Larval Dispersal of Reef Fish in the Great Barrier Reef: Connectivity and Metapopulation Analysis

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Abstract

Understanding spatially heterogeneous metapopulations of reef fish, like those on the Great Barrier Reef (GBR), is integral to effective management of these systems and their resources. Because almost all reef fish have a pelagic larval stage, during which they disperse throughout the system, understanding the metapopulation requires an understanding of this pelagic phase, which in turn necessitates understanding how the hydrodynamics of the marine environment affect the larval dispersal.

Tracking larvae during the pelagic stage is not feasible. As a result, biophysical hydrodynamic models have recently been used to simulate larval dispersal patterns at regional scales. These models output data in the form of connectivity matrices, which detail the proportions of larvae from one reef that settle on each reef. Analysis of these matrices can help us construct hypotheses about what drives larval distribution patterns, so that we can better understand the dynamics of reef fish metapopulations.

In this thesis I have developed tools to extract useful information from connectivity matrices. In particular, these tools can determine dominant directions of larval transport using the concepts of matrix reducibility and primitivity. They can also compare the strengths of different dispersal pathways, and use correlation analysis to test whether or not specified groups of reefs act in concert when they send larvae to other reefs.

These methods were used to analyse the connectivity matrices that have been generated by a hydrodynamic model centred on the Cairns section of the GBR.
Matrix reducibility showed that there was a strong, unidirectional flow southward through the Cairns section of the GBR. This flow separated the metapopulation into two distinct subsections, either side of latitude 16.2°S. The northern part of the metapopulation was found to be effectively independent of that in the southern section. However, the southern section required larval input from the northern population to persist, when the metapopulation dynamics were assumed to be recruitment limited. Although both populations were well connected within themselves, and the northern population sent significant amounts of larvae to the southern section, the only larval transport from the southern to the northern section of the reef occurred via a small set of “gateway” reefs.

Correlation analysis showed that reef fish populations on groups of spatially proximate reefs frequently acted in concert when sending their larvae to other reefs. Larval transport from the north and south of a specific reef was found to be negatively correlated, which acts to reduce the variability of the local population on the reef. This negative correlation was presumably due to the overall unidirectional flow, as revealed by the reducibility analysis.

This predominant flow pattern also affected the simulated recovery of the GBR metapopulation from extinction. Larval transport from the southern section to the northern section was limited. Any recolonisation of the extinct metapopulation that began in the southern section took much longer for the modelled section of the GBR to recover, than in the case when recolonisation began on a northern reef.

These characteristics of the spatial metapopulation, as revealed by our analyses of the hydrodynamic dispersal models, show that local reef fish populations on the GBR are connected in different ways from those assumed previously. The arrangement of the GBR metapopulation is similar to a source-sink setup, with the northern section representing the source. This is likely to be important in formulating management strategies that affect the GBR’s reef fish species.
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Chapter 1

Introduction

1.1 The importance of coral reef fish

Fish account for roughly one fifth of all animal protein in the human diet worldwide, and around 1 billion people rely on fish as their primary protein source. New projections, however, suggest that the contribution of fish to the global food supply is likely to decrease in the next two decades, as demand for fish increases and production flags (Laureti, 1996). In the developing world, reef fisheries form an important but often imperiled source of food for many tropical nations (Russ, 1991; Polunin and Roberts, 1996). For first world countries, fish help sustain the economy through tourism, as well as through exploitative fishing.

According to the FAO, 60% of the world’s important fish stocks are in urgent need of management, either to rehabilitate them or to keep them from being overfished. “The effects [of human disturbance] are apparent even on the Great Barrier Reef (GBR), despite intensive protection over the past three decades” (Jackson et al., 2001). These effects partly result from our lack of understanding of how the GBR acts as a whole, rather than as a collection of isolated reefs and animals. Knowledge of the mechanisms underlying population dynamics is fundamental to effective management of fisheries (Rothschild, 1986; Cushing, 1995). Nowhere is this as true as on the GBR: “Coral reefs are the most structurally complex and taxonomically diverse marine ecosystems” (Jackson et al., 2001), and the GBR is the largest collection of coral reefs on the planet.
1.2 Modelling the Great Barrier Reef

“Distributions of pelagic organisms such as larvae of reef fish cannot be understood fully without an understanding of the physical oceanography of the study area . . . and of the 100 families of bony fish associated with coral reefs, only four plus a single species from a fifth family are known to lack a pelagic early life history stage” (Leis, 1991).

To understand reef fish on the GBR, scientists must understand how their pelagic lifestage affects their benthic lifestage. The benthic life stage of fish on the GBR is understood better than the pelagic, about which less is known – both because it was initially considered less important than the benthic stages, and because the study of reef fish in their larval stage is difficult, and almost impossible in situ (Leis, 1991; Meekan et al., 1993).

Post-settlement mortality of reef fish is thought to be a function of the amount of settlement (Millicich and Doherty, 1994), and so the density of adult fish depends on the number of larvae successfully settling on a reef. The importance of the pelagic larval stage is such that it would not be an exaggeration to state that “reef fish [are] pelagic animals with a benthic reproductive phase” (Leis, 1991).

Reefs in the GBR support local populations of fish that do not exchange significant amounts of adult fish, but which can be considered open to some extent through the fishes’ larval reproductive stage. By open, we mean that local populations interact by exchanging larvae with other local populations; thus, their dynamics are not independent of those of other local populations in the system. This frequent emigration and immigration through larval exchange means that the larvae arriving at a reef prior to settlement could have been drawn from a large set of spawning habitats (Armstrong, 2000). Therefore, the dynamics of any particular local population on the GBR depend on both local (i.e., in the vicinity of the reef itself) and external (i.e., the other local populations in the system) dynamics.

The relationships between the local populations are not simple. Larvae are not
consistently spread throughout the reef system, nor are the strongest transports necessarily to local populations on nearby reefs. The local population at a reef in any particular year is dependent not only on the complex currents that weave their way through the many channels and lagoons of the GBR (James et al., 2001), but also on the state of every other population in the system. When a group of local populations is interrelated in such a way, we call them members of a \textit{spatially heterogeneous metapopulation} (Levins, 1969). All factors that affect these inter-relations must be taken into account when we try to understand the ecology of reef fish in any ecological system as complex as the GBR.

\section*{1.2.1 Hydrodynamic Models}

One way (perhaps the only feasible way) to deal with this complexity is by the use of hydrodynamic models. Using these models, we can simultaneously track millions of particles, representing dispersing larvae. It is thus possible to create data sets (e.g., matrices that quantify inter-reefal “connectivity”) spanning decades in a few days. Recent developments in larval dispersal models have seen the introduction of behavioural attributes of reef fish larvae, thereby enhancing the reliability and realism of the predicted dispersal patterns. This means that for a fraction of the cost of empirical studies, it is possible to provide a unique insight into the pelagic life stage of reef fish. This will help in developing an understanding of the importance of the interaction of currents and reefs on the GBR, and other similarly complex ecosystems.

Hydrodynamic models for use in larval fish studies were first formulated by Power (1984), who discussed the physical and biological requirements of modelling the pelagic stage of fish. In the GBR, hydrodynamic modelling had been applied a decade or so ago to the Crown of Thorns starfish problem (Black and Gay, 1987; James \textit{et al.}, 1990; Dight \textit{et al.}, 1990ab). For some time, many biologists’ attitudes towards these models were cautious, because they felt the models inadequately addressed the biological considerations.
Recently, modellers have begun to address the biological factors involved by formulating integrated bio-physical models, which take into account the sensory and motive capabilities of late stage larvae (Armsworth, 2000). Larval abilities have been found to be quite incredible. Able to swim for large distances over long time scales without rest, and to reach speeds significantly above those of the ambient currents (Fisher et al., 2000), late stage larvae are anything but passive particles. Furthermore, field experiments by Leis et al. (1996) show that larvae can detect the location of nearby reefs up to a kilometre away, while Wolanski et al. (1997) provided evidence that this sensory capability is independent of the current.

When analysing connectivity, we must always keep in mind that the numerical values come from simulations of larval dispersal, and thus only approximate the true system. Their testability it limited also, as comparative empirical data is scarce. For example, although the hydrodynamic model used to generate the connectivity matrices used in this thesis shows agreement with empirical studies performed by Jones et al. (1999), the error associated with this empirical model precludes drawing definitive conclusions. As well, any such validation would only be based on one connectivity, in a single year.

A depth-integrated model with a number of biophysical properties, incorporating the ability of larvae to actively affect their dispersal, has been formulated by James et al. (2001). Biologists have justifiably considered this a necessary inclusion in any realistic larval dispersal model (Leis, 1991), yet we must always remember that this ability is limited. Despite the surprising laboratory measurements of larval swimming capabilities, regional scale dispersal will be mainly determined by the prevailing hydrodynamic regimes. Regional scales are very large, and it is unlikely that larvae can alter their dispersal patterns significantly over such extensive distances (Armsworth 2000).
1.2.2 Connectivity Matrices

Hydrodynamic larval transport models typically output data about how reef fish larvae disperse in the form of connectivity matrices, denoted $P$. These are two-dimensional matrices whose $p_{ij}$ elements represent the proportion of larvae created by a local population at reef $i$ that arrive at reef $j$, before any post-settlement mortality occurs. Combined with a realistic population model for the local population on each separate reef, these connectivity matrices help make it possible to understand the causes of temporal fluctuations and dispersal pattern structure in a spatially distributed metapopulation.

As an example, consider a simple metapopulation comprising five local populations, as shown in Figure 1.1. The connectivity matrix, $P$ describing the interrelation of

![Diagram of a five-reef metapopulation](image)

**Figure 1.1:** Schematic diagram of a hypothetical five-reef metapopulation.
the local populations, is shown below:

\[
P = \begin{pmatrix}
  p_{11} & p_{12} & p_{13} & p_{14} & 0 \\
  p_{21} & p_{22} & 0 & p_{24} & 0 \\
  p_{31} & p_{32} & p_{33} & p_{34} & 0 \\
  0 & p_{42} & 0 & p_{44} & p_{45} \\
  0 & 0 & 0 & 0 & p_{55}
\end{pmatrix}
\]

In this state, it is often quite difficult to either comprehend, or to derive useful conclusions about dispersal patterns from these connectivity matrices. The Cairns sector of the GBR, for example (see Figure 1.2), contains 199 reefs, and the section of the GBR focused on later in this thesis contains 321 reefs. Each year the model will produce a different connectivity matrix, due to the variability associated with the input parameters, the winds and currents. In Chapter 3, I devise methods to determine the important correlations between the \( p_{ij} \) elements, without calculating every correlation in the system, which would produce \( 10^{10} \) coefficients.

To cope with this daunting complexity, we must invent and adapt methods that can be used in understanding how the complexity and heterogeneity of hydrodynamic flows and spatial structure of the GBR influence the distribution of its reef fish. One of the primary benefits of spatial metapopulation models is that they allow us to determine characteristics of the system that are integral to the long term persistence of the metapopulation. In the case of the GBR, these could include local populations (reefs), whose persistence is vital to the viability of many others. Currents and larval exchange pathways, which supply otherwise isolated local populations, have potentially enormous importance to the metapopulation. Until they can be identified, any vulnerability associated with them may leave large sections of the metapopulation endangered. The main task of this thesis is thus:

\begin{quote}
In a heterogeneous metapopulation, there will be regions that are more important than others to the persistence of the metapopulation as a whole. I aim to identify these regions in the hope that protecting them will help in the persistence of the metapopulation.
\end{quote}
Tools and methods must be designed to extract useful information from the connectivity matrices, which will help in the completion of this task. Fortunately, there are many methods in the realm of linear algebra and statistics that can be adapted to this task.

In Chapter 3, I have collected a toolbox of techniques, which have proven valuable in the analysis of connectivity matrices. I also discuss a number of ideas relevant to interpreting the output of larval transport models.

In Chapter 4, these techniques are applied to a set of connectivity matrices describing a region of the GBR, which includes the Cairns section, between latitudes 14 and 19°S, in the years from 1967 to 1998. Interesting structure, which became apparent in the reef system, is also noted in this chapter. The matrices used in the analysis were generated by a hydrodynamic model of larval transport. The model

\[1.2\text{Map showing the analysis region of the GBR. Inner boundary marks the Cairns Section, outer boundary indicates the model boundary. The abscissa and ordinate denote longitude (°E) and latitude (°S), respectively.}\]
was developed by a team at James Cook University, specifically for pelagic larvae on the GBR (James et al., 2001).

A population model is formulated in Chapter 5, using these connectivity matrices, to capture the metapopulation behaviour of the GBR. I will investigate the effects that the structure observed in Chapter 4 has on the dynamics of the GBR. Certain implications that the metapopulation dynamics have for our understanding of the GBR will also be examined. The model equations are linearised in this chapter, using established statistical techniques (Cox and Miller, 1966; Roughgarden, 1975). The variance of noted features will be analysed, according to ideas about correlations in connectivity, arising from the theory developed in Chapter 3.
Chapter 2

Modelling reef fish dynamics

Following the review by Leis (1991), I aim to provide some basic ideas surrounding coral reef fish with a pelagic larval stage, which should be known before attempting either to understand metapopulations of reef fish, or to model their dynamics.

2.1 The larval stage

Most reef fish on the GBR have a pelagic (open ocean) larval stage, which can last for weeks or months (and occasionally as long as a year). During this open ocean stage, larvae grow rapidly while being exposed to extreme mortality. In their later developmental stages, they have been found to have exceptional swimming abilities (Bellwood and Fisher, 2000), although these are not the same throughout families, or even species (Stobutzki, 1998). They can also use their abilities to affect their vertical and horizontal position (Job and Bellwood, 1999). Feeding while in the open ocean is thought to have a pronounced effect on their swimming, and also their condition at settlement on a reef (Green and McCormick, 1999; Fisher and Bellwood, 2001). This condition could dramatically affect their probability of post-settlement survival (McCormick, 1998).

Of larval capabilities, there is considerable laboratory evidence, but few in situ data. Models of larval behaviour thus have little choice but to include the simplest of assumptions until further evidence can be provided. This topic is discussed at more length in Chapter 5.
2.2 Larval settlement

Once a particular larva has survived in the pelagic stage long enough to develop to the point that it is ready to settle, it must find a suitable reef. Many larvae do not, and die in the open ocean. Upon settlement, they must survive extreme post-settlement mortality, and only those few fish that survive make up the first age cohort.

2.3 The benthic stage

Although there are a host of biological traits evidenced by coral reef fish (see the collection of reviews by Sale (1991)), the fish being modelled are gonochoristic (i.e., have two distinct sexes), and males typically saturate the system. The limiting reproductive factor is therefore the number of females, and it is the population of these that we model.

Once females reach sexual maturity, they begin to produce larvae in amounts typically proportional to their volume (Sadovy, 1996).

2.4 Specific assumptions of the model

In modelling reef fish populations in this thesis, certain assumptions were made about their behaviour and life history. First, the lifetime of the fish was described using a number of discrete age classes. Once the larvae have survived post-settlement mortality and settled, they belong to the first age class. There is an upper limit to the reproductive life of these fish. Each year the adults have a probability \(q_i\) of reaching the next age class, and a probability \((1 - q_i)\) of dying. There is a set number of age classes \(\omega\), and after spending one year in the oldest age class and reproducing, all such individuals are removed from the system (either by mortality or senescence).
We assume that the fish reproduce after they grow to the next age class, and therefore only if they survive the mortality associated with that ageing.

It is important that we know how many larvae an average fish will produce in its lifetime, and using age classes allows useful simplification. Those larvae that survive post-settlement mortality at reef $k$ will produce $f_i$ (their fecundity at year $i$) larvae in their $i$th year. After the initial density-dependent mortality upon recruitment, the probability of an adult fish surviving to the next age class is $q_k$, until the maximum age of $\omega$. We will assume that $q_k$ is the same for each age class ($q$), and $q_\omega = 0$. For convenience, we define $q_0 = 1$. These assumptions allow us to determine the size of any age cohort ($a$), at a particular local population $i$, ($N_i^a(t)$), given the number of fish that survived post-settlement density-dependent mortality $a$ years before, $N_i^1(t - a)$. Thus,

$$N_i^{a+1}(t) = q^a N_i^1(t - a).$$

Given the number of fish that survive post-settlement mortality, the constant mortality each year, and the fecundity of each age class, we can calculate $R$, the average lifetime larval output of a fish surviving post-settlement mortality, the net reproductive value of the average individual.

$$R = \sum_{i=1}^{\omega} f_i q^{i-1} \quad (2.1)$$

(Caswell, 2001; Armstrong, 2000). The net reproductive value of the fish is important, because it removes the need for explicit consideration of each separate age class. If the probability of surviving to the next age class is constant, then knowing the size of the settling cohort allows us to extrapolate the size of this cohort in one year, in two years, and so on. Modelling the dynamics of the metapopulation reduces to the simpler affair of modelling just the first age cohort, using their net reproductive value. Subsequently, when describing fish population with age structure, the notation $N_i$ is used to specify the size of the first age class in the local population at reef $i$. 

11
Chapter 3

Analytical Tools

An important feature of spatial population models for fish with life histories involving both benthic and pelagic stages is how, and to what extent, discontinuous spatial populations (on the reefs) exchange larvae. This feature is integral to understanding both persistence over ecological time, and the evolution of fish species. As an example, because long range recruitment encompasses multiple habitats, it limits opportunities for local adaption, and thereby increases the importance of phenotypically plastic traits (Warner, 1997).

Connectivity matrices for specific years simulate this information, and if taken over a sufficient number of years they will also include the temporal variation in this exchange. Unfortunately, the matrices are too large and unstructured for any patterns in these data to be immediately evident, and so we must develop tools to isolate important structure embedded in the connectivity matrices. It is through these methods, applied to the raw connectivity matrices, that we can attempt to understand the structure of spatial metapopulations. Such techniques will become even more important if the hydrodynamic model were to be extended to the entire GBR. This would involve an order of magnitude increase in the number of reefs considered, and consequently perhaps as much as two orders of magnitude increase in the complexity of any analysis.
3.1 Static mean patterns

3.1.1 Primitivity

A non-negative matrix $A$ is primitive iff there is a positive integer $p$ such that $A^p > 0$ (Caswell, 2001; Meyer, 2000).

If the matrix $A^p > 0$, every element in that matrix is itself greater than zero.

An important aspect of metapopulation dynamics is how well the individual local populations are connected to one another – this is the notion of Primitivity. Obviously, if each element in the connectivity matrix is positive (i.e., $P > 0$), then each local population in the metapopulation is connected to every other local population at each timestep. However, this typically will not be the case, and there might be two local populations which, although they are not directly connected, still exchange information through an intermediate local population.

As an example of this situation, let us consider a three-reef metapopulation consisting of reefs $a$, $b$ and $c$, with a local population on each reef. In the first case, $P > 0$, and thus two-way exchange exists between the populations on reefs $a$ and $b$, $b$ and $c$, and $a$ and $c$. In the second case, only those on reefs $a$ and $b$, and $b$ and $c$ have two way exchange. There is no direct exchange between the populations on reefs $a$ and $c$. These two cases have the respective connectivity matrices:

$$P_1 = \begin{pmatrix} p_{aa} & p_{ab} & p_{ac} \\ p_{ba} & p_{bb} & p_{bc} \\ p_{ca} & p_{cb} & p_{cc} \end{pmatrix},$$

$$P_2 = \begin{pmatrix} p_{aa} & p_{ab} & 0 \\ p_{ba} & p_{bb} & p_{bc} \\ 0 & p_{cb} & p_{cc} \end{pmatrix},$$

$$P_2^2 = \begin{pmatrix} p_{aa}^2 + p_{ab}p_{ba} & p_{aa}p_{ab} + p_{ab}p_{bb} & p_{ab}p_{bc} \\ p_{ba}p_{aa} + p_{bb}p_{ba} & p_{ba}p_{ab} + p_{bb}^2 + p_{bc}p_{cb} & p_{bb}p_{bc} + p_{bc}p_{cc} \\ p_{cb}p_{ba} & p_{cb}p_{bb} + p_{cc}p_{cb} & p_{cb}p_{bc} + p_{cc}^2 \end{pmatrix}.$$
**Figure 3.1:** Schematic Diagram of metapopulation comprising of three local populations. (a) represents $P_1$ and (b) represents $P_2$.

In two timesteps, however $P_2^2 > 0$, and so the local populations on reefs $a$ and $c$ do exchange information, via reef $b$. In general, if all the local populations in an $n$-reef metapopulation exchange information in $n$ timesteps or fewer, the associated connectivity matrix will be primitive.

In the context of reef fish metapopulations, I define:

> A connectivity matrix of $n$ local populations is **Primitive** iff for each local population $i$ in the metapopulation, the descendants of fish from a local population on reef $i$ will reach **every** other reef in the metapopulation (including returning to the reef $i$ itself) in $n$ timesteps or fewer.

An increasing body of evidence suggests that local populations on many reefs can be classified as “sinks” (Pulliam, 1988; Thomas and Kunin, 1999). This means that they depend on external larval supply for their persistence (Armsworth 2000), although this point of view is not without its detractors (Jones *et al.*, 1999). If source-sink dependencies are common in reef fish metapopulations, however, metapopulation persistence may depend on marine park managers being able to identify
local populations that output larvae vital for the persistence of other local populations – the sinks (James et al., 2001).

Such source-sink systems may exist in chains. That is, the survival of a local population on a particular reef is dependent on larvae supplied by a local population upstream, while the survival of that population is dependent in turn on a local population upstream from it. The collapse of a population on a reef near the “top” of such a chain would have disastrous consequences for a host of populations downstream.

Isolating these downstream chains could therefore be an important factor when siting marine reserves. The connectivity matrices can be used to identify these chains, if they exist. \( \mathbf{P} \) cannot determine anything about paths longer than one timestep, although information about longer chains can be computed from it.

In a metapopulation of \( n \) local populations, the longest possible chain is of length \( n - 1 \) – a chain back to the original reef, after passing through every other local population. Any longer chains involve a repeated step or loop somewhere in the chain, and could be reduced to \( n \) steps or fewer by removing this. Thus, since

\[
\mathbf{P} = \begin{pmatrix}
    p_{11} & p_{12} & \cdots & p_{1n} \\
    p_{21} & p_{22} & \cdots & p_{2n} \\
    \vdots & \ddots & \ddots & \vdots \\
    p_{n1} & \cdots & \cdots & p_{nn}
\end{pmatrix},
\]

matrix \( \mathbf{P}^2 \) has the form

\[
[\mathbf{P}^2]_{ij} = \sum_{k=1}^{n} p_{ik}p_{kj},
\]

and thus the matrix \( \mathbf{P}^r \) can be expressed as

\[
[P^r]_{ij} = \sum_{k_1,k_2,\ldots,k_{r-1}=1}^{n} p_{i_1k_1}p_{k_1k_2} \cdots p_{k_{r-2}k_{r-1}}p_{k_{r-1}j}.
\]

We can find local populations that are connected over more than one timestep by searching for reefs where

\[
[P^r]_{ij} \neq 0, \quad r > 1.
\]
The next problem lies in determining just how *strong* such multiple-timestep connections are. For example, when investigating matrix $P^2$, the importance of the two-step connection between local populations on reefs $i$ and $j$, via reef $k$, would not necessarily be determined by the value $p_{ik}p_{kj}$, which would generally be of smaller order than most single timestep connections. $p_{ik}p_{kj}$ gives the proportion of larvae from the local population at reef $i$ that travel to reef $k$, multiplied by the proportion of larvae from the local population on reef $k$ that travel to reef $j$. A better indicator of the importance of the path $i \rightarrow k \rightarrow j$ would be the number of larvae reaching reef $j$, from reef $k$, whose ancestors lived on reef $i$.

Including the reproductive step on the intermediate reefs of a chain changes the relative importance of particular larval dispersal paths considerably.

If a metapopulation does exist on the reefs being studied, we assume that, given a static connectivity matrix, the size of the population on each of these reefs attains a stable value, or an equilibrium. Using the notation for the net reproductive value, we express the size of a local population at a particular reef using only the size of the first age class post-settlement. The equilibrium size of this population on a reef $i$ is denoted by $\hat{N}_i$.

The relative importance of the route $i \rightarrow k \rightarrow j$ is calculated as follows: we multiply the number of larvae created at the local population on reef $i$ ($R\hat{N}_i$) by the proportion of larvae from reef $i$ that reach reef $k$ ($p_{ik}$).

The average mortality experienced by these incident larvae would be subtracted from this, leaving the number of new juveniles in the local population on reef $k$ that came from reef $i$. We assume that mortality will be density dependent, and so the mortality the juveniles suffer will be different at each reef, depending on how saturated that reef is with settling larvae each year. We have not assumed that the net reproductive value of a juvenile changes, however, and so $R$ is a constant throughout the system. The surviving juveniles on reef $k$ will each produce $R$ larvae in their lifetime, and the proportion of these larvae that are transported to reef $j$ is $p_{kj}$. 

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Analysis is limited to a single, spatial pathway. A single spawning season on reef \( i \) produces a set amount of larvae: how many of the larvae that arrive at reef \( j \) in subsequent years had ancestors born in that initial season? This path does not include any feedback, so that we are not including larvae whose ancestry included a self-recruitment step, nor one that went in the opposite direction to the path described above. So, for example, we would not include the path \( i \rightarrow k_1 \rightarrow k_2 \rightarrow k_1 \rightarrow k_2 \rightarrow j \), as we could reduce it to the path \( i \rightarrow k_1 \rightarrow k_2 \rightarrow j \).

Mathematically, the number of larvae that travelled to reef \( j \) by the pathway \( i \rightarrow k \rightarrow j \) can be expressed as

\[
T_{ikj} = \hat{N}_i R^2 m_k p_{ik} p_{kj},
\]

where \( T_{ikj} \) is called the “transport”, the number of larvae descended from the local population on reef \( i \) that reach reef \( j \) via reef \( k \). The proportion of larvae incident on reef \( k \) that survive post-settlement mortality is denoted by \( m_k \).

In general, therefore, the relative importance of the path \( i \rightarrow k \rightarrow j \) will be measured by \( T_{ikj} \), compared with all other transports to reef \( j \).

For an \( l \)-stage path from reef \( i \rightarrow j \), equation (3.4) generalises to

\[
T_{ik_1k_2\ldots k_{l-1}j} = R^l \hat{N}_i p_{ik_1} \left( \prod_{s=1}^{l-1} m_{k_s} \prod_{r=1}^{l-2} p_{k_r,k_{r+1}} \right) p_{k_{l-1}j}.
\]

These \( T \) values scale the importance of a particular path to a local population’s persistence. They make it possible to find the most important larval source \( i \), of a specific local population \( j \), in terms of actual numbers of larvae, rather than just proportions. It is possible that paths with small \( \prod p_{k_1}, \ldots, p_{k_{l-1}j} \) might be more important than their proportions indicate. In turn, it is possible to find the important sources of \( i \), and so on, thus establishing a chain of dependence. Armstrong (2000) notes that “The important dispersal paths are those that induce some degree of closedness.” These would be represented by paths \( T_{ik_1k_2\ldots k_{l-1}i} \). By performing simulations where sets of reefs are removed from the metapopulation, James et al. (2001) show that reefs for which self-recruiting larvae are a significant proportion of the total settling cohort, are disproportionately important to the long-term per-
sistence of the metapopulation on the GBR. It would be interesting to see whether removing self-recruiting paths where the self-recruiting larvae formed a significant proportion of the total settling cohort would give similar results.

On the other hand, if we wish to find local populations that never exchange larvae (in at least one direction), we seek reefs $i$ and $j$ where

$$\sum_{r=1}^{n} [P^r]_{ij} = 0. \quad (3.6)$$

Here, the populations on reefs $i$ and $j$ could be involved in a “unidirectional chain”, or could be spatially separated (e.g., both closed). The existence of unidirectional chains implies that the connectivity matrix is imprimitive (since descendants of fish from the local population at reef $i$ would never reach reef $j$ – contradicting our definition of primitivity). These two reefs could lie in a strong, unidirectional current, as shown in Figure 3.2. Reef $j$ is downstream from reef $i$, so larvae from the local population on reef $j$ never reach reef $i$. The converse is not necessarily true.

![Figure 3.2: Example of unidirectional flow.](image)

Imprimitivity in the connectivity matrices has important consequences for the metapopulation. If $\sum_{r=1}^{n} [P^r]_{ji} = 0$, then there is no chance that the local population at reef $i$ could be recolonised by larvae from reef $j$, if the population of $i$ were pushed to extinction. Analyses of metapopulation dynamics typically assume that local populations exchange larvae in both directions (Armstrong, 2000), and that extinction
of a species at one reef is only temporary, since recolonisation of an entire metapopulation can occur in following timesteps as long as the colony survives somewhere (Sale and Tollermeri, 2000; Armsworth, 2001). These results may not hold where sections of the metapopulation are linked via unidirectional chains.

Equation (3.6) allows us to find pairs of reefs that are involved in unidirectional flow or are spatially separated, but if whole sections of the metapopulation can only exchange larvae in one direction, the scale of the problem is much greater. Accordingly, I have developed methods using reducible matrices to solve such problems.

### 3.1.2 Reducible Matrices and Perron Frobenius

Much work in theoretical ecology has used the findings of the Perron Frobenius theorem (PFT) to make statements about the general structure of matrices (Armsworth 2000; Caswell, 2000). The PFT is a set of results which refer to the properties of the eigenvalues of non-negative matrices. This makes the PFT useful for single population Leslie matrix methods. Because population stability and persistence depend heavily on the size of the dominant eigenvalue of matrices similar to the Leslie matrix (a non-negative matrix), this theorem has found a useful place in theoretical population ecology. Results about the persistence of a population can thus be determined from the general form of the Leslie matrix.

Because connectivity matrices are also non-negative, I initially assumed the PFT could provide insights into the characteristics of certain connectivity matrices. A matrix is *reducible* if there exists a permutation matrix $S$ such that

$$S^T P S = \begin{pmatrix} X & 0 \\ Y & Z \end{pmatrix},$$

(3.7)

where $X$, $Y$ and $Z$ are block diagonal matrices, and $X$ and $Z$ are both square. Otherwise $P$ is said to be *irreducible*. $S^T P S$ is a *symmetric permutation* of $P$, as the permutation swaps the same columns of $P$ as it swaps rows. This is important, because although the ordering of the reefs is arbitrary, it must be the same down the rows as it is along the columns, so that any element $[P]_{ij}$ has a consistent
interpretation.

A reducible matrix is imprimitive. This follows from the definition of a reducible matrix and the first general definition of primitivity (the matrix from equation (3.7), raised to any power, can never have nonzero elements in its upper right block matrix). Importantly, in the reef fish context, it means that it is possible to prove that sections of the GBR are members of a unidirectional chain, if we can symmetrically permute our connectivity matrix $P$ to the form of equation (3.7). If $X$ is of dimensions $x$, and $Z$ of dimensions $z$, then the downstream section of the metapopulation has $x$ reefs, and the upstream section $z$. Matrix $X$ defines how the downstream section is interrelated within itself, and $Z$ does the same for the upstream reefs. Matrix $Y$ defines how much transfer there is from the upstream to the downstream sections, and the matrix of zeros shows that there is no transfer upstream from the first $x$ reefs to the last $z$ reefs.

Therefore, given a system of $n$ local populations, if it can be shown that the connectivity matrix corresponding to this system is reducible, then it can no longer be viewed as a metapopulation of $n$ interrelated local populations. An alternative view might see two smaller meso-populations arranged in a source-sink pair, the mesopopulations having sizes $n - x$ and $x$, respectively. These exchange larvae in only one direction. The matrices $X$ and $Z$ may in turn be further reducible.

Permutation matrices such as $S$ are simple to construct, as they are identity matrices with elements interchanged, corresponding to the rows and columns that the $S^T P S$ permutation will swap. The problem is knowing which rows and columns to interchange - i.e., which reefs will be upstream, and which downstream. Fortunately, one of the results concerning primitivity can help. Restricting attention to static patterns, we calculate all possible paths, and store them in the matrix $P_{total}$, defined by

$$P_{total} = \sum_{r=1}^{n} P^r.$$  

If there are any elements in that matrix such that $|P_{total}|_{ij} = 0$, then reef $i$ is downstream from reef $j$. We note all such reefs, $i$. When we perform a symmetric
permutation of the original connectivity matrix, all these $i$ reefs are moved to the
top of the matrix. As long as one such reef exists, $P$ will be in reducible form,
although trivially. In this simple case, $X$ would be a $1 \times 1$ matrix, corresponding to
a population that only received larvae, and contributed nothing to any other reef.

A result relevant to the metapopulation, rather than just a few reefs, would arise if
the symmetric permutation were to separate the metapopulation into two roughly
equal subsections: the downstream reef sector (local populations on the first $x$ reefs)
would exchange larvae with other downstream reefs, but not the upstream reefs;
the upstream reefs would exchange larvae with the other upstream reefs, and also
contribute larvae to the downstream reefs.

Thus, if a given connectivity matrix can be symmetrically permuted into the form of
equation (3.7), our understanding of the reef system would alter significantly. Any
regional analysis of the reef system would need to take into account this split in the
metapopulation. In many cases, the spatial structure of the system might suggest
where this schism lies, and reducibility would make it possible to rigorously test the
proposal by focusing on a certain vicinity.

As an example, in a unidirectional flow, the resilience of the total metapopulation
might be overestimated if the vulnerability of the downstream population to events
in the upstream section is not considered, and the metapopulation will be assumed
to be better connected than in fact it is. The downstream population would be
especially vulnerable if it depended on larval supply from the northern population
for persistence. In the next chapter, we show that simulations of a metapopulation
on the GBR have this characteristic for some parameter values.
3.2 Temporal variation

3.2.1 Correlations in larval connectivity

Defining what a single “reef” actually is has always been problematic. Estimates of the number of reefs on the GBR have ranged from 2500 to almost 4200 (Hughes et al., 1999; World Conservation Monitoring Service, 2001), simply because there is no unambiguous definition of what constitutes an individual reef. Protecting metapopulations through the creation of marine reserves on specific reefs involves selecting sub-regions of the metapopulation that are judged to be crucial to the persistence of species on the GBR, but how these regions should be chosen has been the subject of much debate. Black (1993) maintains that “A better understanding of reef connectedness is central to establishing appropriate management strategies for the GBR.” I propose here that groups of reefs whose larval destinations are correlated will be important when making that choice. In effect, a reef will be partially defined by the larval dispersal from the fish in its local population.

If the larval transport from two reefs to a third reef is correlated, then the local populations on the first two reefs act in concert when sending larvae to the other reef, within statistically significant variance. Positive correlations imply that when the transport from one reef is above average, the transport from the positively correlated reef is likely to also be above average. Negative correlations imply that if transport from one reef is above average, then in general the transport from the other reef will be below average.

In a stochastic environment, a protection scheme that takes larval dispersal into account would best serve the GBR by ensuring that those local populations open to exploitation receive sufficient larvae every year, thus guaranteeing their persistence. Much recent debate has centred on recruitment limitation, a theory which postulates that because local population are usually under-stocked, fluctuations in larval recruitment dominate the size of cohorts at a later time, since levels are never sufficiently large for density-dependent mortality to affect the population size (Do-
herty, 1981; Doherty and Williams, 1988; Armsworth, 2001). Although the debate has been polarised (see Sale and Tolimieri (2000) for a review), there is growing evidence that the recruitment limitation hypothesis is justified to some extent. If recruitment limitation is incorporated into fishing strategies, managing fish as a resource will become slightly simpler: a below average recruitment year would result in a smaller number of adult fish at some later time, and fishing at that later time would need to be scaled down accordingly, in order to avoid the possibility of depressing the population below an extinction threshold.

If recruitment limitation is found to be important, it would be beneficial to protect pairs of reefs whose larval transport to an exploited local population is significantly negatively correlated. In that way, if the larval transport in a particular year to the exploited target reef is below average for one of the pair, then in general the larval transport from the other will be above average, ensuring the population on the target reef receives a more uniform larval supply. Marine reserves could be structured in groups of three reefs: a target reef, which is open to exploitation; and two protected reefs (or groups of reefs) whose transports to the target reef are negatively correlated, an arrangement shown schematically in Figure 3.3. Since the target reef receives a more steady supply of larvae, its older cohorts will be of a more uniform size.

**Figure 3.3:** Negatively correlated transport to the target reef ensures its population has minimum variance. \( p_{12} \) and \( p_{32} \) are negatively correlated.

There are some caveats associated with this method, however. The local population on the target reef cannot depend on self-recruitment for its persistence, and the two chosen supply reefs must provide sufficient larvae for persistence on the target reef. Although this may seem an unlikely scenario, there is evidence that such
situations can exist. Jackson et al. (2001) note that in the 1960s, “reef fish all around Jamaica ... rarely reached reproductive maturity, so that the abundant recruits of fish on Jamaican reefs at that time must have come from undiscovered populations in Jamaica or elsewhere.” Thus, external recruitment from larval dispersal sometimes can be sufficient to maintain large adult populations on reefs that cannot receive self-recruited larvae. The two supplying reefs in the metapopulation must have sufficient self-recruitment to sustain their own populations at sufficiently high levels, although this is because the metapopulation being analysed has been simplified to only three populations.

To prove that if the transports from the two supply reefs are negatively correlated, then the population variance on the target reef will be minimised, we consider only local populations on the three reefs 1, 2 and 3, as in Figure 3.3. The populations of juveniles on reefs 1 and 3 are assumed constant, and denoted by $\hat{N}_i$ ($i = 1, 3$). This is a simplifying assumption, but it can be justified if, on those two reefs, larval supply is saturating. If the populations on reefs 1 and 3 are unexploited, it is possible that the fish populations could approach the carrying capacity of the two reefs.

We use the $R$ notation of equation (2.1) to show that the fish on each of these reefs produces on average $R\hat{N}_i$ larvae every year. Of these larvae, a proportion $p_{i2}$ \((i = 1, 3)\) will be transported to the target reef (reef 2) each year.

Due to environmental variability, this proportion, $p_{i2}$, will fluctuate. We assume that it is a second order stationary process (meaning that it is a distribution with a constant mean and variance), varying randomly about some mean proportion $A_{i2}$, so that

$$p_{i2}(t) = A_{i2} + a_{i2}(t) \quad i = 1, 3,$$

(3.8)

where $a_{i2}(t)$ has a mean of zero and a variance of $\text{Var}(a_{i2})$.

Since self-recruitment is zero, the amount of larvae ($L$), incident upon reef 2 in any particular year is
\[ L = \dot{N}_1 R p_{12}(t) + \dot{N}_3 R p_{32}(t) \]  
\[ = \dot{N}_1 R (A_{12} + a_{12}(t)) + \dot{N}_3 R (A_{32} + a_{32}(t)) \]  
\[ = [\dot{N}_1 R A_{12} + \dot{N}_3 R A_{32}] + [\dot{N}_1 R a_{12}(t) + \dot{N}_3 R a_{32}(t)], \]  

where the first term is constant and the second varies with time. If the two connections are negatively correlated, we can express \( a_{32} \) as a function of \( a_{12} \). That is,

\[ a_{32}(t) = \kappa a_{12}(t) + \epsilon(t), \]  

where \( \epsilon \) is a random, independent variable with mean zero, and \( \kappa \) is a negative number. Ideally, we want to minimise the variance of the larvae arriving at reef 2.

\[
\text{Var}(L) = \text{Var}(\dot{N}_1 R a_{12}(t) + \dot{N}_3 R a_{32}(t))
\]

\[
= \dot{N}_1^2 R^2 \text{Var}(a_{12}) + \dot{N}_3^2 R^2 \text{Var}(a_{32}) + 2 \dot{N}_1 \dot{N}_3 R^2 \text{Cov}(a_{12}(t), a_{32}(t))
\]

\[
= R^2 (\dot{N}_1 + \kappa \dot{N}_3)^2 \text{Var}(a_{12}) + R^2 \dot{N}_3^2 \text{Var}(\epsilon).
\]

Thus to ensure a stable yield, we should choose groups of reefs where \( p_{12} \) and \( p_{32} \) are close to the form of equation (3.12), where the coefficient \( \kappa = -\dot{N}_1/\dot{N}_3 \).

Correlations in recruitment can be found if connectivity matrices are available over a number of years. Then the extent to which different connections are correlated can be determined using the equation

\[ r = \frac{\sum[(x - \bar{x})(y - \bar{y})]}{(n - 1)s_x s_y}, \]  

where \( r \in [-1, 1] \) is the strength of the correlation between the transport of the populations on the reefs \( x \) and \( y \) to the target reef; \( s_x, s_y \) are the respective sample standard deviations of \( p_{12} \) and \( p_{32} \).

We only accept correlations above a 95% confidence level. The correlation coefficient has a conditional \( t \) distribution with \( n - 2 \) degrees of freedom (with \( n \) years of connectivity data). Thus

\[
\frac{r \sqrt{n - 2}}{\sqrt{1 - r^2}} \sim t^* (n - 2).
\]  

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These formulae (Hogg and Tannis, 1993) should allow us, given a particular target reef, to determine which reefs’ transports to the target reef are negatively correlated at the 95% confidence level.
Chapter 4

Application of methods to the GBR

The methods discussed in the previous chapter can provide results about a complex and stochastic reef system from temporal and static analyses of the connectivity matrices, results that would be difficult to realise otherwise. The set of matrices provided by James et al. (2001) provide an excellent opportunity to test these techniques.

A complete set of connectivity matrices must span all the reefs in a large region. Although “how far juvenile [larvae] normally travel from their natal area is an unanswered question in marine biology” (Jones et al., 1999), it is thought that “the pelagic phase may disperse at scales . . . [of] thousands of kilometres.” (Leis, 1991). Thus analyses should be performed on a regional scale, to better understand the full metapopulation dynamics. The connectivity matrices need to span a significant timescale, as larval dispersal is influenced by inter-annual events such as the El Niño/La Niña cycles, which have long periods, typically decadal. The impact of their variability can only be gauged correctly if we incorporate matrices over appropriately large time scales.

These connectivity matrices contain information about the distribution of larvae from 321 reefs, including and surrounding the Cairns Section of the GBR. From this point onwards I will refer to this subset as the GBR. The techniques will equally apply if connectivity matrices can be generated for larger portions of, or even the entire, GBR.
4.1 Simulations

The simulations in the following sections all use the nondimensionalised model defined in Appendix 1. They use the set of 32 connectivity matrices to simulate the dynamics on the 321 local populations in the modelling region. To reproduce the stochasticity of the environment, the connectivity in the metapopulation is determined each year by randomly selecting a connectivity matrix from the given set of 32.

The number of larvae that survive the density-dependent mortality upon settlement is described by the Beverton-Holt relationship (Caswell, 2001). This is a function of the dimensionless parameter, $\beta$, as described in Appendix 1. It is $\beta$ that determines the strength of recruitment limitation acting on the settling larvae, which is why some of the experiments involved manipulating $\beta$. Figure 4.1 shows that for different $\beta$ values, and a given fecundity, a settling larval cohort of a particular size will intersect the Beverton-Holt curve at different points. Diminishing $\beta$ values mean that a particular cohort size moves increasingly into the linear part of the Beverton-Holt curve, corresponding to more recruitment limited conditions.

4.2 Primitivity

Upon analysis, only two of the 32 connectivity matrices proved to be primitive. Primitivity requires, in this situation, that $\sum_{r=1}^{321} P^r > 0$, meaning that in 321 years a fish on any reef might be able to send its descendants to any reef in the system.

The years 1983 and 1996 were the two cases that were found to be primitive, and their connectivity matrices became positive within 5 and 2 years, respectively. Yet by inspection, these two years did not appear to be significantly different from the other years being considered. Something happened in these years which caused the matrices to be primitive.

Figure 4.2a–c show how, in the imprimitive years, the reefs whose populations cause
**Figure 4.1:** Three Beverton-Holt curves for different values of $\beta$. For different values of $\beta$, a particular incoming larval cohort will undergo different levels of density-dependent mortality.

The imprimitivity appears in the matrix $\sum_{i=1}^{n} [P^t]_{ij}$: the dots indicate where there are zero values. The entire row associated with a reef causing the imprimitivity is zero, meaning that the population on this particular reef contributes no larvae to any other reefs, including itself. Such a local population is completely dependent on larval supply from other reefs, and truly fits the definition of a *sink* reef. The position of these reefs on the GBR is seen in Figure 4.3. Their most obvious similarity is latitudinal position – they are all at the southern end of the system.

This provides some evidence for the existence of unidirectional flows in this region of the GBR. Analysis of the entire time series, however, showed that whilst these reefs frequently belonged to the set of reefs not contributing to the system, none of them was found in all the sets – there were times when their larvae did settle on reefs in the system. This is found to be frequently the case when analysing connectivity.
Figure 4.2: Sparsity plots of $\sum_{i=1}^{n} P^i$ matrices, simulating the years (a) 1988, (b) 1975, (c) 1968, (d) 1972, (e) 1974 and (f) 1976. The black dots indicate the zero elements that cause imprimitivity. In the last three years the imprimitivity is obviously important.

matrices: there are no constants, and conclusions must be appended with a variance. Another explanation of why these populations might not have contributed to the rest of the system is because of their proximity to the model’s southern boundary. The hydrodynamic model that generated the matrices considered larval propagules transported across this boundary to be lost from the system, so that they cannot return. The oscillatory nature of currents in the GBR Lagoon (both tidal and wind driven), means that some of those propagules might have returned and settled, had they not been removed upon their excursion from the system. Through this mechanism, their lack of contribution might have been exacerbated, and hence we should exercise caution when analysing results for reefs near the northern and southern boundaries of the model.

Thus, the imprimitivity exhibited by these reefs probably does not point to any significant structure in the GBR. The connectivity matrices shown in Figure 4.2d–f
**Figure 4.3:** Reefs that do not contribute larvae to the system in 1968 are denoted by red dots. They are at the southern extent of the model domain. These three years were unique in the time series: there were no others with such significant imprimitivity, but this is not to say that the findings they generated were not applicable to the rest of the time series.

A significant implication of this imprimitivity is that with respect to the GBR, the Perron Frobenius theorem can provide no results, as the necessary and sufficient condition is that the matrix is irreducible. This condition is violated if our matrix is imprimitive.
4.3 Reducibility of the Great Barrier Reef

The imprimitivity of the system allows us to prove that the GBR is caught in a definite unidirectional flow, as imprimitivity guarantees reducibility (although not necessarily significant reducibility). In the years 1972, 1974 and 1976, however, the matrices were what we can deem to be significantly reducible, and the GBR was definitely split into two roughly equal parts, arranged in a downstream flow (Figure 4.4). So pronounced was the divide, in fact, that in the above years, the GBR could well be considered as two smaller subsections involved in regional scale source-sink dynamics, with the northern section acting as a source for the southern sink.

![Figure 4.4](image_url)

**Figure 4.4:** Split in the Cairns section of the GBR predicted by the connectivity matrix for 1972.
4.3.1 The Gateway Reefs

In the remaining years, the connectivity matrices were only trivially reducible, with fewer than 20 reefs being part of the downstream chain. When the symmetric permutations from the significantly reducible years were applied to the other matrices, however, their new arrangements were almost arranged in a downstream chain. Only the populations on the few reefs shown in Figure 4.5 transported larvae upstream to the northern section, and over the years modelled, this particular set of reefs, which I have labelled gateway reefs remained fairly constant, a set of predominantly large reefs confined to a single region.

These reefs are: Rudder Reef, Tongue Reef, Batt Reef, Opal Reef, Reef 16—022, Reef 16—024, Reef 16-008, High Islets and Low Islets.

Finding the extent to which the GBR was reducible was difficult, however, and a systematic method had to be developed to algorithmically identify the reefs that form the down- and upstream sections. Downstream sections are actually easier to identify, because their row in the $\sum_{r=1}^{n} [P^r]_{ij}$ matrix will have zero elements – upstream reefs to which they cannot send larvae. Once the $k$ rows, $r_1 \ldots r_k$, which correspond to these downstream reefs have been identified, we construct a permutation matrix $S$ such that:

\[
\text{for } i = 1:k \\
\quad S(i,i) = 0 \\
\quad S(r(i),r(i)) = 0 \\
\quad S(i,r(i)) = 1 \\
\quad S(r(i),i) = 1 \\
\text{end}
\]

We then perform the symmetric permutation $P_{\text{reduced}} = S^T P S$.

The drawback with this method is that it will not find matrices that are almost reducible. It would not be helpful, for example, if our connectivity matrix had two
Figure 4.5: The set of Gateway reefs, those that transported larvae from the southern to the northern section.

distinct sections (an up- and downstream), but there was just one gateway reef, making the matrix primitive. If this were the case, an alternative method would be to try each possible permutation of the connectivity matrix, and then select the ordering of the reefs that maximised the number of zeros in one of the off-diagonal block matrices, while keeping the diagonal block matrices square. At a rough estimate, this method would need to perform in the order of $n!$ permutations to be sure of the optimal ordering (in the case of our $321 \times 321$ connectivity matrices,
Figure 4.6: The connectivity matrix from 1972 before and after the reducing symmetric permutation. The permutation has reordered the connectivity matrix into the form of equation (3.7). In this figure, the black dots indicate non-zero elements in the matrix.

This would be impossible to achieve, let alone accomplish for the entire GBR.

Another, more intelligent procedure might test suggested sections. The proposed downstream reefs would be ordered first, followed by the upstream. Observation of the connectivity matrix, permuted in this manner, would provide some idea of whether the proposal had merit.

In the case of the connectivity matrices for the GBR, this was precisely the problem that occurred. Most of the connectivity matrices were irreducible except for the reefs mentioned earlier – those that sent larvae to no other reefs. In other cases the reducibility was trivial, and the downstream component comprised a set of six or fewer reefs. These corresponded to the same reefs, although in this case, they exchanged some larvae amongst themselves, and lost all the rest from the system.

The years 1972, 1974 and 1976 were different. In these years, the unidirectional flow was pronounced, and the connectivity matrices were significantly reducible. Figure 4.6 shows the 1972 connectivity matrix before and after the symmetric permutation. It is obvious that the matrix is reducible.

However, because the row indices are not necessarily related to the position of the
**Figure 4.7:** Demonstration that the connectivity matrices can be permuted into approximately reducible form by the permutation matrix from 1972: (a) and (b) before and after \( S_{1972} \) is applied to \( P_{1969} \); (c) and (d) similarly for \( P_{1984} \). The black dots indicate non-zero elements in the matrix. The black dots in the upper right block matrix indicate northward larval dispersal from the down- to the upstream section, by the group of gateway reefs.

reefs, I needed to determine what this reducibility meant in terms of the *spatial* structure of the GBR: that is, which reefs were located in the downstream component, and which in the upstream? Figure 4.4 clearly shows that in 1972, the GBR is broken into two distinct parts, and that there is a very definite line where this break occurs, between latitudes 16.1 and 16.2°S.

Furthermore, application of the 1972 permutation matrix (\( S_{1972} \)) to other years in the time series yielded a similar form for the connectivity matrix. Figure 4.7 shows the connectivity matrices for 1969 and 1984, before and after \( S_{1972} \) was applied. These two years were chosen at random, but are representative of all years. They show that permuting the connectivity matrices with \( S_{1972} \) yields an almost reducible state, except for the few recurring “gateway” reefs.

These gateway reefs are the only reefs in the southern section that are able to
transport larvae against the predominant flow, to many of the reefs in the northern region. This transport is both consistent and significant – the gateway reefs are all in the top 2% of larval transports on the GBR, and the same set makes up the gateway reefs throughout the 32 year time series.

4.3.2 Independence of the northern and southern regions

Importantly, we need to determine how independent these two sub-sections are. Could either of them survive if the other was removed? How would the dynamics in one be affected by events in the other?

Analysing the independence of the two populations gives some interesting results. If the two metapopulations are independent, then we would expect them to persist without larval input from the other. If the dominant larval transport is indeed unidirectional, however, then we would expect the upstream population not to be affected by the removal of the downstream population, but not the converse, especially in conditions of extreme recruitment limitation. Intuitively, we would expect the northern population to be independent of the southern population, and the southern population to depend on the northern population to some extent.

Simulations to test this hypothesis were performed, where we assumed first that the northern and southern populations were completely independent of each other, and then subsequently that they were interconnected by strong southward flow, as predicted by the connectivity matrices. The results are shown in Figure 4.8.

It is immediately obvious that the northern population is not significantly affected by the southern population’s existence, i.e., the northern section of the GBR is independent of the south. On the other hand, over a wide range of $\beta$ values, the southern population depends on the northern population for its persistence, i.e., it is dependent heavily on the northern section. This is because the dominant transport within the GBR is the southward flow – the northern population exists without input from the south for much of the time. The small amount of northward larval transport provided by the gateway reefs is not important to the maintenance of the
Figure 4.8: Equilibrium population of northern and southern sections of the GBR for different values of the dimensionless Bewerton-Holt parameter, $\beta$. Equilibrium with and without larval exchange between the sections is compared. Dashed lines denote $\pm 1$ standard deviation. The population measurements are averaged over all the reefs in the system.

Possibly because of superior inter-connectedness, the northern population is able to persist at $\beta$ values for which the southern population alone is not sustainable – when the system is severely recruitment limited. In these cases, the existence of southward larval transport will allow the southern section to exist. When $\beta$ increases to a level where the southern section can exist independently, the existence of southward flow will increase the population of the south, as shown in Figure 4.8.

Once the existence of southward flow is established, some corollaries become evident. If the northern section were damaged, then the southern section would be impacted as well. If the south were to be affected however, this would not change the northern section at all.

In Figure 4.9, the simulated population is allowed to converge to equilibrium, and
then at 250 timesteps the downstream (southern) population is perturbed downwards to 10% of its equilibrium levels. At 350 timesteps the upstream (northern) population is also perturbed to 10% of equilibrium levels. Since the up- and downstream components are monitored separately, it is possible to observe the effect that each perturbation has on the other population. Figure 4.9 shows this effect agrees with the supposition that events in the upstream population impact the downstream population, but not \textit{vice versa}. The figure shows the average of 15 simulations.

This impact of this structure can be positive – from Figure 4.9 we can see that the recovery of the southern population is significantly faster than the recovery of the northern population. This is presumably because larvae received from the northern population speeds the recovery of the southern population.

![Figure 4.9](image)

**Figure 4.9:** Effects of perturbations in one sub-section of the GBR on the other. At 250 timesteps, the southern population is damaged. At 350 timesteps, the northern population is damaged ($\beta = 40$). Average of 15 simulations, with dotted curves indicating $\pm 1$ standard deviation.
Although they do not significantly affect metapopulation parameters such as the mean and variance of the populations, the gateway reefs are important, just as the inherent structure and reducibility of the GBR is. Both are evidence of the fact that the GBR is not uniformly connected. There are weak links in the connections between the separate reefs and also between sections of the GBR, and these affect the dynamics of the entire metapopulation.

4.3.3 Extinction

As an example of how the heterogeneity of the GBR might affect its dynamics, we investigate a simple perturbation example, which might correspond to extensive coral bleaching over the entire Cairns section of the GBR.

In late 1997 to early 1998, coral reefs around the world suffered from a mass bleaching which has been linked with higher than average sea temperature fluctuations. The “1997-1998 Mass Bleaching”, as it became known, recorded mortalities of shallow water coral of up to 95%, as well as unprecedented mortality in coral species usually resistant to bleaching, such as boulder and plate corals (Wilkinson, 1998).

Such events force us to consider what would happen if mass extinction of coral were to occur over large sections of the GBR. Corals comprise the fundamental organism of the GBR, and their partial mortality would have serious ramifications for reef fish, which depend directly and indirectly on them for survival.

Using the metapopulation model, I show that, for fish that depend on live coral, severe repercussions would follow a large scale bleaching event. Extinction would take place in particular sections of the GBR until conditions improve, or until the entire metapopulation goes extinct. The particulars of recovery underline the break between the northern and southern sections of the GBR, and the importance of flow regimes to the metapopulation’s dynamics. The northern sector can survive longer than the southern, and overall recovery has a greater probability of occurring if it begins in the northern section. Furthermore, it is possible, if the metapopulation were to go extinct, to restock the entire GBR from a single, well chosen reef (as
long as the conditions returned to pre-bleaching states). This simulation shows the fragility of the entire metapopulation to a major downturn, such as that which would follow a mass bleaching event.

In the event of mass coral bleaching, certain fish populations would suffer increased mortality as their coral habitat is damaged by increased water temperatures. High levels of coral mortality could happen in a single year, and increased density-dependent mortality would result from a decrease in habitable space and resources, in reef fish species dependent on live coral. In our non-dimensionalised metapopulation model (Appendix 1), this would result in a decrease in $\beta$, corresponding to an increase in the strength of density-dependent mortality.

We will not consider the effects of increased competition on post-settlement mortality, nor its effects on fecundity – these will be assumed constant throughout the experiment. The effect of the coral bleaching will be to decrease the number of larvae able to find safe habitats, and thus survive.

In the first simulation, the metapopulation is allowed to equilibrate with a value of $\beta$ that corresponds to a recruitment limited situation: all the reefs have fish, but they could support larger populations. Then in 5 years, the value of $\beta$ is decreased to 50% of its equilibrium levels. The effect of this downturn is noted, as populations on reef after reef become extinct across the GBR. When the conditions drop to this extent, the population of the GBR falls to zero. The GBR is then allowed to remain unpopulated for 100 years to equilibrate. Assuming the metapopulation is closed (the GBR does not receive larvae from outside its boundaries), then this metapopulation will remain at extinction until larvae are added to the system.

Two processes are thus begun. First, we assume that the corals begin to recover. If the bleaching does not result in 100% mortality, then once conditions begin to improve, we assume that the corals begin to slowly recover, over an extended period of 50 years. Second, in an attempt to restock the GBR, we begin to saturate a reef with larvae for the 50 years of improving conditions, followed by a further 10 years, after which the larval saturation is stopped. We choose a set of reefs in the south,
and a set in the north, and a set of the gateway reefs to saturate in this manner. We run 20 replicate simulations of each scenario, and compare how long it takes the GBR to fully recover (for there to be 90% of pre-bleaching levels of fish on each reef in the metapopulation). The model was run for 200 years after the recovery, and then the GBR was tested to see how long it took for all the local populations to regain 90% of their equilibrium levels.

With the return of favourable conditions, complete recolonisation is possible. Using the metapopulation model, we find that the speed of recolonisation of the GBR depends not only on the size of equilibrium populations, but also on the position of that reef in the hydrodynamic framework of the GBR.

In the northern sector of the GBR, we arbitrarily chose as candidates for initial recolonisation: Lizard Island, Harrier Reef, Ribbon Reef No. 10, and Beatrice Reef. In the south, the set included: Sudbury Reef, Howie Reef, Moore Reef, Arlington Reef and Flora Reef. We chose two of the gateway reefs, Rudder Reef and Opal Reef. The reefs selected are marked on the map in Figure 4.10.

When the simulations were run, we found that if the reef chosen was situated in the northern section of the GBR, recolonisation was quite rapid, but southern recovery took much longer on average. The size of the equilibrium population did play a factor, but the position of the reef in the system was more important. The sizes relative to the largest reef, and recovery times, are listed in Table 1.

Although it was the smallest reef in the entire set, Harrier was able to recolonise the system quickly because of its proximity to the Ribbon reefs, especially Ribbon Reef No. 10.

In the southern sector, it proved to be extremely difficult to recolonise the GBR unless the seeded reef is very large. Even then, recovery times were much longer than for northern reefs. Even though they were all larger than Harrier, or even Beatrice Reef, the southern reefs of Arlington, Howie and Sudbury all took longer to recolonise the GBR.
Figure 4.10: The red dots show the positions of the reefs on which the recolonisation simulation was attempted.
<table>
<thead>
<tr>
<th>Reef Name</th>
<th>Position</th>
<th>Size</th>
<th>$\mu$</th>
<th>$\sigma$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Harrier</td>
<td>Northern</td>
<td>0.03</td>
<td>105</td>
<td>8.8</td>
</tr>
<tr>
<td>Lizard Is.</td>
<td>Northern</td>
<td>0.19</td>
<td>57</td>
<td>1.5</td>
</tr>
<tr>
<td>Beatrice</td>
<td>Northern</td>
<td>0.02</td>
<td>135</td>
<td>8.0</td>
</tr>
<tr>
<td>Ribbon No.10</td>
<td>Northern</td>
<td>0.82</td>
<td>30</td>
<td>1.3</td>
</tr>
<tr>
<td>Rudder</td>
<td>Gateway</td>
<td>0.40</td>
<td>107</td>
<td>8.9</td>
</tr>
<tr>
<td>Opal</td>
<td>Gateway</td>
<td>0.20</td>
<td>134</td>
<td>8.4</td>
</tr>
<tr>
<td>Moore</td>
<td>Southern</td>
<td>0.14</td>
<td>X</td>
<td>—</td>
</tr>
<tr>
<td>Arlington</td>
<td>Southern</td>
<td>0.56</td>
<td>146</td>
<td>9.3</td>
</tr>
<tr>
<td>Sudbury</td>
<td>Southern</td>
<td>0.77</td>
<td>156</td>
<td>12.4</td>
</tr>
<tr>
<td>Howie</td>
<td>Southern</td>
<td>1.00</td>
<td>186</td>
<td>8.8</td>
</tr>
<tr>
<td>Flora</td>
<td>Southern</td>
<td>0.08</td>
<td>X</td>
<td>—</td>
</tr>
</tbody>
</table>

Table 4.1: Time taken for the GBR metapopulation to reach 90% of equilibrium levels, on every reef in the system. “Size” refers to equilibrium population size relative to equilibrium population size on Howie Reef. Mean recovery time (years) is given by $\mu$. Standard deviation of recovery time is denoted by $\sigma$. X denotes cases where recovery did not occur in the simulation’s timeframe.

It is not generally a problem for southern reefs to recolonise the southern sector of the GBR. The problem, once this has been done, is to colonise the northern sector. The gateway reefs provide the means to do this, and simulations show that once they are colonised, the region directly to the north of them is colonised immediately, because of their strong northward larval dispersal. Gateway reefs are able to project larvae northwards, and we see that the time taken for recolonisation if they are saturated is disproportionate to their sizes, and more like the time taken for a northern reef to recolonise the metapopulation.

The speed of recolonisation, if a well-placed northern reef is chosen, is partially due to the rapid southward dispersal of larvae originating on the Ribbon Reefs, especially No. 10 (because of its size), carried on the dominant southward current, which was commented upon previously. The Ribbon Reefs take advantage of a
strong southward oceanic current, which runs past the outer reefs and can rapidly
transport larvae over large distances.

Many of these concepts are best described using graphical means. The CD included
with this thesis contains QuickTime movies of the above recolonisation scenarios,
which provide not only an easily understandable format for the information, but
also show many other facets of connectivity on the GBR, not explicitly noted here.

A traditional understanding of the GBR would suggest that the metapopulation
is connected to such an extent that recolonisation would occur at a similar rate,
irrespective of where the initial population was situated. This would depend on
homogeneous connectivity. In contrast, we have demonstrated that such a model
is over-simplistic, and unlikely to be effective in explaining the dynamics of the
metapopulation.

4.4 Negative correlations to a target reef

Correlations could be perhaps the most important tool in determining structure
on the GBR from the connectivity matrices (Maurice James, pers. comm.). The
question is, how can we possibly hope to simplify the $10^{10}$ correlations that exist
within the GBR transports, for just the present section of the GBR?

One possible way to do so is to focus on the correlations to a particular reef. How
are the connections to a chosen target reef correlated? I have discussed earlier the
ramifications that negative correlation between transports to the target reef would
have for the exploitation of that reef, and I show in this section that such scenarios
can exist on the GBR.

Using the definitions for correlation given in equation (3.13), we correlate only those
connections that involve amounts of larvae which could theoretically sustain fish on
the target reef. I have chosen to include only the largest 5% of all transports between
reefs in the system, including self-recruitment. Using this reduced set of connections,
we determine which pairs of $p_{ij}$ elements would be considered correlated at a 95%
confidence level. In almost all cases, only transports from pairs of reefs in close proximity to the target reef satisfy both these requirements.

To visually demonstrate these correlations, we plot a map of all the important reefs on a diagram, and draw green lines between pairs of reefs whose transports to a chosen target reef are positively correlated. Pairs of reefs whose transport to the target reef are negatively correlated are joined by red lines. If we have a scenario similar to that described in Chapter 3, then we would expect reefs that consistently acted together to be joined by green lines. If such a group of reefs were negatively correlated to another such group, then these two groups would be joined by red lines. This is exactly what we find.

The three reefs examined in Figures 4.11, 4.12 and 4.13, Otter Reef, Pixie Reef and Ribbon Reef No. 10 respectively, are indicative of many of the reefs throughout the GBR. The findings shown here can be found for many other reefs on the GBR, irrespective of their size or position.

Because of the predominantly alongshore flow, there are typically groups of reefs that are positively correlated to the north and south of the target reef. Groups to the north and south are joined with negative correlations (red lines). Many reefs’ populations are more stable, due to negatively correlated transport, than they would be in random, chaotic flow. I also find that certain groups of reefs are positively correlated in their transport to many target reefs, which implies that they work together when sending larvae, independent of the prevailing flow.

Figure 4.14 shows just such a group of reefs acting together in their transport to three different reefs. The group centered about (18°S and 146.8°E) has consistently correlated transport to the three reefs shown (Otter Reef, Britomart Reef, and Reef 18-022), and a number of others.

The implication of such similar behaviour is that, instead of focusing on individual reefs when considering management strategies, it might be wiser to also consider how groups of reefs act. It could be preferable that groups of reefs be considered as a single entity when discussing marine reserves. On the other hand, if two reefs have
Figure 4.11: Close-up of reefs whose transport to Otter Reef are positively correlated (joined by green lines), and negatively correlated (joined by red lines).
Figure 4.12: Close-up of reefs whose transport to Pixie Reef are positively correlated (joined by green lines), and negatively correlated (joined by red lines). Pixie Reef is obscured by the blue dot, due to its small size.
Figure 4.13: Close-up of reefs whose transport to Ribbon Reef No. 10 are positively correlated (joined by green lines), and negatively correlated (joined by red lines).
Figure 4.14: Three groups of reefs that are strongly positively correlated: they act in unison when sending larvae to other reefs.
highly positively correlated transport, this redundancy could mean that exploiting one of them might minimise, or at least reduce, any impacts on the metapopulation.

Given that the groups of reefs whose transport is positively correlated are usually to the north and south of the target reef (probably because the dominant winds are NW/SE), it might be wise to arrange marine reserves as bands of reefs, based on the cross-shelf distance.

In these cases, and perhaps in others, the correlations between the transports of reefs should be included in formulating management decisions.
Chapter 5

Metapopulation Modelling

5.1 Modelling of stochastic systems

The dynamics of a reef fish metapopulation are inherently stochastic, primarily because they depend on the size of each year’s recruitment. A deterministic model of the metapopulation would thus be overly simplistic, as it would rely on the mean proportions matrix, which would lose the information contained in the variance of the connections between reefs. Although a deterministic model should provide a reasonable estimate of the mean population size, it would tell us nothing about its variance. The variance of the metapopulation (and of each local population) is necessary for an informed idea of population stability, and it is believed that variances are more useful measures of population dynamics on coral reefs than are means (Stuart Sandin, pers. comm.).

Armsworth (2000) developed a deterministic metapopulation model to help understand the dynamics of reef fish with a pelagic larval stage, and the analysis contained in this chapter is largely based on that model.

Linear approximations to nonlinear systems are applicable to both predictable and unpredictable fluctuations in population parameters (Roughgarden, 1975), and previous applications of linearisation to nonlinear populations have proved very accurate (Roughgarden, 1975; Roughgarden et al., 1985; Hughes and Roughgarden, 1998). Their application to recruitment-limited processes is useful, because it allows us to apply known results from the field of auto-regressive processes to determine the
effects of correlations in connectivity on population variance.

Linearised functions are simpler forms of the full, nonlinear population equations. We assume the metapopulation has a stable equilibrium, and that negative feedback acts on any small perturbations in the metapopulation, to return it to this equilibrium state. In our nonlinear metapopulation model, these perturbations are caused by fluctuations in the connectivities, which we have explained are variable. We must assume regularity in this variation, however, so we assume the connectivities are second-order stationary stochastic processes. Such a process does not have a fixed value; rather, it has a fixed distribution, with a constant mean and variance.

This assumption allows us to express the connectivities $p_{ij}(t)$, as

$$p_{ij}(t) = A_{ij} + a_{ij}(t), \quad (5.1)$$

where $a_{ij}$ is a random variable with a zero mean and a known variance. The perturbations $a_{ij}$ in the connectivity are smaller than the mean values of the connectivities, $p_{ij}$.

A first order Taylor series expansion of the nonlinear equations is taken with respect to all stochastic variables, about the equilibrium values. Dropping all but the first order terms theoretically means that the approximation is only valid for small deviations from equilibrium, but in practice, the nonlinear and linear equations are almost indistinguishable for most realistic deviations (Roughgarden, 1975).

One drawback of linearised equations is that population values will be estimated consistently higher than for the full nonlinear model. This is because nonlinear models restore deviations above equilibrium more strongly than they restore deviations below. On the other hand, linearised models restore deviations below equilibrium more strongly than nonlinear models, as the linearised model’s larval output is based about the larval output of the equilibrium population. A negatively displaced nonlinear model will produce less larvae, due to its lower population.

These drawbacks are relatively unimportant, however, and the simplicity and ease of use of linearised model outweighs them near equilibrium. Finding the equilibrium
value of the metapopulation becomes the problem.

5.2 Linearisation

Armsworth (2001) developed a metapopulation model for pelagic larvae on the GBR. It assumed that the GBR metapopulation could be expressed as a system of partially-open local populations, which exchanged larvae once a year through pelagic larvae. Every year, each local population produced larvae based on the number of fish in each age class, and the fecundity of each class. These pelagic larvae exit the local reef and spend a certain precompetent period in the open ocean, before settling on a local population.

Upon settlement, it is thought that the larvae suffer density dependent mortality. Certainly, post-settlement mortality is severe. Coral reef fish are known to undergo 30–78% mortality in the first week, post-settlement (Doherty and Sale, 1985; Victor, 1986; Booth, 1991; Carr and Hixon, 1995; McCormick, 1998), and it is thought that the mortality is density-dependent (Steel, 1997; Armsworth, 2001). We model this density dependence using a Beverton-Holt relationship, whereby for each local population, every year,

\[ N_i(t+1) = \Gamma(S_i(t)) = \frac{\gamma S_i(t)}{1 + \beta S_i(t)}. \]  

(5.2)

\( N_i(t) \) is the number of year old juveniles on reef \( i \) at time \( t \), \( S_i(t) \) is the number of fish trying to settle on the reef at time \( t \), and \( \Gamma(S_i(t)) \) is the number of those larvae that survive density dependent mortality. Using the net reproductive value of the year old fish, equation (2.1), means that only the first year age class needs to be considered.

The Beverton-Holt relationship is a compensatory density dependent function. Compensatory density dependence means that as the size of the settling cohort increases, the number of surviving juveniles approaches a limit. Overcompensatory density dependence means that more larvae can result in a smaller cohort of juveniles.
Armstrong (2000) justifies the use of this particular form by citing four independent studies of reef fish that can be described accurately by the Beverton-Holt relationship: Jones (1990), Doherty and Fowler (1994), Steel (1997), and Schmitt and Holbrook (1997).

The number of larvae, $S_j(t)$, settling at a particular reef $j$ in an $M$-metapopulation depends not only on the larval output of every population in the metapopulation, but also how those populations are connected to the particular reef. If we keep our definition of the connectivity matrix consistent, then the element $p_{kj}$ is the proportion of larvae produced at reef $i$ that settle upon reef $j$:

$$S_j(t) = R \sum_{k=1}^{M} p_{kj}(t) N_k(t).$$ \hspace{1cm} \text{(5.3)}

These larvae suffer density dependent mortality, so that the number surviving at the first census is:

$$N_j(t + 1) = \Gamma (S_j(t)) = \frac{\gamma R \left( \sum_{k=1}^{M} p_{kj} N_k(t) \right)}{1 + \beta \left( R \sum_{k=1}^{M} p_{kj} N_k(t) \right)}.$$ \hspace{1cm} \text{(5.4)}

A useful simplification of this nonlinear model is nondimensionalisation. Appendix 1 demonstrates this nondimensionalisation, which changes the form of the density dependent Beverton-Holt function only slightly, yet allows significant simplification. Firstly, the number of parameters in the model is reduced to one. The population values at each reef are no longer expressed as absolute numbers of fish, but instead as proportions of the saturation number of fish at each location.

Equation (5.4) is the nonlinear model used to generate our linearised model. Assume for now that we can deterministically calculate the mean populations at each of the $M$ populations, the $\bar{N}_i$ values. The perturbation of these populations from their mean values is given by $n_i(t)$, making the local population $i$ at time $t$ equal to $\bar{N}_i + n_i(t)$. This stochasticity is due to the $a_{ij}$ values, equation (5.1). Performing the required first order Taylor expansion yields the linear model in discrete time:

$$n_j(t + 1) = \gamma R \sum_{k=1}^{M} \left[ n_k(t) A_{kj} + \bar{N}_k a_{kj}(t) \right] \frac{1}{[1 + \beta R \left( \sum_{k=1}^{M} A_{kj} \bar{N}_k \right)]^2}.$$ 55
A useful application of this model will be the entire GBR metapopulation in its reducible form, which has two main sections. It will also allow us to investigate the importance of correlations in a $2 \times 2$ connectivity matrix, specifically the impact that correlations in recruitment have on the stability of a population.

### 5.3 Linearised two-population model

A system of two populations is the largest system that we can solve analytically. Armsworth (2001) showed that a system of $M$ populations had $2^M$ equilibria, of which only one was interior. Finding the interior equilibrium of a two population system requires the solving of a quartic, which is possible analytically. A three population system would require the roots of an eighth degree polynomial, which cannot be done analytically (although numerical methods could be used). Fortunately we do not have to solve a quartic to get our interior equilibrium in this case, as the existence of a known (extinction) equilibrium reduces the equation to a cubic. The extinction state is an unstable equilibrium for all possible closed systems.

The full, dimensional, nonlinear equations of the two population system at the internal equilibrium are

$$
\dot{N}_1 = \frac{\gamma R (A_{11} \dot{N}_1 + A_{21} \dot{N}_2)}{1 + \beta R (A_{11} N_1 + A_{21} N_2)}
$$

$$
\dot{N}_2 = \frac{\gamma R (A_{12} \dot{N}_1 + A_{22} \dot{N}_2)}{1 + \beta R (A_{12} N_1 + A_{22} N_2)},
$$

and the solution for $N_2$, for example, requires us to solve the cubic

$$
0 = N_2^3 \left[ -R^3 \beta^2 A_{11} A_{22} \right]
+ N_2^2 \left[ R^2 \beta^2 A_{22} A_{12} - R^3 \gamma \beta A_{11} A_{12} A_{22} + 2R^2 \beta A_{11} A_{22} + 2R^3 \gamma \beta^2 A_{11} A_{22}^2 - R\beta A_{12} \right]
+ N_2 \left[ R^3 \gamma^2 \beta A_{11} A_{12} A_{22} - R^2 \gamma \beta A_{11} A_{12} - R^3 \gamma^2 \beta A_{11} A_{12} A_{22} \right]
+ 2R^2 \gamma \beta A_{11} A_{22} - R^3 \gamma^2 \beta^2 A_{11} A_{12} A_{22} - R\beta A_{11} - R^2 \gamma \beta A_{12} A_{22} + R\beta A_{12} + R^2 \gamma \beta A_{12} A_{22} - R\gamma A_{12} \right]
+ \left[ R^3 \gamma^3 A_{11} A_{12} A_{22} - R^2 \gamma^2 A_{11} A_{12} - R^2 \gamma^3 A_{11} A_{22} + R A_{12} \right]
$$

(5.7)
This can be done analytically, if not simply. Murray (1989) gives an analytic solution to a general cubic. Although the solution was calculated, it will not be used here.

For metapopulations with more than two local populations, we are forced to look for other methods of solution. Using the solution of equation (5.7) as a benchmark, we find that very few iterations of the full deterministic model are needed for metapopulation convergence, and that equilibrium can be used in the linearisation. Comparison of the numerical equilibrium with the analytical equilibrium for the two population system resulted in perfect agreement.

### 5.4 Analysis of the linear equations

Linearised population equations are especially useful because they allow analysis using matrix methods. For \(M\) populations, we can express the linear equations as the matrix equation

\[
\mathbf{n}_{t+1} = \mathbf{Dn}_t + \mathbf{z}_t, \tag{5.8}
\]

where

\[
[D]_{ij} = C_j A_{ij},
\]

\[
\mathbf{n}_t = \begin{pmatrix} n_1(t) \\ n_2(t) \\ \vdots \\ n_M(t) \end{pmatrix},
\]

\[
\mathbf{z}_t = \begin{pmatrix} z_1 = \sum_{k=1}^{M} C_1 \hat{N}_k a_{k1}(t) \\ z_2 = \sum_{k=1}^{M} C_2 \hat{N}_k a_{k2}(t) \\ \vdots \\ z_M = \sum_{k=1}^{M} C_M \hat{N}_k a_{kM}(t) \end{pmatrix}, \tag{5.9}
\]
\[ C_j = \frac{\gamma R}{(1 + \beta R \sum_{k=1}^M A_{kj} N_j)^2}, \]  
(5.10)

a constant at each local population in the metapopulation. The \( a_{ij}(t) \) are the random variations in the connectivity, whose covariance we will examine.

We can diagonalise this system if the matrix \( D \) has a complete set of linearly independent eigenvectors. Matrix \( D \) depends on matrix \( A \), and \( A \) is a non-negative, asymmetric matrix, which does not necessarily have this property. However, our linear system can be perturbed in any direction in the \( M \)-dimensional space (where each dimension describes the population at one of the local reefs), and the linear system must be able to return this system to its equilibrium. For this to be so, the matrix \( A \) must span the entire space, requiring it to have a full set of \( n \) linearly independent eigenvectors. Hence we can diagonalise the equations as follows.

\[ n_{i+1}^s = T^{-1} DT n_i^s + z_i^s = \Lambda n_i^s + z_i^s, \]  
(5.11)

where \( \Lambda \) is the diagonal matrix comprising the eigenvalues of \( D \):

\[ \Lambda = \begin{pmatrix} 
\lambda_1 & 0 & \ldots & 0 \\
0 & \lambda_2 & \ldots & 0 \\
\vdots & \ddots & \ddots & \vdots \\
0 & \ldots & \ldots & \lambda_n
\end{pmatrix}, \]

and

\[ n_i^s = T^{-1} n_i, \]  
(5.12)

\[ z_i^s = T^{-1} z_i. \]  
(5.13)

This is a standard diagonalisation of such a matrix expression – see Meyer (2000) for a full explanation. We construct the matrix \( T \) from the column eigenvectors of
D, and we refer to it using the following notation:

\[ T = \begin{pmatrix}
  t_{11} & t_{12} & \cdots & t_{1M} \\
  t_{21} & t_{22} & \cdots & t_{2M} \\
  \vdots & \vdots & \ddots & \vdots \\
  t_{M1} & \cdots & \cdots & t_{MM}
\end{pmatrix} \]

and

\[ T^{-1} = \begin{pmatrix}
  t_{11}^{-1} & t_{12}^{-1} & \cdots & t_{1M}^{-1} \\
  t_{21}^{-1} & t_{22}^{-1} & \cdots & t_{2M}^{-1} \\
  \vdots & \vdots & \ddots & \vdots \\
  t_{M1}^{-1} & \cdots & \cdots & t_{MM}^{-1}
\end{pmatrix}. \]

This diagonalisation is beneficial because the variables are uncoupled in the new system, and each \( \mathbf{n}_i^*(t + 1) \) can be expressed as a function of \( \mathbf{n}_i^*(t) \) and its random variable \( \mathbf{z}_i^*(t) \), as

\[ \mathbf{n}_i^*(t + 1) = \lambda_i \mathbf{n}_i^*(t) + \mathbf{z}_i^*(t). \quad (5.14) \]

Successive substitution yields

\[ \mathbf{n}_i^*(t + 1) = \sum_{k=0}^{\infty} \lambda_i^k \mathbf{z}_i^*(t - k). \quad (5.15) \]

Equation (5.14) has the form of a first order autoregressive process. As the effects of each perturbation decrease over time when the system returns to equilibrium, we can assume all \( \lambda_i < 1 \). A lot of work has been done on first-order processes in the field of time series analysis, and so there are general results we can apply. Equation (5.15) shows that the present state of the population is a sum of the previous fluctuations, weighted by the eigenvalues of the connectivity matrix, and the time since the perturbation occurred.

All the above results are general, although after this point only two populations will be considered. The results are applicable for as many populations as are necessary.
Analysis of two populations will have an application to the GBR’s southern and northern regions. Consequently the vectors are two-dimensional, and we can revert to scalar notation.

The working in this section is analogous to that done by Hughes and Roughgarden (1998), with a few significant differences. Whereas their analysis focused on a single point population of two species, I have constructed the models for a single species, with two spatially separate, partially open, local populations. Hughes and Roughgarden examined the importance of the interaction term between the two species, and their model forced a random variable on the population sizes to make them second order stationary processes. Their random variables \( z_1 \) and \( z_2 \) were considered independent, and thus were assumed uncorrelated.

Such an assumption is not necessarily valid for the metapopulation problem. In Figure 3.2 we can see how, for metapopulation connections, this would not be a valid assumption. If the northern and southern sections of the GBR are involved in a similar flow, it is possible that the transport between them would be correlated in some way. If there were unidirectional flow from the northern to the southern section, then we might expect \( a_{12}(t) \) and \( a_{21}(t) \) to be negatively correlated.

The following section will determine the effects of such a correlation on the variance of each individual population (\( \text{Var}(n_1) \), \( \text{Var}(n_2) \)), and also on the total population \( \text{Var}(n_1 + n_2) \), the biomass of the system.

Our new variables \( n_1^* \) and \( n_2^* \) are linear combinations of the populations of the two reefs being analysed. This linear combination can be expressed as a function of the reef populations and the elements of the matrix of the eigenvectors, \( \mathbf{T} \).

\[
\begin{align*}
  n_1(t) &= t_{11} n_1^* + t_{12} n_2^*, \\
  n_2(t) &= t_{21} n_1^* + t_{22} n_2^*. 
\end{align*}
\]

(5.16) (5.17)

It is useful to express the variance of the transformed random variables as functions of the original \( z_i(t) \) values:

\[
z_1^* = t_{11}^{-1} z_1 + t_{12}^{-1} z_2,
\]

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\[ z_2^* = t_{21}^{-1}z_1 + t_{22}^{-1}z_2. \quad (5.18) \]

Therefore

\[
\begin{align*}
\text{Var}(z_1^*) &= (t_{11}^{-1})^2 \text{Var}(z_1) + (t_{12}^{-1})^2 \text{Var}(z_2) + 2t_{11}^{-1}t_{12}^{-1} \text{Cov}(z_1, z_2), \\
\text{Var}(z_2^*) &= (t_{21}^{-1})^2 \text{Var}(z_1) + (t_{22}^{-1})^2 \text{Var}(z_2) + 2t_{21}^{-1}t_{22}^{-1} \text{Cov}(z_1, z_2),
\end{align*}
\]

(5.19)

where \( \text{Cov}(z_1, z_2) \) denotes the covariance of \( z_1 \) and \( z_2 \).

We need to link the variance of the perturbations from the equilibria, \( n_1 \) and \( n_2 \), to the variance and covariance of our stochastic \( a_{ij} \) variables. We can do this by expressing the random perturbations, \( z_1 \) and \( z_2 \), as functions of the \( a_{ij} \) elements. The form of the \( z \) variables is defined in equation (5.9). For our two populations they simplify to

\[
\begin{align*}
z_1(t) &= C_1(\hat{N}_1 a_{11}(t) + \hat{N}_2 a_{21}(t)), \\
z_2(t) &= C_2(\hat{N}_1 a_{12}(t) + \hat{N}_2 a_{22}(t)),
\end{align*}
\]

(5.20)

and their variances can be expressed (Cox, 1968; p. 279) as

\[
\begin{align*}
\text{Var}(z_1) &= C_1^2(\hat{N}_1^2 \text{Var}(a_{11}) + \hat{N}_2^2 \text{Var}(a_{21}) + 2\hat{N}_1 \hat{N}_2 \text{Cov}(a_{11}, a_{21})), \\
\text{Var}(z_2) &= C_2^2(\hat{N}_1^2 \text{Var}(a_{12}) + \hat{N}_2^2 \text{Var}(a_{22}) + 2\hat{N}_1 \hat{N}_2 \text{Cov}(a_{12}, a_{22})).
\end{align*}
\]

(5.21)

If \( \lambda_i < 1 \), the variance of the first order autoregressive variable \( n_i^* \) can be expressed as

\[
\text{Var}(n_i^*) = \frac{\text{Var}(z_i^*)}{1 - \lambda_i^2}
\]

(5.22)

(Cox and Miller, 1968).

Thus from equations (5.16)

\[
\begin{align*}
\text{Var}(n_1) &= t_{11}^2 \text{Var}(n_1^*) + t_{12}^2 \text{Var}(n_2^*) + 2t_{11}t_{12} \text{Cov}(n_1^*, n_2^*), \\
\text{Var}(n_2) &= t_{21}^2 \text{Var}(n_1^*) + t_{22}^2 \text{Var}(n_2^*) + 2t_{21}t_{22} \text{Cov}(n_1^*, n_2^*).
\end{align*}
\]

(5.23)
Substituting equation (5.22) for $\text{Var}(n_i^*)$ gives

$$\text{Var}(n_1) = \frac{(t_{11} t_{11}^{-1})^2 \text{Var}(z_1) + (t_{12} t_{12}^{-1})^2 \text{Var}(z_2) + 2t_{11} t_{12}^{-1} t_{12} t_{12}^{-1} \text{Cov}(z_1, z_2)}{1 - \lambda_1^2}$$

$$+ \frac{(t_{12} t_{12}^{-1})^2 \text{Var}(z_1) + (t_{12} t_{12}^{-1})^2 \text{Var}(z_2) + 2t_{12} t_{12}^{-1} t_{12} t_{12}^{-1} \text{Cov}(z_1, z_2)}{1 - \lambda_2^2}$$

$$+ 2t_{11} t_{12} \text{Cov}(n_1^*, n_2^*) \tag{5.24}$$

$$\text{Var}(n_2) = \frac{(t_{21} t_{21}^{-1})^2 \text{Var}(z_1) + (t_{21} t_{21}^{-1})^2 \text{Var}(z_2) + 2t_{21} t_{21}^{-1} t_{22} t_{22}^{-1} \text{Cov}(z_1, z_2)}{1 - \lambda_1^2}$$

$$+ \frac{(t_{22} t_{22}^{-1})^2 \text{Var}(z_1) + (t_{22} t_{22}^{-1})^2 \text{Var}(z_2) + 2t_{22} t_{22}^{-1} t_{22} t_{22}^{-1} \text{Cov}(z_1, z_2)}{1 - \lambda_2^2}$$

$$+ 2t_{21} t_{22} \text{Cov}(n_1^*, n_2^*) \tag{5.25}$$

Eventually we want to express $\text{Cov}(n_1^*, n_2^*)$ in terms of the variations in the connectivity coefficients $a_{ij}(t)$. Now

$$\text{Cov}(n_1^*, n_2^*) = E[n_1^* n_2^*] - E[n_1^*]E[n_2^*], \tag{5.26}$$

where $E$ denotes expectation, and $E[n_i^*] = 0$. Also,

$$E[n_1^* n_2^*] = E \left[ \sum_{i=0}^{\infty} \lambda_1^i z_1^i (t - i) \sum_{j=0}^{\infty} \lambda_2^j z_2^j (t - j) \right],$$

since terms in different timesteps are independent,

$$= E \left[ \sum_{i=0}^{\infty} \lambda_1^i \lambda_2^j z_1^i (t - i) z_2^j (t - j) \right]$$

$$= \sum_{i=0}^{\infty} (\lambda_1 \lambda_2)^i \text{Cov}(z_1^i, z_2^j)$$

$$= \text{Cov}(z_1^*, z_2^*)$$

$$= \frac{E[z_1^* z_2^*] - E[z_1^*]E[z_2^*]}{1 - \lambda_1 \lambda_2}.$$ 

In addition, $E[z_2^*] = 0$, so that

$$E[n_1^* n_2^*] = \frac{E[(t_{11}^{-1} z_1 + t_{12}^{-1} z_2)(t_{21}^{-1} z_1 + t_{22}^{-1} z_2)]}{1 - \lambda_1 \lambda_2}$$
and
\[
\text{Cov}(n_1^*, n_2^*) = \frac{t_{11}^{-1} t_{21}^{-1} \text{Var}(z_1) + t_{12}^{-1} t_{22}^{-1} \text{Var}(z_2) + (t_{12}^{-1} t_{21}^{-1} + t_{11}^{-1} t_{22}^{-1}) \text{Cov}(z_1, z_2)}{1 - \lambda_1 \lambda_2}.
\]

If we are to express \(\text{Cov}(n_1^*, n_2^*)\) as a function of the \(a_{ij}(t)\) elements, we have to finally expand \(\text{Cov}(z_1, z_2)\) in terms of their definitions in equation (5.9):
\[
\text{Cov}(z_1, z_2) = E[z_1 z_2] - E[z_1]E[z_2],
\]
and since \(E[z_i] = 0\),
\[
\text{Cov}(z_1, z_2) = E[z_1 z_2]
\]
\[
= E[C_1(\hat{N}_1 a_{11} + \hat{N}_2 a_{21})C_2(\hat{N}_1 a_{12} + \hat{N}_2 a_{22})]
\]
\[
= C_1 C_2(\hat{N}_1^2 \text{Cov}(a_{11}, a_{12}) + \hat{N}_2^2 \text{Cov}(a_{21}, a_{22})
\]
\[
+ \hat{N}_1 \hat{N}_2 [\text{Cov}(a_{11}, a_{22}) + \text{Cov}(a_{21}, a_{12})]).
\]

Thus we can now express the variance in each population as a function of the variance of the transports.

\[
\text{Var}(n_1) = \frac{(t_{11}^{-1} t_{11}^{-1})^2 \text{Var}(z_1) + (t_{11}^{-1} t_{12}^{-1})^2 \text{Var}(z_2) + 2 t_{11}^{-1} t_{11}^{-1} t_{12}^{-1} \text{Cov}(z_1, z_2)}{1 - \lambda_1^2}
\]
\[
+ \frac{(t_{12}^{-1} t_{21}^{-1})^2 \text{Var}(z_1) + (t_{12}^{-1} t_{22}^{-1})^2 \text{Var}(z_2) + 2 t_{12}^{-1} t_{21}^{-1} t_{22}^{-1} \text{Cov}(z_1, z_2)}{1 - \lambda_2^2}
\]
\[
+ \frac{2 t_{11} t_{12}}{1 - \lambda_1 \lambda_2} \left( t_{11}^{-1} t_{21}^{-1} \text{Var}(z_1) + t_{12}^{-1} t_{22}^{-1} \text{Var}(z_2) \right)
\]
\[
+ (t_{12}^{-1} t_{21}^{-1} + t_{11}^{-1} t_{22}^{-1}) C_1 C_2 \left[ \hat{N}_1^2 \text{Cov}(a_{11}, a_{12}) + \hat{N}_2^2 \text{Cov}(a_{21}, a_{22})
\]
\[
+ \hat{N}_1 \hat{N}_2 (\text{Cov}(a_{11}, a_{22}) + \text{Cov}(a_{21}, a_{12})].
\]

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\[
\text{Var}(n_2) = \frac{(t_{21}t_{11}^{-1})^2\text{Var}(z_1) + (t_{22}t_{12}^{-1})^2\text{Var}(z_2) + 2t_{21}^2t_{11}^{-1}t_{12}^{-1}\text{Cov}(z_1, z_2)}{1 - \lambda_1^2} \\
+ \frac{(t_{22}t_{21}^{-1})^2\text{Var}(z_1) + (t_{22}t_{22}^{-1})^2\text{Var}(z_2) + 2t_{22}^2t_{21}^{-1}t_{22}^{-1}\text{Cov}(z_1, z_2)}{1 - \lambda_2^2} \\
+ \frac{2t_{21}t_{22}}{1 - \lambda_1\lambda_2} \left[ t_{11}^{-1}t_{21}^{-1}\text{Var}(z_1) + t_{12}^{-1}t_{22}^{-1}\text{Var}(z_2) \\
+ (t_{12}^{-1}t_{21}^{-1} + t_{11}^{-1}t_{22}^{-1})C_1C_2 \left[ \hat{N}_1^2\text{Cov}(a_{11}, a_{12}) + \hat{N}_2^2\text{Cov}(a_{21}, a_{22}) \\
+ \hat{N}_1\hat{N}_2(\text{Cov}(a_{11}, a_{22}) + \text{Cov}(a_{21}, a_{12})) \right] \right].
\]

The variance of the biomass can be expressed in terms of the variance of the \( z_i \) and the covariance between the \( a_{ij} \) elements:

\[
\text{Var}(n_1 + n_2) = \text{Var}(n_1) + \text{Var}(n_2) + 2\text{Cov}(n_1, n_2),
\]

(5.31)

where \( \text{Cov}(n_1, n_2) \) can be written as

\[
\text{Cov}(n_1, n_2) = E[n_1, n_2] - E[n_1]E[n_2]
\]

and \( E[n_i] = 0 \). Therefore,

\[
\text{Cov}(n_1, n_2) = E[(t_{11}n_1^i + t_{12}n_2^i)(t_{21}n_1^s + t_{22}n_2^s)] \\
= t_{11}t_{21}\text{Var}(n_1^i) + t_{12}t_{22}\text{Var}(n_2^i) + \text{Cov}(n_1^i, n_2^i)(t_{11}t_{22} + t_{12}t_{21}).
\]

All the quantities of interest are now defined in terms of the variances and covariances between the \( a_{ij} \) elements.

### 5.5 Effects of covariance in the \( a_{ij} \) terms

Imagine that we have a small, two-reef metapopulation. If there were a fairly strong but fluctuating current flowing through the system along the north–south axis, what effect would this have on the connections between the reefs? An obvious assumption is that when the flow was directed strongly toward the south, the proportion \( p_{12} \) would be above its mean, and \( p_{21} \) would be below. When the flow was northward,
the converse would occur. Making assumptions about the effects of such flow on
self-recruitment is problematic, as flow regimes near reefs are very complex, and the
factors that influence self-recruitment are largely unknown (Wolanski, 1997).

In the case of unidirectional flow, we therefore assume that the proportions \( p_{12}(t) \)
and \( p_{21}(t) \) are negatively correlated, which would mean the random fluctuations
\( a_{12}(t) \) and \( a_{21}(t) \) are negatively correlated. We can therefore simplify the equations
for the variance of the populations and the biomass by letting \( \text{Cov}(a_{11}, a_{21}) \) and
\( \text{Cov}(a_{12}, a_{22}) \) equal zero in equations (5.21). Similarly, we set all occurrences of
\( \text{Cov}(a_{11}, a_{22}) \) to zero also.

Assume, for example, that the matrix \( \mathbf{D} \) is

\[
\mathbf{D} = \begin{pmatrix}
0.5 & 0.3 \\
0.3 & 0.5
\end{pmatrix}.
\]  

(5.32)

Here, we call the metapopulation symmetric – the two local populations will have
the same equilibria, and will be virtually indistinguishable. In the symmetric case,
the two populations are roughly equal, and we can define the equilibrium \( [\hat{N}_1, \hat{N}_2] \).

Immediately we can plot the effects of covariance in the stochastic parameters \( a_{12} \)
and \( a_{21} \), as shown in Figure 5.1, a plot of the variance and coefficient of variation
(CV) of each population as functions of the correlation between \( a_{12} \) and \( a_{21} \). The
variance of each population is affected only slightly by the correlations in the \( a_{ij} \)
terms. It changes so little, in fact, that when plotted on the same axis the change in
variance of the individual populations is difficult to notice. This might be expected,
as the correlation concerns the inter-reef dispersal, and thus mainly affects the relative
size of the populations at each timestep. In the symmetric case, this has little
effect on the variance of each of the populations; its main effect is on the relationship
between the fluctuations in each population, not the size of those fluctuations.

The variance of the biomass is very much concerned with how those fluctuations are
interrelated, as the biomass is the sum of the two populations. Negative correlation
between the inter-reef dispersal means that when \( p_{12}(t) \) is above average, \( p_{21}(t) \) is
below average. The effect of this is that, when population 1 is larger than usual,
Figure 5.1: The effect of correlation on the variance, and coefficient of variation, of each population and the biomass of the system. The variance and coefficient of variation indicate population stability. The solid lines denote the biomass of the system, the dotted lines denote the local populations.

population 2 will be smaller. This has the effect of reducing the variance of the biomass. We would therefore expect the lowest possible biomass variance to occur when the correlation is perfectly negative: \( r = -1 \), as confirmed in Figure 5.1. The variance is not zero at this point, but equal to the variance of one of the populations. When the two connectivities are uncorrelated, the variance of the biomass is simply the sum of the variances of two independent populations.

Thus linearisation allows us to analytically investigate the effects of correlations in the inter-reef dispersal on the variance of the local and metapopulations. This is only a small fraction of what could be done, however, in this area of research. The assumption of symmetry, for example, could be relaxed to a pair of metapopulations whose inter-reef dispersal is negatively correlated, but where one of the transports is
much larger than the other. This is the scenario corresponding to the reduced version of the GBR, as hypothesised in Chapter 4. Linearised models have a history of successful application in community dynamics, and the benefits of the analytical linearised approach to metapopulation modelling are significant, but to my knowledge they have yet to be applied to any important problems on the GBR.
Chapter 6

Discussion and Conclusions

Successful management of reef fish populations on the GBR requires understanding the effect of pelagic larval dispersal patterns and variability, on local and regional-scale population dynamics. The aim of this thesis was to provide tools to aid in the understanding of spatially heterogeneous systems in general, and the GBR in particular. It has also made a number of suggestions as to how these tools could be used, and the ramifications of some specific findings.

These methods were designed for reef fish metapopulations. A metapopulation is essentially a group of smaller, local populations which are partially open (i.e., they interact by exchanging larvae through dispersal), and partially closed (i.e., the benthic adults are unable to migrate between local populations). In other words, we are forced to view local populations both as entities within themselves, and also as pieces of a much larger structure. Such scale transitions are difficult to accommodate, yet are fundamental to our understanding of metapopulations.

In Chapter 3, a number of tools were developed for use with connectivity matrices. The tools find underlying structure in systems driven by biophysical interaction – structure which might not be immediately apparent from the spatial distribution of the populations. Obtaining connectivity matrices, sometimes expressed as dispersal kernels, is a fundamental goal for modellers studying marine organisms with benthic/pelagic lifestages, as well as other systems with spatially heterogeneous and discrete populations. These matrices contain enormous amounts of information, yet due to their complexity, much of this information, and its significance, is difficult
to obtain. The magnitude of the problem will increase markedly if the region of analysis is increased to the entire GBR.

Significant simplification is possible if we are able to separate a metapopulation into smaller, more manageable sub-sections. It would be simplistic to consider members of an interlinked metapopulation as disparate and independent local populations, but by analysing the reducibility of the connectivity matrices, we can expose large-scale structure in the metapopulation without losing detail.

The work reported here on reducibility can isolate structure in a larger metapopulation, caused by dominant directions of transport or migration (Shulman and Birmingham, 1995). It is worth noting that the dominant directions of flow are not always as obvious as they proved to be in the analysis of the GBR – there might be cases when a secondary, opposite flow will make it difficult to permute the matrix into a completely reduced form. If judicious choices are made as to the regions examined, however, and if only the larger transports are incorporated, the primary direction of larval flow/migration can still become evident.

Correlation analysis is a simple statistical method, which I have implemented here to determine if local populations on different reefs act in concert, when considering the dispersal of their larvae to a specific target reef.

There is much more statistical analysis to be done in determining how such inter-reef alliances work, and what are the major causes. It would be beneficial to determine the important physical processes governing this cooperation: some possible causes might include the El Niño cycles of the Pacific, or perhaps the point where the East Australian Current (EAC) bifurcates against the continental shelf. The most likely cause, however, is the way by which wind-driven currents force specific flow patterns.

When these methods were applied to the GBR, it became obvious, through both metapopulation modelling and the analysis of the connectivity matrices, that there was a significant biological-hydrodynamic split in the Cairns section of the GBR. This split was centered about the gateway reefs (16.5°S, 145–146°E). The local pop-
ulations within the northern and southern segments displayed significant interconnections within themselves, and there was significant transport from the northern to the southern section. South to north transports between the sections, on the other hand, was rare. The only reefs that were capable of connecting the southern section with the northern section belonged to the small set of gateway reefs.

The gateway reefs re-emerged in a hypothetical analysis of metapopulation extinction, which argued that, in the event of a catastrophic loss of fish, rates of recolonisation of the GBR would depend on where the introduction of larvae took place. Near extinction, the heterogeneity of the GBR was underlined, as was the importance of both the reducibility of the system and the gateway reefs. If the recolonisation began on one of the southern reefs, then although the southern section of the GBR was recolonised rapidly, it was difficult to send enough larvae northward to recolonise the northern sector, and the gateway reefs became vital in linking the southern section with the northern section.

The reducibility of the GBR can be used to test the veracity of the larval dispersal model. One example of how this division of the GBR could be used to test hypotheses, is in realising larval dispersal paths. Many ideas are being generated in marine biology about what reef fish larvae can do, but there are very few data at all concerning what the fish actually do. If the hydrodynamic and dispersal of the system finds that, with only a limited range of sensory and motive capabilities, the larvae cannot disperse from southern reefs to northern reefs, then we have the makings of an empirical test.

Recent work by Jones et al. (2000) proved that it is possible (if both difficult and expensive) to track larvae throughout the pelagic stage, using techniques such as fluorescent otolith dyeing. The model of James et al. (2001) predicts that, in the 32 years considered, there was no transport whatsoever between certain reefs in the south, and certain reefs in the north. The reefs that never send larvae north are marked in Figure 6.1. Some of these are close enough to the division that, on the basis of spatial proximity alone, we would conclude they were sufficiently close to the northern reefs to transport larvae to them. The findings of the James et al.
Figure 6.1: The reefs marked in red are members of the southern region of the GBR, and never send larvae to the northern sector. Reducibility on the GBR is important to how we view the metapopulation. Simulations have shown that the northern section of the population is considerably more robust than the southern, and that the southern section of the GBR is to some
extent dependent on the north. If the GBR is involved in regional scale source-sink dynamics, this information should affect its management at the largest scale.

The methods that analysed the effects of high correlations on fish populations were shown to have some applications on the GBR. Negative correlations between different groups of reefs (whose members’ transports were positively correlated) were observed, meaning that certain regions in the system act in concert with respect to the destination of their larvae, and act in a complementary fashion with other groups of reefs.

In Chapter 5, the model used to explain the dynamics of a species of fish with a pelagic dispersal phase was defined, and non-dimensionalised in Appendix 1. Why such an environment is stochastic was explained, and one possible method of rigorously understanding the effects of this stochasticity, linearisation, was applied to a simple metapopulation. This method allows the effects of variations in the larval connections to be understood, and the impact on the variations on local population and biomass variance was thereby investigated.

The linearisation performed here employs techniques used in a similar context by Roughgarden and Hughes (1998, 2000) and Ives et al. (1999). It contains a solid argument for the inclusion of stochastic parameters, and in doing so it allows detailed analysis of covariance in the processes responsible for the variability. Simulations can provide a simple and effective way of complementing the analytical methods, and the combination of the two will offer more insight into the processes at work than either could alone.

The biomass of the system analysed was more stable when inter-population correlations were negatively correlated. A simple extension of this linearisation might consider the effects of an asymmetric connectivity matrix on the stability of the biomass, and the individual populations.

These methods help in understanding the complexity of a system like the GBR. Chesson (1997) notes, “the inclusion of spatial detail often quantitatively and qualitatively changes fundamental properties of population dynamics”.

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Recent work on the GBR by James et al. (2001), and Armsworth (2001) has used close ties with marine biologists to develop and implement biophysical factors into metapopulation, hydrodynamic models. Connolly and Roughgarden (1998) have done similarly innovative work on explaining latitudinal gradients in sessile organisms (barnacles), using an integrated framework of community dynamics and oceanographic processes. Many others (e.g., Chesson, (1997); Olson and Hood, (1994)) are expanding this field as well.

In marine metapopulations, especially those with a benthic/pelagic (or, more correctly, pelagic/benthic) life history, much of this spatial heterogeneity is due to the effects of hydrodynamic features in the environment. We must avoid falling into the trap of assuming that because two populations are spatially close, their inhabitants must be interlinked to a greater extent than when populations are more distant from one another. In reality, the spatial proximity of populations can be deceptive. Once we begin to include complex, strong and variable currents (especially in an environment where the spatial pattern of reefs further confounds these hydrodynamics), and physically active larvae, we find that in some cases neighbouring reefs might act as though they are on opposite sides of the system.

The only feasible way we can deal with these problems is by the use of innovative, biophysical models, and a closer collaboration between oceanography and ecology. Large scale modelling, and the analysis of its results, has an important place in ecology alongside empirical studies, so that they might augment, criticise and above all, act to corroborate each other.

In this thesis I have explored a number of new techniques, which have revealed interesting structure when applied to the GBR. Both the tools and the results offer the prospect for novel and potentially valuable insights into the complex ecosystem dynamics of the GBR.
Appendix 1

Metapopulation Model – Nondimensionalisation

The metapopulation model discussed in Chapter 5 can be nondimensionalised with a minimum of difficulty. Based on the Beverton-Holt density dependent relationship, the full metapopulation model needs a number of parameters to determine the specific function being considered. Nondimensionalisation can allow us to express the density of fish on a reef as a proportion of that reef’s carrying capacity, the maximum number of fish sustainable there.

The number density of the first age cohort on reef $j$ ($N_j(t)$) in year $t$, which results from a settlement of $S(t)$ larvae, can be expressed by the Beverton-Holt relationship,

$$N_j(t + 1) = \frac{\gamma S(t)}{1 + \beta S(t)}.$$  \hfill (A.1)

Obviously density dependence will be a function of the settling larval density, rather than the number of settling larvae.

If this reef is saturated with larvae (as $S(t) \to \infty$),

$$N_s = \frac{\gamma}{\beta},$$  \hfill (A.2)

which is denoted as the saturation density, and is the same on all reefs in the system.

Using equations (A.1 and A.2)

$$\frac{N_j(t + 1)}{N_s} = \frac{\beta S(t)}{1 + \beta S(t)} = F(t).$$ \hfill (A.3)

$$= F(t).$$ \hfill (A.4)
As a constant proportion of the settling cohort survive each year, the population density at any time is dependent on the number of fish settling in the last \((\omega - 1)\) years, where we recall that \(\omega\) is the maximum age of the fish. In the model used to generate the data in Chapter 4, \(\omega = 5\).

Therefore, the population density on reef \(j\) at any time is

\[
N_j(t) = \sum_{i=1}^{\omega} q^{i-1} N_j(t - i + 1)
\]

(A.5)

\[
= \sum_{i=1}^{\omega} N_a q^{i-1} F(t - i).
\]

(A.6)

If we consider the entire metapopulation, we can use the above equations to construct a dimensionless analogue to equation (5.4).

The number of larvae arriving per unit area on a particular reef \(b\) is dependent on the total output of every other reef in the system, multiplied by the proportion \((p_{ab})\) of larvae from each reef that are transported to reef \(b\). This is called \(T_{ab}\), the transport density from some reef to reef \(b\), and can be expressed as:

\[
T_{ab} = \frac{p_{ab}(t) A_a}{A_b} f_1 \sum_{i=mat}^{\omega} q^{i-1} \phi_i N_a(t - i + 1)
\]

(A.7)

where \(A_b\) is the area of reef \(b\), and \(\phi_i\) is the fecundity of the \(i\)th age class, relative to \(f_1\), the fecundity of the first breeding age class. \(N_a\) is the number of fish in the first age class on reef \(a\), and \(mat\) is the age of reproductive maturity.

\(Z_b\), the size of the total settling cohort on reef \(b\) is the sum of the \(T_{ab}\) contributions over the \(M\) reefs in the metapopulation. We would rather not specify the absolute fecundity of the fish at all, so we normalise by dividing through by the maximum number of larvae that a unit area can produce. Thus we define a new \(Z'_b\) as the larval supply density, relative to the maximum possible larval supply density. Hence

\[
Z'_b = \sum_{a=1}^{M} \frac{p_{ab}(t) A_a}{A_b} f_1 \sum_{i=mat}^{\omega} \phi_i q^{i-1} N_a(t - i)
\]

(A.8)

\[
= \frac{f_1 \sum_{i=mat}^{\omega} \phi_i q^{i-1} N_a}{f_1 \sum_{i=mat}^{\omega} \phi_i q^{i-1} N_a} \sum_{a=1}^{M} \frac{p_{ab}(t) A_a}{A_b} f_1 \sum_{i=mat}^{\omega} \phi_i q^{i-1} N_a(t - i)
\]

(A.9)
\[
\sum_{a=1}^{M} \frac{P_{ab}(t)A_a}{A_b} \sum_{i=\text{mof}}^{\omega} \phi_i q^{-i} F_a(t - i) /
\sum_{i=\text{mof}}^{\omega} \phi_i q^{-i}.
\]  \hspace{1cm} (A.9)

This leaves us with a significantly simpler expression for the number density of first
generation individuals relative to the maximum number at that particular reef:

\[
F(t) = \frac{\beta' Z'(t)}{1 + \beta' Z'(t)}.
\]  \hspace{1cm} (A.10)

For simplicity, the new nondimensional parameter, \(\beta'\), is referred to in the rest of
the text as \(\beta\).
Bibliography


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