

A Lattice Model for Two Different Life-History Strategies of Corals in a Coral Reef

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<p>Coral reefs form important marine ecosystems and simultaneously are at risk of deterioration due to rapidly changing environments as a consequence of human actions. Understanding their dynamics is thus important in order to be able to protect them from being destroyed.</p> <p>In this thesis we construct a lattice model for two life-history strategies of corals, brooders and spawners. These two strategies differ mainly in their modes of sexual reproduction, but also differences in growth and death rates as well as competitive ability are considered. We use pair approximation to help analyse the model while keeping its spatial structure.</p> <p>Numerical analysis is used to find the equilibria of the system as well as their stabilities, first for a single strategy and then for the two-strategy system.</p> <p>We find that the two strategies are able to coexist if the spawners have a higher growth rate and higher death rate and are competitively superior to brooders. This requires some reproduction over distance and a trade-off between growth and death rates. Thus we find that brooders are focusing a bigger part of their energy on long-distance reproduction, while spawners are dominating over short distances and having a higher turnover.</p> <p>We also find that both mutual invasibility and coexistence in the broader sense are only possible for low rates of sexual reproduction for both strategies. For higher rates of sexual reproduction we find that whichever strategy invades the lattice first will stay and the other cannot invade.</p> <p>Lastly we look at the effect of a change in environmental conditions, namely the acidification and temperature increase of oceans, on the two strategies and find that it affects the two strategies differently. The spawners are quickly driven to extinction by the change in environmental conditions, while brooders initially benefit from the changing conditions and only start to suffer themselves after the spawners have gone extinct.</p>			
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Chapter 1

Introduction

It is well known that coral reefs are at big risk of deterioration due to rapidly changing environments. The main factors affecting coral reefs as a consequence of human actions are changes in ocean temperatures and acidity, as well as habitat destruction due to fishing, pollution, sedimentation. Changes in ocean temperatures and acidity contribute to coral bleaching, which is the process when corals lose their symbiotic zooxanthellae and thus eventually die. Coral reefs form important marine ecosystems, which is why understanding their dynamics is important in order to be able to protect them from being destroyed.

Life-history strategies are characteristics that are consistent inside one species and affect their fitness. Traditionally they are split into two or three strategies, however in their paper Darling et al. [1] recently found four strategies for corals. Previous mathematical models for corals in reefs do not take these differences into account, but rather consider all corals as just one type. The goal of this thesis is to make a realistic model for the two most important strategies, brooders and spawners. With the help of such a model we can understand the dynamics of coral reefs better, and can make some conclusions about coexistence of and competition between the different strategies. Finally, we will take a look at what happens in the model under changing environmental conditions.

As a basis for the model, we will use a model for lattice population dynamics for plants developed by Harada and Iwasa [2]. Their model includes propagation and long-distance seed dispersal. The model consists of an infinite lattice with one type of individual that goes through three different kinds of transitions: death, vegetative propagation and recruitment by seeds. For their analysis they use pair approximation. Corals have similar dynamics to plants in that they are immobile with local growth as well as global dispersal of offspring. Thus taking a model like the one by Harada and Iwasa [2] as a starting point allows us to take spatial factors into consideration when it comes to both competition and reproduction, using pair approximation methods to simplify the model while keeping the

spatiality.

For analysis of the model, numerical analysis will be necessary, since the model for two strategies consists of multiple differential equations each with a number of independent parameters. For this purpose, the software Mathematica [3] will be used and the results will also be plotted to ensure proper understanding.

Chapter 2

Background

In this chapter we cover some of the most relevant parts of coral biology and ecology, as well as the most important mathematical methods used in the thesis. The most important part of coral biology for the scope of this thesis are their different modes of reproduction, which will form the basis of the different life-history strategies modelled here.

2.1 Coral Reproduction

Corals can reproduce both asexually and sexually. Most corals reproduce asexually by releasing a piece of the coral or a polyp either intentionally or as the consequence of stress. It can then settle on a new surface and form a new, genetically identical colony.[4] They also spread by propagation into their immediate surroundings.

Sexual reproduction of corals is split into broadcast spawning (from now on only spawning) and brooding. Most coral species reproduce at least by spawning, whereas brooding is restricted to a limited number of species [1]. Spawners release their eggs and sperm into the water in mass spawning events that usually happen once a year. Fertilisation then happens in the water and the embryos develop into larvae in a few days. On the other hand, brooders reproduce during months or even around the year and fertilisation happens either on the surface of the coral or inside it. Thus the brooders release larvae that are immediately ready to settle.[5]

2.2 Life-History Strategies of Corals

Life-history strategies are collections of characteristics that are consistent inside one species. They can be used to understand trade-offs between these different characteristics.

The simplest theory is the so called r/K selection theory that was coined by Robert MacArthur and Edward O. Wilson [6]. This is a theory that consists of only two different life-history strategies: the fast (r) strategy and the slow (K) strategy. This two-strategy framework is nowadays often seen as too simple, and instead a three-strategy model is used. A famous three-strategy framework is Grime's model for plants that consists of competitive, stress-tolerant and ruderal life-history strategies [7].

Darling et. al [1] used hierarchical clustering on different coral species to find four different life-history strategies: competitive, weedy, stress-tolerant and generalist. Here the first three strategies coincide with those of Grime's model and generalist is a new strategy that combines characteristics of the other three. In the categorisation found in the paper, competitive species are fast growing, large, branching and plating species that reproduce by spawning. The weedy species have smaller colony sizes and reproduce by brooding (as well as by spawning). The stress-tolerant species grow slowly, reproduce by spawning and have high fecundity. Out of the three strategies, competitive species are the most sensitive to environmental changes while the other two can manage them relatively well. The generalist strategy exhibited characteristics of the other three, and its existence as a separate strategy as opposed to just a sub-strategy of one of the other three is uncertain. Darling et al. also used random forest analysis to find out which traits were the most important in distinguishing the life-history strategies from each other. They found the three most important characteristics to be colony growth form, growth rate and reproductive mode.

2.3 Lattice Models and Pair Approximation in Population Dynamics

A lot of population dynamics models use mean-field approximations that assume the whole population is well-mixed and ignore spatial structure. However, in many cases this kind of an approximation is far from accurate. In the case of corals, which are immobile for a large part of their life cycle, many interactions can only occur between immediate neighbours.

Lattice models take space into account in the form of discrete sites that each fit a single individual. This allows for a more realistic approach to the modelling of reproduction and competition, which often require direct contact between individuals.

The simplest lattice model is the so called contact process, which consists of a single type of individual on a lattice undergoing two different kinds of processes: death at a constant rate and birth attempts at a constant rate but depending on whether the target site is empty.

To simplify the calculations of lattice models a pair approximation is often used. Mat-

suda et al. [8] developed the pair approximation method for lattice population models. The pair approximation is the approximation that the probability of finding a site occupied by an individual of type X next to an individual of type Y is independent of the other neighbours of the individual of type X . This means that only interactions between individuals right next to each other are considered for the local dynamics, any intermediate interactions (like triplets) are approximated to pairs. The justification for the pair approximation is that any further neighbours will have a smaller effect than the nearest neighbour. Mathematically speaking, the pair approximation is a form of moment closure in space.

Chapter 3

Building the Model

Following the different life-history strategies for corals, we build a model for two different ones, brooders (denoted by B) and spawners (denoted by S). These correspond to the weedy and competitive strategies of the four-strategy model of Darling et al [1], respectively. This model is loosely based on the lattice model for plants by Harada and Iwasa [2]. The model will consist of equations for the global densities p_B and p_S as well as equations for pair densities ρ_{XY} for X and Y corresponding to either brooders, spawners or empty sites. Here a global density p_X refers to the probability of finding an individual of type X at a randomly chosen site, whereas the pair density ρ_{XY} refers to the probability of finding an individual of type X and an individual of type Y at a randomly chosen pair of neighbouring sites. We also need the conditional probability $q_{X/Y}$, which refers to the probability of finding an individual of type X on a site given that its neighbour is of type Y as well as the conditional probability $q_{X/YZ}$, which refers to the probability of finding an individual of type X on a site given that its neighbour is of type Y and the neighbour of that individual is of type Z .

3.1 Individual-Level Processes

We start by writing down the individual-level processes for the two strategies. The processes for both are the same, only with different rates. Thus we will write down the processes for only one of the two, the brooder strategy. The processes for the spawners are equivalent, changing each B for an S in the first three processes. The two different processes in competition are the same for the two different strategies. In the symbolic equations for the processes, 0 will denote an empty site.

$$\begin{aligned}
(3.1) \quad \text{death:} & \quad B \xrightarrow{d_B} 0 \\
(3.2) \quad \text{growth/propagation:} & \quad (B, 0) \xrightarrow{b_B} (B, B) \\
(3.3) \quad \text{reproduction:} & \quad 0 \xrightarrow{m_B} B \\
(3.4) \quad \text{competition:} & \quad (B, S) \xrightarrow{c_S} (S, S) \\
(3.5) & \quad (B, S) \xrightarrow{c_B} (B, B)
\end{aligned}$$

For the parameter values, we make the following assumptions based on Darling et al. [1] and as described in (2.2):

$$\begin{aligned}
d_S &> d_B \\
b_S &> b_B \\
c_S &> c_B
\end{aligned}$$

We define the parameter for competition such that $c_X = P_X b_X$ where P_X is the probability for X to win a conflict between two adjacent individuals of different strategies. This is equivalent to setting $c_S = P b_S$ and $c_B = (1 - P) b_B$ where P is the probability that the spawner wins this conflict.

3.2 Reproduction

The parameter m_X will include all different kinds of reproduction over distance, asexual reproduction (budding, breaking of pieces from polyps) as well as both spawning and brooding reproduction. Both strategies are assumed to reproduce asexually with rate β , as well as by spawning, but spawners have a higher rate of spawning than brooders ($\gamma_S > \gamma_B$). Brooding on the other hand only takes place for the brooders. Brooding is modelled in two parts, one which is similar to spawning in that it happens over distance and refers to far-travelling sperm cells that reach the egg cells on or inside the coral (with rate α) and one that happens due to the sperm cells of nearby individuals (with rate $\eta q_{B/B}$). The growth parameter b_X can also be considered a form of reproduction since we assume that a single coral covering two sites will act in the same way as two separate corals of the same type on neighbouring sites. The parameter b_X is however not included here in m_X . We also ignore the fact that spawning is a yearly event and model it as if it were a continuous one. This is purely a simplification choice.

Thus m_X will be as follows for brooders and spawners:

$$(3.6) \quad m_B = (\beta + \gamma_B p_B + \alpha p_B + \eta q_{B/B}) p_B = (\beta + \gamma_B p_B + \alpha p_B) p_B + \eta \rho_{BB}$$

$$(3.7) \quad m_S = (\beta + \gamma_S p_S) p_S$$

3.3 Global and Local Equations

Now that we have the processes for the individuals of the two strategies, we can write down the equations for the global and pair densities. Let us start with the global densities:

$$\begin{aligned} \frac{dp_B}{dt} &= -d_B p_B + b_B q_{0/B} p_B + m_B p_0 + c_B q_{S/B} p_B - c_S q_{S/B} p_B \\ &= -d_B p_B + b_B q_{0/B} p_B + m_B (1 - p_B - p_S) + (c_B - c_S) q_{S/B} p_B \\ \frac{dp_S}{dt} &= -d_S p_S + b_S q_{0/S} p_S + m_S p_0 + c_S q_{B/S} p_S - c_B q_{B/S} p_S \\ &= -d_S p_S + b_S q_{0/S} p_S + m_S (1 - p_B - p_S) + (c_S - c_B) q_{B/S} p_S \end{aligned}$$

For the pair densities we have 9 different ones: $\rho_{BB}, \rho_{0B}, \rho_{B0}, \rho_{SB}, \rho_{BS}, \rho_{S0}, \rho_{0S}, \rho_{SS}, \rho_{00}$. Now since these 9 densities must add up to 1, it is enough to find an expression for 8 of them in order to have a comprehensive description of the system. We will leave out ρ_{00} since it does not involve any corals and is thus the least interesting one of the pair densities. After this, we note that for any X, Y we have $\rho_{XY} = \rho_{YX}$, since the probability of finding a pair XY is the same as finding a pair YX (the order does not matter). Thus it is in fact enough to find the expressions for 5 different pair densities: $\rho_{BB}, \rho_{0B}, \rho_{SB}, \rho_{0S}, \rho_{SS}$.

We start with the doublet density ρ_{BB} :

$$\begin{aligned} \frac{d\rho_{BB}}{dt} &= -2d_B \rho_{BB} - 2\frac{c_S}{z}(z-1)q_{S/BB}\rho_{BB} + \frac{c_B}{z}(z-1)q_{B/SB}(\rho_{SB} + \rho_{BS}) \\ &\quad + \frac{c_B}{z}(\rho_{SB} + \rho_{BS}) + \frac{b_B}{z}(\rho_{0B} + \rho_{B0}) + \frac{b_B}{z}(z-1)q_{B/0B}(\rho_{B0} + \rho_{0B}) + m_B(\rho_{B0} + \rho_{0B}) \\ &= \rho_{BB} \left(-2d_B - 2\frac{c_S}{z}(z-1)q_{S/BB} \right) + 2\rho_{SB} \left(\frac{c_B}{z}(z-1)q_{B/SB} + \frac{c_B}{z} \right) \\ &\quad + 2\rho_{0B} \left(\frac{b_B}{z} + \frac{b_B}{z}(z-1)q_{B/0B} + m_B \right) \end{aligned}$$

The other doublet density ρ_{SS} looks similar:

$$\begin{aligned}\frac{d\rho_{SS}}{dt} &= \rho_{SS} \left(-2d_S - 2\frac{c_B}{z}(z-1)q_{B/SS} \right) + 2\rho_{SB} \left(\frac{c_S}{z}(z-1)q_{S/BS} + \frac{c_S}{z} \right) \\ &\quad + 2\rho_{0S} \left(\frac{b_S}{z} + \frac{b_S}{z}(z-1)q_{S/0S} + m_S \right)\end{aligned}$$

Now for the cross density ρ_{0B} :

$$\begin{aligned}\frac{d\rho_{0B}}{dt} &= \left(\frac{d\rho_{B0}}{dt} \right) - d_B\rho_{0B} - \frac{b_B}{z}\rho_{0B} - \frac{b_B}{z}(z-1)q_{B/0B}\rho_{0B} - \frac{b_S}{z}(z-1)q_{S/0B}\rho_{0B} \\ &\quad - m_B\rho_{0B} - m_S\rho_{0B} - \frac{c_S}{z}(z-1)q_{S/B0}\rho_{0B} + d_B\rho_{BB} + d_S\rho_{SB} \\ &\quad + \frac{b_B}{z}(z-1)q_{B/00}\rho_{00} + m_B\rho_{00} + \frac{c_B}{z}(z-1)q_{B/S0}\rho_{0S}\end{aligned}$$

And now since $\rho_{00} = 1 - \rho_{BB} - 2\rho_{0B} - 2\rho_{SB} - 2\rho_{0S} - \rho_{SS}$ we get:

$$\begin{aligned}\frac{d\rho_{0B}}{dt} &= \rho_{0B} \left(-d_B - \frac{b_B}{z} - \frac{b_B}{z}(z-1)q_{B/0B} - \frac{b_S}{z}(z-1)q_{S/0B} - m_B - m_S \right. \\ &\quad \left. - \frac{c_S}{z}(z-1)q_{S/B0} - 2\frac{b_B}{z}(z-1)q_{B/00} - 2m_B \right) \\ &\quad + \rho_{BB} \left(d_B - \frac{b_B}{z}(z-1)q_{B/00} - m_B \right) \\ &\quad + \rho_{SB} \left(d_S - 2\frac{b_B}{z}(z-1)q_{B/00} - 2m_B \right) \\ &\quad + \rho_{0S} \left(\frac{c_B}{z}(z-1)q_{B/S0} - 2\frac{b_B}{z}(z-1)q_{B/00} - 2m_B \right) \\ &\quad + (1 - \rho_{SS}) \left(\frac{b_B}{z}(z-1)q_{B/00} + m_B \right)\end{aligned}$$

And analogously for ρ_{0S} we get:

$$\begin{aligned}
\frac{d\rho_{0S}}{dt} &= \left(\frac{d\rho_{S0}}{dt} = \right) \rho_{0S} \left(-d_S - \frac{b_S}{z} - \frac{b_S}{z}(z-1)q_{S/0S} - \frac{b_B}{z}(z-1)q_{B/0S} - m_S \right. \\
&\quad \left. - m_B - \frac{c_B}{z}(z-1)q_{B/S0} - 2\frac{b_S}{z}(z-1)q_{S/00} - 2m_S \right) \\
&\quad + \rho_{SS} \left(d_S - \frac{b_S}{z}(z-1)q_{S/00} - m_S \right) \\
&\quad + \rho_{SB} \left(d_B - 2\frac{b_S}{z}(z-1)q_{S/00} - 2m_S \right) \\
&\quad + \rho_{0B} \left(\frac{c_S}{z}(z-1)q_{S/B0} - 2\frac{b_S}{z}(z-1)q_{S/00} - 2m_S \right) \\
&\quad + (1 - \rho_{BB}) \left(\frac{b_S}{z}(z-1)q_{S/00} + m_S \right)
\end{aligned}$$

Finally for the last cross density, ρ_{SB} we get:

$$\begin{aligned}
\frac{d\rho_{SB}}{dt} &= \left(\frac{d\rho_{BS}}{dt} = \right) - d_B \rho_{SB} - d_S \rho_{SB} - \frac{c_S}{z} \rho_{SB} - \frac{c_B}{z} \rho_{SB} - \frac{c_S}{z}(z-1)q_{S/BS} \rho_{SB} \\
&\quad - \frac{c_B}{z}(z-1)q_{B/SB} \rho_{SB} + \frac{b_B}{z}(z-1)q_{B/0S} \rho_{0S} + \frac{b_S}{z}(z-1)q_{S/0B} \rho_{0B} \\
&\quad + m_B \rho_{0S} + m_S \rho_{0B} + \frac{c_B}{z}(z-1)q_{B/SS} \rho_{SS} + \frac{c_S}{z}(z-1)q_{S/BB} \rho_{BB} \\
&= \rho_{SB} \left(-d_B - d_S - \frac{c_S}{z} - \frac{c_B}{z} - \frac{c_S}{z}(z-1)q_{S/BS} - \frac{c_B}{z}(z-1)q_{B/SB} \right) \\
&\quad + \rho_{0S} \left(\frac{b_B}{z}(z-1)q_{B/0S} + m_B \right) + \rho_{0B} \left(\frac{b_S}{z}(z-1)q_{S/0B} + m_S \right) \\
&\quad + \frac{c_B}{z}(z-1)q_{B/SS} \rho_{SS} + \frac{c_S}{z}(z-1)q_{S/BB} \rho_{BB}
\end{aligned}$$

3.4 Pair Approximation

Now that we have the expressions for the pair densities, we can do a pair approximation. This means that we approximate any triplet probability $q_{X/YZ}$ (for any X, Y, Z) with $q_{X/Y}$. [8] Doing this can be justified by a decrease in the effect on individuals that are not direct neighbours.

With the pair approximation, we get the following expressions for the pair densities:

$$\begin{aligned}\frac{d\rho_{BB}}{dt} &= \rho_{BB} \left(-2d_B - 2\frac{c_S}{z}(z-1)q_{S/B} \right) + 2\rho_{SB} \left(\frac{c_B}{z}(z-1)q_{B/S} + \frac{c_B}{z} \right) \\ &\quad + 2\rho_{0B} \left(\frac{b_B}{z} + \frac{b_B}{z}(z-1)q_{B/0} + m_B \right)\end{aligned}$$

$$\begin{aligned}\frac{d\rho_{SS}}{dt} &= \rho_{SS} \left(-2d_S - 2\frac{c_B}{z}(z-1)q_{B/S} \right) + 2\rho_{SB} \left(\frac{c_S}{z}(z-1)q_{S/B} + \frac{c_S}{z} \right) \\ &\quad + 2\rho_{0S} \left(\frac{b_S}{z} + \frac{b_S}{z}(z-1)q_{S/0} + m_S \right)\end{aligned}$$

$$\begin{aligned}\frac{d\rho_{0B}}{dt} &= \frac{d\rho_{B0}}{dt} = \rho_{0B} \left(-d_B - \frac{b_B}{z} - \frac{b_B}{z}(z-1)q_{B/0} - \frac{b_S}{z}(z-1)q_{S/0} \right. \\ &\quad \left. - 3m_B - m_S - \frac{c_S}{z}(z-1)q_{S/B} - 2\frac{b_B}{z}(z-1)q_{B/0} \right) \\ &\quad + \rho_{BB} \left(d_B - \frac{b_B}{z}(z-1)q_{B/0} - m_B \right) \\ &\quad + \rho_{SB} \left(d_S - 2\frac{b_B}{z}(z-1)q_{B/0} - 2m_B \right) \\ &\quad + \rho_{0S} \left(\frac{c_B}{z}(z-1)q_{B/S} - 2\frac{b_B}{z}(z-1)q_{B/0} - 2m_B \right) \\ &\quad + (1 - \rho_{SS}) \left(\frac{b_B}{z}(z-1)q_{B/0} + m_B \right)\end{aligned}$$

$$\begin{aligned}\frac{d\rho_{0S}}{dt} &= \frac{d\rho_{S0}}{dt} = \rho_{0S} \left(-d_S - \frac{b_S}{z} - \frac{b_S}{z}(z-1)q_{S/0} - \frac{b_B}{z}(z-1)q_{B/0} \right. \\ &\quad \left. - 3m_S - m_B - \frac{c_B}{z}(z-1)q_{B/S} - 2\frac{b_S}{z}(z-1)q_{S/0} \right) \\ &\quad + \rho_{SS} \left(d_S - \frac{b_S}{z}(z-1)q_{S/0} - m_S \right) \\ &\quad + \rho_{SB} \left(d_B - 2\frac{b_S}{z}(z-1)q_{S/0} - 2m_S \right) \\ &\quad + \rho_{0B} \left(\frac{c_S}{z}(z-1)q_{S/B} - 2\frac{b_S}{z}(z-1)q_{S/0} - 2m_S \right) \\ &\quad + (1 - \rho_{BB}) \left(\frac{b_S}{z}(z-1)q_{S/0} + m_S \right)\end{aligned}$$

$$\begin{aligned}
\frac{d\rho_{SB}}{dt} &= \frac{d\rho_{BS}}{dt} = \rho_{SB} \left(-d_B - d_S - \frac{c_S}{z} - \frac{c_B}{z} - \frac{c_S}{z}(z-1)q_{S/B} - \frac{c_B}{z}(z-1)q_{B/S} \right) \\
&+ \rho_{0S} \left(\frac{b_B}{z}(z-1)q_{B/0} + m_B \right) + \rho_{0B} \left(\frac{b_S}{z}(z-1)q_{S/0} + m_S \right) \\
&+ \frac{c_B}{z}(z-1)q_{B/S}\rho_{SS} + \frac{c_S}{z}(z-1)q_{S/B}\rho_{BB}
\end{aligned}$$

Now that we have the expressions for the global and pair densities, we only need to express all the conditional probabilities $q_{X/Y}$ in terms of densities to have a closed system. This goes according to the formula $q_{X/Y} = \frac{\rho_{XY}}{p_Y}$ (from the formula for conditional probability, where $q_{X/Y}$ is the conditional probability of X given Y , ρ_{XY} is the probability of the intersection of X and Y and p_Y is the probability of Y).

3.5 System of Differential equations

Here we collect the system of differential equations built in chapters (3.3) and (3.4) with the conditional probabilities expressed in terms of densities and with slight other rearrangements in order to make the equations easier to understand. We also substitute the expressions for each m_X built in chapter (3.2). We have altogether seven different equations, two for global densities and 5 for pair densities.

$$(3.8) \quad \frac{dp_B}{dt} = -d_B p_B + b_B \rho_{0B} + ((\beta + \gamma_B p_B + \alpha p_B) p_B + \eta \rho_{BB}) (1 - p_B - p_S) + (c_B - c_S) \rho_{SB}$$

$$(3.9) \quad \frac{dp_S}{dt} = -d_S p_S + b_S \rho_{0S} + (\beta + \gamma_S p_S) p_S (1 - p_B - p_S) + (c_S - c_B) \rho_{SB}$$

$$(3.10) \quad \begin{aligned}
\frac{d\rho_{BB}}{dt} &= -2\rho_{BB} \left(d_B + \frac{c_S}{z}(z-1) \frac{\rho_{SB}}{p_B} \right) + 2\rho_{SB} \left(\frac{c_B}{z}(z-1) \frac{\rho_{SB}}{p_S} + \frac{c_B}{z} \right) \\
&+ 2\rho_{0B} \left(\frac{b_B}{z} + \frac{b_B}{z}(z-1) \frac{\rho_{0B}}{1 - p_S - p_B} + (\beta + \gamma_B p_B + \alpha p_B) p_B + \eta \rho_{BB} \right)
\end{aligned}$$

(3.11)

$$\begin{aligned} \frac{d\rho_{SS}}{dt} = & -2\rho_{SS} \left(d_S + \frac{c_B}{z}(z-1) \frac{\rho_{SB}}{p_S} \right) + 2\rho_{SB} \left(\frac{c_S}{z}(z-1) \frac{\rho_{SB}}{p_B} + \frac{c_S}{z} \right) \\ & + 2\rho_{0S} \left(\frac{b_S}{z} + \frac{b_S}{z}(z-1) \frac{\rho_{0S}}{1-p_S-p_B} + (\beta + \gamma_S p_S) p_S \right) \end{aligned}$$

(3.12)

$$\begin{aligned} \frac{d\rho_{0B}}{dt} = \frac{d\rho_{B0}}{dt} = & -\rho_{0B} \left(d_B + \frac{b_B}{z} + 3\frac{b_B}{z}(z-1) \frac{\rho_{0B}}{1-p_S-p_B} + \frac{b_S}{z}(z-1) \frac{\rho_{0S}}{1-p_S-p_B} \right. \\ & \left. + 3((\beta + \gamma_B p_B + \alpha p_B) p_B + \eta \rho_{BB}) + (\beta + \gamma_S p_S) p_S + \frac{c_S}{z}(z-1) \frac{\rho_{SB}}{p_B} \right) \\ & + \rho_{BB} \left(d_B - \frac{b_B}{z}(z-1) \frac{\rho_{0B}}{1-p_S-p_B} - ((\beta + \gamma_B p_B + \alpha p_B) p_B + \eta \rho_{BB}) \right) \\ & + \rho_{SB} \left(d_S - 2\frac{b_B}{z}(z-1) \frac{\rho_{0B}}{1-p_S-p_B} - 2((\beta + \gamma_B p_B + \alpha p_B) p_B + \eta \rho_{BB}) \right) \\ & + \rho_{0S} \left(\frac{c_B}{z}(z-1) \frac{\rho_{SB}}{p_S} - 2\frac{b_B}{z}(z-1) \frac{\rho_{0B}}{1-p_S-p_B} - 2((\beta + \gamma_B p_B + \alpha p_B) p_B + \eta \rho_{BB}) \right) \\ & + (1 - \rho_{SS}) \left(\frac{b_B}{z}(z-1) \frac{\rho_{0B}}{1-p_S-p_B} + (\beta + \gamma_B p_B + \alpha p_B) p_B + \eta \rho_{BB} \right) \end{aligned}$$

(3.13)

$$\begin{aligned} \frac{d\rho_{0S}}{dt} = \frac{d\rho_{S0}}{dt} = & -\rho_{0S} \left(d_S + \frac{b_S}{z} + 3\frac{b_S}{z}(z-1) \frac{\rho_{0S}}{1-p_S-p_B} + \frac{b_B}{z}(z-1) \frac{\rho_{0B}}{1-p_S-p_B} \right. \\ & \left. + 3(\beta + \gamma_S p_S) p_S + (\beta + \gamma_B p_B + \alpha p_B) p_B + \eta \rho_{BB} + \frac{c_B}{z}(z-1) \frac{\rho_{SB}}{p_S} \right) \\ & + \rho_{SS} \left(d_S - \frac{b_S}{z}(z-1) \frac{\rho_{0S}}{1-p_S-p_B} - (\beta + \gamma_S p_S) p_S \right) \\ & + \rho_{SB} \left(d_B - 2\frac{b_S}{z}(z-1) \frac{\rho_{0S}}{1-p_S-p_B} - 2(\beta + \gamma_S p_S) p_S \right) \\ & + \rho_{0B} \left(\frac{c_S}{z}(z-1) \frac{\rho_{SB}}{p_B} - 2\frac{b_S}{z}(z-1) \frac{\rho_{0S}}{1-p_S-p_B} - 2(\beta + \gamma_S p_S) p_S \right) \\ & + (1 - \rho_{BB}) \left(\frac{b_S}{z}(z-1) \frac{\rho_{0S}}{1-p_S-p_B} + (\beta + \gamma_S p_S) p_S \right) \end{aligned}$$

(3.14)

$$\begin{aligned}
\frac{d\rho_{SB}}{dt} = \frac{d\rho_{BS}}{dt} = & -\rho_{SB} \left(d_B + d_S + \frac{c_S}{z} + \frac{c_B}{z} + \frac{c_S}{z}(z-1)\frac{\rho_{SB}}{p_B} + \frac{c_B}{z}(z-1)\frac{\rho_{SB}}{p_S} \right) \\
& + \rho_{0S} \left(\frac{b_B}{z}(z-1)\frac{\rho_{0B}}{1-p_S-p_B} + (\beta + \gamma_B p_B + \alpha p_B) p_B + \eta \rho_{BB} \right) \\
& + \rho_{0B} \left(\frac{b_S}{z}(z-1)\frac{\rho_{0S}}{1-p_S-p_B} + (\beta + \gamma_S p_S) p_S \right) \\
& + \frac{c_B}{z}(z-1)\frac{\rho_{SB}}{p_S} \rho_{SS} + \frac{c_S}{z}(z-1)\frac{\rho_{SB}}{p_B} \rho_{BB}
\end{aligned}$$

3.6 One Strategy Model

We will start by analysing the model for just one strategy. Here is the system of differential equations for just one strategy, brooders, as simplified from the system in (3.5). We are doing this analysis for brooders since the system for spawners can easily be constructed from this one by setting $\alpha = 0$ and $\eta = 0$.

(3.15)

$$\frac{dp_B}{dt} = -d_B p_B + b_B \rho_{0B} + ((\beta + \gamma_B p_B + \alpha p_B) p_B + \eta \rho_{BB}) (1 - p_B)$$

(3.16)

$$\frac{d\rho_{BB}}{dt} = -2\rho_{BB} d_B + 2\rho_{0B} \left(\frac{b_B}{z} + \frac{b_B}{z}(z-1)\frac{\rho_{0B}}{1-p_B} + (\beta + \gamma_B p_B + \alpha p_B) p_B + \eta \rho_{BB} \right)$$

(3.17)

$$\begin{aligned}
\frac{d\rho_{0B}}{dt} = \frac{d\rho_{B0}}{dt} = & -\rho_{0B} \left(d_B + \frac{b_B}{z} + 3\frac{b_B}{z}(z-1)\frac{\rho_{0B}}{1-p_B} + 3((\beta + \gamma_B p_B + \alpha p_B) p_B + \eta \rho_{BB}) \right) \\
& + \rho_{BB} \left(d_B - \frac{b_B}{z}(z-1)\frac{\rho_{0B}}{1-p_B} - (\beta + \gamma_B p_B + \alpha p_B) p_B - \eta \rho_{BB} \right) \\
& + \left(\frac{b_B}{z}(z-1)\frac{\rho_{0B}}{1-p_B} + (\beta + \gamma_B p_B + \alpha p_B) p_B + \eta \rho_{BB} \right)
\end{aligned}$$

In fact we can now rewrite (3.15) and (3.16) again in terms of only p_B and ρ_{BB} . This is possible since we have that $p_B = \rho_{BB} + \rho_{0B}$.

Thus we get the model:

$$\frac{dp_B}{dt} = -d_B p_B + b_B (p_B - \rho_{BB}) + ((\beta + \gamma_E p_B + \alpha p_B) p_B + \eta \rho_{BB}) (1 - p_B)$$

$$\frac{d\rho_{BB}}{dt} = -2\rho_{BB} d_B + 2(p_B - \rho_{BB}) \left(\frac{b_B}{z} + \frac{b_B}{z} (z-1) \frac{p_B - \rho_{BB}}{1 - p_B} + (\beta + \gamma_E p_B + \alpha p_B) p_B + \eta \rho_{BB} \right)$$

We choose to work with $z = 4$ from now on since we have a 2D lattice. This now gives the model:

$$(3.18)$$

$$\frac{dp_B}{dt} = -d_B p_B + b_B (p_B - \rho_{BB}) + ((\beta + \gamma_E p_B + \alpha p_B) p_B + \eta \rho_{BB}) (1 - p_B)$$

$$\frac{d\rho_{BB}}{dt} = -2\rho_{BB} d_B + 2(p_B - \rho_{BB}) \left(\frac{b_B}{4} + \frac{3b_B}{4} \frac{p_B - \rho_{BB}}{1 - p_B} + (\beta + \gamma_E p_B + \alpha p_B) p_B + \eta \rho_{BB} \right)$$

Chapter 4

Model Analysis

4.1 Equilibrium of One Strategy Model

Solving the model (3.18) for the equilibrium $\frac{dp_B}{dt} = 0$ and $\frac{d\rho_{BB}}{dt} = 0$ we get the equation for ρ_{BB} :

$$(4.1) \quad \rho_{BB} = \frac{-b_B p_B - \beta_B p_B + d_B p_B - \alpha p_B^2 + \beta_B p_B^2 - \gamma_B p_B^2 + \alpha_B p_B^3 + \gamma_B p_B^3}{-b_B + \eta - \eta p_B}$$

Which then gives the following equation for p_B (after dividing by p_B in order to get rid of the trivial solution $p_B = 0$):

$$(4.2) \quad \begin{aligned} & (\alpha^2 b_B + 2\alpha b_B \gamma_B + b_B \gamma_B^2) p_B^5 \\ & + (-2\alpha^2 b_B + 2\alpha b_B \beta + 3\alpha b_B \eta - 4\alpha b_B \gamma_B + 2b_B \beta \gamma_B + 3b_B \eta \gamma_B - 2b_B \gamma_B^2) p_B^4 \\ & + (\alpha^2 b_B + \alpha b_B^2 - 4\alpha b_B \beta + b_B \beta^2 + 2\alpha b_B d_B - 7\alpha b_B \eta + 3b_B \beta \eta - 4\alpha d_B \eta + 2b_B \eta^2 - 4d_B \eta^2 \\ & + 2\alpha b_B \gamma_B + b_B^2 \gamma_B - 4b_B \beta \gamma_B + 2b_B d_B \gamma_B - 7b_B \eta \gamma_B - 4d_B \eta \gamma_B + b_B \gamma_B^2) p_B^3 \\ & + (-2\alpha b_B^2 + 2\alpha b_B \beta + b_B^2 \beta - 2b_B \beta^2 - 6\alpha b_B d_B + 2b_B \beta d_B + 5\alpha b_B \eta + b_B^2 \eta - 7b_B \beta \eta + 8\alpha d_B \eta \\ & - 5b_B d_B \eta - 4\beta d_B \eta - 5b_B \eta^2 + 8d_B \eta^2 - 2b_B^2 \gamma_B + 2b_B \beta \gamma_B - 6b_B d_B \gamma_B + 5b_B \eta \gamma_B + 8d_B \eta \gamma_B) p_B^2 \\ & + (\alpha b_B^2 - 2b_B^2 \beta + b_B \beta^2 + 4\alpha b_B d_B - 3b_B^2 d_B - 6b_B \beta d_B + b_B d_B^2 - \alpha b_B \eta - 2b_B^2 \eta + 5b_B \beta \eta - 4\alpha d_B \eta \\ & + 8b_B d_B \eta + 8\beta d_B \eta - 4d_B^2 \eta + 4b_B \eta^2 - 4d_B \eta^2 + b_B^2 \gamma_B + 4b_B d_B \gamma_B - b_B \eta \gamma_B - 4d_B \eta \gamma_B) p_B \\ & + b_B^2 \beta + 3b_B^2 d_B + 4b_B \beta d_B - 4b_B d_B^2 + b_B^2 \eta - b_B \beta \eta - 3b_B d_B \eta - 4\beta d_B \eta + 4d_B^2 \eta - b_B \eta^2 = 0 \end{aligned}$$

Equations (4.1) and (4.2) can now be adapted to get the equivalent equations for spawners by changing each b_B for b_S , d_B for d_S , γ_B for γ_S and p_B for p_S and setting $\alpha, \eta = 0$. Thus for spawners the equations would be:

$$(4.3) \quad \rho_{SS} = \frac{-b_S p_S - \beta_S p_S + d_S p_S + \beta_S p_S^2 - \gamma_S p_S^2 + \gamma_S p_S^3}{-b_S}$$

$$(4.4) \quad \begin{aligned} & \gamma_S^2 p_S^5 + (2\beta\gamma_S - 2\gamma_S^2)p_S^4 + (-4\beta\gamma_S + 2\gamma_S d_S + \gamma_S^2 + \beta^2 + b_S \gamma_S)p_S^3 \\ & + (-6\gamma_S d_S - 2\beta^2 + 2\beta d_S + 2\beta\gamma_S - 2b_S \gamma_S + \beta b_S)p_S^2 \\ & + (\beta^2 - 6\beta d_S + d_S^2 + 4\gamma_S d_S - 2\beta b_S + b_S \gamma_S - 3b_S d_S)p_S \\ & + (3b_S d_S - 4d_S^2 + \beta b_S + 4\beta d_S) = 0 \end{aligned}$$

4.2 One Strategy Model Without Sexual Reproduction

We start by looking at equation (4.4) when $\gamma_S = 0$, in other words when there is no sexual reproduction present. It is worth noting that this equation is the same for brooders if there is no sexual reproduction (i.e. when $\gamma_B = \alpha = \eta = 0$). This gives the cubic (the subscripts have been dropped for clarity):

$$\begin{aligned} & \beta^2 p^3 + (-2\beta^2 + 2\beta d + \beta b)p^2 + (\beta^2 - 6\beta d + d^2 - 2\beta b - 3bd)p \\ & + (3bd - 4d^2 + \beta b + 4\beta d) = 0 \end{aligned}$$

Now we divide by d^2 and set $b^* = \frac{b}{d}$ and $\beta^* = \frac{\beta}{d}$ in order to decrease the number of free parameters to get:

$$(4.5) \quad \begin{aligned} & \beta^{*2} p^3 + (-2\beta^{*2} + 2\beta^* + \beta^* b^*)p^2 + (\beta^{*2} - 6\beta^* + 1 - 2\beta^* b^* - 3b^*)p \\ & + (3b^* - 4 + \beta^* b^* + 4\beta^*) = 0 \end{aligned}$$

Which only depends on 2 parameters, b^* and β^* . Similarly for ρ we get (from (4.3)):

$$(4.6) \quad \rho = \frac{-b^* p - \beta^* p + p + \beta^* p^2}{-b^*}$$

Now we can find the equilibrium values in terms of these 2 parameters, b^* and β^* .

4.2.1 Stability of Extinct Equilibrium

We start by looking at the stability of the extinct equilibrium, $(p, \rho) = (0, 0)$. In this case we have the Jacobian:

$$J(0, 0) = \begin{bmatrix} -1 + b^* + \beta^* & -b^* \\ \frac{b^*}{2} & -2 - \frac{b^*}{2} \end{bmatrix}$$

Which has $\text{Det } J = 2 - \frac{3b^*}{2} - 2\beta^* - \frac{\beta^*b^*}{2}$ and $\text{Tr } J = -3 + \frac{b^*}{2} + \beta^*$.

Now, we need to find a condition for b^* and β^* such that the extinct equilibrium is unstable (and thus we have a positive, stable equilibrium). More specifically, the extinct equilibrium needs to be a saddle. This is due to the fact that for small values of b^* and β^* the extinct equilibrium is a stable node, and with an increase in these parameters, the positive equilibrium needs to come into the positive region through a transcritical bifurcation, leaving the extinct equilibrium a saddle. Additionally it can be said that the extinct equilibrium could not be a focus since it would imply negative values of p , which is impossible.

Thus we get that for the extinct equilibrium to be a saddle and for us to have a stable positive equilibrium, we need $\text{Det } J < 0$, i.e.:

$$2 - \frac{3b^*}{2} - 2\beta^* - \frac{\beta^*b^*}{2} < 0$$

Which gives:

$$4 < 3b^* + 4\beta^* + \beta^*b^*$$

This means that in order to find a positive, stable equilibrium, we need to find b^* and β^* such that they fulfil the condition above. In the extreme case $b^* = 0$, we thus need $\beta^* > 1$ and if $\beta^* = 0$ we need $b^* > \frac{4}{3}$.

4.2.2 Finding Positive Equilibria

To find the positive equilibria of (4.5) in terms of b^* and β^* we use Mathematica [3]. This gives the equilibrium values for $p \in [0, 1]$ as seen in the contourplot (4.1).

It can be seen that there is a curve below which we get no positive equilibrium solutions for $p \in (0, 1]$. In this region we do get one positive, unstable equilibrium, however it is greater than 1 and thus biologically meaningless. This curve is $\beta^* = \frac{4-3b^*}{4+b^*}$, which corresponds to the condition for instability of the extinct equilibrium found in (4.2.1) and thus to the transcritical bifurcation line. Below this line the extinct equilibrium is stable.

We can also calculate the equilibrium values for ρ based on the equilibrium values for p using equation (4.6). These can be seen in figure (4.2).

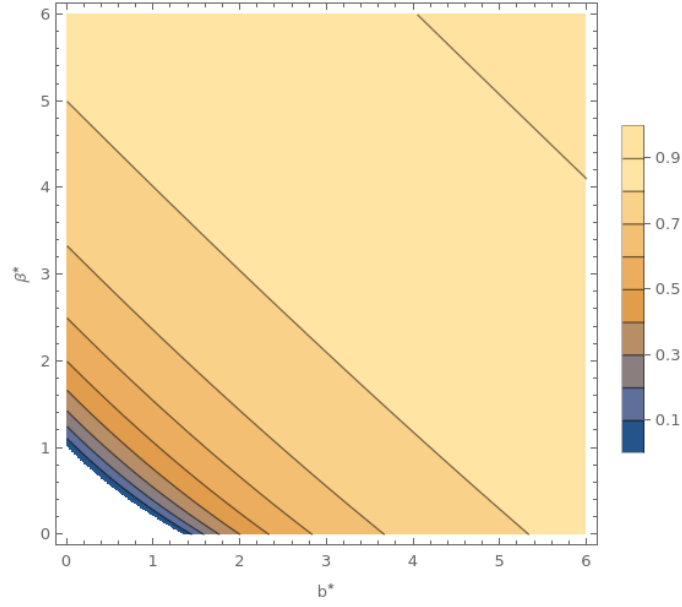


Figure 4.1: Contourplot of the equilibrium value of p for different b^* and β^*

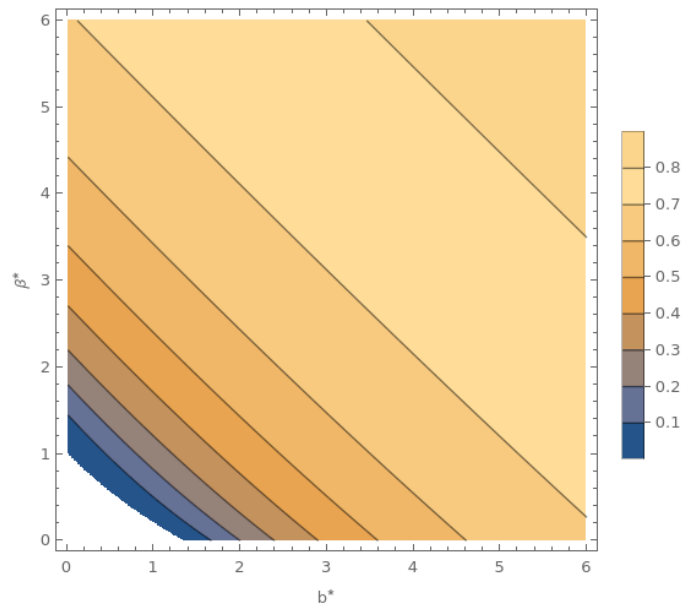


Figure 4.2: Contourplot of the equilibrium value of ρ for different b^* and β^*

4.2.3 Stability Analysis

Next we check the stability of the positive equilibria calculated in section (4.2.2). In this case (with no sexual reproduction) the Jacobian is:

$$J(p, \rho) = \begin{bmatrix} -1 + b^* + \beta^* - 2\beta^*p & -b^* \\ \frac{b^*}{2} + \frac{3b^*}{2} \frac{p-\rho}{1-p} \left(1 + \frac{1-\rho}{1-p}\right) + 4\beta^*p - 2\beta^*\rho & -2 - \frac{b^*}{2} - 3b^* \frac{p-\rho}{1-p} - 2\beta^*p \end{bmatrix}$$

By inserting each pair of values p, ρ calculated for specific b^* and β^* (as well as the b^* and β^* themselves) we can calculate the determinant and trace for each equilibrium value found in (4.2.2).

By doing so we see that for all the pairs of $p, \rho \in (0, 1]$, $\text{Det } J > 0$ and $\text{Tr } J < 0$ and thus the positive equilibria are stable. This can be seen in figures (4.3) and (4.4).

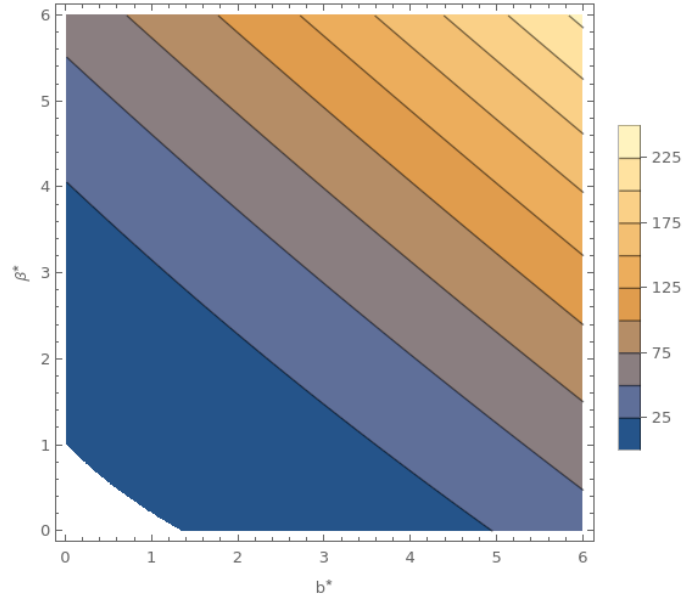


Figure 4.3: Contourplot of the values of the determinant of the Jacobian for different b^* and β^*

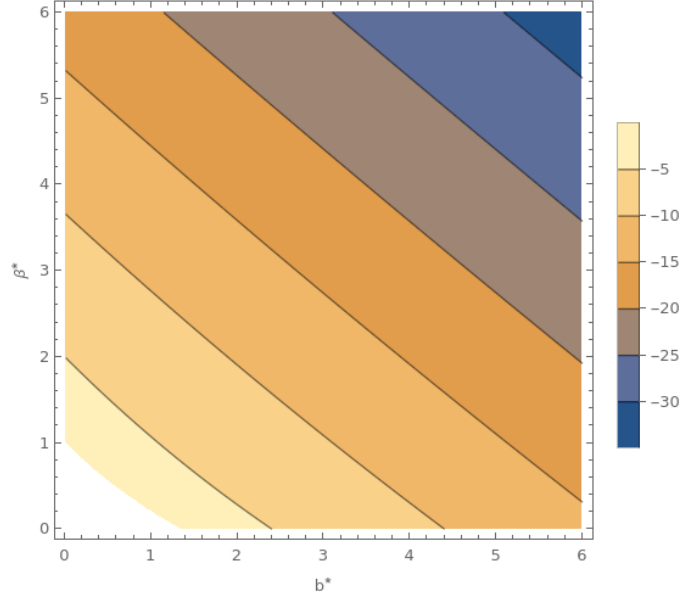


Figure 4.4: Contourplot of the values of the trace of the Jacobian for different b^* and β^*

4.3 One Strategy Model Under Introduction of Sexual Reproduction

Next we will take a look at the one strategy model with sexual reproduction. We start with equation (4.4) similarly to the analysis in section (4.2), but now instead of setting $\gamma_S = 0$, we set $\beta = 0$. By doing this we should be able to find how much sexual reproduction is needed to add a positive, stable equilibrium to the region where we have a stable extinct equilibrium.

The equation we get from equation (4.4) is thus (leaving out the subscripts once again):

$$\begin{aligned} &\gamma^2 p^5 - 2\gamma^2 p^4 + (2\gamma d + \gamma^2 + b\gamma)p^3 + (-6\gamma d - 2b\gamma)p^2 \\ &+ (d^2 + 4\gamma d + b\gamma - 3bd)p + (3bd - 4d^2) = 0 \end{aligned}$$

And by dividing by d^2 and setting $b^* = \frac{b}{d}$ and $\gamma^* = \frac{\gamma}{d}$, we get:

$$(4.7) \quad \begin{aligned} &\gamma^{*2} p^5 - 2\gamma^{*2} p^4 + (2\gamma^* + \gamma^{*2} + b^* \gamma^*) p^3 + (-6\gamma^* - 2b^* \gamma^*) p^2 \\ &+ (1 + 4\gamma^* + b^* \gamma^* - 3b^*) p + (3b^* - 4) = 0 \end{aligned}$$

Similarly for ρ from equation (4.3) we get:

$$\rho = \frac{-b^*p + p - \gamma^*p^2 + \gamma^*p^3}{-b^*}$$

Now for the extinct equilibrium $(p, \rho) = (0, 0)$ we have the Jacobian:

$$J(0, 0) = \begin{bmatrix} -1 + b^* & -b^* \\ \frac{b^*}{2} & -2 - \frac{b^*}{2} \end{bmatrix}$$

With $\text{Det } J = 2 - \frac{3b^*}{2}$ and $\text{Tr } J = -3 + \frac{b^*}{2}$. The stability of the extinct equilibrium now depends only on b^* , so we get that the extinct equilibrium is stable if $b^* < \frac{4}{3}$ and unstable if $b^* > \frac{4}{3}$, corresponding to where the determinant changes sign and thus the transcritical bifurcation, similar to what we found in (4.2.1). If $b^* > \frac{4}{3}$ we thus get a positive, stable equilibrium.

When $b^* = \frac{4}{3}$, the presence of a positive equilibrium depends on the value of γ^* . The equation in this case becomes:

$$\gamma^{*2}p^5 - 2\gamma^{*2}p^4 + (\gamma^{*2} + \frac{10}{3}\gamma^*)p^3 - \frac{26}{3}\gamma^*p^2 + (\frac{16}{3}\gamma^* - 3)p = 0$$

Now we can look at the derivative near $p = 0$ to see in which direction the graph $f(p) = \gamma^{*2}p^5 - 2\gamma^{*2}p^4 + (\gamma^{*2} + \frac{10}{3}\gamma^*)p^3 - \frac{26}{3}\gamma^*p^2 + (\frac{16}{3}\gamma^* - 3)p$ goes. We see that the graph $f(p)$ has value $f(1) = \gamma^{*2} - 2\gamma^{*2} + \gamma^{*2} + \frac{10}{3}\gamma^* - \frac{26}{3}\gamma^* + \frac{16}{3}\gamma^* - 3 = -3$ for all values of γ^* . Now, if the derivative $\frac{df(p)}{dp}$ at $p = 0$ is negative and $\frac{df(p)}{dp} \leq 0$ for all $p \in [0, 1]$, the graph will necessarily have negative values for all $p \in [0, 1]$, whereas if it is positive, the graph will cross the x-axis between 0 and 1 and the equation thus must have a positive equilibrium. The derivative is:

$$\frac{df(p)}{dp} = \left(5\gamma^{*2}p^4 - 8\gamma^{*2}p^3 + (3\gamma^{*2} + 10\gamma^*)p^2 - \frac{52}{3}\gamma^*p + (\frac{16}{3}\gamma^* - 3) \right)$$

Which has value $\frac{16}{3}\gamma^* - 3$ at $p = 0$.

Figure (4.5) shows the values of the derivative $\frac{df(p)}{dp}$ for $\gamma^* \in [0, \frac{9}{16}]$ and $p \in [0, 1]$, showing that the derivative takes negative values for all of these values of γ^* and p . Thus for $\gamma \leq \frac{9}{16}$ we do not get a positive equilibrium.

However, for $\frac{16}{3}\gamma^* - 3 > 0$, i.e. $\gamma^* > \frac{9}{16}$, we get a positive value for the derivative at $p = 0$ and thus we must have a positive equilibrium value for $p \in (0, 1]$. Thus we have that the lower limit for γ^* for a positive equilibrium when $b^* = \frac{4}{3}$ is $\gamma^* > \frac{9}{16}$.

The interesting case to study is now the part where the extinct equilibrium is stable, so when $b^* < \frac{4}{3}$, because the introduction of sexual reproduction can introduce a second

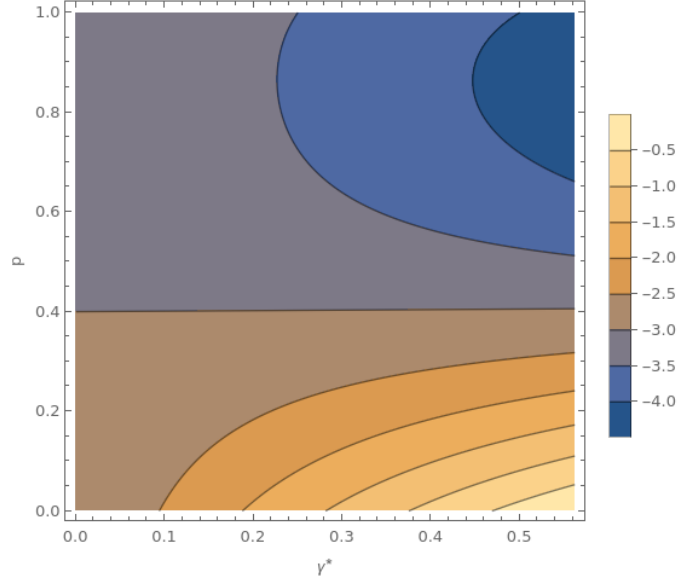


Figure 4.5: Value of derivative $\frac{df(p)}{dp}$ for $\gamma^* \in [0, \frac{9}{16}]$ and $p \in [0, 1]$.

stable, positive equilibrium in the range $[0, 1]$ through a fold bifurcation. For each b^* value we have a γ^* value above which two new, positive equilibria are introduced. The b^* and γ^* value pairs at which these new equilibria are created form the fold bifurcation line. We know that at this bifurcation line, both the value of equation (4.7) and its derivative must be 0, so we can use these conditions to find the γ^* value at the bifurcation line for each specific value of b^* . We do this by first solving at $b^* = 0$ and then using continuation of equilibria (using FindRoot function in Mathematica [3] with a small step size and using the previous result as the initial estimate for the next one) to continue the line. Figure (4.6) shows the fold bifurcation line and the transcritical bifurcation at $b^* = \frac{4}{3}$. These bifurcation lines divide the positive parameter space into 3 regions.

Now the Jacobian with sexual reproduction included (and $\beta = 0, \eta = 0$) is:

$$J(p, \rho) = \begin{bmatrix} -1 + b^* + 2\gamma^*p - 3\gamma^*p^2 & -b^* \\ \frac{b^*}{2} + 2\gamma^*p^2 + \frac{3b^*(p-\rho)}{1-p} + 4\gamma^*p(p-\rho) + \frac{3b^*(p-\rho)^2}{2(1-p)^2} & -2 - \frac{b^*}{2} - 2\gamma^*p^2 - \frac{3b^*(p-\rho)}{1-p} \end{bmatrix}$$

Thus we can characterise the regions in figure (4.6) according to number of equilibria and their stability. We only consider equilibria in $p \in [0, 1]$. In the region below the fold bifurcation line we have no equilibria in $(0, 1]$ and the extinct equilibrium is stable. Above it we have 2 positive equilibria $(0, 1]$ with the larger of these being stable and the lower one unstable (a saddle), and the extinct equilibrium being stable. To the right of the

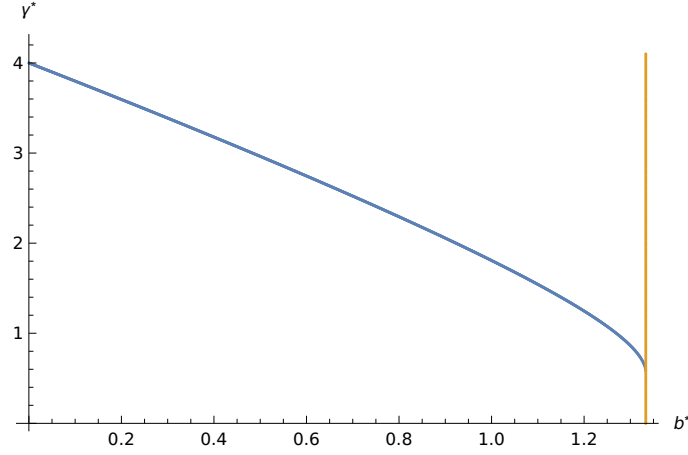


Figure 4.6: Fold and transcritical bifurcation lines. The fold bifurcation line is only plotted until the transcritical bifurcation line because past it, the fold bifurcation happens outside $p \in [0, 1]$.

transcritical bifurcation line the extinct equilibrium is unstable and there is one positive, stable equilibrium in $(0, 1]$. As was stated earlier, at $b^* = \frac{4}{3}$ we have a positive equilibrium in the $(0, 1]$ range if and only if $\gamma^* > \frac{9}{16}$, corresponding to the point where the fold and transcritical bifurcation lines meet.

4.3.1 Model For Different η Values

Now, taking a look at the model for brooders instead of spawners, we have the fifth order equation (4.2). Here we can look at $(\gamma_B + \alpha)$ together as an equivalent to γ_S for spawners. We can rewrite (4.2) as (removing all subscripts):

$$\begin{aligned}
& b(\gamma + \alpha)^2 p^5 + (2b\beta(\gamma + \alpha) - 2b(\gamma + \alpha)^2 + 3b\eta(\gamma + \alpha)) p^4 \\
& + (b^2(\gamma + \alpha) + b(\gamma + \alpha)^2 + 2bd(\gamma + \alpha) - 4b\beta(\gamma + \alpha) + b\beta^2 - 7b\eta(\gamma + \alpha) - 4d\eta(\gamma + \alpha) \\
& + 3b\beta\eta + 2b\eta^2 - 4d\eta^2) p^3 + (-2b^2(\gamma + \alpha) + 2b\beta(\gamma + \alpha) - 6bd(\gamma + \alpha) + 5b\eta(\gamma + \alpha) \\
& + 8d\eta(\gamma + \alpha) + b^2\beta - 2b\beta^2 + 2bd\beta + b^2\eta - 7b\beta\eta - 5bd\eta - 4d\beta\eta - 5b\eta^2 + 8d\eta^2) p^2 \\
& + (b^2(\gamma + \alpha) - 2b^2\beta + b\beta^2 + 4bd(\gamma + \alpha) - 3b^2d - 6b\beta d + bd^2 - b\eta(\gamma + \alpha) - 2b^2\eta \\
& + 5b\beta\eta - 4d\eta(\gamma + \alpha) + 8bd\eta + 8\beta d\eta - 4d^2\eta + 4b\eta^2 - 4d\eta^2) p \\
& + b^2\beta + 3b^2d + 4b\beta d - 4bd^2 + b^2\eta - b\beta\eta - 3bd\eta - 4\beta d\eta + 4d^2\eta - b\eta^2 = 0
\end{aligned}$$

Which, if we set $\eta = 0$ and $\alpha = 0$ gives us back the model for spawners, as found in equation (4.4).

Now we can repeat the analysis done in (4.3), but for some different values of η . Let us start by setting $\beta = 0$ and dividing by d^3 and setting $b^* = \frac{b}{d}$, $\gamma^* = \frac{\gamma}{d}$, $\alpha^* = \frac{\alpha}{d}$, $\eta^* = \frac{\eta}{d}$. We get:

$$\begin{aligned}
& b^*(\gamma^* + \alpha^*)^2 p^5 + (-2b^*(\gamma^* + \alpha^*)^2 + 3b^*\eta^*(\gamma^* + \alpha^*)) p^4 + (b^{*2}(\gamma^* + \alpha^*) + b^*(\gamma^* + \alpha^*)^2 \\
& + 2b^*(\gamma^* + \alpha^*) - 7b^*\eta^*(\gamma^* + \alpha^*) - 4\eta^*(\gamma^* + \alpha^*) + 2b^*\eta^{*2} - 4\eta^{*2}) p^3 \\
& + (-2b^{*2}(\gamma^* + \alpha^*) - 6b^*(\gamma^* + \alpha^*) + 5b^*\eta^*(\gamma^* + \alpha^*) + 8\eta^*(\gamma^* + \alpha^*) + b^{*2}\eta^* \\
& - 5b^*\eta^* - 5b^*\eta^{*2} + 8\eta^{*2}) p^2 + (b^{*2}(\gamma^* + \alpha^*) + 4b^*(\gamma^* + \alpha^*) - 3b^{*2} + b^* - b^*\eta^*(\gamma^* + \alpha^*) \\
& - 2b^{*2}\eta^* - 4\eta^*(\gamma^* + \alpha^*) + 8b^*\eta^* - 4\eta^* + 4b^*\eta^{*2} - 4\eta^{*2}) p \\
& + 3b^{*2} - 4b^* + b^{*2}\eta^* - 3b^*\eta^* + 4\eta^* - b^*\eta^{*2} = 0
\end{aligned}$$

In this case we have for the extinct equilibrium:

$$J(0, 0) = \begin{bmatrix} -1 + b^* & -b^* + \eta^* \\ \frac{b^*}{2} & -2 - \frac{b^*}{2} \end{bmatrix}$$

And so we get $\text{Det } J = 2 - \frac{3b^*}{2} - \frac{b^*\eta^*}{2}$, which means that for the extinct equilibrium to be unstable, we need $2 - \frac{3b^*}{2} - \frac{b^*\eta^*}{2} < 0$, i.e. $b^* > \frac{4}{3+\eta^*}$.

Figures (4.7), (4.8), (4.9) and (4.10) show the bifurcation lines for four different values of η^* : 0.1, 0.2, 0.5 and 1.0, respectively. These lines divide the positive parameter space into three regions similarly to the case with $\eta^* = 0$, as was explained in section (4.3). Comparing the case with $\eta^* = 0$ and these 4 cases of different values of η^* , it becomes clear that an increase in η^* moves the transcritical bifurcation line to the left, in other words for higher η^* , a lower b^* is needed to destabilise the extinct equilibrium. We also notice that an increase in η^* lowers the fold bifurcation line, so that for higher η^* , a lower $\gamma^* + \alpha^*$ is needed to create a stable, positive equilibrium in the region where the extinct equilibrium is stable.

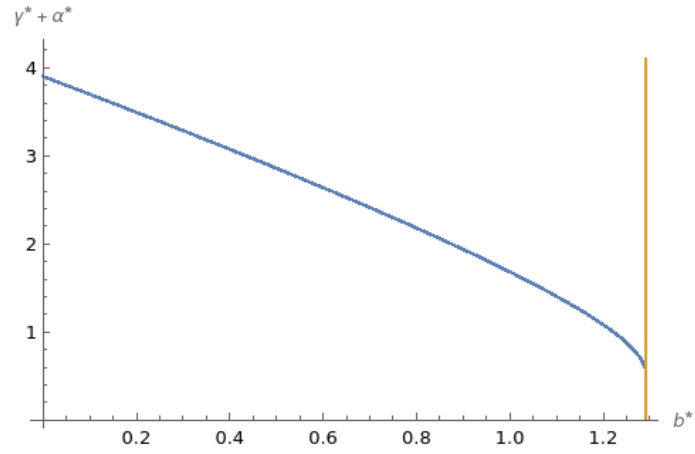


Figure 4.7: Fold and transcritical bifurcation lines for $\eta^* = 0.1$. The fold bifurcation line is only plotted until the transcritical bifurcation line because past it, the fold bifurcation happens outside $p \in [0, 1]$.

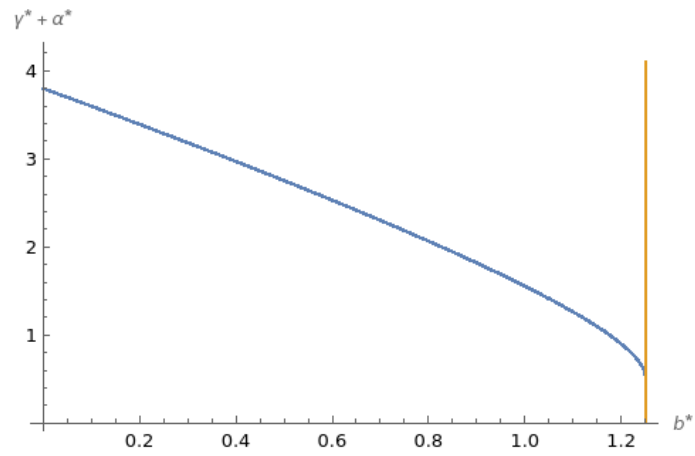


Figure 4.8: Fold and transcritical bifurcation lines for $\eta^* = 0.2$. The fold bifurcation line is only plotted until the transcritical bifurcation line because past it, the fold bifurcation happens outside $p \in [0, 1]$.

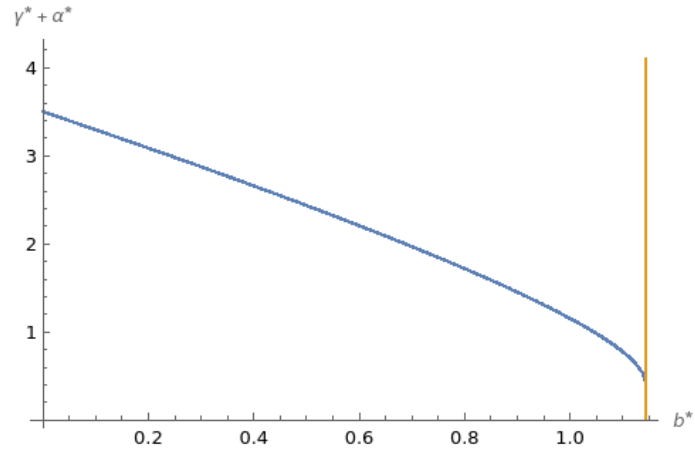


Figure 4.9: Fold and transcritical bifurcation lines for $\eta^* = 0.5$. The fold bifurcation line is only plotted until the transcritical bifurcation line because past it, the fold bifurcation happens outside $p \in [0, 1]$.

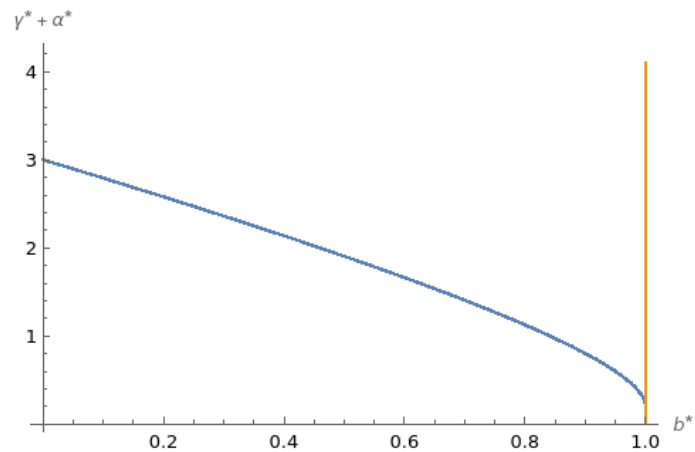


Figure 4.10: Fold and transcritical bifurcation lines for $\eta^* = 1.0$. The fold bifurcation line is only plotted until the transcritical bifurcation line because past it, the fold bifurcation happens outside $p \in [0, 1]$.

4.3.2 Stability analysis

We calculated the determinant and trace of the Jacobian at each of the 3 equilibria in the $\{b^*, (\gamma^* + \alpha^*)\}$ parameter space for the different values of η^* to check their stability. The Jacobian is:

$$J(p, \rho) = \begin{bmatrix} -1 + b^* + (\gamma^* + \alpha^*)(2 - 3p)p - \eta^* \rho & -b^* + \eta^*(1 - p) \\ \frac{b^*}{2} + (\gamma^* + \alpha^*)(6p - 4\rho)p + \frac{3b^*(p-\rho)}{1-p} + \frac{3b^*(p-\rho)^2}{2(1-p)^2} + \eta^* \rho & -2 - \frac{b^*}{2} - 2(\gamma^* + \alpha^*)p^2 - \frac{3b^*(p-\rho)}{1-p} + 2\eta^*(p - 4\rho) \end{bmatrix}$$

It became clear that only the middle equilibrium is both biologically admissible and stable, for all the values of η^* (0, 0.1, 0.2, 0.5 and 1.0). This is consistent with what we know about the bifurcation lines. At values to the left of the transcritical bifurcation line the extinct equilibrium is stable, and thus above the fold bifurcation line we get one saddle and one stable equilibrium, which must be the higher of the two, alongside the already existing unstable equilibrium (which is not biologically admissible). At the transcritical bifurcation the saddle goes through the extinct equilibrium and exchanges stability with it, leaving the extinct equilibrium unstable but not affecting the other positive equilibria.

Figures (4.11) and (4.12) show the determinant and trace of the middle equilibrium for $\eta = 0.1$ as an example. From these it can be seen that the determinant is always positive wherever this equilibrium exists and the trace is always negative, giving that the equilibrium is always stable. Figures (4.13) and (4.14) also show the p and ρ values of the middle equilibrium for $\eta^* = 0.1$ for comparison.

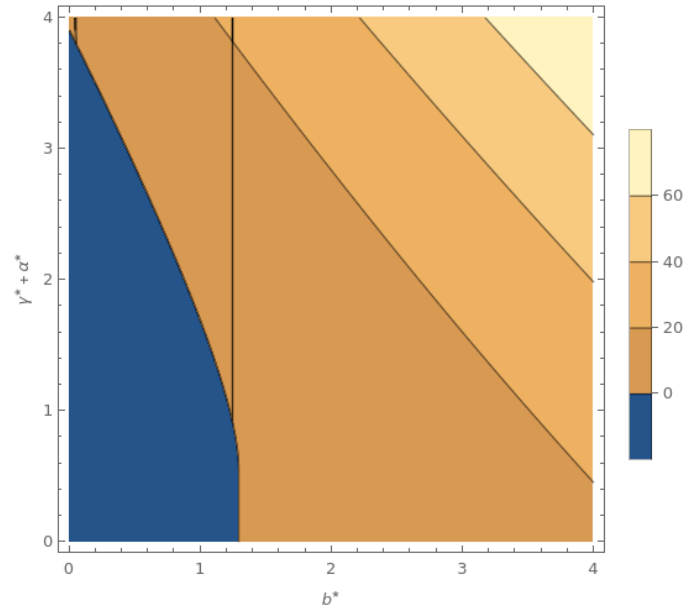


Figure 4.11: Contourplot of the value of the determinant of the Jacobian for the middle equilibrium for $\eta^* = 0.1$. In the blue region this equilibrium does not exist. The vertical black lines are plotting artefacts and do not carry any meaning.

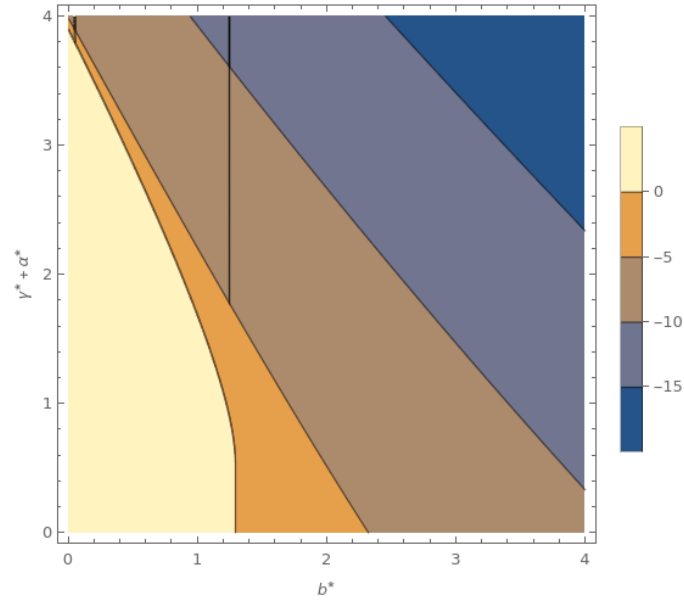


Figure 4.12: Contourplot of the value of the trace of the Jacobian for the middle equilibrium for $\eta^* = 0.1$. In the yellow region this equilibrium does not exist. The vertical black lines are plotting artefacts and do not carry any meaning.

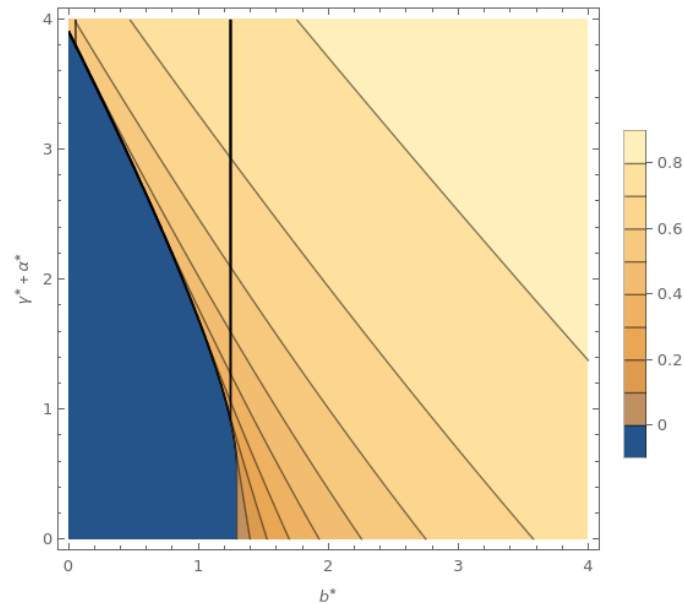


Figure 4.13: Contourplot of the p value for the middle equilibrium for $\eta^* = 0.1$. In the blue region this equilibrium does not exist. The vertical black lines are plotting artefacts and do not carry any meaning.

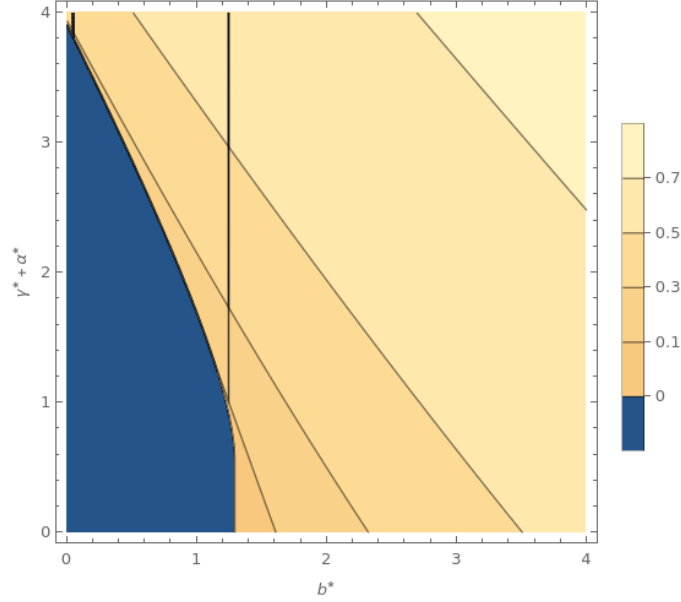


Figure 4.14: Contourplot of the ρ value for the middle equilibrium for $\eta^* = 0.1$. In the blue region this equilibrium does not exist. The vertical black lines are plotting artefacts and do not carry any meaning.

4.4 Invasion Analysis

Now that we have characterised the one-strategy model, we will do an invasion analysis to find out conditions for coexistence of the two strategies.

Let us start with spawners as the resident population, at equilibrium (as found in section (3.6)). We then want to find under which conditions brooders can invade this population, starting from a small population with p_B close to 0. We have the differential equation for p_B :

$$\frac{dp_B}{dt} = (-d_B + b_B q_{0/B} + (\beta + \gamma_B p_B + \alpha p_B + \eta q_{B/B}) (1 - \hat{p}_S - p_B) + (c_B - c_S) q_{S/B}) p_B$$

We can see that when p_B is close to 0, it grows very slowly. However, we want to find such conditions that it grows, even if slowly. This is equivalent to:

$$\begin{aligned} \lim_{p_B \rightarrow 0} & (-d_B + b_B q_{0/B} + (\beta + \eta q_{B/B}) (1 - \hat{p}_S) + (c_B - c_S) q_{S/B}) \\ & = -d_B + b_B q_{0/B} + (\beta + \eta q_{B/B}) (1 - \hat{p}_S) + (c_B - c_S) q_{S/B} > 0 \end{aligned}$$

So now we need to find the differential equations for the conditional probabilities $q_{B/B}$, $q_{0/B}$ and $q_{S/B}$ and find their quasi-equilibria when $p_B = 0$. However since they are conditional probabilities: $q_{0/B} + q_{B/B} + q_{S/B} = 1$. Thus we can express $q_{0/B}$ in terms of the other two to get:

$$(4.8) \quad -d_B + b_B (1 - q_{S/B} - q_{B/B}) + (\beta + \eta q_{B/B}) (1 - \hat{p}_S) + (c_B - c_S) q_{S/B} > 0$$

To find the conditional probabilities, it is worth remembering that $q_{X/Y} = \frac{\rho_{XY}}{p_Y}$ and that by the chain rule $\frac{dq_{X/Y}}{dt} = \frac{d}{dt} \left(\frac{\rho_{XY}}{p_Y} \right) = \frac{1}{p_Y} \frac{d\rho_{XY}}{dt} - \frac{q_{X/Y}}{p_Y} \frac{dp_Y}{dt}$ for any X, Y . Thus we get:

$$\begin{aligned} \frac{dq_{B/B}}{dt} &= -2q_{B/B} \left(d_B + \frac{3c_S}{4} q_{S/B} \right) + 2q_{S/B} \left(\frac{3c_B}{4} q_{S/B} \frac{p_B}{\hat{p}_S} + \frac{c_B}{4} \right) \\ &+ 2q_{0/B} \left(\frac{b_B}{4} + \frac{3b_B}{4} q_{0/B} \frac{p_B}{1 - \hat{p}_S - p_B} + (\beta + \gamma_B p_B + \alpha p_B) p_B + \eta q_{B/B} p_B \right) \\ &+ d_B q_{B/B} - b_B q_{0/B} q_{B/B} - (\beta + \gamma_B p_B + \alpha p_B + \eta q_{B/B}) (1 - \hat{p}_S - p_B) q_{B/B} \\ &- (c_B - c_S) q_{S/B} q_{B/B} \end{aligned}$$

Giving:

$$\begin{aligned} \lim_{p_B \rightarrow 0} \frac{dq_{B/B}}{dt} &= q_{B/B} \left(-d_B - \frac{3c_S}{2} q_{S/B} \right) + q_{S/B} \frac{c_B}{2} \\ &+ (1 - q_{S/B} - q_{B/B}) \left(\frac{b_B}{2} - b_B q_{B/B} \right) - (\beta + \eta q_{B/B}) (1 - \hat{p}_S) q_{B/B} \\ &- (c_B - c_S) q_{S/B} q_{B/B} \end{aligned}$$

Now we also need to find the differential equation for $q_{S/B}$:

$$\begin{aligned} \frac{dq_{S/B}}{dt} &= -q_{S/B} \left(d_B + d_S + \frac{c_S}{4} + \frac{c_B}{4} + \frac{3c_S}{4} q_{S/B} + \frac{3c_B}{4} q_{S/B} \frac{p_B}{\hat{p}_S} \right) \\ &+ \hat{\rho}_{0S} \left(\frac{3b_B}{4} \frac{q_{0/B}}{1 - \hat{p}_S - p_B} + \beta + \gamma_B p_B + \alpha p_B + \eta q_{B/B} \right) \\ &+ q_{0/B} \left(\frac{3b_S}{4} \frac{\hat{\rho}_{0S}}{1 - \hat{p}_S - p_B} + (\beta + \gamma_S \hat{p}_S) \hat{p}_S \right) \\ &+ \frac{3c_B}{4} \frac{q_{S/B}}{\hat{p}_S} \hat{\rho}_{SS} + \frac{3c_S}{4} q_{S/B} q_{B/B} + d_B q_{S/B} - b_B q_{0/B} q_{S/B} \\ &- (\beta + \gamma_B p_B + \alpha p_B + \eta q_{B/B}) (1 - \hat{p}_S - p_B) q_{S/B} - (c_B - c_S) q_{S/B}^2 \end{aligned}$$

Which gives:

$$\begin{aligned}
\lim_{p_B \rightarrow 0} \frac{dq_{S/B}}{dt} &= -q_{S/B} \left(d_S + \frac{c_S}{4} + \frac{c_B}{4} + \frac{3c_S}{4} q_{S/B} \right) \\
&+ \hat{\rho}_{0S} \left(\frac{3b_B}{4} \frac{1 - q_{S/B} - q_{B/B}}{1 - \hat{p}_S} + \beta + \eta q_{B/B} \right) \\
&+ (1 - q_{S/B} - q_{B/B}) \left(\frac{3b_S}{4} \frac{\hat{\rho}_{0S}}{1 - \hat{p}_S} + (\beta + \gamma_S \hat{p}_S) \hat{p}_S \right) \\
&+ \frac{3c_B}{4} \frac{q_{S/B}}{\hat{p}_S} \hat{\rho}_{SS} + \frac{3c_S}{4} q_{S/B} q_{B/B} - b_B q_{S/B} (1 - q_{S/B} - q_{B/B}) \\
&- (\beta + \eta q_{B/B}) (1 - \hat{p}_S) q_{S/B} - (c_B - c_S) q_{S/B}^2
\end{aligned}$$

So now we can find the quasi-equilibria of $q_{B/B}$ and $q_{S/B}$ by setting $\lim_{p_B \rightarrow 0} \frac{dq_{B/B}}{dt} = 0$ and $\lim_{p_B \rightarrow 0} \frac{dq_{S/B}}{dt} = 0$. This is easily done due to the fact that the expression for $\lim_{p_B \rightarrow 0} \frac{dq_{S/B}}{dt}$ is linear in $q_{B/B}$. The general expressions for the conditional probabilities however are long and will not be presented here. By substituting these expressions for the conditional probabilities $q_{B/B}$ and $q_{S/B}$ into the equation for the growth of brooders from p_B near 0 found before, we can now calculate whether brooders can invade the spawners for specific values of parameters (invasion is possible if the growth expression is positive, i.e. if inequality (4.8) holds).

Similarly, we can look at invasion of spawners when brooders are the resident population. Following similar reasoning as before, we need that:

$$(4.9) \quad \lim_{p_S \rightarrow 0} (-d_S + b_S q_{0/S} + (\beta + \gamma_S p_S) (1 - \hat{p}_B - p_S) + (c_S - c_B) q_{B/S})$$

$$(4.10) \quad = -d_S + b_S (1 - q_{B/S} - q_{S/S}) + \beta (1 - \hat{p}_B) + (c_S - c_B) q_{B/S} > 0$$

So again, we need to find the quasi-equilibria of $q_{S/S}$ and $q_{B/S}$. We get:

$$\begin{aligned}
\lim_{p_S \rightarrow 0} \frac{dq_{S/S}}{dt} &= q_{S/S} \left(-d_S - \frac{3c_B}{2} q_{B/S} \right) + q_{B/S} \frac{c_S}{2} + (1 - q_{B/S} - q_{S/S}) \left(\frac{b_S}{2} - b_S q_{S/S} \right) \\
&- \beta (1 - \hat{p}_B) q_{S/S} - (c_S - c_B) q_{B/S} q_{S/S} = 0
\end{aligned}$$

$$\begin{aligned}
\lim_{p_S \rightarrow 0} \frac{dq_{B/S}}{dt} &= -q_{B/S} \left(d_B + \frac{c_S}{4} + \frac{c_B}{4} + \frac{3c_B}{4} q_{B/S} \right) \\
&+ (1 - q_{B/S} - q_{S/S}) \left(\frac{3b_B}{4} \frac{\hat{\rho}_{0B}}{1 - \hat{p}_B} + (\beta + \gamma_B \hat{p}_B + \alpha \hat{p}_B) \hat{p}_B + \eta \hat{\rho}_{BB} \right) \\
&+ \hat{\rho}_{0B} \left(\frac{3b_S}{4} \frac{1 - q_{B/S} - q_{S/S}}{1 - \hat{p}_B} + \beta \right) + \frac{3c_B}{4} q_{B/S} q_{S/S} + \frac{3c_S}{4} \frac{q_{B/S}}{\hat{p}_B} \hat{\rho}_{BB} \\
&- b_S (1 - q_{B/S} - q_{S/S}) q_{B/S} - \beta (1 - \hat{p}_B) q_{B/S} - (c_S - c_B) q_{B/S}^2 = 0
\end{aligned}$$

So now by inserting the conditional probabilities into the equation for the growth of spawners from p_S near 0, we can calculate whether spawners can invade for specific values of parameters (invasion is possible when inequality (4.9) holds).

By finding the parameter values for which brooders can invade spawners and vice versa, we can now find the region in the parameter space where mutual invasibility is possible.

4.4.1 Mutual Invasibility Without Sexual Reproduction

We start by looking at mutual invasibility when no sexual reproduction is present, i.e. when γ_S , γ_B , α and η are all 0. In this case, the differential equations for brooders and spawners are the same, so for coexistence to be possible we will need a trade-off in the parameters. Looking at the assumptions made in (3.1) about the parameter values as well as based on the life-history strategies found in Darling et al [1], it seems logical to start from a trade-off between death rate and growth and competition. Thus we define $d_X = ab_X$ where a is a constant between 0 and 1. We also remember that $c_S = Pb_S$ and $c_B = (1 - P)b_B$ where P is the probability that the spawner wins this conflict. Since we want the spawners to be better competitors, we only look for $P > 0.5$.

Now we can look at different combinations of a and P values and screen for combinations that give mutual invasibility in the region that fulfils the conditions:

$$\begin{aligned}
d_S &> d_B \\
b_S &> b_B \\
c_S &> c_B
\end{aligned}$$

Which, since all of these rates for one strategy are now proportional to each other, is the same as looking at just the region where $b_S > b_B$. It is worth remembering that we only look for $P > 0.5$, which guarantees the third condition if $b_S > b_B$.

We looked at a number of combinations of a and P values for $\beta = 0.0, 0.1, 0.2$ and 0.5 and were able to find mutual invasibility. For $\beta = 0.0$, no mutual invasibility could be found. Table (4.1) shows the combinations of a and P that give mutual invasibility when $\beta = 0.1$. For $\beta = 0.2$ the table looked the same, for $\beta = 0.5$ no mutual invasibility was found for $a = 0.8$.

From this it becomes clear that at least some reproduction over distance (in this case in the form of budding and breaking of pieces, β) is needed for mutual invasibility. This is due to the fact that without this form reproduction, the normal birth/growth rate b cannot make up for the death rate d for higher values of a , whereas for lower values of a , invasion is not possible due to the resident taking over most of the lattice. We also see that in general, a relatively high value of a , $a \geq 0.8$, is needed for mutual invasibility in the region we are looking at, $b_S > b_B$.

$\beta = 0.1$		P										
		0.50	0.55	0.60	0.65	0.70	0.75	0.80	0.85	0.90	0.95	1.00
a	0.0											
	0.1											
	0.2											
	0.3											
	0.4											
	0.5											
	0.6											
	0.7											
	0.8		X	X	X	X	X	X	X	X	X	X
	0.9		X	X	X	X	X	X	X	X	X	X
1.0		X	X	X	X	X	X	X	X	X	X	

Table 4.1: Combinations of parameters a and P that give mutual invasibility such that $b_S > b_B$ (represented by X in the table), for $\beta = 0.1$.

Figure (4.15) shows the area of mutual invasibility for an example set of parameters, $\beta = 0.1$, $a = 0.8$ and $P = 0.8$. These were chosen out of the ones that give mutual invasibility due to the fact that they are somewhat intermediate values and because they give a clear region of mutual invasibility in the (b_S, b_B) -plane.

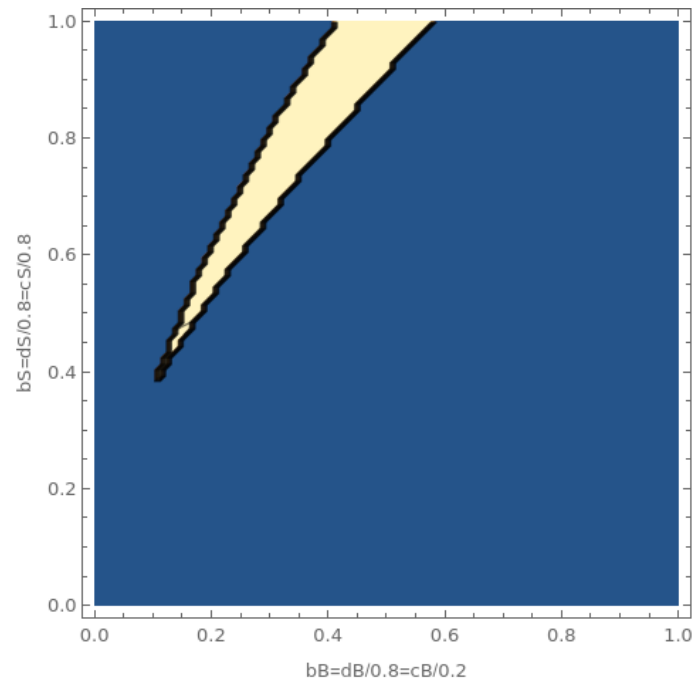


Figure 4.15: Region of mutual invasibility (yellow) for different b_S and b_B values when $\beta = 0.1$, $a = 0.8$ and $P = 0.8$, and no sexual reproduction is present.

4.4.2 Mutual Invasibility and Coexistence Under the Addition of Sexual Reproduction

Next we take a point in the region of mutual invasibility in the parameter space and add sexual reproduction, to see how this affects coexistence.

We start with the same parameter values as in figure (4.15) and choose the values $b_S = 0.80$ and $b_B = 0.35$ due to their location inside the region of mutual invasibility.

First we take a look at the mutual invasibility for different γ_S and $\gamma_B + \alpha$ values. We do not consider different values of η for this analysis, but set $\eta = 0$. Figure (4.16) shows that mutual invasibility is only possible for small rates of sexual reproduction. This is due to the fact that sexual reproduction only becomes significant at higher population densities, a phenomenon known as the Allee effect. More specifically, this is because sexual reproduction depends on the square of the population density (since two parents are needed), and if the population density is already near 0, its square becomes negligible. In practice this means that sexual reproduction only helps the resident strategy and not the invader, which is why at high rates of sexual reproduction for the resident the resident is able to reproduce very effectively and it does not make a difference how high sexual reproduction for the invader is, invasion will not be possible.

Next we see if coexistence can be extended to higher rates of sexual reproduction where mutual invasibility is not possible. This could be possible due to the Allee effect, since sexual reproduction does not help the invader, but can keep a strategy from going to extinction when it is already present in the population.

We do this by setting first $\gamma_B + \alpha$ to a few specific values and finding all positive equilibria for different values of γ_S and then the other way around. Lastly we look at a case where $\gamma_B + \alpha$ and γ_S change proportionally to each other.

Firstly, by setting $\gamma_B + \alpha = 0$ and finding all equilibrium values for different values of γ_S , we find that in this case no positive equilibria exist outside the region of mutual invasibility, i.e. for $\gamma_S > 0.0327$. Figure (4.17) shows the equilibrium values of p_B , showing clearly that at $\gamma_S = 0.0327$ the equilibrium undergoes a transcritical bifurcation and the boundary equilibrium with $p_B = 0$ becomes stabilised.

Doing the same with $\gamma_S = 0$ and finding the equilibria for different values of $\gamma_B + \alpha$ shows the same thing, with no positive equilibria existing outside the region of mutual invasibility and the boundary equilibrium, in this case $p_S = 0$, becoming stabilised at $\gamma_B + \alpha = 0.0393$ through a transcritical bifurcation.

Next, we set $\gamma_B + \alpha$ to some different values below 0.0393, i.e. in the range that allows for mutual invasibility. We find that for $\gamma_B + \alpha$ in the range $[0.0273, 0.0393[$ we get coexistence outside the region of mutual invasibility. Figure (4.18) shows the equilibrium values of p_B for different γ_S values in one such case, for $\gamma_B + \alpha = 0.0360$. Here we can see that we still get a transcritical bifurcation at $\gamma_S = 0.0327$, only in this case it is due

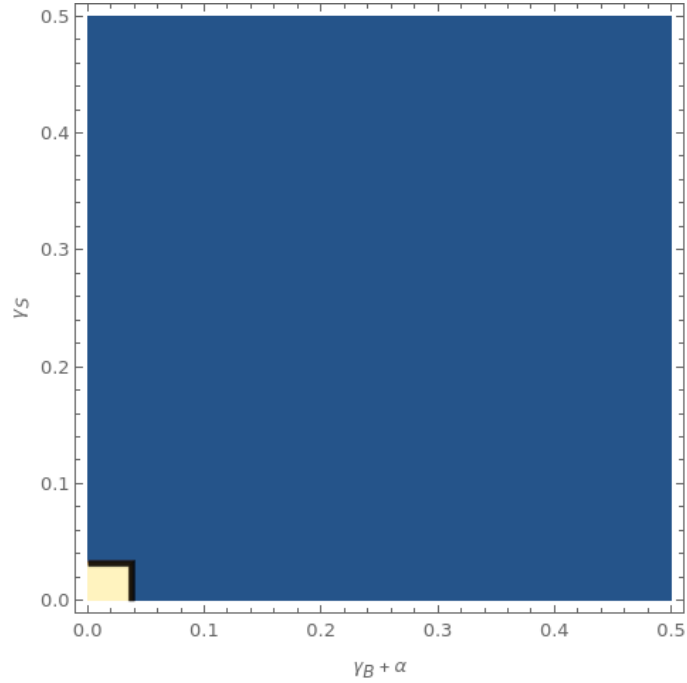


Figure 4.16: Region of mutual invasibility (yellow) for different γ_S and $\gamma_B + \alpha$ values when $\beta = 0.1$, $a = 0.8$ and $P = 0.8$, and $b_S = 0.80$ and $b_B = 0.35$

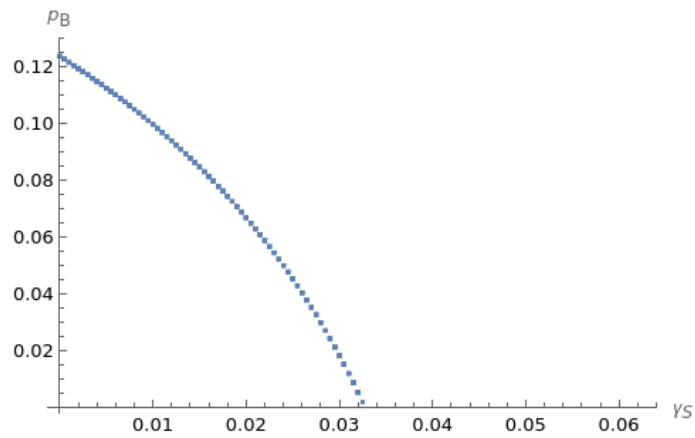


Figure 4.17: Positive equilibrium values of p_B for different values of γ_S when $\gamma_B + \alpha = 0$ and $\beta = 0.1$, $a = 0.8$, $P = 0.8$, $b_S = 0.80$ and $b_B = 0.35$

to an equilibrium that comes into the positive region through the boundary equilibrium at $p_B = 0$, stabilising the boundary equilibrium and creating a saddle. Thus there is a range of γ_S values outside the region of mutual invasibility where we have one unstable positive equilibrium and one stable positive one, until these two come together in a fold bifurcation.

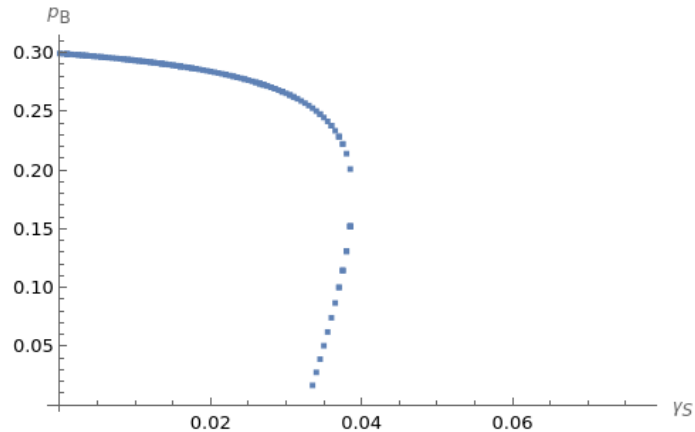


Figure 4.18: Positive equilibrium values of p_B for different values of γ_S when $\gamma_B + \alpha = 0.0360$ and $\beta = 0.1$, $a = 0.8$, $P = 0.8$, $b_S = 0.80$ and $b_B = 0.35$

We also looked at some set values of γ_S between 0 and 0.0327 with varying values of $\gamma_B + \alpha$, but were not able to find any extensions of the region of coexistence outside the region of mutual invasibility.

Lastly, we set $\gamma_S = \gamma_B + \alpha$ and find all the positive equilibria for different values of these, as can be seen in figure (4.19) for p_B . This corresponds to looking at the diagonal line in the $\{\gamma_S, \gamma_B\}$ -parameter space. This diagonal line passes through the area in the parameter space that has simultaneously an unstable and a stable positive equilibrium, as was found before, and this can also be seen in figure (4.20) which shows a closeup of this range in $\gamma_S = \gamma_B + \alpha$. It can be seen that an equilibrium enters the positive region through a transcritical bifurcation, stabilising the boundary equilibrium $p_B = 0$ and creating a saddle. The positive stable equilibrium then exits the positive region through the other boundary equilibrium $p_S = 0$, stabilising this boundary equilibrium and only leaving the saddle. Thus in the region where both γ_S and $\gamma_B + \alpha$ are large, both boundary equilibria are stable and there is a priority effect where the strategy that is first present on the lattice will reach a stable positive equilibrium and the other strategy cannot invade.

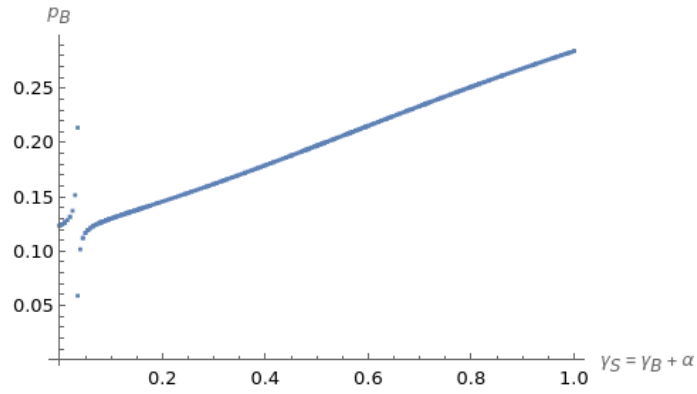


Figure 4.19: Positive equilibrium values of p_B for different values of $\gamma_S = \gamma_B + \alpha$ when $\beta = 0.1$, $a = 0.8$, $P = 0.8$, $b_S = 0.80$ and $b_B = 0.35$

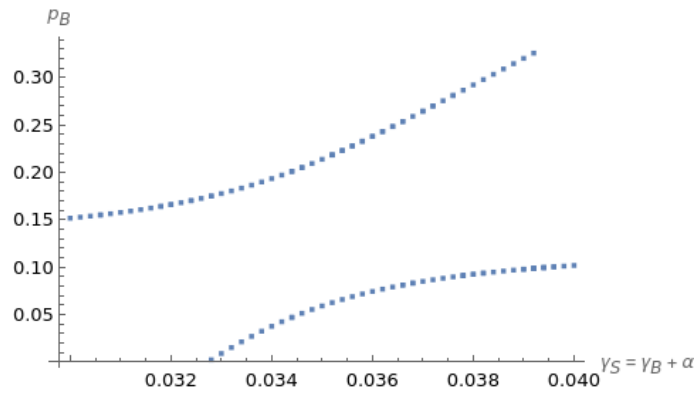


Figure 4.20: Closeup of region with two positive equilibrium values of p_B for different values of $\gamma_S = \gamma_B + \alpha$ when $\beta = 0.1$, $a = 0.8$, $P = 0.8$, $b_S = 0.80$ and $b_B = 0.35$

4.5 Modelling of Environmental Impacts on Corals

Darling et al. [1] hypothesised that human and environmental impacts such as fishing, pollution, sedimentation, ocean acidification and temperature increase would have a disproportionately large effect on the competitive species of corals (in our case the spawners) and possibly lead to their replacement by corals exhibiting other strategies (such as brooders).

We choose to take a look at ocean acidification and temperature increase, which affect the entire coral population equally. The most straight-forward way to model this is by an increased death rate.

So, we start again from the same point in the region of coexistence as in the previous chapters, where $\beta = 0.1$, $b_S = 0.80$, $b_B = 0.35$ and $P = 0.8$, $a = 0.8$, and no sexual reproduction is present. Now we keep the rest of the parameters the same, but increase a to increase the death rate (remember that $d_X = ab_X$ and we are keeping the growth rate b_X constant) and do a continuation of equilibria. Figure (4.21) shows what happens to the global densities of brooders and spawners when the death rate increase. We see that spawners quickly go extinct, with an increase in a from 0.800 to only 0.814, whereas brooders increase in density until this point and then start to decline with any further increases to a .

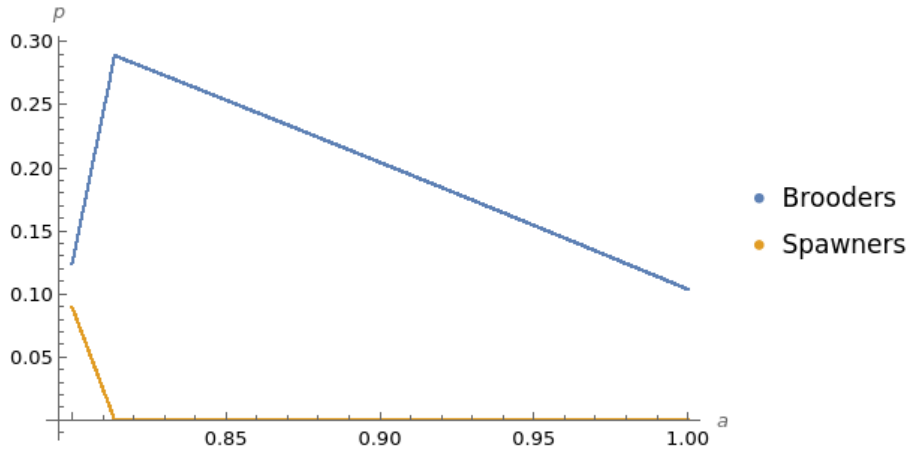


Figure 4.21: Global densities p_B and p_S for an increase in death rate. The other parameters are $\beta = 0.1$, $P = 0.8$, $b_S = 0.80$, $b_B = 0.35$, $\gamma_S = 0$, $\gamma_B + \alpha = 0$ and $\eta = 0$.

Since $d_X = ab_X$, an increase in a affects the death rate of the spawners more strongly than the brooders, due to the difference in their growth rates. The brooders in fact first benefit from the changing conditions due to the spawners going to extinction, and only then with further increases in the death rate start to suffer themselves. This is consistent

with the hypothesis made by Darling et al. [1] about the effects of environmental changes on the different strategies.

Chapter 5

Discussion

In this thesis we developed a pair approximation lattice model for two different life history strategies of corals on a coral reef. The main focus was on the two different reproductive strategies, brooding and spawning, since these make up the most important component in differentiating strategies from each other.

We started by analysing the model for one strategy only. We found that asexual reproduction rates b and β over the the death rate d (i.e. the viability) when no sexual reproduction is present must fulfill condition $4 < 3\frac{b}{d} + 4\frac{\beta}{d} + \frac{\beta}{d}\frac{b}{d}$ in order for a stable positive equilibrium to be present (section (4.2.1)). Then we looked at how sexual reproduction can extend this stable positive equilibrium into the region where before there was no stable positive equilibrium (section (4.3)). We found that there is always a rate of sexual reproduction that can create a positive stable equilibrium, even for the extreme case where no asexual reproduction is present. However, due to the Allee effect, sexual reproduction only becomes substantial at higher population densities, which means that even if we have a stable positive equilibrium, there is no invasion. This means that a large perturbation due to for example an environmental catastrophe could lead to extinction.

From the invasion analysis in section (4.4) it became clear that the two strategies can coexist under certain conditions which fit the biological assumptions based on Darling et al. [1]. These assumptions were that spawners have a higher growth rate, a higher death rate and are better competitors than brooders. From our invasion analysis, we found that some reproduction over distance is needed for coexistence, as is a strong trade-off between growth and death rates. A skew in the competition is also necessary. With these conditions, we find a stable equilibrium where brooders have a significantly lower growth and thus death rate than spawners, which have the competitive advantage. Brooders are thus focusing a bigger part of their energy on long-distance reproduction, while spawners are dominating over short distances and having a higher turnover.

In section (4.4.2) we looked at the effect of sexual reproduction on invasibility and

coexistence. We found that mutual invasibility is possible only for low rates of sexual reproduction for both strategies. This is explained by the fact that effectively only the resident population is performing sexual reproduction and thus a high rate of sexual reproduction for the resident will give it an advantage, whereas increasing the rate of sexual reproduction for the invader has practically no effect. We also looked at whether coexistence could be extended to where no mutual invasibility was possible. We found there was a small region where coexistence was possible outside the region of mutual invasibility, however it was only a very small extension. For higher rates of sexual reproduction no stable positive equilibrium was found, only the boundary equilibria are stable and thus whichever strategy gets established first will stay and the other cannot invade.

Due to the differences in their strategies mentioned above, we also found that a change in the environmental conditions, namely the acidification and temperature increase of oceans, affects the two strategies differently (section (4.5)). Since spawners have a higher growth rate and a higher death rate, the increase in death rate caused by the changing conditions affects them negatively and quickly leads to extinction, with brooders being much more resistant to the changing conditions. We found that the brooders in fact first benefit from the changing conditions due to the spawners going extinct, and only with further changes start to suffer themselves. This result is similar to the result found by Nee and May in their paper on habitat destruction [9]. They looked at the Levins-Culver model and found that habitat destruction leads to a decrease in patches occupied by the superior competitor but an increase in patches occupied by the inferior one, even if the total number of patches is decreasing. The patches occupied by the inferior competitor only start to decrease once the superior competitor has gone extinct. This is similar to the original increase in the density of brooders that we observe in this model. In his model for habitat destruction in a coral reef ecosystem, Stone [10] also found a similar result looking at a system of multiple coral species arranged in a competitive hierarchy.

5.1 Limitations and Future Improvements

There are many ways in which this model could be extended and improved. The most obvious one would be extending the model to include the other two life history strategies as per Darling et al. [1], the stress-tolerant and generalist strategies. However, as the model is already complex with many equations and parameters, even adding one more strategy would make the model computationally heavy and perhaps impossible to analyse.

In the two strategy framework, one improvement that could be made would be to model spawning as a yearly event. In the current model it is modelled as a continuous one, but this is not biologically realistic. This could be improved by modelling all the other processes continuously, as in the current model, but making spawning a discrete

event where the release of egg and sperm cells and the settling down of the newly formed corals all happens instantaneously. Modelling the temporal aspects of the two different reproductive strategies would allow us to truly understand their differences and reactions to changes to the environment.

The differences in the sexual reproduction between brooders and spawners could also be analysed in more detail. This model included the parameter η to model brooding between neighbours, but this parameter was set to 0 for most of the analysis performed in order to simplify it. The next step would be to look at mutual invasibility and coexistence as well as the effect of environmental changes for some different values of η .

We modelled the effect of environmental changes in the shape of changing ocean temperatures and acidity, but habitat destruction also affects corals. Fishing, pollution and sedimentation affect the corals by destroying the reef, sometimes even permanently. This could be modelled by reducing the number of available sites in the model, like was done by Stone [10] in his model. This sort of habitat destruction would affect large patches of the reef at once, which would effectively mean decreasing the survival rates of globally dispersed offspring, since the offspring landing on destroyed sites could not survive. Locally it would only affect the corals on the edges of the destroyed patches, which could be ignored if the areas destroyed are only few, large areas as assumed, since the number of sites on the edges would then be negligible on the infinite lattice.

In the future, the parameters in the model could be fixed based on real data about birth, growth and death rates from coral species. The whole model could also be compared to real density data from reefs where coral species corresponding to the different life history strategies are known to coexist. Thus we could confirm the model's accuracy not only qualitatively as has been done now, but also quantitatively. The model as it is serves as a good starting point for such future work.

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