

Impact of Biased Movement on Marine Protected Area Effectiveness

by  
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A PROJECT

submitted to  
Oregon State University  
University Honors College

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degree of

Honors Baccalaureate of Science in Mathematics  
(Honors Scholar)

Presented June 2, 2015  
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Enrique Thomann

Fish mobility affects the distribution of commercially caught fish species in marine protected areas (MPAs) and unprotected areas, which we will call fishing grounds (FGs). Previous theoretical findings predicted that highly mobile fish would benefit little if at all from protection in MPAs (Demartini 1993, Walters et al. 1999). However, Claudet et al. (2010) found that more mobile fish respond at least as well as less mobile fish to MPA protection, hypothesizing that MPAs may increase habitat quality and cause fish to preferentially remain in the MPA. Following Langebrake et al. (2010) we use biased movement ODE models in which fish preferentially remain in MPAs in an attempt to capture the impact of mobility on MPA effectiveness found in Claudet et al. (2010). A general mathematical background is developed and we show that constant recruitment and logistic growth ODE models with biased movement conditionally exhibit increasing steady state relative abundance with increasing mobility.

Key Words: marine protected area, biased movement, population diffusion

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I understand that my project will become part of the permanent collection of Oregon State University, University Honors College. My signature below authorizes release of my project to any reader upon request.

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James Alexander Rekow, Author

# Impact of Biased Movement on Marine Protected Area Effectiveness

by

James Rekow

## 1 Introduction

We define an MPA to be a no fishing zone. The creation of MPAs is guided by a drive to protect endangered fish species, biodiversity, critical habitats, and in some cases to increase fishing yields as well. Mathematical models of fish populations in MPAs and the surrounding FG can be used to predict the affect of an MPA on a particular fish species and this prediction can be used to inform efforts to protect fish or increase fishery yields. Previous theoretical findings have predicted that the effectiveness of MPAs will decrease as fish mobility increases (Gerber et al. 2003, Mofitt et al. 2009). However, empirical evidence from at least one study suggests that MPA effectiveness does not decrease as fish mobility increases (Claudet et al. 2010). In an attempt develop a mathematical theory that agreed with this observation Langebrake et al. (2011) used biased movement models to describe the diffusion of fish in MPA FG systems. In a biased movement model, fish preferentially remain in the MPA. Reduced disturbance, increased habitat quality, and increased food availability could all decrease the propensity of fish to leave MPAs. In their study, Langebrake et al. (2010) assumed a constant recruitment rate and showed that for sufficiently strong movement biases their models predicted increased MPA effectiveness for more mobile fish. Our goal is to extend their result and find more general biased movement ODE models (such as logistic growth models) that predict an increase in MPA effectiveness (as measured by relative abundance) as fish mobility increases. We analyze two mathematical models that describe the diffusion of fish in a system with two spatial regions: a single MPA and a FG. These models are a constant recruitment ODE model, and a logistic growth ODE model.

## 2 Mathematical Background

### 2.1 Measuring Mobility

In Claudet et al. (2010) mobility is defined using "...an expert opinion approach in which three independent referees, with specific knowledge of the life history of target fish for the region of interest, assigned traits to species...mobility was sedentary (fish that swim less than 50% of the time), vagile (fish that swim more than 50% of the time), and very vagile (fish that swim almost all of the time)". This is a fairly qualitative measure of mobility. In order to make the idea of mobility mathematically precise, one could tag fish with sensors that measure position and velocity over time. The simplest way to define mobility would be

$$\eta = \frac{1}{t_1 - t_0} \int_{t_0}^{t_1} \|\vec{v}(t)\| dt$$

where  $\eta$  is the mobility,  $\vec{v}(t)$  the velocity of the fish, and  $t_0, t_1$  the times at which measurement begins and ends, respectively. However, in the context of diffusion it might be more appropriate to weight the speed with which a fish moves by how far it is from home to capture the fact that seeing new territory is more relevant than swimming in circles. To do this, let  $f$  be a real monotone increasing function and define the effective mobility to be

$$\eta_e = \frac{1}{t_1 - t_0} \int_{t_0}^{t_1} f(\|\vec{x}(t)\|) \|\vec{v}(t)\| dt$$

where  $\vec{x}(t)$  is the position of the fish and its "home" is at the origin.

## 2.2 Creating the Mathematical Models

The heat equation is a linear, second-order partial differential equation that describes the diffusion of heat in a region. It arises in many areas of mathematics and is often used to model other diffusive phenomena. We derive a biological analog of the heat equation to model the diffusion of fish in a region containing an MPA and a FG. To begin, consider the population of fish of a given species  $Y$  in some region  $\Omega \subseteq \mathbb{R}^3$ , and let the density of this population in  $\Omega$  be given by some function  $\rho(\vec{x}, t)$ . Define another function  $w(\vec{x}, t)$  on  $\Omega$ , where  $w$  is the mass of a single organism of species  $Y$  at a point  $\vec{x} \in \mathbb{R}^3$ . We now define the function  $b(\vec{x}, t)$  in  $\Omega$  to be the biomass density of species  $Y$  and we assume that  $b(\vec{x}, t) \simeq w(\vec{x}, t)\rho(\vec{x}, t)$  ( $b$  is our analog of energy density  $e$  in the heat equation derivation). Now consider some region  $V \subseteq \Omega$ . The total biomass in  $V$  is the quantity  $\iiint_V b(\vec{x}, t) d\vec{x}$ . Assume that the flux of biomass  $q(\vec{x}, t)$  is proportional to the density gradient. That is,  $q(\vec{x}, t) = -m(\vec{x}, t)\nabla\rho(\vec{x}, t)$ , where  $m(\vec{x}, t)$  is the mobility of fish species  $Y$ . Note that in this application the gradient and Laplacian are taken with respect to the spatial variable  $\vec{x}$  only, not with respect to the time variable  $t$ . We want to conserve biomass, so

$$\frac{d}{dt} \iiint_V b(\vec{x}, t) d\vec{x} = - \iint_{\partial V} q(\vec{x}, t) \cdot \vec{\eta} d\vec{s} = - \iiint_V \nabla \cdot q(\vec{x}, t) d\vec{x}$$

where  $\vec{\eta}$  is the outward normal vector on  $\partial V$  and the second equality follows from Gauss's Divergence Theorem. Suppose now that

$$\frac{d}{dt} \iiint_V b(\vec{x}, t) d\vec{x} = \iiint_V \frac{\partial}{\partial t} b(\vec{x}, t) d\vec{x}$$

so that

$$- \iiint_V \nabla \cdot q(\vec{x}, t) d\vec{x} - \iiint_V \frac{\partial}{\partial t} b(\vec{x}, t) d\vec{x} = - \iiint_V \left[ \frac{\partial}{\partial t} b(\vec{x}, t) + \nabla \cdot q(\vec{x}, t) \right] d\vec{x} = 0$$



$\forall V \subseteq \Omega \Rightarrow \frac{\partial b}{\partial t} = -\nabla \cdot q(\vec{x}, t)$ . It makes physical sense that  $w(\vec{x}) > 0 \forall \vec{x} \in \mathbb{R}^3$ . We are interested in models with weight  $w$  and mobility  $m$  that do not change with time and which are piecewise constant in space, so

$$\frac{\partial b}{\partial t} = -\nabla \cdot q(\vec{x}, t) \Rightarrow \frac{\partial \rho}{\partial t} = -\frac{\nabla \cdot q(\vec{x}, t)}{w(\vec{x}, t)}. \quad (2.1)$$

We will consider two possible fluxes in this paper, which we call Fourier flux and Fickian flux. The Fourier flux is given by  $q(\vec{x}, t) = -m(\vec{x}, t)\nabla\rho(\vec{x}, t)$  and the Fickian flux is  $q(\vec{x}, t) = -m(\vec{x}, t)\nabla b(\vec{x}, t)$ . Fourier flux models the fish as diffusing based on population density, while Fickian flux models them as diffusing based on biomass density. Assuming Fourier flux, (2.1) becomes

$$\frac{\partial \rho}{\partial t} = \frac{m(\vec{x}, t)}{w(\vec{x}, t)} \Delta \rho(\vec{x}, t),$$

and assuming Fickian flux (2.1) becomes

$$\frac{\partial \rho}{\partial t} = m(\vec{x}, t) \Delta \rho(\vec{x}, t).$$

Note that  $m(\vec{x}, t)$  is not the same in Fickian flux models as it is in Fourier flux models. It must have different units in each model.

### 2.3 Physical Systems

Presented here are three basic models describing the diffusion of fish in an MPA/FG system. In all of these models  $\mu(\vec{x}, t)$  is the mortality due to both natural causes and fishing, and  $R(\vec{x}, t)$  is the birth rate. However, these equations are different in each model. In particular, the units of  $R(\vec{x}, t)$  depend on which model one is using.

**Pure Diffusion:** Fish diffuse and population remains constant.

$$\begin{aligned} 0 &= \frac{d}{dt} \int_V b(\vec{x}, t) d\vec{x} = - \int_{\partial V} q(\vec{x}, t) \cdot \vec{\eta} d\vec{s} = - \int_V \nabla \cdot q(\vec{x}, t) d\vec{x} \\ &\Rightarrow \int_V \left( \frac{\partial}{\partial t} [b(\vec{x}, t)] + \nabla \cdot q(\vec{x}, t) \right) d\vec{x} = 0 \Rightarrow \frac{\partial b}{\partial t} = -\nabla \cdot q(\vec{x}, t) \end{aligned} \quad (2.2)$$

**Diffusion with constant growth and fishing:** fish are born at a constant rate, they die at a constant rate, and they diffuse.

$$0 = \frac{d}{dt} \int_V b(\vec{x}, t) d\vec{x} = - \int_{\partial V} q(\vec{x}, t) \cdot \vec{\eta} d\vec{s} + \int_V R(\vec{x}, t) d\vec{x} - \int_V \mu(\vec{x}, t) \rho(\vec{x}, t) d\vec{x}$$

$$\begin{aligned} \Rightarrow \int_V \frac{\partial}{\partial t} [b(\vec{x}, t)] + \nabla \cdot q(\vec{x}, t) + \mu(\vec{x}, t)\rho(\vec{x}, t) - R(\vec{x}, t) \, d\vec{x} &= 0 \\ \Rightarrow \frac{\partial b}{\partial t} &= R(\vec{x}, t) - \mu(\vec{x}, t)\rho(\vec{x}, t) - \nabla \cdot q(\vec{x}, t) \end{aligned} \quad (2.3)$$

**Diffusion with logistic growth and fishing:** fish are born at a density dependent rate, they die at a constant rate, and they diffuse. Here  $k(\vec{x}, t)$  is the carrying capacity.

$$\begin{aligned} 0 &= \frac{d}{dt} \int_V b(\vec{x}, t) \, d\vec{x} = - \int_{\partial V} q(\vec{x}, t) \cdot \vec{n} \, d\vec{s} + \int_V R(\vec{x}, t)\rho(\vec{x}, t)[k(\vec{x}, t) - \rho(\vec{x}, t)] \, d\vec{x} - \int_V \mu(\vec{x}, t)\rho(\vec{x}, t) \, d\vec{x} \\ \Rightarrow \int_V \frac{\partial}{\partial t} [b(\vec{x}, t)] + \nabla \cdot q(\vec{x}, t) + \mu(\vec{x}, t)\rho(\vec{x}, t) - R(\vec{x}, t)\rho(\vec{x}, t)[k(\vec{x}, t) - \rho(\vec{x}, t)] \, d\vec{x} &= 0 \\ \Rightarrow \frac{\partial b}{\partial t} &= -\rho^2(\vec{x}, t)R(\vec{x}, t) + \rho(\vec{x}, t)[k(\vec{x}, t)R(\vec{x}, t) - \mu(\vec{x}, t)] - \nabla \cdot q(\vec{x}, t) \end{aligned} \quad (2.4)$$

## 3 Results and Examples

### 3.1 ODE Models

We derived several PDE models for the diffusion of fish in a bounded system partitioned into two parts: an MPA and a FG. These PDE models provide a general background for the study the diffusion of fish in MPA/FG systems. For the remainder of this paper we focus on ODE models. These models simplify the situation by reducing the MPA and FG to two distinct points rather than regions of space. Making this simplification sacrifices predictive power for mathematical ease in solving the resulting system of equations. Our goal in this section is to find a system of ODEs that models the observed data from Claudet et al. (2010). More specifically, if  $\rho^*$  is the steady state ratio of the density of fish in the MPA to the density of fish in the FG we want  $\frac{d\rho^*}{d\alpha} < 0$  and  $\frac{d\rho^*}{dm} > 0$  so that the steady state relative abundance increases as mobility increases and as preference for the MPA becomes stronger. We consider two systems of ODEs and identify conditions under which they satisfy the preceding criteria. These systems are a constant recruitment model and a logistic growth model. We begin by studying the constant recruitment model.

#### 3.1.1 Constant Recruitment Model

Before proceeding we must define our variables and parameters and state the system of ODEs we seek to analyze. First, we define two functions  $u^+$  and  $u^-$  by  $u^+ = \max\{0, u\}$  and  $u^- = \max\{0, -u\} = (-u)^+$ . Next, define  $x_1$  and  $x_2$  to be the population density of fish in the MPA and FG respectively. Let  $\alpha$  denote a

parameter representing the preference or bias of the fish towards the MPA. If  $n$  fish would leave the MPA in unbiased conditions then in biased conditions  $\alpha n$  fish leave the MPA instead, where  $0 \leq \alpha \leq 1$ . This reflects a reluctance of fish to leave the MPA. Other models could explore the impact of  $\alpha > 1$ , which reflects a preference towards leaving the MPA, but that case is not considered here. The parameter  $m$  denotes the mobility of the fish species,  $\mu$  denotes the mortality due to natural causes (i.e. deaths not caused by fishing),  $f$  is the mortality due to fishing, and  $\tilde{\mu} = \mu + f$  ( $\tilde{\mu} \geq \mu$ ) denotes the combined mortality of the fish due to natural causes and fishing. We assume in this model that the growth rate of the fish is constant and denote it by  $R$ . The system of differential equations that make up this model is as follows:

MPA fish population:

$$\frac{dx_1}{dt} = -\mu x_1 + R + m[(x_2 - x_1)^+ - \alpha(x_1 - x_2)^+] \quad (3.1)$$

FG fish population:

$$\frac{dx_2}{dt} = -\tilde{\mu} x_2 + R - m[(x_2 - x_1)^+ - \alpha(x_1 - x_2)^+]. \quad (3.2)$$

Although we do not consider it in this paper, it could be interesting to consider a modification of (3.1) and (3.2) in which  $R$  is piecewise constant and takes on different values in the MPA and FG. Fish in MPAs live longer and grow larger than fish in FGs, so they have a higher per capita reproductive output. Allowing  $R$  to take on different values in the MPA and FG could capture this aspect of real MPA/FG systems.

**Theorem:** The above model has a unique, positive steady state  $X^* = \begin{pmatrix} x_1^* \\ x_2^* \end{pmatrix}$ , and the steady state ratio  $\rho^* = \frac{x_1^*}{x_2^*}$  is increasing with mobility if and only if  $\alpha$  is a function of  $m$  with the property that  $\frac{d\alpha}{dm} < -\frac{\alpha(m)}{m} \leq 0$ .

**proof:** One easily computes that at an equilibrium  $X^* = \begin{pmatrix} x_1^* \\ x_2^* \end{pmatrix}$  the ratio  $\rho^*$  is

$$\rho^* = \frac{x_1^*}{x_2^*} = 1 + \frac{f}{\mu + 2m\alpha}. \quad (3.3)$$

Thus,  $\rho^*$  is unique and by adding the equations (3.1) and (3.2) at equilibrium we find that

$$0 = -\mu x_1^* - \tilde{\mu} x_2^* + 2R = 2R - x_2^*(\mu\rho^* + \tilde{\mu}) \Rightarrow x_2^* = \frac{2R}{\mu\rho^* + \tilde{\mu}}.$$

The above computations show that  $X^*$  is positive and unique. Using (3.3) we compute the change in the steady state density with respect to preference to be

$$\frac{d\rho^*}{d\alpha} = \frac{-2mf}{(\mu + 2m\alpha)^2}$$

and the change in steady state density with respect to mobility to be

$$\frac{d\rho^*}{dm} = \frac{-2\alpha f}{(\mu + 2m\alpha)^2}.$$

If  $\alpha$  is constant, then  $\rho^*$  is decreasing with  $m$ . It follows that a necessary condition for  $\rho^*$  to be increasing with  $m$  is that  $\alpha$  is a non-constant function of  $m$ . So suppose that  $\alpha$  is a function  $\alpha(m)$  of  $m$ . Then  $\rho^* = 1 + \frac{f}{\mu + 2m\alpha(m)}$ . Using this we obtain the following:

$$\frac{d\rho^*}{d\alpha} = \frac{-2mf}{(\mu + 2m\alpha(m))^2}$$

and additionally

$$\frac{d\rho^*}{dm} = \frac{-2f}{(\mu + 2m\alpha(m))^2} \alpha(m) + m \frac{d\alpha}{dm}$$

It follows that  $\frac{d\rho^*}{dm} > 0 \iff \frac{d\alpha}{dm} < \frac{-\alpha(m)}{m} \leq 0 \Rightarrow \alpha(m) \leq \frac{C}{m}$ , where  $C$  is a constant of integration.  $\square$

Note that the two expressions we derived for  $\frac{d\rho^*}{dm}$  agree if  $\alpha(m)$  is constant. In Figure 1 below we provide a qualitative illustration of the effect of mobility on the steady state density ratio if  $\alpha$  is constant or if  $\alpha$  is a function of  $m$  such that  $\alpha(m) \leq \frac{1}{m}$  for  $m \in [0, 1]$ .

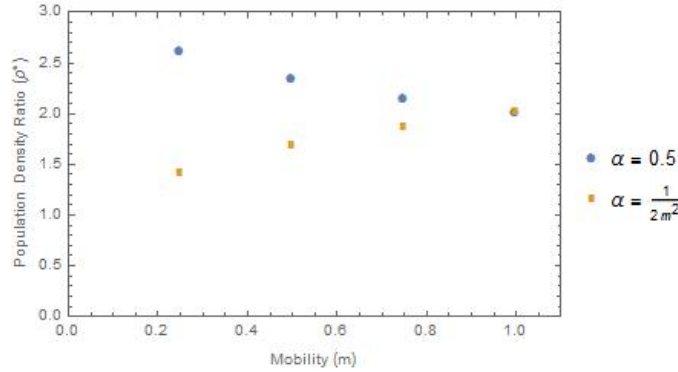


Figure 1: Impact of mobility on steady state population density ratio.

As expected, if  $\alpha$  is constant then  $\rho^*$  decreases as  $m$  increases and if  $\alpha = \frac{1}{2m^2}$  then  $\rho^*$  increases as  $m$  increases. According to the preceding theorem an increasing trend for the steady state ratio as a function of mobility implies that the bias parameter  $\alpha$  is a function of mobility  $m$  which is bounded above by a function of order  $m^{-1}$ . In particular, if  $\alpha$  is constant, then the data in Claudet et al. (2010) showing that log ratios of fish densities in MPAs versus fish densities in FGs increased as fish mobility increased cannot be explained using this model. In the next section we consider a slightly more complicated logistic system of differential equations used to model the same physical situation. In the logistic model the growth rate of the fish is not constant but instead is density dependent.

### 3.1.2 Logistic Growth Model

All variables and parameters introduced in the previous section concerning the constant recruitment model will continue to be used in the same manner in this section. In addition, we introduce the new parameters  $r, \tilde{r}$ , the per unit growth rate of the fish species in the MPA and FG respectively, and  $k, \tilde{k}$ , the carrying capacity of the MPA and FG respectively. These parameters satisfy the following relations:  $\tilde{r} = r - f \leq r$ , and  $\tilde{k} = \frac{k(r-f)}{r} \leq k$ . Additionally, we assume  $r > f$  so that  $\tilde{r}, \tilde{k} > 0$ . The following pair of ODEs define this model:

MPA fish population:

$$\frac{dx_1}{dt} = rx_1 \left(1 - \frac{x_1}{k}\right) + m [(x_2 - x_1)^+ - \alpha(x_1 - x_2)^+] \quad (3.4)$$

FG fish population:

$$\frac{dx_2}{dt} = \tilde{r}x_2 \left(1 - \frac{x_2}{\tilde{k}}\right) - m [(x_2 - x_1)^+ - \alpha(x_1 - x_2)^+]. \quad (3.5)$$

As before, we are interested in the steady state solutions of this coupled system of ODEs. At equilibrium  $\frac{dx_1}{dt} = 0 = \frac{dx_2}{dt}$ , so that

$$0 = r \left(1 - \frac{x_1}{k}\right) + m \left[ \frac{x_2}{x_1} - 1 - \alpha \left(1 - \frac{x_2}{x_1}\right) \right]$$

and

$$0 = \tilde{r} \left(1 - \frac{x_2}{\tilde{k}}\right) - m \left[ 1 - \frac{x_1}{x_2} - \alpha \left(\frac{x_1}{x_2} - 1\right) \right].$$

We distinguish two cases:  $\rho \geq 1$  and  $\rho < 1$ .

$\rho < 1$  : If  $\rho < 1$  then

$$0 = r - \frac{r}{k}x_1 + m\frac{1}{\rho} - m$$

which gives

$$x_1 = k + \frac{km}{r} \left(\frac{1}{\rho} - 1\right).$$

and

$$0 = \tilde{r} - \frac{\tilde{r}}{\tilde{k}}x_2 + m(\rho - 1)$$

which gives

$$x_2 = \tilde{k} + \frac{km}{r}(\rho - 1).$$

Next,

$$\rho = \frac{x_1}{x_2} \iff x_1 = \rho x_2 \Rightarrow \frac{km}{r} \frac{1}{\rho} - 1 + k = \frac{km}{r} \rho^2 + \tilde{k} - \frac{km}{r} \rho.$$

Let  $h_-(\rho) = \frac{km}{r} \frac{1}{\rho} - 1 + k$  and let  $p_-(\rho) = \frac{km}{r} \rho^2 + \tilde{k} - \frac{km}{r} \rho$ . Then  $h_-(1) = k$  and  $p_-(1) = \tilde{k}$ .

$\rho \geq 1$  : If  $\rho \geq 1$  then

$$0 = r - \frac{r}{k} x_1 - \alpha m + \alpha m \frac{1}{\rho}$$

which gives

$$x_1 = k + \frac{\alpha km}{r} \frac{1}{\rho} - 1 \quad (3.6)$$

and

$$0 = 1 - \frac{1}{\tilde{k}} x_2 + \frac{m\alpha}{\tilde{r}} (\rho - 1)$$

which gives

$$x_2 = \tilde{k} + \frac{\alpha km}{r} (\rho - 1).$$

Next,

$$\rho = \frac{x_1}{x_2} \iff x_1 = \rho x_2 \Rightarrow k + \frac{\alpha km}{r} \frac{1}{\rho} - 1 = \tilde{k} \rho + \frac{\alpha km}{r} (\rho^2 - \rho).$$

Let  $h_+(\rho) = k + \frac{\alpha km}{r} \frac{1}{\rho} - 1$  and let  $p_+(\rho) = \tilde{k} \rho + \frac{\alpha km}{r} (\rho^2 - \rho)$ . Then  $h_+(1) = k$  and  $p_+(1) = \tilde{k}$ .

Thus,  $h_-(1) = h_+(1)$  and  $p_-(1) = p_+(1)$ . It follows that the functions  $h = \begin{cases} h_- & \rho < 1 \\ h_+ & \rho \geq 1 \end{cases}$  and  $p = \begin{cases} p_- & \rho < 1 \\ p_+ & \rho \geq 1 \end{cases}$

$\begin{cases} p_- & \rho < 1 \\ p_+ & \rho \geq 1 \end{cases}$  are continuous, as desired.

**Theorem:** The  $\omega$ -limit set of all flows with initial value  $X_0 = \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}$ ,  $x_1, x_2 > 0$  is the singleton consist-

ing of the unique non-zero equilibrium solution  $X^* = \begin{pmatrix} x_1^* \\ x_2^* \end{pmatrix}$ ,  $0 < \tilde{k} < x_2^* < x_1^* < k$ .

**proof:** Define the set  $\Omega$  to be the open, bounded set whose boundary is the right triangle with vertices  $A = \begin{pmatrix} 1 \\ \frac{1}{2} \end{pmatrix} \begin{pmatrix} \tilde{k} \\ \tilde{k} \end{pmatrix}$ ,  $B = 2 \begin{pmatrix} k \\ k \end{pmatrix}$ ,  $C = \begin{pmatrix} 2k \\ \tilde{k} \\ \frac{1}{2} \end{pmatrix}$ . More precisely,  $\Omega = \left\{ X = \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} \in \mathbb{R}^2 \mid 0 < \frac{\tilde{k}}{2} < x_2 < x_1 < 2k \right\}$ .

The proof will proceed in two steps. First, we will show that all flows with initial value  $X_0 = \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}$ ,  $x_1, x_2 > 0$  enter the region  $\Omega$  in finite time. Second, we use the Poincare-Bendixson and Bendixson-Dulac

Theorems to prove that the  $\omega$ -limit set of all flows that enter  $\Omega$  is  $X^*$ . Figure 2 shows several qualitative flows entering the region  $\Omega$ .

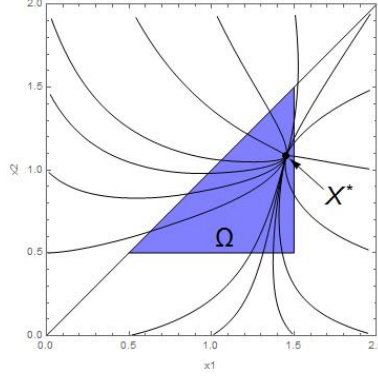


Figure 2: All flows enter the region  $\Omega$  in finite time.

Part 1:

Let  $\theta = \tan^{-1} \frac{x_2}{x_1}$ , so that  $\frac{d\theta}{dt} = \frac{x_1 \frac{dx_2}{dt} - x_2 \frac{dx_1}{dt}}{x_1^2 + x_2^2}$ . From this it follows that

$$\begin{aligned} \frac{d\theta}{dt} = \frac{1}{x_1^2 + x_2^2} & \left[ \tilde{r} x_1 x_2 \left( 1 - \frac{x_2}{k} - m x_1 [(x_2 - x_1)^+ - \alpha (x_1 - x_2)^+] - r x_1 x_2 \left( 1 - \frac{x_1}{k} \right. \right. \right. \\ & \left. \left. \left. - m x_2 [(x_2 - x_1)^+ - \alpha (x_1 - x_2)^+] \right] \right) \right] \iff \end{aligned}$$

$$\frac{d\theta}{dt} = \frac{1}{x_1^2 + x_2^2} \left[ \frac{r}{k} x_1 x_2 (x_1 - x_2) - m (x_1 + x_2) [(x_2 - x_1)^+ - \alpha (x_1 - x_2)^+] - f x_1 x_2 \right].$$

We will now evaluate this expression for  $\frac{d\theta}{dt}$  on lines of constant  $\rho$ . Before we do this, observe that our definition of  $\theta$  is oriented so that  $\theta$  increases in the ccw direction and decreases in the cw direction. From (3.1) and (3.5) it is clear that the first quadrant is an invariant set. If  $\rho < 1$  then

$$\frac{d\theta}{dt} = \frac{1}{x_1^2 + x_2^2} \left[ \frac{r}{k} x_1 x_2 (x_1 - x_2) - m (x_1 + x_2) (x_2 - x_1) - f x_1 x_2 \right].$$

Let  $z = \frac{1}{\rho}$ . Then  $x_2 = z x_1$  and

$$\frac{d\theta}{dt} = \frac{1}{(1 + z^2) x_1^2} \left[ \frac{r}{k} z x_1^2 (1 - z) x_1 - m (z + 1) (z - 1) x_1^2 - f z x_1^2 \right] \iff$$

$$\frac{d\theta}{dt} = \frac{1}{(1 + z^2) x_1^2} \left[ \frac{r}{k} z (1 - z) x_1^3 - m (z^2 - 1) x_1^2 - f z x_1^2 \right] < \frac{-m z^2 - f z + m}{1 + z^2}.$$

Define the function  $g : \{z \in \mathbb{R} | z > 1\} \rightarrow \mathbb{R}$  by  $g(z) = \frac{-mz^2 - fz + m}{1 + z^2}$ . It follows that  $g'(z) = \frac{fz^2 - 4mz - f}{(1 + z^2)^2}$ . Next, define the function  $h : \{z \in \mathbb{R} | z > 1\} \rightarrow \mathbb{R}$  by  $h(z) = fz^2 - 4mz - f$ . Observe that

$$g'(z) = 0 \iff h(z) = 0 \iff z = \frac{2m}{f} \pm \sqrt{\frac{4m^2}{f^2} + 1}$$

and that

$$\frac{2m}{f} - \sqrt{\frac{4m^2}{f^2} + 1} < 0 < 1 < \frac{2m}{f} + \sqrt{\frac{4m^2}{f^2} + 1}.$$

Now,  $\text{sgn}(g'(z)) = \text{sgn}(h(z))$ ,  $g'(z)$  and  $h(z)$  are continuous, and

$$\begin{aligned} \lim_{z \rightarrow \infty} h(z) = \lim_{z \rightarrow -\infty} h(z) = \infty > 0 &\Rightarrow g''(z) > 0 \Rightarrow \\ \Rightarrow g(z^*) = g\left(\frac{2m}{f} + \sqrt{\frac{4m^2}{f^2} + 1}\right) &= \min\{g(z) | z \in \mathbb{R} \text{ and } z > 1\} \end{aligned}$$

and

$$\begin{aligned} \max\{g(z) | z \in \mathbb{R} \text{ and } z > 1\} &= \max\{g(1), \lim_{z \rightarrow \infty} g(z)\} = \max\left\{-m, \frac{-f}{2}\right\} \Rightarrow \\ \Rightarrow \frac{d\theta}{dt} \Big|_X < g(z) &\leq \max\left\{-m, \frac{-f}{2}\right\} < 0 \end{aligned}$$

for all  $X = \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}$ ,  $x_2 > x_1 > 0$ .

If  $\rho = 1$  then

$$\frac{d\theta}{dt} = \frac{-fx_1^2}{2x_1^2} = \frac{-f}{2} < 0.$$

At this point we have shown that all flows with initial condition  $X_0 = \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}$ ,  $x_2 \geq x_1 > 0$  enter the region  $\rho > 1$  in finite time and that solutions in this region remain there for all time.

Next, we will show that all flows that enter the region  $\rho > 1$  enter the region  $\Omega$  in finite time. To do



this, suppose that  $\rho > 1$  and  $0 < x_2 \leq \frac{\tilde{k}}{2}$ . Let  $g(x_2) = \tilde{r}x_2 \left(1 - \frac{x_2}{\tilde{k}}\right)$  and let  $X_0 = \begin{pmatrix} x_1^0 \\ x_2^0 \end{pmatrix}$ , where  $0 < x_2^0 < x_1^0$  and  $x_2^0 \leq \frac{\tilde{k}}{2}$ . Now,  $g(x_2)$  is a quadratic polynomial,  $g(x_2) = 0 \iff x_2 = 0, \frac{\tilde{k}}{2}$ , and

$$\lim_{x_2 \rightarrow \pm\infty} g(x_2) = -\infty \Rightarrow \max\{g(x_2) | x_2 \in \mathbb{R}\} = \frac{\tilde{k}}{2}, \min_{x_2^0 \leq x_2 \leq \frac{\tilde{k}}{2}} g(x_2) = g(x_2^0).$$

Thus,

$$\frac{dx_2}{dt} \Big|_X = \tilde{r}x_2 \left(1 - \frac{x_2}{\tilde{k}}\right) + m\alpha(x_1 - x_2) > g(x_2) \geq g(x_2^0)$$

for all  $X = \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}$ , where  $0 < x_2 \leq \frac{\tilde{k}}{2}$  and  $\rho > 1$ .

Suppose that  $\rho > 1$ , and  $x_1 \geq 2k$ . Let  $g(x_1) = rx_1 \left(1 - \frac{x_1}{k}\right)$ . Then  $\frac{dx_1}{dt} = rx_1 \left(1 - \frac{x_1}{k}\right) - m\alpha(x_1 - x_2) < g(x_1)$ . Observe that  $\max\{g(x_1) | x_1 \geq 2k\} = g(2k) = -2rk < 0$ .

We have now shown that all flows enter the region  $\Omega$  in finite time.

### Part 2:

We use the Bendixson-Dulac Theorem to show that there are no periodic flows lying entirely within

$\Omega \subseteq^{op} \mathbb{R}^2$ . Let  $X' = \begin{pmatrix} f(x_1, x_2) \\ g(x_1, x_2) \end{pmatrix} = \begin{pmatrix} \frac{dx_1}{dt} \\ \frac{dx_2}{dt} \end{pmatrix}$  and let  $\phi(x_1, x_2) = \frac{1}{x_1x_2}$ . Now,  $\phi \in C^1(\Omega)$  and

$$\begin{aligned} \frac{\partial(f\phi)}{\partial x_1} + \frac{\partial(g\phi)}{\partial x_2} &= \frac{\partial}{\partial x_1} \left[ \frac{1}{x_1x_2} \left( rx_1 \left(1 - \frac{x_1}{k}\right) - m\alpha(x_1 - x_2) \right) \right] + \\ &\quad + \frac{\partial}{\partial x_2} \left[ \frac{1}{x_1x_2} \left( \tilde{r}x_2 \left(1 - \frac{x_2}{\tilde{k}}\right) + m\alpha(x_1 - x_2) \right) \right] = \\ &= \frac{\partial}{\partial x_1} \left[ r \frac{1}{x_2} - \frac{r}{k} \frac{x_1}{x_2} - m\alpha \frac{1}{x_2} + m\alpha \frac{1}{x_1} \right] + \frac{\partial}{\partial x_2} \left[ \tilde{r} \frac{1}{x_1} - \frac{r}{k} \frac{x_2}{x_1} + m\alpha \frac{1}{x_2} - m\alpha \frac{1}{x_1} \right] = \\ &= -\frac{r}{k} \frac{1}{x_2} - m\alpha \frac{1}{x_1^2} - \frac{r}{k} \frac{1}{x_1} - m\alpha \frac{1}{x_2^2} < 0. \end{aligned}$$

Thus, by the Bendixson-Dulac Theorem there are no periodic solutions lying entirely within  $\Omega$ . Since all flows with initial value  $X = \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}$ ,  $x_1 > 0$  or  $x_2 > 0$  enter the region  $\Omega$  in finite time and remain there for all time it follows that there are no periodic solutions at all (other than the trivial case when  $x_1 = x_2 = 0$ ). Now, our logistic system of ODEs is a differentiable real dynamical system in  $\Omega \subseteq^{op} \mathbb{R}^2$  and using the

Bendixson-Dulac Theorem we showed that there are no periodic solutions in  $\Omega$  so if we can show that the equilibrium solution  $X^*$  is unique then all flows will limit to  $X^*$ , since homoclinic and heteroclinic orbits can only occur if there are multiple fixed points in  $\Omega$ .

Let  $\rho^* = \frac{x_1^*}{x_2^*}$ , where  $X^* = \begin{pmatrix} x_1^* \\ x_2^* \end{pmatrix}$ . We have shown that  $\rho^* > 1$  and that  $h_+(\rho^*) = p_+(\rho^*)$ , where

$h_+(\rho) = k + \frac{\alpha km}{r} \frac{1}{\rho} - 1$  and  $p_+(\rho) = \tilde{k}\rho + \frac{\alpha km}{r}(\rho^2 - \rho)$ . Now,  $h_+(1) = k > \tilde{k} = p_+(1)$  and in the region  $\rho > 1$   $h_+$  is strictly monotone decreasing and  $p_+$  is strictly monotone increasing so

$h_+(\rho) = p_+(\rho)$  for exactly one  $\rho \in \mathbb{R}, \rho > 1$ . Thus,  $\rho^*$  is unique. Suppose that  $X^* = \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}$  and

$X^{*'} = \begin{pmatrix} x_1' \\ x_2' \end{pmatrix}$  are both equilibrium solutions to the logistic system of equations. Then we find that

$0 + 0 = 0 = r + \tilde{r} - \frac{r}{k}(x_1 + x_2) \iff x_1 + x_2 = x_2(1 + \rho^*) = 2k - \frac{fk}{r} \Rightarrow x_1^*$  and  $x_2^*$  are unique  $\Rightarrow X^*$  is unique. Thus,  $X^*$  is globally stable.  $\square$

This means that for any non-zero initial distribution of fish the number of fish in the MPA and the FG will approach  $x_1^*$  and  $x_2^*$  respectively as time goes on.

### 3.1.3 Effect of Mobility on Relative Abundance of Fish at Equilibrium

Let  $z = m\alpha(m)$  and let  $\rho^* = \frac{x_1^*}{x_2^*}$  be the relative abundance of fish at equilibrium. We just showed that  $\rho^* > 1$  so the pair of ODEs describing the system can be rewritten as

$$\frac{dx_1}{dt} = 0 = r - \frac{r}{k}x_1^* - z + z\frac{1}{\rho^*}$$

$$\frac{dx_2}{dt} = 0 = 1 - \frac{1}{\tilde{k}}x_2^* + \frac{1}{\tilde{r}}z\rho - \frac{1}{\tilde{r}}z$$

Using these equations we continue to compute

$$x_1^* = k - \frac{k}{r}z + \frac{k}{r}z\frac{1}{\rho^*}$$

$$x_2^* = \tilde{k} - \frac{k}{r}z\rho^* - \frac{k}{r}z.$$

From which we find that

$$\begin{aligned}
\rho^* &= \frac{x_1^*}{x_2^*} = \frac{k - \frac{k}{r}z + \frac{k}{r}\frac{1}{\rho^*}}{\tilde{k} - \frac{k}{r}z\rho^* - \frac{k}{r}z} \\
0 &= -\frac{k}{r}z\rho^{*2} - \frac{k}{r}z\rho^* + \tilde{k}\rho^* - k + \frac{k}{r}z - \frac{k}{r}z\frac{1}{\rho^*} \\
\frac{d}{dz}(0) &= 0 = \frac{d}{dz} \left[ -\frac{k}{r}z\rho^{*2} - \frac{k}{r}z\rho^* + \tilde{k}\rho^* - k + \frac{k}{r}z - \frac{k}{r}z\frac{1}{\rho^*} \right] \\
0 &= -\frac{k}{r}\rho^{*2} - \frac{2k}{r}z\rho^* \frac{\partial \rho^*}{\partial z} - \frac{k}{r}\rho^* - \frac{k}{r}z \frac{\partial \rho^*}{\partial z} + \tilde{k} \frac{\partial \rho^*}{\partial z} + \frac{k}{r} - \frac{k}{r}\frac{1}{\rho^*} + \frac{k}{r}z \frac{1}{\rho^{*2}} \frac{\partial \rho^*}{\partial z} \\
\frac{\partial \rho^*}{\partial z} &= \frac{\rho^{*2} + \rho^* + \frac{1}{\rho^*} - 1}{-2\rho^* + \tilde{r} - z + z\frac{1}{\rho^{*2}}}. \tag{3.7}
\end{aligned}$$

Now,  $\rho^* > 1$  so the numerator in (3.7) is positive and by (3.6) we see that

$$\begin{aligned}
x_1^* &= k + \frac{km\alpha(m)}{r} \left[ \frac{1}{\rho^*} - 1 \right] = k + \frac{k}{r}z \left[ \frac{1}{\rho^*} - 1 \right] > 0 \iff \\
&\iff r\rho^* - z\rho^* + z > 0 \iff \rho^* > \frac{1}{1 - \frac{r}{z}} \Rightarrow \frac{z}{\rho^{*2}} < \frac{z}{\rho^*} < z - r \Rightarrow \\
&\Rightarrow -2\rho^* + \tilde{r} - z + \frac{z}{\rho^{*2}} < -2\rho^* + \tilde{r} - z + z - r = -(2\rho^* + f) < 0.
\end{aligned}$$

Thus, the denominator in (3.7) is negative and  $\frac{\partial \rho^*}{\partial z} < 0$ . Using the chain rule we obtain

$$\frac{\partial \rho^*}{\partial m} = \frac{\partial \rho^*}{\partial z} \frac{\partial z}{\partial m} > 0 \iff \frac{\partial z}{\partial m} < 0.$$

Now,  $z = m\alpha(m)$ , so  $\frac{\partial z}{\partial m} = \alpha(m) + m\frac{\partial \alpha}{\partial m} < 0$ . This occurs precisely when  $\frac{\partial \alpha}{\partial m} < -\frac{\alpha(m)}{m}$ . From this differential inequality it follows that  $\alpha(m) < \frac{C}{m}$  for some real constant  $C$ , exactly as in the constant recruitment model.

In this section we analyzed two ODE models for the diffusion of fish in a system with an MPA and a FG: a constant recruitment model and a logistic growth model. Both models predict a single stable equilibrium that attracts all nonzero solutions. This equilibrium occurs in the region  $x_1 > x_2$ , so both models predict that the equilibrium population of fish in the MPA will be greater than the equilibrium population

of fish in the FG. This prediction is reasonable because the ODE model ignores the relative size of the MPA and FG and so one would expect more fish in the MPA at equilibrium because there is no fishing in the MPA and they have a preference  $\alpha$  for remaining in the MPA. In this model the steady state interface density ratio  $\rho^*$  increases with mobility if and only if  $\frac{\partial \alpha}{\partial m} < -\frac{\alpha(m)}{m}$ .

## 4 Discussion

Two mathematical models have been developed to describe the growth and diffusion of single species fish populations in a region with one MPA and one FG. First, we studied the constant recruitment ODE model with biased diffusion at the interface, for which the derivative of relative abundance of fish at equilibrium with respect to mobility is positive if and only if the preference is a function  $\alpha(m)$  of mobility satisfying the inequality  $\frac{d\alpha}{dm} < -\frac{\alpha(m)}{m}$ . Second, we considered a logistic ODE model with biased diffusion at the interface and showed that it has a unique nonzero, globally stable fixed point that attracts all other nonzero solutions. Just as in the constant recruitment model, the derivative of relative abundance with respect to mobility is positive in this model if and only if the preference is a function  $\alpha(m)$  of mobility satisfying the inequality  $\frac{d\alpha}{dm} < -\frac{\alpha(m)}{m}$ .

## 5 Conclusions

### 5.1 Comparing Mathematical Models with Empirical Evidence

We identified conditions in our constant growth and logistic growth ODE models that are necessary and sufficient for steady state solutions in those models to predict an increase in relative abundance as fish mobility increases. In particular, it must occur that preference is a function of mobility and satisfies the inequality  $\frac{d\alpha}{dm} < -\frac{\alpha(m)}{m}$ . Roughly speaking, more mobile fish must have less preference towards remaining in the MPA. It is difficult to say whether or not fish preference is correlated with fish mobility in real systems. Thus, our ODE models conditionally agree with empirical observations that more mobile fish respond better to MPAs, but it is unknown whether or not those conditions are reasonable.

The logistic ODE model was shown to have a unique positive steady state solution that attracts all other positive solutions. This is a nice property for a model to have and under the assumption that the fish species under consideration is fished at the same rate year round it is a reasonable prediction that there would be a unique steady state. However, many fish are harvested seasonally and therefore are not harvested at a constant rate. A simplifying assumption made throughout this paper was that fishing rates did not depend on time. This assumption makes the problem more mathematically tractable but could lead to predictions that differ wildly from empirical observations. It is worth noting that the empirical observations are not necessarily observations of a steady state, but could in fact be observations of fish populations that are not

in equilibrium. Steady state predictions of the models presented here conditionally agree with empirical data in Claudet et al. (2010), but that data may have been collected from MPA/FG systems that were not in equilibrium.

## 5.2 Future Research

We considered only very simple cases in this paper. It remains to analyze the problem with PDEs, in two and three dimensions, to consider biased diffusion within each region in addition to the discontinuity at the interface, to analyze the problem using a logistic growth model, to analyze general, non-steady state solutions, and to compare more fully the differences between predictions made by models using Fourier and Fickian flux. Ideally, a general theory will be developed that describes solutions to interface value problems with piecewise continuous diffusion coefficients, perhaps as a specific type of limit of solutions to interface value problems with continuous diffusion coefficients. Such a theory would be widely applicable as diffusion across interfaces with piecewise continuous diffusion coefficients can be used as a mathematical model to describe situations other than MPA/FG systems such as heat diffusion across an interface between two substances with different thermal properties and diffusion of people across borders.

## 6 Appendix

Included is some preliminary work for related PDE models. In this section we analyze two one-dimensional PDE models with time independent flux of biomass ( $q$ ) for the same MPA/FG system and consider the steady state solutions in these models. The models analyzed are constant growth and affine growth models. We begin our analysis of PDE models with the constant growth model.

Let the entire one-dimensional body of water that comprises the system be represented by the region  $[-a, b]$ , with the MPA being the region  $[-a, 0]$  and the FG being the region  $(0, b]$ . In all of the PDE models considered here we will make several simplifying assumptions. First, we work in one dimension, so that  $\vec{x} = x$  and we assume that  $\rho(x, t)$  is separable so that  $\rho(x, t) = X(x)T(t)$  for some functions  $X$  and  $T$ . Next, we assume that fish mortality ( $\mu(x, t)$ ), mobility ( $m(x, t)$ ), and weight ( $w(x, t)$ ) are piecewise constant and defined to be

$$h(x, t) = \begin{cases} h_- : x \in [-a, 0] \\ h_+ : x \in (0, b] \end{cases}$$

for  $h = m, \mu, w$ . This models the fish in a given region as having a fixed weight, mobility, and mortality as long as they remain in that region. For any function  $g(x, t)$  we adopt the convention that

$$g(x, t) = \begin{cases} g_-(x, t) : x \in [-a, 0] \\ g_+(x, t) : x \in (0, b] \end{cases}$$

to simplify computations.

We now consider the case of diffusion with constant growth and fishing in one spatial dimension. In this model we assume that the fish grow at a piecewise constant rate, depending on whether they are in the MPA or the FG, given by  $R(x, t) = r\rho(x, t)$  for some  $r \in \mathbb{R}$ , and that fish diffuse according to Fourier flux conditions  $q(x, t) = -m(x, t)\frac{\partial \rho}{\partial x}$ . It follows from (2.3) that

$$\begin{aligned} \frac{\partial b}{\partial t} &= r\rho(x, t) - \mu(x, t)\rho(x, t) + m(x, t)\frac{\partial^2 \rho}{\partial x^2} \\ \iff \frac{\partial}{\partial t}[w(x, t)\rho(x, t)] &= w(x)\frac{\partial \rho}{\partial t} = \rho(x, t)(r - \mu(x, t) + m(x, t))\frac{\partial^2 \rho}{\partial x^2} \\ \Rightarrow w(x)X(x)\frac{dT}{dt} &= X(x)T(t)(r - \mu(x, t)) + m(x, t)T(t)\frac{d^2 X}{dx^2} \\ \frac{T'}{T} &= \frac{r - \mu(x, t)}{w(x)} + \frac{m(x, t)X''}{w(x)X} \\ \Rightarrow \frac{T'}{T} &= \frac{r - \mu(x)}{w(x)} + \frac{m(x)X''}{w(x)X} = \Lambda \end{aligned}$$

for some constant  $\Lambda \in \mathbb{R}$ . From the above computation we find that

$$T' = \Lambda T \Rightarrow T(t) = ke^{\Lambda t},$$

and also that

$$\begin{aligned} (r - \mu(x))X + m(x)X'' &= \Lambda w(x)X \\ \Rightarrow X'' &= \frac{\Lambda w(x) + \mu(x) - r}{m(x)}X. \end{aligned}$$

Let  $\tilde{\Lambda}_\pm = \frac{\Lambda w_\pm + \mu_\pm - r}{m_\pm}$ . If  $\tilde{\Lambda}_\pm < 0$  then we can let  $\lambda_\pm = \sqrt{|\tilde{\Lambda}_\pm|}$  so that

$$X''(x) = -\lambda_\pm^2 X(x).$$

The general solution to this differential equation is given by

$$X_-(x) = c_1^- \cos(\lambda_- x) + c_2^- \sin(\lambda_- x)$$

$$X_+(x) = c_1^+ \cos(\lambda_+ x) + c_2^+ \sin(\lambda_+ x)$$

Fish cannot leave the domain so we impose Neumann boundary conditions

$$q(-a) = 0 = q(b)$$

$$m_- X'_-(-a) = 0 = m_+ X'_+(b).$$

Some simple computation with the above equation yields the following two relations:

$$-c_1^- \sin(\lambda_- a) = c_2^- \cos(\lambda_- a) \quad (6.1)$$

$$c_1^+ \sin(\lambda_+ b) = c_2^+ \cos(\lambda_+ b) \quad (6.2)$$

The fluxes across the interface must be equal, which leads to the interface condition

$$q_-(0^-) = q_+(0^+)$$

$$-m_- T(t) X'_-(0^-) = -m_+ T(t) X'_+(0^+)$$

$$m_- X'_-(0^-) = m_+ X'_+(0^+).$$

This relationship implies that

$$m_- \lambda_- c_2^- = m_+ \lambda_+ c_2^+ \Rightarrow \lambda_+ = \frac{m_- c_2^-}{m_+ c_2^+} \lambda_-. \quad (6.3)$$

This shows that  $\lambda_-$  and  $\lambda_+$  are dependent. Finally, we also impose the condition that the density of fish at the interface satisfy a chosen ratio

$$\beta_- \rho_-(0^-) = \beta_+ \rho_+(0^+)$$

$$\beta_- T(t) X_-(0^-) = \beta_+ T(t) X_+(0^+)$$

$$\beta_- X_-(0^-) = \beta_+ X_+(0^+)$$

where  $\beta_+, \beta_- \geq 0$  and  $\beta_+ + \beta_- = 1$ . It immediately follows that that

$$\beta_- c_1^- = \beta_+ c_1^+. \quad (6.4)$$

We have four parameters  $c_1^-, c_2^-, c_1^+, c_2^+$  determined by the measurable quantity  $X_+(b)$ , four additional parameters  $\beta_-, \beta_+, \lambda_-, \lambda_+$ , and four equations relating them: two equations from the Neumann boundary conditions, one equation from equality of flux at the interface, and one equation from fixed density ratio at the interface. Thus, we can solve for  $\beta_-, \beta_+, \lambda_-, \lambda_+$  in terms of  $c_1^-, c_2^-, c_1^+, c_2^+$ . In particular, this allows us to solve for  $\beta_-$  and  $\beta_+$  in terms of  $c_1^-, c_2^-, c_1^+, c_2^+$ , which shows that the steady state interface density ratio is fixed. Starting with (6.2) and using (6.3), (6.1) and then (6.4) we calculate

$$\begin{aligned}
c_1^+ &= \cot(\lambda_+ b) c_2^+ = \frac{m_- \lambda_-}{m_+ \lambda_+} \cot(\lambda_+ b) c_2^- = -\frac{m_- \lambda_-}{m_+ \lambda_+} \cot(\lambda_+ b) \tan(\lambda_- a) c_1^- \\
\beta_- c_1^- &= -\beta_+ \frac{m_- \lambda_-}{m_+ \lambda_+} \cot(\lambda_+ b) \tan(\lambda_- a) c_1^- \\
\beta_- \tan(\lambda_+ b) &= -\beta_+ \frac{c_2^+}{c_2^-} \tan(\lambda_- a) \\
\beta_- \tan \lambda_- \frac{b m_- c_2^-}{m_+ c_2^+} &= -\beta_+ \frac{c_2^+}{c_2^-} \tan(\lambda_- a). \tag{6.5}
\end{aligned}$$

**Theorem:** An infinite number of distinct values of  $\lambda_-$  satisfy equation (6.5).

**proof:** Let  $B = \frac{b m_- c_2^-}{m_+ c_2^+}$ . Define a function  $f : \mathbb{R} \rightarrow \mathbb{R}$  by  $f(\lambda_-) = \beta_- \tan(\lambda_- B) + \beta_+ \frac{c_2^+}{c_2^-} \tan(\lambda_- a)$ . Then (6.5) is satisfied if and only if  $f(\lambda_-) = 0$ . Note that  $\frac{B}{a} \in \mathbb{Q}$  xor  $\frac{B}{a} \in \mathbb{R} - \mathbb{Q}$ .

$\frac{B}{a} \in \mathbb{Q}$ : We know  $B, a > 0$ , which means that  $\frac{B}{a} > 0$  and we are assuming that  $\frac{B}{a} \in \mathbb{Q}$  so there exist  $n, m \in \mathbb{N}$  such that  $\frac{B}{a} = \frac{n}{m}$ . Let  $d \in \mathbb{N}$  and let  $\lambda_- = \frac{dn\pi}{B} = \frac{dm\pi}{a}$ . Then  $f(\lambda_-) = \beta_- \tan(dn\pi) + \beta_+ \frac{c_2^+}{c_2^-} \tan(dm\pi) = 0 \Rightarrow f(\lambda_-) = 0$  for all  $d \in \mathbb{N}$ . Thus, there are an infinite number of distinct roots of  $f(\lambda_-)$ .

$\frac{B}{a} \in \mathbb{R} - \mathbb{Q}$ : Define  $T_+ = \frac{\pi}{B}$  and  $T_- = \frac{\pi}{a}$ , so that  $T_+$  is the period of  $\tan(\lambda_- B)$  and  $T_-$  is the period of  $\tan(\lambda_- a)$ . Now,  $\frac{B}{a} \notin \mathbb{Q} \Rightarrow$  that there do not exist  $n, m \in \mathbb{N}$  such that  $nT_+ = mT_-$ . Define a sequence  $\{\ell_n\}$  by  $\ell_1 = \max\{T_+, T_-\}$  and  $\ell_{k+1} = \min\{nT_+, mT_- | n, m \in \mathbb{N} \text{ and } nT_+, mT_- > \ell_k\}$ . Now define a sequence  $\{A_n\}$  by  $A_n = (\ell_n, \ell_{n+1})$  for all  $n \in \mathbb{N}$ . Next,  $f(\lambda_-)$  is continuous on the set  $G = \{x \in \mathbb{R} | x \neq nT_+ \text{ and } x \neq nT_- \forall n \in \mathbb{Z}\}$  and  $A_n \subseteq G \forall n \in \mathbb{N} \Rightarrow f$  is continuous on  $A_n$  for all  $n \in \mathbb{N}$ . Finally,  $\lim_{\lambda_- \rightarrow \ell_n^-} f(\lambda_-) = \infty$  and  $\lim_{\lambda_- \rightarrow \ell_n^+} f(\lambda_-) = -\infty$ , and  $A_n$  continuous implies by the intermediate value theorem that for all  $n \in \mathbb{N}$  there exists  $z_n \in A_n$  such that  $f(z_n) = 0$ . Thus,  $f(\lambda_-) = 0$  for infinitely many  $\lambda_- \in \mathbb{R}$ .  $\square$



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