



Figure 1.2 Vito Volterra (Volterra, 1926)

In recent years we have seen an increase in the need for marine preservation due to our current climate crisis (United Nations., 2023) along side a growing demand for fishery goods (Supartini et al., 2018). This growing demand for fishery goods puts in-demand species at a higher risk of being over fished or depleted of its population. For this reason, the need for effective conservation has increased. A popular method of preservation comes in the form of marine protected areas (MPAs), commonly referred to as MPAs. As defined by the International Union for the Conservation of Nature (IUCN) a protected area is a "clearly defined geographical space, recognised, dedicated and managed to achieve the long term conservation of nature" (International Union for the Conservation of Nature, 2020). MPAs were endorsed by the US government as a method of conservation in 2001. As of 2020 there are 29 coastal states with a federal and/or state MPA program in place (Wenzel et al., 2020). Research concerning MPAs and conservation initially sought to determine whether MPAs were effective as a conservation effort. It was found that MPAs resulted in an increase of biomass of populations within its protected borders (Perez-Ruzafa et al., 2008). Now, research into how size, location, population(s) of interest, etc. affect the efficacy an MPA network have been of great interest in the past twenty years.



Figure 1.3 Marine Protected Area Coverage by US Ocean Region (US Ocean Region, 2023)

While the majority of MPAs allow some fishing within its boundaries this study explores a notake marine reserve meaning there is no fishing within the boundaries of an MPA. There are other methods of conservation, besides MPAs, already in place for marine life. Conservation efforts such as limitations on catch size and quantity, license requirements, seasonal restraints, etc. are common (Reef Resilience Network, 2023), but when these methods are used in tandem with the information gained from modelling, these methods have the potential to be more effective and efficient. The mismanagement of fisheries can have detrimental effects not only on the populations of interest, but also on our local and national economy. Managing and utilizing these fisheries has created nearly two million jobs and generated more than 250 billion in sales (Raimondo & Spinrad, 2020). Thus, the understanding of how these species interact with and affect the systems they belong to has become a popular topic of research.





In this study we utilize a multi-species model to analyze the impact mobility can have on two species in competition living within an MPA network made up of protected areas and fishing zones. Given the economic importance of fisheries we also explore how the implementation of a MPA network affects sustainable yield. Sustainable yield being the harvesting amount of a species that still allows that species to replenish what's been taken from its population.

This thesis is organized as follows: In Chapter 2, we begin by introducing the widely known Lotka-Volterra competitive species model. Several variations and generalizations of this model along with our proposed setting and mathematical equations in dimensionless forms are provided in the subsections. Applicable numerical solution methods for the governing partial differential equations are illustrated in Chapter 3. The adopted finite difference scheme formulation for our model is described in the subsection 3.2. Our main results and applications appear in Chapter 4. Our numerical results are applied to the practical fishing scenario involving brown and pink shrimps. The historical overview of brown and pink shrimp habitats and their existence in Marine Protected Areas (MPAs) are narrated in the respective subsections. The parameters required in the diffusion and harvesting model are reported in the subsection 4.3. The determination of biomass

density and the sustainable biomass are crucial to the survival of brown and pink shrimps. In subsections 4.4 and 4.5, the evaluation and interpretation of these quantities in multiple fishing zones including MPAs network is demonstrated in detail. The computed results are portrayed graphically in the respective subsections as well. Finally, in Chapter 5, we document the main findings of the thesis and give a brief mention of possible future work.

2: DIFFUSION MODEL TO TRACK BIOMASS DENSITY OF BROWN AND PINK SHRIMP

In this Chapter, we provide definitions and a brief overview of the models in population biology. Then we start with the spatially uniform distribution model and augment a diffusion term to obtain system of coupled pde's.

2.1 Models in Population Dynamics

Applications of simple mathematical concepts to growth and decline of population in nature and struggle of species to predominate over one another has been a subject of interest centuries ago. Among the works on mathematical population models, Malthus (1798), Verhulst (1838), Pearl and reed (1908) and so on, the work done by Lotka and Volterra (1920's and 1930's) and Kermack and McKendrik (1927) had a profound effect on the field of population biology (Edelstein-Keshet, 2005).

Lotka and Volterra were the first to study models with interacting species by making simple assumptions that led to a tractable mathematical problem. Among these work, a notable contribution was by Kermack and McKendrick(1927) who addressed the problem of outbreak of epidemic in a population. Critics of these models often argue that factors like environmental effects are not considered in these models. However the importance should not rely on accuracy of predictions but rather the principles they are laid on like competiting species excluding one another.

Over the past three decades, the appreciation of Lotka Volterra Models are mixed, nevertheless it is interesting to note that these models have helped the research directions greatly.

2.2 Spatially Uniform Distribution

We consider a simple two species Lotka-Volterra competition model wherein principle of competition exclusion holds. The LVCM is a logistic equation with a self limiting component-carrying capacity. This describes a population whose growth is proportional to the remaining amount of some constant limited resource; as the population increases the amount of the limited resource decreases. In addition to the self limiting component there is a competition term to describe the effect of the competing species on other population.

7

Let u and v represent brown and pink shrimp competing for their life in marine protected area(MPA). Species u has a low transport and species v has a high transport. We would like to investigate competition and coexistence of species u and v (inside MPA). Both the species have logistic type of growth in absence of the other. We also like to investigate harvesting model and calculate the maximum sustainable yield for LVCM. Later we would like to add in the transport term to the above model and rename it as Lotka Volterra competition- diffusion system. Now we would like to bring in reserves in this model and see which species wins. The biomass density of two species u and v are formulated by system of ODEs:

$$\frac{du}{dt} = r_1 u \left(1 - \frac{u}{K_1} - b_{12} \frac{v}{K_1} \right) - f u \tag{2.1}$$

$$\frac{dv}{dt} = r_2 v \left(1 - \frac{v}{K_2} - b_{21} \frac{u}{K_2} \right) - f v$$
(2.2)

where r_1 , r_2 are the birth rates, K_1 , K_2 denotes the carrying capacities, b_{12} , b_{21} are the measure of competition of species v on u and measure of competition of species u on v. We then define the non-dimensional quantities such that

$$\tilde{u} = \frac{u}{K_1}, \tilde{v} = \frac{v}{K_2}, \tilde{t} = r_1 t, \rho = \frac{r_2}{r_1}, a_{12} = b_{12} \frac{K_2}{K_1}, a_{21} = b_{21} \frac{K_1}{K_2}, \tilde{f} = \frac{f}{r_1}$$
(2.3)

The non dimensionalized system of ode's (after dropping tilda's) are as follows:

$$\frac{du}{dt} = u(1 - u - a_{12}v) - fu = F_1(u, v))$$
(2.4)

$$\frac{dv}{dt} = \rho v (1 - v - a_{21}u) - f v = F_2(u, v)$$
(2.5)

The steady states (u^*, v^*) are solutions of $F_1(u, v) = F_2(u, v) = 0$.

Now we augment the above system with diffusion term to obtain the system of partial differential equations to track biomass density of pink and brown shrimp.

2.3 Diffusion Model to Track Biomass Density of Brown and Pink Shrimp

The corresponding system of equations are as follows.

$$\frac{\partial u}{\partial t} = \mu_1 \Delta u + r_1 u \left(1 - \frac{u}{K_1} - b_{12} \frac{v}{K_1} \right) - f u \tag{2.6}$$

$$\frac{\partial v}{\partial t} = \mu_2 \Delta v + r_2 v \left(1 - \frac{v}{K_2} - b_{21} \frac{u}{K_2} \right) - f v$$
(2.7)

To start with, we reduce the model to 1-D system of partial differential equations

$$\frac{\partial u}{\partial t} = \mu_1 \frac{\partial^2 u}{\partial x^2} + r_1 u \left(1 - \frac{u}{K_1} - b_{12} \frac{v}{K_1} \right) - f u$$
(2.8)

$$\frac{\partial v}{\partial t} = \mu_2 \frac{\partial^2 v}{\partial x^2} + r_2 v \left(1 - \frac{v}{K_2} - b_{21} \frac{u}{K_2} \right) - f v$$
(2.9)

where u(x,t), v(x,t) are biomass density of brown and pink shrimp population respectively. Equation (2.8) helps to track biomass density of the brown shrimp population at location x and time t. It is controlled by three processes: diffusion, reproduction and mortality. The first term in the right hand side of equation (2.8) describes diffusion, that is, random motion of species with μ as its diffusion coefficient. Density dependent reproduction and mortality are represented by the second and the third term of equation (2.8) respectively. Also μ is the transport coefficient. Equation (2.9) gives biomass density of the pink shrimp population at a location x and time t. It is controlled by three processes: transport, reproduction and mortality. The first term describes diffusion: random motion of a population. The second term represents density dependent reproduction and the last term denotes the density dependent mortality.

We now discuss the dimensions of the variables and the parameters in the above system. uand v are biomass density of brown and pink shrimp population per unit domain with dimensions $\frac{KG}{L}$. In one-dimension the domain is a unit line, and in two- dimensions, the domain is a unit area .The carrying capacity in the parent stock 'K' is the total biomass KG per unit domain length with dimensions L. Parameter r_1 and r_2 are maximum instantaneous per capita birth rate of brown and pink shrimp population respectively with dimensions $\frac{1}{T}$ and f natural instantaneous per capita fishing mortality rate with dimensions $\frac{1}{T}$. In order to reduce the number of parameters, we shall non-dimensionalize the system of reaction-diffusion equations. We then define the non-dimensional quantities such that

$$\tilde{u} = \frac{u}{K_1}, \tilde{v} = \frac{v}{K_2}, \tilde{t} = r_1 t, \tilde{x} = \frac{x}{L_m}, \tilde{f} = \frac{f}{r_1}$$

The non dimensionalized system of pde's (after dropping tilda's) are as follows:

$$\frac{\partial u}{\partial t} = a \frac{\partial^2 u}{\partial x^2} + u(1 - u - dv) - fu$$
(2.10)

$$\frac{\partial v}{\partial t} = b \frac{\partial^2 v}{\partial x^2} + cv(1 - v - eu) - fv$$
(2.11)

where

$$a = \frac{\mu_1}{r_1 L_m^2}, b = \frac{\mu_1}{r_1 L_m^2}, c = \frac{r_2}{r_1}, d = b_{12} \frac{K_2}{K_1}, e = b_{21} \frac{K_1}{K_2}$$

In the next Chapter, we discuss numerical methods used to solve partial differential equations.

3: NUMERICAL METHODS TO SOLVE PARTIAL DIFFERENTIAL EQUATONS

Partial differential equations arise in the mathematical modelling of many physical, chemical and biological phenomena and many diverse subject areas such as fluid dynamics, electromagnetism, material science, astrophysics, economy, financial modelling, etc. Very frequently the equations under consideration are so complicated that finding their solutions in closed form or by purely analytical means is either impossible or impracticable, and one has to resort to seeking numerical approximations to the unknown analytical solution. In this Section, we discuss numerical techniques for the approximate solution of partial differential equations: finite element methods and finite difference methods.

First seminal work in the field of FEM was done by Richard Courant (Courant, 1943) in 1943. Unfortunately, the relevance of this article was not recognised at the time and the idea was forgotten. In the early 1950's the method was rediscovered by engineers, but the mathematical analysis of finite element approximations began much later, in the 1960's, the first important results being due to Milos Zlamal in 1968. Since then finite element methods have been developed into one of the most general and powerful class of techniques for the numerical solution of partial differential equations and are widely used in engineering design and analysis. The finite element method determines an approximate soution that is a linear combination of some specified basis functions. This method is typically based on some "weak form" or "variational formulation" of the differential equation, that leads to a system of linear equations.

Finite difference method (FDM) is one of the simplest and oldest approximation approaches to solve the ODEs and PDEs (Shankara Narayana Rao, 2016). The calculus of finite differences is used to develop an approximation formula and is based on the Taylor's series expansion. L. Euler in 1768 was the first to use this method to solve differential equations in one dimension of space and then this method was extended to two dimensions by C. Runge in 1908. In 1928, FDM was further established in a fundamental theoretical paper by Courant, Friedrichs, Lewy (Courant et al., 1967). Around 1950's, with the emergence of computer the FDM was used to solve time-dependent problems. Since then, FDM has been extensively used to study significant problems in

scientific and engineering fields. Its simplicity allows for fast and efficient calculations reducing computational cost. In addition, the FDM helps establish stability and makes error analysis more simple. And while the FDM can have some loss of accuracy for higher order derivatives, this method is appropriate for our model given it's a second order PDE system.

In order to implement FDM, one must generate a mesh with grid points (x_i, t_j) , where we want to find an approximate solutions. Then, we replace the derivative terms in a partial differential equation by divided difference formulae at each grid point, producing a system of algebraic equations. The numerical solution of these algebraic equations are discrete equations; this is the characteristic part of numerical analysis of partial differential equations. Finally, the error analysis can be done by analysing stability, consistency, convergence for the given partial differential equation and error analysis in the numerical results is done by using grid convergence technique.

3.1 Finite Difference Approximations

Suppose we want to approximate f'(x). Using the definition of derivative we have

$$f'(x) = \lim_{h \to 0} \frac{f(x+h) - f(x)}{h}.$$
(3.12)

We discretize the domain of a given function f(x) with a set of points x_i , i = 0, 1, 2, N and define the sequence of x_i values in terms of mesh size h, that is, $x_{i+1} = x_i + h$. Then the definition (3.12) at a discrete point x_i can be written as

$$f'(x_i) = \lim_{h \to 0} \frac{f(x_i + h) - f(x_i)}{h}$$

= $\frac{f_{i+1} - f_i}{h}$ (3.13)

where h is sufficiently small. This formula uses the forward difference approximation and hence the name forward Euler approximation (LeVeque, 2007). Similarly there are two other difference approximations. Backward Euler and Central difference approximations (LeVeque, 2007) are given by

$$f'(x_i) = \lim_{h \to 0} \frac{f(x_i) - f(x_i - h)}{h}$$

= $\frac{f_i - f_{i-1}}{h}$, (3.14)

$$f'(x_i) = \lim_{h \to 0} \frac{f(x_i + h) - f(x_i - h)}{h}$$
$$= \frac{f_{i+1} - f_{i-1}}{2h}$$
(3.15)

respectively. Now the obvious question is "which is a better approximation?" To answer this question and also to analyze the error in the difference approximation, one might have to use a Taylor's series. The Taylor series expansion of function f about the point x_i is given by

$$f(x_i + h) = f(x_i) + hf'(x_i) + \frac{1}{2}h^2 f''(x_i) + \frac{1}{6}h^3 f'''(x_i) + O(h^4).$$
(3.16)

Here $O(\cdot)$ is the big O notation. It is important to note that Taylor's series expansions are valid when f is sufficiently smooth. Now rearranging the terms in the above series, we get

$$\frac{f(x_i+h)-f(x_i)}{h} - f'(x_i) = \frac{1}{2}hf''(x_i) + \frac{1}{6}h^2f'''(x_i) + O(h^3).$$
(3.17)

The error in forward Euler approximation is given by this expression (3.17). The expression in the right hand side of the above expression can be referred to as truncation error, which is the error obtained by truncating the series. Similarly, we can derive truncation errors for backward Euler and central difference approximations. Expanding the function values of f about the point x_i , we get

$$f(x_i - h) = f(x_i) - hf'(x_i) + \frac{1}{2}h^2 f''(x_i) - \frac{1}{6}h^3 f'''(x_i) + O(h^4)$$
(3.18)

which on rearranging gives the truncation error for backward Euler,

$$\frac{f(x_i) - f(x_i - h)}{h} - f'(x_i) = -\frac{1}{2}hf''(x_i) + \frac{1}{6}h^2f'''(x_i) + O(h^3).$$
(3.19)

The truncation error for forward and backward Euler approximations are proportional to h and hence these approximations are referred to as first order approximations. Now combining equations (3.16) and (3.18), we get

$$f(x_i+h) - f(x_i-h) = 2hf' + \frac{1}{3}h^3 f'''(x_i) + O(h^5).$$
(3.20)

This can be further reduced in the form,

$$\frac{f(x_i+h) - f(x_i-h)}{h} - f'(x_i) = \frac{1}{6}h^2 f'''(x_i) + O(h^4)$$
(3.21)

This shows that the truncation error is proportional to h^2 and hence the approximation is referred to as second order approximation (Shankara Narayana Rao, 2016). Now we illustrate finite difference approximation using two examples.

Example 1: We now briefly discuss finite difference formulation for second order non-homogeneous Dirichlet problem (Shankara Narayana Rao, 2016). Suppose $u : \overline{\Omega} \to \mathbb{R}$ for a bounded domain $\Omega = (0, 1) \subset \mathbb{R}$. Here $\overline{\Omega} = \Omega \cup \partial \Omega$, where $\partial \Omega$ is the boundary.

$$-u'' + c \ u(x) = f(x) \tag{3.22}$$

$$u(0) = \alpha, u(1) = \beta \tag{3.23}$$

Equations (3.22) and (3.23) together represent 1D-BVP, where $c \in \mathbb{R}$, f(x) is any given function of *x*, defined on $\overline{\Omega}$, $c \ge 0$. Here

$$x_i = ih, \ 0 \le i \le N+1,$$
 (3.24)

is the grid point and

$$h = \frac{1}{N+1} \tag{3.25}$$

is the mesh width (distance between any two grid points x_i and x_{i+1}), N is an integer. At each of these grid points, we attempt to compute a numerical value of the solution

$$U_0, U_1, U_2, \dots, U_N, U_{N+1}$$
(3.26)

where U_i is the approximation to the solution $u(x_i)$. Now using the boundary conditions from equation (3.23),

$$U_0 = \alpha, \ U_{N+1} = \beta.$$
 (3.27)

We now have N unknowns to compute: $U_1, U_2, ..., U_N$. By replacing the second order derivative by central difference approximation, we obtain

$$\frac{U_{i+1} - 2U_i + U_{i-1}}{h^2} + c \ U_i = F_i \tag{3.28}$$

where $U_i = u(x_i)$ and $F_i = f(x_i)$. The example discussed above gives an essence of the finite difference scheme. The reader is directed to references (LeVeque, 2007; Shankara Narayana Rao, 2016) for different types of finite difference schemes for both ODEs and PDEs.

Example 2: In this illustration, we consider a one dimensional parabolic PDE, which is a time dependent problem. We want to find $u : [0,T] \times \overline{\Omega} \to \mathbb{R}$ such that

$$\frac{\partial u}{\partial t} - \frac{\partial^2 u}{\partial x^2} + c u(x,t) = f(x,t), \ x \in (0,1), \ t \ge 0$$
(3.29)

$$u(0,t) = u(1,t) = 0, \qquad t \ge 0$$
 (3.30)

$$u(x,0) = u_0(x), \ x \in (0,1)$$
(3.31)

We formulate a grid with grid points (x_i, t_n) , where

$$x_i = ih, \quad t_n = nk. \tag{3.32}$$

Here $h = \Delta x$ is the mesh spacing on the spatial axis x and $k = \Delta t$ is the time step. Suppose U_i^n is the numerical approximation to the solution $u(x_i, t_n)$ at the grid point (x_i, t_n) ,

$$U_i^n \approx u(x_i, t_n). \tag{3.33}$$

Then using forward difference approximation for time derivative and central difference approximation for space derivative, we get

$$\frac{U_i^{n+1} - U_i^n}{k} = \frac{U_{i+1}^n - 2U_i^n + U_{i-1}^n}{h^2} + c \ U_i^n + F_i^n,$$
(3.34)

where $F_i^n = f(x_i, t_n)$. We refer to the above forward time central space approximation as the finite difference scheme for given PDEs (3.29). Now rearranging scheme (3.34),

$$U_i^{n+1} = U_i^n + \frac{k}{h^2} \left(U_{i+1}^n - 2U_i^n + U_{i-1}^n \right) + c \ k \ U_i^n + k F_i^n.$$
(3.35)

Using the above equation (3.35), one can compute U_i^{n+1} explicitly using the values from the previous time step and hence the name an explicit method. For the sake of simplicity, we set c = 0 and f = 0 in equation (3.29). Then the PDE (3.29) reduces to

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} \tag{3.36}$$

The corresponding scheme for (3.36) is

$$U_i^{n+1} = U_i^n + \frac{k}{h^2} \left(U_{i+1}^n - 2U_i^n + U_{i-1}^n \right).$$
(3.37)

There are several important results and estimates for equation (3.29) with applications in the field of biology (Kolmogorov et al., 1937).

So from the two illustrations, one can infer that the finite difference scheme results from an approximation of a given equation using a Taylor expansion.

In the next subsection we will discuss different finite difference schemes for a one dimensional parabolic partial differential equation, which is a time dependent problem.

3.1.1 Finite Difference Schemes

The backward difference approximation for time derivative and central difference approximation for space derivative in the example above results in implicit scheme:

$$\frac{U_i^n - U_i^{n-1}}{k} = \frac{U_{i+1}^n - 2U_i^n + U_{i-1}^n}{h^2} + c \ U_i^n + F_i^n, \tag{3.38}$$

This requires solving a system of linear equations to compute the values U_i^n at the time t_n using the values of previous time level t_{n-1} .

Convex combination of explicit and implicit schemes are defined for $0 \le \theta \le 1$ and called as θ -scheme:

$$\frac{U_i^n - U_i^{n-1}}{k} = \theta \frac{U_{i+1}^n - 2U_i^n + U_{i-1}^n}{h^2} + (1-\theta) \frac{U_{i+1}^{n-1} - 2U_i^{n-1} + U_{i-1}^{n-1}}{h^2} + c U_i^n + \theta F_i^n + (1-\theta) F_i^{n-1}.$$
 (3.39)

This gives implicit (resp. explicit) scheme if $\theta = 1$ (resp. $\theta = 0$). For $\theta = \frac{1}{2}$, the scheme is called the Crank-Nicolson scheme.

All these schemes are multi-level schemes as they involve two different time levels U^n and U^{n-1} and the resulting matrix is tridiagonal. A few other multi-level schemes are listed below for the special case c = 0:

Richardson scheme:

$$\frac{U_i^{n+1} - U_i^{n-1}}{2k} = \frac{U_{i+1}^n - 2U_i^n + U_{i-1}^n}{h^2} + F_i^n,$$
(3.40)

DuFort-Frankel scheme:

$$\frac{U_i^{n+1} - U_i^{n-1}}{2k} = \frac{U_{i+1}^n - U_i^{n+1} + U_{i-1}^n - U_i^{n-1}}{h^2} + F_i^n,$$
(3.41)

Now we propose a finite difference based numerical implementation of LVM developed in Chapter 2.

3.2 Formulation of Finite Difference Scheme

To construct the finite-difference method, we need to discretize the domain $[0,T] \times \Omega$. Here $\Omega = [a, b]$, a one dimensional domain. We introduce equidistributed grid points corresponding to a spatial step size *h* and to a time step *k*,

$$h = \frac{1}{N+1} , k = \frac{1}{M+1}$$
(3.42)

where M, N are integers, and define the grid points by

$$(x_i, t_j) = (ih, jk), \ i = 0, 1, 2, \dots N+1, \ j = 0, 1, 2, \dots M+1.$$
 (3.43)

Let u(x,t) and v(x,t) denote the exact solution of the system of equations (2.10) and (2.11). Then we denote the approximate solution at a point (x_i, t_j) by $(u_{i,j}, v_{i,j})$.

Now we refer to scheme (3.45) as the forward time and central space because forward difference and central difference approximations are used for the partial derivative terms

$$\frac{\partial u}{\partial t}$$
 and $\frac{\partial^2 u}{\partial x^2}$, (3.44)

respectively in equation (2.10).

$$\frac{u_{i,j+1} - u_{i,j}}{k} = a \frac{u_{i+1,j} - 2u_{i,j} + u_{i-1,j}}{h^2} + u_{i,j}(1 - u_{i,j} - dv_{i,j}) - fu_{i,j}.$$
(3.45)

Finite difference scheme (3.45) is used to track biomass density of brown shrimp population at a location x and time t. Now grouping the terms we get unknown density at the (i, j + 1)th mesh point in terms of known values along the jth time level. This is called an explicit formula. Note: To calculate the values at the first time level, we have used the initial values at t = 0. The above scheme (3.45) can be further rewritten

$$u_{i, j+1} = zu_{i, j} + a r \left(u_{i+1, j} - 2u_{i, j} + u_{i-1, j} \right) + k u_{i, j} \left(1 - u_{i, j} - dv_{i, j} \right).$$
(3.46)

Here *a*, *d* are the dimensional less rates defined previously in Section ??,

$$a = \frac{\mu_1}{r_1 L_m^2}, \ d = b_{12} \frac{K_2}{K_1} \tag{3.47}$$

and

$$r = \frac{k}{h^2}, \ z = 1 - b_1, \tag{3.48}$$

where

$$b_1 = kf. aga{3.49}$$

Finite difference scheme (3.51) is referred as the forward time and forward space because forward difference approximations are used for the partial derivative terms

$$\frac{\partial v}{\partial t}$$
 and $\frac{\partial v}{\partial x}$, (3.50)

respectively in (2.11).

$$\frac{v_{i,\,j+1}-v_{i,\,j}}{k} = b \frac{v_{i+1,\,j}-2v_{i,\,j}+v_{i-1,\,j}}{h^2} + c v_{i,\,j} (1-v_{i,\,j}-e u_{i,\,j}) - f v_{i,\,j}.$$
(3.51)

Finite difference scheme (3.51) is used to track pink shrimp biomass density at a location x and time t. Now grouping the terms, one can find the mass at the (i, j + 1)th mesh point in terms of known values along the *j*th time level. This is also an explicit formula. Note: To calculate the values at the first time level, we have used the initial values at t = 0. This scheme (3.51) can further be simplified,

$$v_{i, j+1} = zv_{i, j} + b r \left(v_{i+1, j} - 2v_{i, j} + v_{i-1, j} \right) + ck v_{i, j} \left(1 - v_{i, j} - du_{i, j} \right).$$
(3.52)

Here a, e, z denote the dimensionless rates defined previously in Section 3.2,

$$a = \frac{\mu}{\beta L_m^2}, \ e = b_{21} \frac{K_1}{K_2}$$
(3.53)

and

$$r = \frac{k}{h^2} \,. \tag{3.54}$$

We have developed a finite difference scheme for the numerical solution to the system of coupled nonlinear partial differential equations. In the following section, we will apply the model to track density of brown and pink shrimp population in the Gulf Campeche and demonstrate the use of the model.

4: APPLICATION OF THE MODEL TO GULF OF CAMPECHE SHRIMP FISHERY

4.1 Shrimp Fisheries

Shrimping industry provides jobs to millions of people across the globe (Table 6 in (Gillett, 2008)). In light of its economic value, shrimp is one of the most important internationally traded fishery product. Shrimp fisheries are the highest valued fisheries in the southeastern United States (brown shrimp landings in 2014, 105 million pounds, valued at more than 305 million dollars).

Warm-water shrimp fisheries (Gulf of Mexico and southeast Atlantic coast) and the cold-water shrimp fisheries (northeast and northwest of United States of America) are the two main types of shrimp fisheries that are operated in the United States of America. Gulf of Mexico shrimp fisheries target three major species of penaeid shrimp- brown shrimp (*Farfantepenaeus aztecus*), white shrimp ((*Litopenaeus setiferus*), pink shrimp (*Farfantepenaeus duorarum*).

According to a recent 2015 stock assessment (Hart, 2015), the brown shrimp stock in the South Atlantic is not overfished and is not subject to overfishing.

At the beginning of their life cycle, shrimp larvae live among free floating plankton in marine waters. They spend a portion of their life in estuarine waters where they are safe from predators and have access to an abundance of food. Once they reach sub adult length they begin their trip back to marine waters where they continue grow to adult length and spawn the next generation of shrimp. There are a couple of reasons why we chose these shrimp in particular for our model. To start, they are both present in a common area within the Gulf of Mexico and are therefore relevant to study for this area. In addition, the pink and brown shrimp are two of the three most profitable "annual crops" for shrimp fisheries here in Texas. In 2020, Texas shrimp fisheries made more than 84 million dollars on commercially caught pink and brown shrimp alone. This speaks to the importance of maintaining a healthy shrimp population as shrimp fisheries are one of the highest valued fisheries in the United States and contribute to our economy, both locally and nationally

4.1.1 Life History of Biology of Brown and Pink Shrimp

Brown shrimp's growth depends on factors such as water temperature and salinity, and they can reach up to 7 inches in length. They have a short life span, usually less than two years. Brown shrimp are able to reproduce when they reach about 5 ½ inches long. They spawn in relatively deep water. Females typically release about 500,000 to 1 million eggs near the ocean floor. Peak spawning is in spring and summer, with newly hatched shrimp entering estuaries in February and March to settle in their nursery habitat. Brown shrimp larvae feed on plankton (tiny floating plants and animals). Juvenile and adult shrimp feed on the bottom at night. They are omnivorous, and feed on worms, algae, microscopic animals, and various types of organic debris. Sheepshead minnows, water boatmen, and insect larvae eat postlarval shrimp. Grass shrimp, killifishes, and blue crabs prey on young shrimp. A wide variety of finfish feed heavily on juvenile and adult shrimp. (National Oceanic and Atmospheric Administration Brown Shrimp, 2023)

Pink shrimp grow fairly fast, depending on factors such as water temperature and salinity, and can reach over 8 inches in length. They have a short life span, usually less than 2 years, and are often referred to as an "annual crop." Pink shrimp are able to reproduce when they reach about 3.3 inches long. Off North Carolina, they spawn in May through July. In Florida they spawn multiple times, peaking from April through July when the water is warmest. Males mate with females and anchor their sperm to the females. Females release about 500,000 to 1 million eggs near the ocean floor, and the eggs are fertilized as they are released. Newly hatched shrimp travel to their estuarine nursery habitats in late spring and early summer, propelled by shoreward currents. Shrimp that survive the winter grow rapidly in late winter and early spring before returning to the ocean. Pink shrimp larvae feed on plankton (tiny floating plants and animals). Juvenile and adult shrimp are omnivorous, feeding on copepods, small mollusks, diatoms, algae, plant detritus, bacterial films, slime molds, and yeast. Sheepshead minnows, water boatmen, and insect larvae eat postlarval shrimp, and grass shrimp, killifishes, and blue crabs prey on young shrimp. A wide variety of finfish feed heavily on juvenile and adult shrimp.(National Oceanic and Atmospheric Administration Pink Shrimp, 2023)

4.2 Marine Protected Areas

The global perception of dwindling marine resources is triggering a call for more effective mechanisms to protect and conserve marine population (Murray et al., 1999; Lubchenco et al., 2003). This has stimulated interest in and debate of the potential utility of "marine protected areas (MPAs)" as a tool for fisheries management. MPAs is one of the tools that has been increasingly used to protect and conserve marine population (National Marine Protected Areas Center, 2023). In the U.S., more than 1,700 MPAs have been established (Hart, 2015; National MPA center's MPA Inventory, 2012), 41 % of all U.S. waters are in some form of MPA , while 3 % of all U.S. waters are highly protected marine reserves (no-take MPAs), to protect sensitive species and habitats (Hart, 2015; National MPA center's MPA Inventory, 2012). The majority of these MPAs focus on conserving critical marine habitat for fish and rebuilding stocks.

Our focus, in this thesis will be on marine protected areas (MPAs) and how it could be used for protecting migratory species such as brown and pink shrimp.

4.2.1 Background: Theoretical Studies on Marine Protected Areas

Literature on marine protected areas (MPAs) is abundant and has been growing very fast. Presently, studies on MPAs tend to focus on two main issues: benefits from establishing MPAs (in and outside the protected area) and the design of MPAs (NGOC, 2014). Even though the theoretical Berezansky et al. (2010); Christou & Idels (2012); Sanchirico & Wilen (2001); National MPA center's MPA Inventory (2012) and empirical studies (Walters, 2000; Burgess et al., 2009) suggest that MPAs will benefit conservation of species, the debate on benefits of MPAs on the fisheries yields has been only discussed for little more than two decades (De Leo & Micheli, 2015).

Sanchirico and Wilen (Sanchirico & Wilen, 2001) consider a theoretical model with the densitydependent growth, and their results suggest that a protected area may increase the number of individuals of the population, in some cases may increase the sustainable yield. Movement of individuals from MPAs to fishing zones is termed "spillover" in fisheries. "Spillover" refers to the movement of adults and juveniles from MPAs into neighbouring fished areas, and the extent to which this occurs is dependent on the size of the zones, habitat configuration within them, and the abundance and mobility of the species (Marine Parks Authority, 2008). Sanchirico and Wilen (Sanchirico & Wilen, 2001) also emphasise that when the spillover effect is significant, the MPAs could increase number of individuals outside the protected area.

Empirical studies of MPAs need a large amount of population data over different spatial and temporal scales, but such data are rarely available. This makes theoretical studies on marine protected areas very important. Berezansky (Berezansky et al., 2010) discusses the benefits of a theoretical modelling of MPAs, using a delay-differential model, and gives some insights into the type of fisheries data that should be collected in order to design MPA. In a more recent article, Christou (Christou & Idels, 2012) uses Bioeconomic Ricker's model and concludes that greater profits under the optimal harvesting strategy was observed when the convergence to the optimal equilibrium solution was fast (Shankara Narayana Rao, 2016). Studies on theoretical bioeconomic models suggest that, increase in the average size of catch will result in an increase in demand value, and hence the higher market prices per unit of weight (Sanchirico & Wilen, 2001; Pezzey et al., 2000).

4.3 Parameters for Diffusion and Harvesting Model

To show the utility of harvesting and diffusion model developed in Chapter 2, we investigate how the migratory movement of brown and pink shrimp population from MPAs to fishing zone affect the yield in the fishing area and whether the model is able to predict sustainability of brown and pink shrimp outside the MPA. To answer these questions, one might have to parameterize the model and numerically simulate the model.

The parameters for the model and their sources are shown in Table 4.1 .

Table 4.1 List of parameters used in numerical simulation

| Parameter values | | | |
|------------------|---|---------------------|-------------------------------------|
| Symbol | Description | Value | Note |
| K | Total biomass of parent stock per unit length | 6 * 10 ⁷ | (Hart, 2015) |
| t | Time | 1 | Life cycle of shrimp 365 days |
| x | Domain length | 1 | Horizontal distance along the shore |
| L_m | Constant | 0.1 | Used to non-dimensionalize x |

For β , figure 10 from (Nance et al., 1989) was used. We fitted the Beverton-Holt curve, and

obtained the maximum slope $(0.96 * 10^6)$, and finally took the natural log to convert from the finite rate to instantaneous rate.

Now in the following section, we apply the model to brown and pink shrimp population in Gulf of Campeche. In this work, we will use two scenarios as a tool to demonstrate the use of model. First, we investigate the biomass density of brown and pink shrimp in and ouside the protected areas. Second, we examine Sustainable biomass yield.

4.4 Scenario 1: Biomass Density for Brown and Pink Shrimp in and outside Marine Protected

Areas

Biomass density is defined as the number of individuals in an area times the average mass of an individual. To analyse these scenarios, we divide the coastal line into discrete zones of marine protected areas and fishing zones. In this section, we assume 40% of the entire domain length is fishing zone under all models. Here the domain length is equivalent to the coastal line. Now having fixed the total fishing area to be 40 %, we start to allocate the network of MPAs. Starting with one fishing zone in the center, fishing zones spread like a wave reaching the ends of coastline, making up to 2^i fishing zones where i = 0, 1, 2, 3, with equal width in each zone. The remaining 60% of domain length will be considered as the marine protected area. Except for the two fishing zone scenario, MPAs are equally distributed. Starting with there are two MPAs in one fishing zone scenario, MPAs spread like waves and reach corners of the coastal line, making $(2^i - 1)$ MPAs, where i = 2, 3. The Table 4.2 shows the number and width of each fishing zone, number and width of MPAs. We assume a hypothetical situation where biomass density of brown and pink shrimp

| Table 4.2 | | |
|------------------|------------------|----------|
| Number and width | of fishing zone, | and MPAs |

| Fishing Zones | | MP | As |
|---------------|-------|--------|-------|
| Number | Width | Number | Width |
| 1 | 4 | 2 | 3 |
| 2 | 2 | 3 | 2.5/1 |
| 4 | 1 | 3 | 2 |
| 8 | 0.5 | 7 | 0.86 |

population is distributed by an initial profile as shown in Figure 4.1, along one dimensional coastal



Figure 4.1 Hypothetical initial density of brown and pink shrimp population distributed along coastal line

line.

In the following Subsection, we track the density and mass of brown shimp population, in and outside marine protected areas under different diffusive transport rates. It is interesting to investigate how the diffusive transport of population from the MPAs to the fishing zone affect the density and mass of the population. Table 4.3, shows different transport rates, used for numerical simulation.

Table 4.3Low, medium and high diffusive transport rates

| Diffusive Transport Rate μ_1 | Value |
|----------------------------------|-------|
| Low transport | 0.001 |
| Medium transport | 0.01 |
| High transport | 0.1 |

In this section we discuss the asymptotic biomass density of the brown and pink shrimp within the different MPA network setups under three different transport rates. The four network setups are as follows: one fishing zone and two MPAs, two fishing zones and three MPAs, four fishing zones and three MPAs, and eight fishing zones and seven MPAs. In every setup, 40% of the area



Figure 4.2

Asymptotic biomass density of brown shrimp population with a transport rate $\mu_1 = 0.001$ under 2^i fishing zones where i = 0, 1, 2, 3

is composed of MPAs and the remaining 60% is composed of fishing zones. In these results, the advantages of choosing a PDE model over an ODE model are shown. Modelling with ODEs, ordinary differential equations, limits the amount of information that could be gain due to ODEs only providing information of rates over time. By choosing to model with PDEs, partial differential equations, the information gained concerns changes over time as well as changes in location. This is best displayed in our asymptotic biomass density results where we are able to see how the density changes throughout our MPA network setups under different transport rates.

Figures 4.2, 4.3 show the asymptotic biomass density of brown and pink shrimp, respectively, under 2^i fishing zones where i = 0, 1, 2, 3, with equal width in each zone. Looking first at Figure 4.2, concerning brown shrimp, we see high density areas corresponding to MPAs and low density areas corresponding to fishing zones. The same correspondence is present in Figure 4.3, concerning pink shrimp, as well. These results are consistent with existing biomass density data collected inside and outside MPAs (Botsford et al., 2006; Scully, 2022). From these results we see that despite varying the width and number of MPAs and fishing zones, there remains a correspondence between density



Figure 4.3

Asymptotic biomass density of pink shrimp population with a transport rate $\mu_1 = 0.001$ under 2^i fishing zones where i = 0, 1, 2, 3

values and the respective areas for our low mobility species. These results can be explained both mathematically and ecologically.

Mathematically, the high biomass density within the MPAs is due to the low transport rate of the species. For our low mobility results, our diffusion coefficient was 0.001 in our model. The ecological consequence of a low transport rate is a species that moves very slow in the water. As a result, a low mobility species will spend significantly more time within the boundaries of the MPAs since it lacks the ability to move quickly in the water. These MPAs provide protection and allows for an increased reproduction rate in the population which contributes to the high density values seen within the MPAs. In related literature, the extended time spent in a protected area has been shown to increase biomass, density and individual size (Halpern, 2003). The low density values observed in the fishing zones is a direct result of the fishing pressure applied in the areas. Theoretically, a low mobility species is most likely to benefit from the protection of an MPA given how long individuals must remain in its boundaries.

Figures 4.4, 4.5 display the biomass density of medium mobile brown and pink shrimp,



Figure 4.4

Asymptotic biomass density of brown shrimp population with a transport rate $\mu_1 = 0.01$ under 2^i fishing zones where i = 0, 1, 2, 3

respectively. There are high biomass density values found within the MPAs and low biomass density values found within the fishing zones. Fishing pressure brings down the density in fishing zone. This correspondence was also seen in our low mobility density results as well. The biomass density curves Figure 4.4 and Figure 4.5 smoothly taper downwards from the peaks. Mathematically,this is due to the result of the increased mobility of the species from MPAs to fishing zones and the low density gradient in MPA. Ecologically, this is due to spillover that occurs when an individual crosses the boundary from an MPA into fishing zone.

The results for medium mobile species can be compared with a 2019 study conducted in southern California concerning MPA spillover found that density and biomass of spiny lobsters increased in both fishing and non-fishing zones following the implementation of an MPA network (Lenihan et al., 2021).

Figures 4.6 and Figure 4.7 show the biomass density graphs concering brown and pink shrimp under a high transport rate. As the number of MPAs and fishing zones increase throughout the four different fishing zone setups the biomass density curves become more and more dramatically



Figure 4.5

Asymptotic biomass density of pink shrimp population with a transport rate $\mu_1 = 0.01$ under 2^i fishing zones where i = 0, 1, 2, 3

smooth. We see this in both Figures 4.6, 4.7 so we conclude that the increased smoothness is a direct result of the increased transport rate. These results were generated for a diffusion coefficient of 0.1. In terms of mobility, a diffusion coefficient of 0.1 results in a very mobile species. This enables the species to move freely throughout the water resulting in an ability to freely move in and out of the two areas.

The eight fishing zone scenario containing the thinnest MPAs and fishing zones, also experiences the most spillover. With a high mobility species, individuals can effortlessly enter and exit MPA boundaries. This is again due to the decreased width of the areas as a result of the increased number of MPAs and fishing zones. Because individuals are quickly moving from higher density areas to lower density areas, the biomass density curve of the fourth setup appears almost smooth meaning there is little difference in density values between the MPAs and fishing zones. This could have consequences in the implementation of an MPA network as the time spent in an MPA is directly related to the benefits gained from an MPA's protection (Breen et al., 2015).



Figure 4.6

Asymptotic biomass density of brown shrimp population with a transport rate $\mu_1 = 0.1$ under 2^i fishing zones where i = 0, 1, 2, 3

4.5 Scenario 2: Sustainable Biomass Yield in Multiple Fishing Zones Scenario with a Network of Marine Protected Areas

The next set of results concern the sustainable biomass yield of brown and pink shrimp for four different MPA network setups under three different transport rates. The MPA networks are as follows: one fishing zone and two MPAs, two fishing zones and three MPAs, four fishing zones and three MPAs, and eight fishing zones and seven MPAs. These network setups are referred to as setups one through four respectively. The differing setups are of particular interest as they could greatly affect the sustainable biomass yield, given the setups dictate the areas in which fishing is permitted. In addition, analyzing the sustainable yield under the previously mentioned conditions opens the discussion of which network setup(s) are best or better suited for species with different mobilities.

Figure 4.8 depicts the sustainable biomass yield for low mobility brown shrimp under the four different MPA network setups. It can be seen that the first three setups behave similarly for low to average fishing rates with some distinction under higher fishing rates. The fourth setup, however,



Figure 4.7 Asymptotic biomass density of pinkshrimp population with a transport rate $\mu_1 = 0.1$ under 2^i fishing zones where i = 0, 1, 2, 3

was able to achieve higher yield values for lower fishing rates and was able to withstand a higher fishing pressure before declining.

In Figure 4.9 the sustainable biomass yield for pink shrimp under the four different MPA network setups is shown. The sustainable biomass yield begins to decline for the first three setups under high fishing pressure. While the fourth setup is able to achieve higher yield values in comparison to the first three setups, the fourth setup's yield declined under average fishing rates. In comparing the sustainable yield of the low mobility brown and pink shrimp, Figures 4.8 and 4.9 both species achieved higher yield values under the fourth setup but only the brown shrimp were able to support higher fishing rates.

These results show that for a low mobility species an MPA setup with more, and therefore thinner, MPAs and fishing zones is more beneficial, in terms of yield and management, than a setup with fewer, but larger, MPAs and fishing zones (Shankara Narayana Rao, 2016; Wenzel et al., 2020). These results make sense given the low transport rate of the species means individuals spend a significant amount time within the boundaries of the MPAs which results in an increased biomass



Figure 4.8 Sustainable biomass yield for brown shrimp with low mobility

and therefore have an increased reproduction rate (Marshall et al., 2019). Several studies on species with comparable mobility concerning the efficacy of an MPA network also saw results found an increased biomass density and abundance within MPAs, (Roberts & Hawkins, 1997; Tupper & Rudd, 2002). The fourth setup allows for a higher sustainable biomass yield to be reached meaning the populations would be able to support higher fishing rates, particularly when fished at the border of the MPAs, which would help meet the increasing demand for fishery goods alongside an increase in sales (Tupper & Rudd, 2002).

In Figure 4.10 and 4.11 the sustainable biomass yield of brown and pink shrimp under a medium transport rate for the four different MPA setups is shown. It can be observed in Figure 4.10 that all four MPA setups are able to support low to average fishing rates before a decline in yield is seen first in setup one. The second and third setups begin declining for higher fishing rates. The fourth setup shows an increased yield even under higher fishing rates.

In Figure 4.11 we can easily see that as the number of MPAs and fishing zones increase, the ability to support higher fishing rates also increases. Throughout the first three setups the highest fishing rate that can be supported goes from four to six in setups one to three respectively. There is



Figure 4.9 Sustainable biomass yield for pink shrimp with low mobility under a wide range of harvesting rates and 2^i fishing zones where i = 0, 1, 2, 3

a noticeable increase in sustainable biomass yield in the fourth setup where a fishing rate of about nine is shown.

For our medium mobile species the fourth setup seems to be most beneficial as it allows for a higher fishing rate and a larger sustainable biomass yield. This is a result of the increased transport rate. There are two reasons for the higher yield values and ability to support more fishing pressure seen in these results. One, the medium mobile species spends enough time within the protection of the MPAs to benefit from the increased reproduction rate it offers. Second, the increased mobility allows for spillover which happens when an individual crosses the boundary from an MPA into a fishing zone. Spillover occurs in the presence of a high density area and a low density area. These and low density areas can easily be seen in Figures 4.4 and 4.5 where our medium mobile species experiences high biomass density within MPAs and low biomass density within fishing zones. The introduction of spillover results in higher densities within the fishing zones which directly results in higher yield values. These findings are consistent with other studies concerning species of a similar mobility living within an MPA network (Walters, 2000), (Tupper & Rudd, 2002).



Figure 4.10 Sustainable biomass yield for brown shrimp with medium mobility under a wide range of harvesting rates and 2^i fishing zones where i = 0, 1, 2, 3

Our last set of results concerns the sustainable biomass yield for a high mobility species under the four different MPA network setups. Sustainable biomass yields of brown shrimp seen in Figure 4.12 show that all four setups are able to support high fishing pressure while still showing an increase in yield, with the highest yield seen in the fourth setup. Now looking at Figure 4.13, it is interesting to see that only the first setup is able to support higher fishing rates. The first setup, consisting of one fishing zone and two MPAs was able to support higher fishing rates where the fourth setup, consisting of eight fishing zones and seven MPAs was not able to support the same fishing rates. This is due to the mobility of the species. High mobility in a species results in high levels of spillover (Sanchirico & Wilen, 2001).

With the ability to move freely in the water, a high mobile species will frequently enter and exit protected areas. This is more drastically seen in the fourth setups since they contain the highest number of MPAs and fishing zones and therefore contain the thinnest MPAs and fishing zones, which results in a large amount of spillover. This is confirmed by our results in Figures 4.10 and 4.11 where the fourth setup experienced high spillover which lowered the density in MPAs and



Figure 4.11 Sustainable biomass yield for pink shrimp with medium mobility under a wide range of harvesting rates and 2^i fishing zones where i = 0, 1, 2, 3

increased the density in fishing zones resulting in a more smooth curve. The higher transport rate has increased the mobility of the species to the point that individuals are able to freely move within the water and thus can quickly move in and out of the MPAs. This greatly reduces the time spent in the protected areas and therefore greatly reduces the benefits a high mobile species receives from MPAs , (Buxton et al., 2014; Sanchirico & Wilen, 2001). These results suggest a high mobile species is less suited for a smaller width MPA setup (Walters, 2000; Shankara Narayana Rao, 2016). Though a highly mobile species may benefit from an MPA places in areas where more time would be spent like breeding grounds or spawning areas (Breen et al., 2015).

Three different diffusive transport rates (low, medium, high) were used to explore how the mobility of species from MPAs to fishing zone affects (1) biomass density of a population in and outside the protected areas and (2) sustainable biomass yield in the fishing zone. High density gradient term was observed for low mobile species in the MPA due to (1) lower transport rate and (2) fewer number of individuals being transported from the MPA to the fishing zone. However a low density gradient term (for higher number of fishing zones) was observed in the scenario with



Figure 4.12 Sustainable biomass yield for brown shrimp with high mobility under a wide range of harvesting rates and 2^i fishing zones where i = 0, 1, 2, 3

high mobile species due to (1) high transport rate and (2) a large number of individuals in MPAs being transported to the fishing zones.

The numerical results for biomass yield suggests that when we establish a network of marine protected areas along a coastline, starting from two MPAs in one fishing zone scenario to seven MPAs in eight fishing zones scenario, biomass yield is always higher for a species with high mobility when fishing with maximum sustainable fishing rate. Sustainability was captured when the model was tested for wide range of fishing rates with multiple fishing zones and a network of MPAs. The numerical results suggest that, for a low mobile species, when 1) fishing rate is increased and 2) increasing the number of fishing zones, biomass yield becomes sustainable. However, for a medium and high mobile species, when fishing at higher fishing rates, under the four fishing zone scenario biomass yield increases with increase in the fishing rate. So this suggests that there is a need to identify the mobility of species before MPA implementation.

Spatially explicit harvesting strategy was explored. Suppose that MSY for a spatially uniform distribution (ODE models) occur at the fishing rate f_S . When a spatially explicit harvesting



Figure 4.13 Sustainable biomass yield for pink shrimp with high mobility under a wide range of harvesting rates and 2^i fishing zones where i = 0, 1, 2, 3

strategies are considered, MSBY does not occur at f_S . The results shows that depending on the number of fishing zones, MSBY fishing rate is different. So this suggests that, when MPAs are introduced, the fishing rates should be adjusted to reach the MSBY.

5: SUMMARY AND CONCLUSIONS

This study investigated the impact of implementing an MPA network with a wide variety of fishing rates on the sustainable yield of two competing species under three different transport rates. To do this the Lotka-Volterra competition model with harvesting was augmented with a diffusion term resulting in a coupled system of second order PDEs. A numerical approximation was used by applying the finite difference method to establish an explicit finite difference scheme used to calculate the biomass densities of the two species. By using PDEs rather than ODEs the biomass densities were able to be observed at different locations. This was important given part of the investigation was the effects of implementing a MPA network which has multiple areas with differing densities.

Numerical results show that the mobility of a species can greatly affect the sustainable yield when managed under an effective MPA network setup. There were three different transport rates used in this study: low ($\mu = 0.001$), medium ($\mu = 0.01$), and high ($\mu = 0.1$). These transport rates directly affected the densities of the populations found in either MPAs or fishing zones. This is reflected in the ecological outcomes seen in the application of the model. For the low mobility species the population densities were highest within the MPAs and lowest within the fishing zones due to their mobility limiting their ability to easily cross the boundaries of an area. The extended time spent in the MPAs contributed to their ability to support higher fishing rates. This is in agreement with other studies that found the protection offered by MPAs increases the biomass of the species an MPA network setup with more frequent and thinner zones resulted in the highest sustainable yield values.

Under the medium transport rate the asymptotic density results showed evidence of spillover in the high density gradient curves as a result of the increased mobility. The effects of spillover are also seen in the yield results under a medium transport rate. The yield results showed that a medium mobile species is able to sustain higher than average fishing rates with the highest sustainable biomass yield achieved under an MPA network setup with more MPAs and fishing zones that are thinner. However, there is still some decrease in sustainable yield for higher fishing rates. A species with medium mobility will spend less time within the MPAs but will spend enough time to experience the benefits of the MPAs, though at a lesser extent compared to a low mobility species (Lenihan et al., 2021; Walters, 2000). The thinner zones allow for the medium mobile species to spillover into fishing zones, increasing the sustainable biomass yield. Though how long a medium mobile species will be able to sustain these yield values given the decreased time spent within the MPAs is in question.

For our high mobility species substantial spillover in can be seen in the asymptotic density results as the curves are dramatically smoother, particularly in the fourth setup. This makes sense since a high mobile species can quickly exit an MPA and since the fourth setup contains the thinnest zones, the spillover effect is quite dramatic (Sanchirico & Wilen, 2001). Though the high mobile species will spend some time in the MPAs it is not enough time to benefit from the protection (Buxton et al., 2014). Since the highly mobile species spends more time outside of the MPAs there is more time spent in the fishing zones which results in higher sustainable yield values. However, similar to the medium mobile species, a question of how long a highly mobile species can support higher fishing rates is in question.

To discuss competition, we see a significant difference in the outcomes of the brown and pink shrimp and found the brown shrimp to be the dominate species. Overall, the brown shrimp performed better as it was able to achieve higher sustainable yields and support higher fishing rates compared to the pink shrimp. This can be seen in the asymptotic density results where pink shrimp consistently had lower density values in both the MPAs and fishing zones compared to the brown shrimp. Also seen in the yield results, pink shrimp always achieved lower yield values and could not support higher fishing rates that the brown shrimp could. This is partly due to the pink shrimp having a smaller initial population and partly due to the effects of competition with the brown shrimp.

This study investigated the effects of varying mobilities within an MPA network established in an area where the species spends its adult life and will spawn the next generation. However, many fish will travel to other areas in search of food, protection, shelter, breeding grounds, etc. As such, migratory behaviors have not been considered in this study. The effect of implementing an MPA network in several areas where a migratory species is known to spend extended time would be interesting to investigate. For example, as previously mentioned, breeding grounds or areas used for protection from predators or areas with a highly desirable food source could be areas where fish could benefit from the protection offered by an MPA network. While this study focused on competition between two species in an MPA network, considering a predator prey dynamic could yield interesting results as well. Considering a third species would also be interesting. With the inclusion of a third species, the complexity of the problem is likely to increase but given that most ecosystems are influenced by more than two species it may be a worthy endeavor.

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