# A multi-species spatially-explicit bio-economic model of a marine reserve 

By
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A report submitted in partial fulfilment of the requirements for the MSc and/or the DIC.

11th September 2007

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#### Abstract

This study describes a model developed to investigate the implications of marine reserve establishment for stocks and harvesters for a mixed fishery for queen conch and Caribbean spiny lobster. Modelling space explicitly allowed the examination of resource distributions over space, as well as the implications of reserve geometry and differential impacts on species with different movement behaviour. Using an agent-based behavioural model to simulate heterogeneities in fisher behaviour allowed the investigation of the effects of reserve establishment and fish distribution changes on fishers with different strategies as well as the implications of varying degrees of illegal fishing.

The model was parameterised with data from an existing reserve in coastal Belize (Gladden Spit marine reserve), and its behaviour verified against expectations through sensitivity analysis. Existing results from the literature were then confirmed and some additional conclusions drawn, namely that: reserves with shorter boundary lengths can maintain greater stock biomass for a particular number of supported fishers than those with longer boundary lengths; adult spillover, whilst occurring to some extent for all reserve configurations, only rarely compensates for the loss of fishing grounds; illegal fishing, whilst relatively unimportant in low effort fisheries, has the capability even at very low levels to undo the benefits of reserves in high effort fisheries; and that under some circumstances particular strategies significantly increase the vulnerability of fishers to changing fishery circumstances, particularly the loss of aggregate catch due to reserve establishment.


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## Glossary of Terms and Abbreviations

| Alle effect | The Allee effect describes a scenario in which <br> populations at low numbers are affected by a <br> positive relationship between population growth <br> rate and density, which increases their likelihood <br> of extinction. |
| :--- | :--- |
| by-catch | Species caught in a fishery intended to target an- <br> other species, as well as reproductively-immature <br> juveniles of the target species. |
| catch per unit effort | (CPUE) The total catch divided by the total amount <br> of effort used to harvest the catch. |
| A group of fish that have the same demographic |  |
| characteristics, such as belonging to the same |  |
| age class of a given stock. |  |

Ideal Free Distribution
marine reserve
meta-population
ontogenetic
overcapacity
patch
recruitment
self-recruitment
sink population
(IFD) A term that describes the way in which animals or harvesters distribute themselves between several patches of resources. Assumes freedom for all to reach all patches, equality amongst individuals and complete knowledge of resource distributions.

An area of ocean or shore that is protected, usually through a complete ban on fishing activity.

A group of spatially seperated populations of the same species which interact at some level, often through movement of larvae from one to another.

Pertaining to the development of an organism, or the stage of development of an organism.

The presence of too many fishers or too many fishing vessels in a fishery. May lead to overfishing and resource degradation.

In modelling, a spatially distinct area and an associated population. Models use multiple patches to distinguish spatially separated populations experiencing different conditions and pressures, but between which there may still be exchange of individuals.

Juvenile recruitment: the movement of juvenile fish from nursery habitat into adult habitat. Recruitment into a fishery: fish reaching an age or size at which they can be harvested by the fishery. Recruitment into an area: the arrival and settling of fish (often juveniles) into a particular area.

Where each successive generation of a population in a specific area are direct descendants of the current adults within that local population.

A population in which there is no self-recruitment and in which each successive generation of individuals is seeded by a separate distance source population.

| source population | A self-recruiting population which also exports <br> larvae to other populations in a meta-population. |
| :--- | :--- |
| spatially explicit modelling | Including an explicit representation of space by <br> modelling more than a single location and allow- <br> ing differences in each to be represented. |
| spawning stock biomass | (SSB) The total biomass of the spawning (ma- <br> ture) adults in a population. |
| spillover | The net export of adult fish from a marine re- <br> serve or no-take zone. |
| stochastic | Synonymous with random. The outcome of <br> stochastic models are at least partially deter- <br> mined based on random trials, whereas deter- <br> ministic models will always produce the same <br> output for a given starting condition. |
| technical interactions | Interactions between species mediated through <br> fishing. For example where increasing sale price <br> of one particular species in a fishery, by increas- <br> ing the total number of fishers supported also <br> increases fishing pressure indirectly on other <br> species. |
| trophic interactions | Essentially consumptive interactions between <br> species through herbivory and predation. |

## Chapter 1

## Introduction

Since the middle of the last century, it has become increasingly apparent that the long-held assumption that the oceans can be considered infinite and inexhaustible is no longer valid. Growth in the human population and the mechanisation of fishing have combined to increase the demand for, and the accessibility of most of the ocean's living resources. As a result, fish stocks have been harvested with increasing vigour and over the last decades have been dwindling alarmingly and in some cases have collapsed entirely (Heyman \& Requena, 2002; Walters, 1996; Pikitch et al., 2004).

In response, a wide variety of management techniques have been tried with varying degrees of success, including: effort control, gear restrictions, seasonal closures, catch quotas, fishing bans and marine reserves. Many of these have been shown to be ineffective at preventing fish stock collapses, in part because they are often dependent upon unreliable information about the state of the stocks being managed (Jonzen \& Lundberg, 1999; Guenette et al., 1998; Russ, 2002). Although management systems which take this uncertainty into account are now being trialled there is scepticism about how successful they may ultimately prove (Lauck et al., 1998).

However, marine reserves (or no-take zones), by permanently protecting a fixed proportion of habitat and especially juveniles (Roberts \& Sargant, 2002), suffer less from inadequacies in information about the stocks under management and hence are likely to be a more resilient and precautionary method
for protecting against stock collapse, as animals within their boundaries are offered full protection (Lauck et al., 1998): Greater levels of enforcement are possible compare to with traditional management for commercial fisheries as a result of the development of global positioning technology that can track the exact location of fleets. In artisanal fisheries because multiple landing points, fishing for personal consumption and sheer number of participants mean that conventional management techniques require unavailable levels of resources to implement.

As a final benefit, the importance of which is coming to be appreciated more and more, marine reserves also extend protection beyond commercial fish stocks to all species and the habitat within their boundaries (Sumaila et al., 2000). Given the complexity of the network of interactions and dependencies between species in an ecosystem and our limited understanding of how they work, measures such as marine reserves which protect a habitat intact are beginning to be considered essential in many cases to ensure the long term health of important marine resources (Guenette et al., 1998).

Alongside a developing understanding of the biology of natural resource management has come the realisation that conservation problems cannot be dealt with in isolation but rather must take into account the economic, social and developmental needs of any dependent human population. Where once exclusion and fences were seen to be the best solution for preventing resource over-use by a local population (Milon, 2000), it is now becoming increasingly apparent that conservation programmes that do not engage with local people, that do not take into account the needs of local people, that do not respect local knowledge and that do not seek to gain approval of local people are often destined for ultimate failure (Russ \& Alcala, 1994). Thus any modern conservation programme with hopes for truly sustainable implementation must always consider the needs of the human population on an equal footing with that of the wildlife.

Such a holistic approach is especially important when considering the management of marine resources, as so many of the world's poorest people are directly or indirectly dependent upon small and medium scale fishing industries often without possible alternative livelihoods (Coutts, 2001). A general
lack of knowledge about fisher behaviour (especially in small-scale artisanal fisheries) means that in many cases the full social implications of a conservation programme may not be realised until some time into implementation. On some occasions this can lead to a failure of the conservation objectives, and in others it can lead to vulnerable sections of a fishing community being put under additional stress. Greater understanding of fisher behaviour and the differential resilience of disparate sections of a fishing community is therefore necessary to ensure positive conservation outcomes (Salas \& Gaertner, 2004a).

Although all forms of fishing restriction can be seen to be threatening to dependent local communities, marine reserves are often viewed with particular hostility (Gell \& Roberts, 2003). This is often in part because of the external imposition of controls on what is often considered a traditional, shared resource, but especially when local stakeholders are not involved in their design, or when changes in circumstances (be they biological or social) are not met with adaptive responses by reserve managers (Guenette et al., 1998). In order to sell a new reserve to a community it is therefore of particularly importance to have considered the likely effects on that community and to present them openly.

Despite having been first formally considered by Beverton and Holt in 1957, marine reserves have only recently started to be used in significant numbers. Consequently there are few long term empirical studies of such reserves (Roberts \& Sargant, 2002), and as a result a large part of the work on characterising the effects of reserves has been carried out through modelling studies (Gerber et al., 2003). It is on the basis of such simulations that most reserves have been justified. Until recently such models have often been highly simplified usually including only a single species and amongst other things leaving out population structure, spatial structure, the relationship between stock and recruitment, the economics and social aspects of fishing and fisher behaviour (Pelletier \& Mahevas, 2005). Recent further research, building on these first generation studies and enabled by increasing understanding (and in some cases, computing power) has shown that such simplifications can lead to misleading conclusions being drawn about the usefulness and applicability
of reserves, often to the detriment of the areas under management (Smith \& Wilen, 2003).

By contrast, this study develops a spatially explicit bio-economic model of a two-species fishery, for Queen Conch (Strombus Gigas) and Caribbean Spiny Lobster (Panulirus Argus) and by including a greater number of components than many existing models, attempts to study the interactions so enabled in order to gain a greater understanding of the implications of fisher behaviour, area closures of differing geometries and other fishing restrictions on the fish stocks and the economic well-being of the dependent fisher population.

Finally, the model will be applied to a data-poor case study artisanal fishery for conch and lobster in the central American state of Belize. It is hoped that sufficient insight will be gained to be able to offer recommendations as to how to improve the effectiveness of the management in order to improve the outcomes for both fish stocks and fishers.

### 1.1 Aims

This thesis presents a multi-species, spatially explicit bio-economic model developed to address these aforementioned issues by including densitydependent movement, multi-species interactions through fishing effort and an agent-based model of fisher behaviour.

The model will be used to investigate the effects of the behaviour of the two different species and different reserve configurations and geometries on spillover and fisheries outcomes, with a view to evaluating marine reserves against more traditional management techniques. Attention will also be paid to the differential effects such management regimes may have on the two species.

This study will also investigate the implications of greater realism of fisher simulation, seeking to explore the economic and social implications for the associated fishery and in particular to explore the effects of differing behaviours on total fisher numbers and on fisher resilience to change.

### 1.2 Objectives

To meet these aims, this study will aim to answer the following questions:

## Spillover

- How the phenomenon of spillover affects the biomass within a reserve and the economics of a dependent fishery.
- How conservation within a reserve and spillover from a reserve is affected by fish behaviour, and in particular by movement behaviour.
- How conservation within a reserve and spillover from a reserve is affected by its geometry (area and boundary length).


## Species interactions through effort redistribution

How reserve establishment can affect the redistribution of fisher effort as a result of the differing behaviour of the species under study.

## Fisher behaviour

How increasing the realism of fisher behaviour can affect the biological, economic and social outcomes of reserve establishment, and what it can tell us about the differing resilience of fishers with different fishing tactics, including by:

- Restricting the knowledge of fishers about fish distributions.
- Requiring fishers to find out about new sites through experimentation or falling back on sites known from previous exploration.
- Allowing varying degrees of communication of known good fishing sites between fishers.
- Allowing a certain percentage of the fisher community to cheat (fish illegally within the no-take zone).


## Chapter 2

## Background

### 2.1 Fisheries management and marine reserves

Most of the world's fish populations are now exploited at or beyond a sustainable level and the habitats and ecosystems upon which they depend have become increasingly degraded by fishing and other human activities (Guenette et al., 1998). Awareness of the problem of overfishing and fishing using destructive techniques has been around for several decades and in that time an increasingly sophisticated literature has developed concerning the sustainable management of the oceans (Russ, 2002; Guenette et al., 1998). Over the same time different techniques for fisheries management have been developed, have come into fashion and have mostly been shown to be inadequate - either through inadequate enforcement and illegal fishing, political unacceptability, lack of understanding of the dynamics of a fishery or through large uncertainties in data about stock health (Russ, 2002). The most notorious of such failures was the collapse of the Newfoundland Grand Banks cod stock, a fishery that was under active scientific management, but where overconfidence in stock assessment models and the poor quality of stock assessment data were nevertheless able to take a once unprecedentedly productive fishery beyond the brink of collapse (Walters, 1996).

As a result of these failures and the realisation of the additional growing
pressures arising as a result of global environmental change, there is a growing understanding that fisheries management must be more responsive and more iterative, more precautionary and must go to greater lengths to ensure that the uncertainty in stock assessment fish and fisher behaviour is properly appreciated and incorporated into management models and procedures. Furthermore it is now apparent that by focusing management solely on maximising the catch of a single species, and ignoring effects on habitat, by-catch species and ecosystems as a whole there have been further unintended consequences - a case in point being the US recreational white marlin fishery in which $90 \%$ of the mortality is through by-catch from the swordfish and tuna long-line fisheries. This risks a two billion dollar industry as well as further threatening a species already being considered for inclusion on the U.S endangered species act list (Pikitch et al., 2004).

### 2.1.1 Overview of effort restrictions

In table 2.1 on the next page the main tools of fishing effort control are outlined along with a brief description of their advantages and disadvantages. It is worth mentioning that although many instances of fisheries management using these tools have resulted in undesirable outcomes, it is often the management methodology rather than the effort control tools that have failed (Caddy \& Cochrane, 2001). However it is true that some of these methods are inherently more suited to precautionary management than others.

In order to attempt to learn from and overcome past failures of management, a new holistic methodology, Ecosystem-based fishery management (EBFM), is being discussed and developed (Hall \& Mainprize, 2004). EBFM, as well as advocating a robustly precautionary approach also broadens the management focus from a single or a few commercially important species to an entire local ecosystem. By doing so EBFM recognises the importance of maintaining a functioning and healthy ecosystem to ensure a similarly healthy fishery, but also acknowledges the wider value of the marine environment. Central to many applications of EBFM are marine reserves (Hall \& Mainprize, 2004), which offer protection to a proportion of habitat through the exclusion of

Table 2.1: Overview of various fishing control methods (McClanahan \& Castilla, 2006)

| Fishing method | Description | Advantages | Disadvantages |
| :---: | :---: | :---: | :---: |
| Gear restric- tions | Restricting the type of fishing gear/techniques allowed. A typical example would be to mandate minimum mesh sizes on nets to prevent the catching of juveniles. Another example would be to ban scuba gear for a dive fishery, thus protecting animals living below the freedive limit of 10 m . | - Offers some protection for juveniles. - Is relatively straightforward to implement. | - Some forms of gear restriction are difficult to police. <br> - Gear selectivity is often not very sharp and juveniles get caught nonetheless. <br> - Selectivity is only appropriate for one species, so doesn't work well in multi-species fisheries or those with significant by-catch. |
| Seasonal closures | Closing some or all of a fishery for particular periods of the year. Often used to ensure protection of spawning stocks, whether over a whole fishery or just a nursery area. | - Offers protection to spawners | - Relies on accurate and precautionary modelling to determine the appropriate length of closures |
| Catch quotas | Restricting the amount that a fishery, vessel or fisher can catch in any given period. | - If knowledge of the state of the stock is good, setting a quota can be an effective way of keeping the catch within a sustainable limit. | - Relies on accurate and complex precautionary modelling of the fishery to determine an appropriate quota. <br> - Global catch quotas can result in vessels and fishers competing to catch as much of the quota themselves as possible. Can lead to overcapacity and shortened fishing season |
| Fishing permits | Restricting fishing to vessels or fishers with an appropriate permit. The number of permits is often controlled in an bid to restrict fishing effort. | - Similarly to catch quotas, if knowledge of the state of the stock is good, can be an effective way of maintaining a sustainable stock level. <br> - If permits can be bought and sold can be a flexible way of devolving entry and exit to and from the fishery. | - Relies on accurate and precautionary modelling <br> - Can be considered culturally unacceptable in some traditional fisheries where the right to fish is considered a traditional entitlement. |
| Effort restric- tions | Restricting the number of fishing days or fishing vessels | - Simple to understand | - Often leads to competition between fishers, escalation of technology, overcapacity and a shortened fishing season. <br> - Particularly damaging when the restrictions do not take into account the increasing CPUE of modern fishing vessels. |
| Outright bans | A total closure of a fishery for an extended period. Used only for extremely depleted stocks where the only alternative is commercial extinction. | - If implemented on time and enforced properly can result in the recovery of very degraded stocks. | - As a last resort measure, often implemented too late to have any effect. <br> - Very politically unacceptable. |
| Marine reserves | A permanent closure, or permanent fishing restrictions within a defined geographic area. | - Can provide a healthy spawning population as an insurance policy against overfishing. <br> - Protects ecosystems as well as individual species | - A simple rule, but can be negative to fishers and hence can be difficult to introduce and enforce. <br> - May rely on good knowledge of species biology and behaviour in order to determine appropriate size, location and geometry. <br> - Reserve establishment often trades stock protection for fishery yields. |

fishing effort. Unlike most other management methods, marine reserves do not require precise, detailed and real-time knowledge of the state of an underlying fishery in order to safeguard the health of a stock. By definitively protecting a proportion of a fish population, they provide a de facto insurance policy against fisheries management failure and as such are beginning to be considered an essential component of any strategy seeking to safeguard the health of the oceans.

### 2.1.2 Marine reserves

Until recently, marine reserves have not been widely used as a fishery management tool. In one of the earliest and most influential analyses of their benefits and drawbacks, Beverton \& Holt (1957) concluded that reserves were (in the context of single-species management) largely equivalent to a combination of more traditional fishing restriction measures. They also concluded from a related modelling study that the effectiveness of reserves was very dependent upon having an accurate model of fish movement behaviour - and that as a result the balance fell more on the side of traditional management measures and against the use of marine reserves. Nonetheless, having subsequently learnt about the difficulties of assuring satisfactory outcomes with traditional fishing methods, the science and application of marine reserves is now making a comeback (Guenette et al., 1998).

One of the most significant outstanding issues with marine reserves is their political acceptability to an affected fishery. Reserves often succeed or fail not on the basis of any biological issue, but as a result of how they are accepted by a dependent fishing community or industry. Central to allowing a reserve the best chance of success is the involvement of the people who will be affected. In Russ \& Alcala (1994), the authors report two starkly different outcomes of reserve establishment in the Philippines. The Apo and Pamilican reserves proved an enduring success because they were supported and managed by local people who believed in the potential benefits from reserve protection. But in another reserve, despite it also having been acknowledged to have positive
effects, the perception that it was being imposed from outside drove fishers to contest its legitimacy ultimately resulting in protection being withdrawn.

Once under the protection of a marine reserve, the populations of fish protected will often increase to concentrations considerably higher than those in surrounding exploited areas. Whether through random diffusion or through migration in search of less densely populated areas (Russ et al., 1992), it is assumed that there will be a considerable degree of export from the reserve into adjacent areas. This export is often used to justify marine reserves to dependent fishing communities and industries and although it only compensates fully for the lost fishing area in particular circumstances, still provides an offset against the losses in catch from fishing grounds no longer accessible (for instance in the case of the spiny lobster fishery in Florida Bay (Davis \& Dodrill, 1989)).

Moreover although some fishing methods are particularly damaging to the habitat in which they are practised, some authors have also concluded that almost all fishing methods cause some degree of environmental damage (Abernethy et al., 2007). It is often the case that a damaged habitat is less able to support a healthy fish population. By extending protection beyond commercial stocks to an entire habitat it has been speculated that through recovering to a more pristine level, an ecosystem could become even more productive than expected once protected by a reserve (Guenette et al., 1998).

Biomass export from marine reserves occurs in two major mechanisms: through the "spillover" of adult fish moving across the reserve boundaries, and through larval export. Through long retention times in the water column, export of pelagic larvae may affect regions many tens or hundreds of kilometres distant from the region protected. Of these two mechanisms, larval export is often considered to provide the greatest aggregate benefits to wider surrounding areas (Guenette et al., 1998). Adult spillover is on the other hand a local effect, providing obvious benefits to local fishermen and hence increasing acceptability. In a connected meta-population spanning great distances, it can be difficult to justify potential damage to local livelihoods by citing benefits to be obtained by people tens or hundreds of kilometres away, potentially even in different countries.

Studies show that for many species, a significant proportion of the subpopulations of a meta-population are not self-recruiting (Acosta, 2002). Thus many areas are reliant on larvae from distant (self-recruiting) source populations. It is doubly important that source populations are ensured full protection - firstly because, being self-recruiting, it is possible to irreversibly collapse a stock by over-extraction, and secondly because should such a collapse occur it could propagate to all dependent sink populations (Sanchirico \& Wilen, 1999). Marine reserves established over source populations can provide a robust insurance policy against a collapse both locally but also in all downstream sink populations and thus have benefits with effect considerably beyond the local (Guenette et al., 1998).

For species which undergo ontogenetic migrations as they develop, it is essential to ensure that both juvenile and adult habitat is protected for the full benefits of a reserve to be felt. The best possible outcomes are possible when a network of reserves is established covering a significant proportion of all important representative habitats (Russ, 2002).

Finally, despite the precautionary nature of marine reserves, it is not enough to assume the mere act of establishment to be in itself sufficient. They must instead be monitored in order to ensure that the anticipated outcomes are being achieved, and when this is not happening, management should be able to adapt to ensure they remain effective (Guenette et al., 1998). Moreover as marine reserve science is still a relatively new discipline with few reserves having been established for long enough for a significant body of empirical findings to have been established, reserves can also be considered an effective learning tool - but without the risk of catastrophic stock collapse inherent in some of the more traditional management methodologies (Lauck et al., 1998).

Until such studies and experiments have been completed, the majority of the science of marine reserve evaluation is being carried out through modelling studies. An overview of the development and state of the art in marine reserve modelling follows below.

### 2.2 Modelling

As scientific understanding of fish behaviour and biology has increased and as the economics of fishing have started to become included, so has the sophistication of modelling grown. This section provides a review of existing models and what they have been able to achieve, starting with the simplest foundational models and progressing through to the most sophisticated contemporary models.

### 2.2.1 Two-patch models

The minimum requirement for modelling the effects of an area closure on a stock is that two distinct populations must be simulated with a different level of fishing effort in each (so-called two-patch models (Pelletier \& Mahevas, 2005)). Even for such a seemingly simple model there are many sources of complexity: should the populations modelled be sink populations or self-recruiting? Should the stocks be represented solely by a single figure representing the biomass contained (a so-called lumped population model), or should they include some level of population structure where age or size or stage is distinguished? How should flow between the two patches be controlled? Should movement be in both directions or one only? Should it be through random diffusion or should it be determined by the relative densities of populations in each patch, or should it be seasonally controlled or reflect the different habitat requirements of a species as it matures? Should growth in the model be dependent on population densities? Should natural mortality be included as well as fishing mortality?

Most of the initial work in marine reserve modelling was carried out using two-patch models incorporating different combinations of the above design options and many of the initial conclusions have proved important and longlasting (Pelletier \& Mahevas, 2005). Simple lumped population models have been used to show that the outcome of reserve establishment is heavily dependent on the movement behaviour and mean movement distance of
the species to be protected, with low mobilities (relative to reserve size) corresponding to better protection and high mobility corresponding to least protection (Pelletier \& Mahevas, 2005).

As well as addressing issues of stock enhancement, two-patch models have been applied to the question of how associated fisheries will react to area closures, and to estimating how much spillover of adult biomass will occur and how that might offset the loss of revenue from the reduction in fishing area (Apostolaki et al., 2002). The best chance of benefits to both fish and fishers are shown to be achieved when species have medium levels of mobility relative to reserve size, and hence some protection is afforded to the fish, but also some export occurs to help offset fishing losses (Apostolaki et al., 2002). In some studies so called "double benefit" situations can occur, where aggregate fishery catch is increased alongside fish stocks - solely through the mechanism of adult spillover. However in most studies such an effect is only seen when a fishery is very heavily exploited (Sanchirico \& Wilen, 2001).

### 2.2.2 Structured populations

When individuals in populations are differentiated by age or size or life stage and are included in two-patch models, some studies have predicted that double benefit situations can occur even in fisheries that are not heavily overexploited. Apostolaki et al. (2002) show that when there is significant juvenile by-catch in a fishery in which there is self-recruitment, marine reserves, by protecting a proportion of juveniles through to maturity can increase both stock levels and aggregate fishery catches by increasing the spawning stock biomass (SSB).

By also including a larval stage in the age structure of such models, and by increasing the number of patches, it becomes possible to investigate the effects of larval export between patches (Smith \& Wilen, 2003). Although in many cases very little is known about larval dynamics, what is known is that not all populations are self-recruiting. In larger connected meta-populations where some areas are sources, some sinks and some a combination of the
two, some modelling studies have confirmed that source populations, being self-recruiting are particularly vulnerable to overfishing (and hence once exhausted may not be able to recover) and particularly important as they are the source of larvae for remote populations in the meta-population structure and hence high priority targets for conservation (Sanchirico \& Wilen, 2001).

### 2.2.3 Multi-species models

A small number of models have simulated multi-species assemblages and have taken into account the interactions between them. In most cases these interactions have been trophic in nature and have investigated the effects of fishing a prey species on a dependent predator species (or vice versa) (Pauly et al., 2000). In some other cases the interactions between species through fishing (so called technical interactions) have also been studied (Laurec, 1991). These studies show that management of one species in a multi-species multi-gear fishery, through changes in the economics of fishing, often has impacts on the level of fishing and hence biomass of the others. They conclude that such fisheries must be managed as a whole, and that attempting to manage each species in isolation would often be futile.

### 2.2.4 Space and geometry

Earlier patch-based models made implicit assumptions about how the geometry of the reserve area relates to biomass export behaviour; whether density-dependent or through random diffusion or as a result of ontogenetic migration. By modelling space more explicitly, often by subdividing areas into a fine grid of patches of equal area representing adjacent regions in space, later models have been able to investigate the effects of movement behaviour and reserve geometry on spillover, fish stocks and fisheries (Pelletier \& Mahevas, 2005) in order to design reserve layout optimally for particular species or combinations of species (Kellner et al., 2007). Other models have considered the effects of habitat heterogeneity on marine reserve location and
have shown that spillover and protection benefits are likely to be maximised by protecting the best habitat within an area (Jonzen \& Lundberg, 1999). However few models have addressed space and movement explicitly in order to derive spillover magnitude and distribution from first principles of fish movement, and few have considered reserve geometry and how it interacts with fish movement, or how different reserve geometries may differentially affect the protection of different species.

### 2.2.5 Effort, economics and fisher behaviour

Whilst earlier studies included fishing as a constant extra level of mortality over and above natural mortality, later models have started to address the reallocation of fisher effort upon reserve establishment (Pelletier \& Mahevas, 2005; Smith \& Wilen, 2003). In the simpler cases this could take several discrete forms: no reallocation, all fishers in the reserve leave the fishery; full reallocation, all fishers in the reserve now fish outside the reserve; or some partial redistribution in-between (Apostolaki et al., 2002). In Smith \& Wilen (2003), the authors compared two models of fishing: a simple model assuming constant fishing effort with predetermined redistribution after reserve establishment (similar to that in the study by Apostolaki et al. 2002), and a more sophisticated economic model of fishing in which effort adjusted with the profitability of the fishery, with fishers leaving when catches became reduced (whether by natural equilibration or after reserve establishment). They found that the simple model of effort, widely used in modelling studies, materially affected the outcome of reserve establishment, in particular by overestimating fishing effort and hence underestimating equilibrium fish population sizes. They concluded that as a result of these systematic errors, studies ignoring economic behaviour will generally result in conclusions that are biased towards the establishment of reserves over other forms of fishing restriction.

Despite a developed literature addressing marine reserves, the field of bioeconomic modelling extends to evaluate all aspects of fisheries and fisheries
management and such models often include a social component to complement the biological component. Thus as well as providing a better estimation of conservation outcomes in managed fisheries, such bio-economic models also allow the impact of changes and restrictions on fisher populations to be studied.

A number of studies have further developed bio-economic modelling by including increasingly sophisticated descriptions of fisher behaviour. Roberts \& Sargant (2002) incorporated the knowledge that fisheries are not heterogeneous in space or time; that there are better places and times for fishing than others, and that fishers target these. Hilborn \& Walters (1987) developed a model of fisher exploration where effort is allocated between fishing grounds by dedicating a fraction of effort to exploratory fishing and the remaining effort to areas with the highest catch rates. Other studies have also explored the implications of fisher learning and exploration behaviour (Moustakas et al., 2006; Dreyfus-Leon, 1999; Xiao, 2004). Still other models have investigated the implications of communication and friendship structure in fishing communications on fishing outcomes and how communication can compensate for differing intrinsic levels of fishing ability or resilience (Curtis \& McConnell, 2004; McClanahan \& Castilla, 2006).

### 2.2.6 Summary

Although many models incorporate some of the aforementioned aspects of modelling/fish behaviour/economics/fisher behaviour, few include more than a small number. Table 2.2 on the following page provides an overview of the features included in a number of the aforementioned modelling studies.

A number of important aspects of reserves are still overlooked. In a review of existing models, Gerber et al. (2003) provide an overview of the results, methods, assumptions and simplifications behind each and identify areas for future development as outlined below:

1. Larval dispersal is rarely modelled explicitly.

2. Few models include density-dependent effects and in particular densitydependent growth.
3. Fisher behaviour is often highly simplified.
4. The social impacts of restrictions are rarely considered, and the complexities, heterogeneities and differential vulnerabilities of livelihoods in real fishing communities are often overlooked.
5. Multi-species interactions are rarely considered whether through trophic or technical interaction (Laurec, 1991).
6. The effect of fishing on vital habitat is ignored.

### 2.3 Biology

The two most commercially important species in the Caribbean are queen conch and spiny lobster. Both are generally fished together in multi-gear artisanal fisheries, and both are currently overexploited in many regions (see section 2.5 for further details). Both have limited movement, known habitats and well documented biology and life history. Together these attributes mean that the two species are of conservation interest, are likely to be coupled through technical and economic interactions and because of their relatively low movement rates are both amenable to protection by reserves and likely to develop measurable spillover. Hence (and because they are also of particular importance to the case study area) they and their fishery are the focus of this study.

### 2.3.1 Recruitment

The life histories of queen conch and spiny lobsters share some similarities. Both have a lengthy pelagic larval stage (6-11 months for lobster, 0.5-1.5 months for conch) (Saul, 2004; Stoner, 1997). Being notoriously difficulty to
study, little is known about the movement dynamics of pelagic larvae. Long distance dispersal is dominated by ocean drift currents which require detailed local study to characterise with any certainty (Saul, 2004; Stoner, 1997). Despite having little control over lateral movement, larval settlement often occurs preferentially in suitable habitat implying that larvae have some control over the process - presumably through control over vertical movements. However as many reef areas are subject to a constant slow drift current, there is no guarantee that there is substantial self-recruitment in any particular local area of reef under study (Acosta, 2002). As a result it is likely that many conch and lobster populations are not self-recruiting but are sink populations for larvae from further upstream, and in turn themselves export larvae downstream.

Larval recruitment occurs throughout the year, but with significant seasonal peaks in August for conch (Appeldoorn, 1988a) and between April and May for lobster (Mark \& Herrnkind, 1986). Both conch and lobster juveniles will settle in sea grass or other shallow vegetated locations as nursery areas (Acosta, 2002). Upon reaching maturity both species will migrate to adult habitats with lobster migrating to deeper offshore reef environments (Saul, 2004) and conch to reef and sandy/algal flats.

### 2.3.2 Mortality

Regardless of fishing pressures, only a certain proportion of individuals survive from one year to the next as a result of natural processes such as predation and disease. Such natural mortality is often relatively consistent for a particular combination of species, location and age. The proportion surviving is often fitted to the following standard equation (Caddy, 1991):

$$
N_{a+1}=N_{a} \cdot e^{-M_{a}}
$$

(Where $N_{a}$ represents the number of individuals at age $a, M_{a}$ is the natural mortality at age $a$ and $e^{-M_{a}}$ represents the proportion of individuals surviving from age $a$ to age $a+1$.)

Natural mortality is not always easy to separate from fishing mortality when studying exploited populations. Combined (natural and fishing mortality) can be represented using the following equation:

$$
N_{a+1}=N_{a} \cdot e^{-Z_{a}}, Z_{a}=M_{a}+F_{a}
$$

(Where $F_{a}$ represents fishing mortality and $Z_{a}$ represents combined fishing and natural mortality. Note that in most uses, this equation makes the strongly simplifying assumption that fishing mortality is an exogenously determined constant and not responsive to fish population levels).

For both Queen Conch and Caribbean Spiny Lobster there are a number of empirical studies which have attempted to determine M. As both species mature, their susceptibility to predation decreases but at different rates and a survey by Cochrane \& Venema (1997) suggest that whereas adult lobster are subject to an effectively constant level of natural mortality as they age, conch, remain vulnerable for considerably longer and experience considerable levels of mortality before their shells thicken into adulthood (Appeldoorn, 1988b). Hence M can be approximated as a constant for lobster whereas for conch M is dependent upon age ( $\overline{\text { CFMC, 1999). }}$

### 2.3.3 Growth

Lobster growth proceeds through successive stages of carapace moulting and regrowth, but can be approximated reasonably using a von Bertalanffy growth equation (Cochrane \& Venema, 1997) as shown below:

$$
L_{a}=L_{\infty} \cdot\left(1-e^{-K\left(a-a_{0}\right)}\right)
$$

(Where $L_{a}$ is the length at age $a, L_{\infty}$ is the asymptotic (maximum possible) length of an individual and $K$ and $a_{0}$ parameters determining the rate at which the asymptotic length is gained for the particular species under consideration.)

Acosta \& Robertson (2002) show that there is a strong correlation between length and weight in adult lobsters that can be used to calculate lobster mass. This can be represented using a power law equation (Mark \& Herrnkind, 1986):

$$
W_{a}=p \cdot\left(L_{a}\right)^{q}
$$

(Where $W_{a}$ is the weight of an individual at age $a, L_{a}$ the length of said individual and $p$ and $q$ constants determining the relationship between length and weight for the particular species under consideration.)

Conch growth proceeds differently, with individuals continuing to increase in weight after their shell has developed to maximum length. As a result it is more appropriate to relate weight directly to age, and this can be done using the Gombertz equation (CFMC, 1999) which takes the form:

$$
W_{a}=x \cdot e^{y \cdot\left(1-e^{-z \cdot a}\right)}
$$

(With $a$ the age of an individual as before and $x, y$ and $z$ being constants determining the rate of growth for the particular species under consideration.)

The mortality and weight relationships for both species are combined in figures 2.1 on the next page and 2.2 on the facing page to show the typical biomass per hectare of each at each particular age.

These relationships are of considerable importance when considering fisheries management strategies. Fisheries in which fishers have the motivation, and are allowed to take individuals at an age to the left of the peak of biomass will experience considerable sustained reductions in yield.

### 2.3.4 Movement

Conch and lobster both have clearly differentiated nursery and adult habitats, and as adults both also occasionally participate in aggregative movement


Figure 2.1: Conch population total biomass at age


Figure 2.2: Lobster population total biomass at age
behaviour. However such aggregative behaviour is infrequent and does not on average substantially affect conch and lobster density patterns. A movement tracking study by Acosta (2002) shows that in normal circumstances both conch and lobster move as individuals in a pattern that is largely similar to a correlated random walk. In a correlated random walk, the movement of an animal is considered to unfold as a series of linear steps in different directions where the direction of each step is correlated to the direction of the previous step (e.g. after each move an animal will only change direction by $\pm 90^{\circ}$ ).

Other studies suggest that fish movement is density-dependent with individuals in high density locations seeking to move to adjacent lower density locations, whether because of territoriality or in order to minimise competition for resources (Abesamis \& Russ, 1995). As movement behaviour is considered likely to be an important determinant of spillover from a reserve (Beverton \& Holt, 1957), where it is not possible to distinguish between the two it is important to be able to evaluate the implications of both. In this study the simulation has been designed to allow the evaluation of both random walk behaviour (an approximation to correlated random walk) and density-dependent movement in order to allow such investigation.

### 2.4 Fisher behaviour

As mentioned earlier, a number of modelling studies have attempted to include more realistic models of fisher behaviour. Conventional bio-economic models, whilst successful at improving the conclusions from fisheries modelling, generally employ a very simplified model of fisher behaviour (Gerber et al., 2003). The most simplified behaviour appropriate to a spatially explicit model, and implicit in many such studies, is the ideal free distribution (IFD) (Fretwell \& Lucas, 1970). The IFD is used to determine fisher decision making over a spatially distributed resource and makes the following assumptions (Fretwell \& Lucas, 1970):

1. That fishers have full (ideal) knowledge of the spatial distribution of the fish stocks.
2. That fishers are free to move to any fishing grounds and catch any prey without constraint or cost.
3. That fishers are indistinguishable in every respect, including fishing ability and the opportunity cost of fishing.
4. That each fisher will (taking into account the distribution of all other fishers) move to the fishing grounds that maximises their returns.

However in real fisheries, especially artisanal fisheries, many of these assumptions do not hold. The distribution of fish is often only dimly perceived, measured locally by each fisher through the process of fishing itself with feedback obtained only in the form of the size of the catch at a particular place on a particular day (Mangel \& Clark, 1983). Fishing trips are normally subject to fuel costs, making more distant grounds more expensive to reach or in some cases inaccessible and fishers are often economically constrained to a single gear type. Moreover individual fishers are frequently neither uniform in fishing ability or in the number of fish they elect to catch. In a study of an artisanal fishery in Anguilla, Abernethy et al. (2007) studied how the behaviour of fishers in a small-scale fishery differs from the IFD and came to the following conclusions: by comparing the number of traps in a particular location with local fish abundance and finding that there was no significant correlation, it was clear that fishers had a very patchy knowledge of fish distributions; that social, economic and physical differences in fishers allowed some to perform better than others whilst preventing opportunistic gear switching; and finally that fishing pressure did not increase with resource availability but that, although some fishers did seek to maximise profits, others did not and caught only for personal consumption.

All the aforementioned deviations in behaviour from the ideal free distribution will materially affect the outcome of both constrained and unconstrained fisheries to some extent, and in general will result in a lower level of exploitation than predicted by the IFD (Abernethy et al., 2007). Such information is important when modelling and designing reserves, as an oversimplified understanding of fisher behaviour could lead to inefficient or incorrect man-
agement procedures and therefore harm the fishery - or more likely alienate the local dependent population (Gerber et al., 2003; Grafton, 2006).

As well as studying the impacts of reserve establishment and other fishery changes on the economics of a fishery, it is also important to consider the social impact. In small-scale artisanal fisheries, fishing may account for a significant proportion of daily food intake and the participants may in some cases have few or no alternative ways of making ends meet (?). Moreover in such communities there are often differences in the circumstances and ability of fishers as well as the tactics they choose when fishing and the strategies they choose over the long term to maintain their livelihoods (Salas \& Gaertner, 2004a). These heterogeneities in the community lead to different levels of vulnerability when changes in circumstances occur. Thus if it is considered important that livelihoods are to be maintained as well conservation objectives met, it is essential to understand how circumstances and tactics can lead to some groups being especially vulnerable in order to identify those groups and to provide them with help with adaptation (Salas \& Gaertner, 2004a).

Finally it is well documented that even in the best managed fisheries there will be some proportion of fishers cheating and ignoring the fishing restrictions (T.J.Pitcher et al., 2002). In some circumstances cheating can be sufficiently prevalent or of sufficient impact to compromise the achievement of fishery management objectives. It is therefore important to consider the complexities involved in enforcement, the implications of cheating and to continuously monitor a fishery to ensure that levels of cheating and their effect are adequately monitored in order to allow enforcement to adapt.

### 2.5 Belize and Gladden Spit Marine Reserve

The Meso-American barrier reef, the second largest in the world, extends along the entire coast of Belize, and is both extensive and diverse with all the main reef types represented as well as associated habitats such as mangroves and sea grass beds. This wealth of variety provides rich habitats for a wide range of marine animal and these in turn support a number of Belizean
industries. Of these the two most important are fishing and tourism. The former is largely artisanal and dependent upon Queen Conch, Caribbean Spiny Lobster and a variety of reef fish including Snappers, Jacks and Groupers (Pomeroy \& Goetze, 2003). Many of the fish caught are consumed locally by the fishers and their families, but there is also an export market which is often focused around local fishing cooperatives (Key, 2002). Until recently many coastal communities were dependent on fishing for their livelihoods, but with recent declines in fish stocks due to over-fishing, tourism has been becoming an increasingly important source of income (Key, 2002).

Queen Conch and Caribbean Spiny lobster are the two most economically important species and are hence subject to heavy exploitation (Acosta, 2002). As a result most coastal populations are in decline, with Queen Conch being particularly vulnerable as a result of Allee effects at low population densities (Stoner \& Ray-Culp, 2000). Declining stock and catches indicate that fishery regulations in many Caribbean countries, including Belize, are insufficient to protect local populations (Acosta, 2002) and marine reserves have been proposed as an alternative management tool to protect populations from extinction.

As the health of reefs worldwide has begun to decline as a result of human activities (including the discharge of pollution, overfishing and disturbance caused by tourism) so local and regional organisations have been formed to campaign for greater environmental protection (FoN, 2007). In 1993, the residents of Placencia, a local fishing village, became sufficiently concerned about the impacts of human activity on the reef that they established a small local NGO, Friends of Nature (FoN), to campaign for protection of the reef and its resources (FoN, 2007). Within a few years of establishment, researchers at FoN became aware that an area of the reef, Gladden Spit, was regularly visited at predictable times by aggregations of a number of species of reef fish in order to spawn. These aggregations had been heavily worked by local fishermen for many years and were also regularly visited by whale sharks (a favourite with tourists). In recent times the fishing activity had become sufficiently intense to threaten the health of these spawning aggregations, as evidenced by the significant decline in numbers of fish arriving from year to
year, and the virtual local extinction of one previously abundant species, the Nassau Grouper (Heyman \& Requena, 2002). With financial assistance from WWF, FoN was able to conduct a series of consultations eventually leading to the Gladden Spit area being declared a marine reserve in May of 2000. The reserve imposes a number of management methods on fishing within its boundaries; most importantly restrictions on the fishing of the spawning aggregations, the prohibition of scuba equipment when fishing for conch and lobster and the enforcement of a small no-take zone.

As mentioned earlier, the establishment and enforcement of marine reserves can cause significant local political difficulties, in large part because local fishermen perceive the reserves as a direct threat to their livelihoods. This is particularly strongly felt in Belize where there is a perception that the establishment of reserves is part of a deliberate conspiracy between the government, the wealthy and foreign conservationists to destroy the livelihoods of local fishermen (Pomeroy \& Goetze, 2003).

It is particularly important to explore the implications of reserve establishment on local communities as well as fish stocks and to present the results to local stakeholders before any management action is taken. There are few resources available locally to study the area in any depth, and so information about the health and level of fish stocks is scarce, making management decision making difficult (Pomeroy \& Goetze, 2003). However Caribbean spiny lobster and queen conch have been widely studied throughout the Caribbean, and a number of local studies provide information about behaviour and maximum stable population sizes that are likely to be relevant to Gladden Spit. Moreover typical sale prices for conch and lobster are obtainable from the fishing cooperative in Placencia (Hargreaves-Allen, 2007), and Friends of Nature have conducted a number studies of the local population (Pomeroy \& Goetze, 2003) which reinforce the assumption that the fishery is small-scale and artisanal, and that the fishers are likely to behave in a way more similar to those studied by Abernethy et al. rather than following an ideal free distribution.

### 2.6 Constants and data sources

Although developed to be applicable to most small-scale multi-species artisanal fisheries, the model in this study is to be applied to a particular case study, and so an attempt has been made to represent the biology and economics of Gladden Spit as closely as possible. As there are few studies completed within the reserve area, or even specifically within Belize, it was necessary to draw upon a wider literature to find appropriate values with which to parametrise the model.

Hence this study includes what is known about local biology, economics and fisher behaviour, estimates parameters where appropriate from similar but more distant regions, and explores the implications of variation in all other parameters in order to gain an understanding of the outcomes that may be predicted for a variety of different management measures.

Table 2.3 on the next page outlines the parameters chosen and their sources.

Table 2.3: Life history and growth parameters for Queen Conch and Caribbean Spiny Lobster

|  | Conch | Lobster |
| :---: | :---: | :---: |
| Age of juvenile recruitment to adult habitat (months) | $\begin{aligned} & \hline \hline 16 \\ & (\text { Acosta, 2002) } \end{aligned}$ | $\begin{aligned} & 12 \\ & (\text { Acosta, 2002) } \end{aligned}$ |
| Magnitude of juvenile recruitment to adult habitat (/ha/month) | $\begin{aligned} & 109-131 \\ & \text { (Acosta, 2002) } \end{aligned}$ | $\begin{aligned} & 12.1-13.1 \\ & (\text { Acosta, 2002) } \end{aligned}$ |
| Month of peak spawning | August | April/May |
| Mortality | $0.44$ <br> (Cochrane \& Venema, 1997) | $\begin{aligned} & M_{t}=\max \left(0.1, \frac{4.330}{t}-\right. \\ & 0.242) \\ & (\text { CFMC 1999) } \end{aligned}$ |
| Carapace length at age (mm) | - - | $\begin{aligned} & C L_{t}=170 *[1- \\ & \left.e^{-0.21 *(t-0.41)}\right] \\ & \text { (Cochrane \& Venema, } \\ & \text { 1997) } \end{aligned}$ |
| Weight at length (g) | ${ }^{-}$ | $W_{t}=0.00158 * C L_{t}^{2.871}$ (Acosta \& Robertson, 2002) |
| Weight at age (g) | $\begin{aligned} & W_{t}=1.263 * 10^{-5} * \\ & e^{17.44 *\left(1.0-e^{-1.126 t}\right)} \\ & (\overline{\text { CFMC, 1999 }} \text { ) } \end{aligned}$ | - - |

## Chapter 3

## Methods

### 3.1 Overview of modelling approach

When designing a modelling study, it is first necessary to consider the types of questions that the model will be developed to answer before choosing which modelling techniques to apply. The most important principle to follow when developing a model is that it must be only as complicated as is required for the questions being asked of it - and no more (Milner-Gulland \& Rowcliffe, 2007). Models that attempt to include every attribute of the behaviour of a system can quickly become so complicated and develop so many interactions that they become almost impossible to interpret. The model developed for this study is a spatially-explicit, age-structured, stochastic, bio-economic, discrete-time dynamic simulation model. In order to justify this complexity, the reasons for the choice of each element are outlined below:

The model is spatially explicit for two reasons: The first reason is that the model is to be used to address the question of spillover from a reserve. As mentioned earlier, in many previous studies, related questions about the implications of area closures on fish population dynamics have been answered with patch-based models (e.g. Apostolaki et al., 2002; Sanchirico \& Wilen, 2001). However because such models do not explicitly model the spatial characteristics of the patches under consideration, the rate of
biomass flow between patches is imposed as an exogenous parameter (at least with relation to patch geometry). The model developed for this study aims amongst other things to explore the relationship between biomass flux and several attributes of reserve geometry (including reserve area and boundary length). By including space explicitly, it becomes possible to simulate how more fundamental biological attributes such as fish movement behaviour and movement distances interact with reserve configurations to affect the flow of biomass. The second reason is to investigate the effects of a range of plausible different spatial behaviours by the dependent fishers, especially how the imperfect knowledge of fish distributions over space affects the biological and economic outcomes of reserve establishment.

The model population is represented as structured rather than lumped in order to allow the simulation of size-selective fishing gear and to allow more insight into the effects of fishing on population structure. The model is age-structured rather than stage- or size-structured primarily because the majority of the biology and modelling papers from which this study derives its simulation parameters are based on age-related studies and hence provide information on mortality and growth rates that is most naturally simulated in an age-structured model.

The model contains a stochastic component in order to model variation in fisher behaviour and to implement random movement of fish. The latter behaviour is important as a reference model to compare against densitydependent movement and to compare the implications of both for spillover.

The model is bio-economic as this study is concerned not only with the effects of reserve establishment on the stocks of fish under investigation but also on the dependent fisher community - and the model assumes that the behaviour of the fishers is largely determined by the economics of fishing.

Finally the model is constrained to be a discrete-time dynamic simulation because the levels of complexity are too high for an analytical model to be tractable.

### 3.2 Biology

The overall structure of the biological component of the model is shown in figure 3.1 (with $N_{1}, N_{2} \ldots$ representing the number of fish in each age class, and $S_{1}, S_{2} \ldots$ representing the proportion of survivors from age class to age class as time progresses). The physical area under simulation is a $100 \mathrm{~km}^{2}$ section of habitat. This area is subdivided for simulation purposes into a grid of 33 by 33 square cells, each of approximately 300 m in width, covering an area of approximately 9 hectares. Within each cell is contained two separate population models, one for conch and one for lobster (any trophic interactions between the two species are ignored). These cells are not independent of one another, but instead form a connected meta-population by which individuals from one cell can move into adjacent cells, either randomly or in a density-dependent way (as described further in section 3.2.2).


Figure 3.1: The structure of the biological component of the model

### 3.2.1 Life history

### 3.2.1.1 Recruitment and mortality

As mentioned in section 2.3.1, the area under study is likely to function largely as a sink with respect to larval recruitment. As a result the model assumes that there will be a seasonally variable but regular supply of larvae arriving within its bounds over the course of each year. The model supports both homogeneous and heterogeneous habitat (as detailed in section 3.2.3) but in the simpler mode it is assumed that the settling larvae are distributed evenly amongst all of the cells of the reserve. Furthermore as little is known about larval mortality, but because there is good data about the arrival of young juveniles into an adjacent reserve (Glover's reef) in Belize (Acosta, 2002) the model does not simulate initial settlement and larval growth but rather starts modelling fish only as young juveniles newly recruited into adult habitat. The level of recruitment varies seasonally with conch juvenile recruitment peaking around October (in the model, fourteen months after spawning) and lobster around April/May (twelve months after spawning) in order to best represent the life histories of the two species.

New individuals entering the model are followed as they grow and as they are subject to natural and fishing mortality. However in an age-structured model each individual is considered to be identical in all aspects other than age. Thus the population in each cell is divided into a number of separate age classes in which each class represents the number of individuals of that particular age present in that cell. For the purposes of this model, there are four age classes per year. New recruits to the model arrive in age class one and every three months all individuals in each age class are moved up into the next age class. Each new group of individuals arriving into the population and progressing upwards through the age classes is referred to as a cohort.

When advancing through the age classes, the numbers in each cohort do not remain constant over time but gradually decrease as the individuals within die off as a result of natural processes such as predation and disease. Within a simulation, such natural mortality is often simplified by assuming that from
one time step to the next, only an age-dependent proportion of the individuals within each cohort survive. The standard equation for natural mortality mentioned earlier is used to determine the number of individuals surviving each time step and following the conclusions of the studies also mentioned earlier, lobsters are modelled as having constant mortality regardless of age whereas conch, being much more vulnerable when younger, are modelled as having mortality that decreases as they advance through the age classes.

### 3.2.1.2 Growth and weight

Although it is necessary to keep track of the number of individuals over time in each age class, it is not sufficient for modelling studies with self recruitment or an economic component. Rather it is important also to know the biomass of fish present: in models with self-recruitment, larval production is related to the size of individuals (Beverton \& Holt, 1957), and for economic studies, the biomass present in a particular catch determines the income a fisher will receive.

As mentioned in section ??, there is a wide literature studying the relationship between age, length and weight for both conch and lobster. In this model, lobster weight is ascertained using a combination of a von Bertalanffy equation to determine length, followed by a power law relationship to determine weight. Conch weight, not being so easily related to shell length, is described using a Gombertz equation relating weight directly to age (section 2.3.3).

### 3.2.2 Movement

As the simulation only starts to model individuals as they are recruited into adult habitat, and because it does not feature qualitatively different habitat types, it is not appropriate to model onotogentic migration from nursery habitat to adult habitat as the fish develop. Moreover, although as mentioned earlier, conch and lobster both engage in aggregative movement behaviour, such effects are not considered likely to contribute significantly to net fish
distributions for any significant length of time Acosta (2002) and are hence unlikely to contribute significantly to answering the questions posed by this study.

As mentioned in section 2.3.4, normal (non ontogenetic, non aggregative) conch and lobster movement behaviour can be represented using a correlated random walk. However such a movement pattern requires that a model keep track of the last movement direction of each individual. As the simulation is not able to keep track of attributes of individual fish, but only the numbers in each age class, it is not possible to simulate this behaviour fully but it can be further approximated using a simple random walk. It has also been mentioned that fish movement may often be density-dependent, and that density-dependence may materially affect the magnitude of spillover from a reserve. As a result the model has also been designed to be able to simulate density-dependent movement.

In this model, random walk behaviour is implemented by assuming that individuals in each cell move at regular intervals from one grid cell to a randomly chosen neighbour cell with the frequency of movement being determined by a species-specific constant (in this study lobster, as a more mobile species, move more frequently than conch). Density-dependent behaviour also constrains movement frequency to species-specific regularly-spaced intervals, but instead of individuals moving to a randomly chosen neighbour cell, they preferentially chose adjacent cells with lower fish densities. In both cases the maximum possible move distance per time-step (day) is a single cell ( $\sim 300 \mathrm{~m}$ ), but in the density-dependent model there is always a known flow of individuals from high density areas to low density areas. It is therefore likely that densitydependent movement will result in increased export from a no-take zone into heavily fished adjacent waters, when compared to random walk behaviour. The steps taken to calculate the net emigration of one age class from one cell for density-dependent movement are shown in figure 3.2 on the next page:


Figure 3.2: Density-dependent movement procedure

### 3.2.3 Habitat

In order to investigate the effect of habitat heterogeneity and changes in fish density distributions over time, the model is capable of simulating a heterogeneous habitat that changes over time. The habitat is generated as a fractal density map using the random midpoint displacement algorithm (Miller, 1986), with each cell being assigned a number representing the suitability of that cell. When in use, the figure in each cell determines the rate of local juvenile settlement and affects adult density-dependent movement, with a high suitability cell being one which is able to support a greater adult biomass without emigration. The underlying density map can be updated at predetermined time intervals in order to stimulate the movement of aggregations of fish and thus to stimulate the need for regular fisher exploration and to investigate fisher behaviour in a dynamic system.

### 3.3 Economics

In order to study the effects of individual fisher behaviour in a spatially distributed system, it is necessary to take a different approach to modelling.

Instead of modelling fishers in a structured, aggregated fashion, it is more useful to model each fisher as an individual (so-called agent based modelling). Thus on each timestep (each day) each fisher is able to take an individual decision about where to fish and with which gear type. Over time the income and outgoings of each fisher can be modelled with individuals adopting the more successful strategies ultimately prospering and those adopting the least successful ultimately needing to leave the fishery.

Moreover in a dynamic system in which fishing is unrestricted for a time and then restrictions are introduced, an individual model of fisher behaviour as described allows for a realistic adjustment of effort if catches should decline (by losing fishers from the fishery). Studying the dynamic adjustment of effort is important both in evaluating outcomes for the fishery as a whole, but also in providing a measure by which to distinguish successful fishing strategies from unsuccessful ones (the former being presumed to be present in greater proportion in fisher populations once stability has been reached).

In this model, the economics of the fish market is not considered. Instead the fishery is considered to be too small-scale to have an effect on market prices which are moreover considered to be fixed for the duration of each simulation.

### 3.3.1 Fisher behaviour

One of the aims of developing the simulation is to evaluate the effects of incorporating more realistic fisher behaviour into a bio-economic model. As a result the model has been designed to allow simulated fisher behaviour to operate in two broad modes: either following the ideal free distribution or following a behavioural model incorporating a number of more realistic assumptions and limitations.

### 3.3.1.1 Ideal free distribution

When operating in IFD mode all fishers in the model are of equal ability, are assumed to have complete knowledge of the number of fish in each cell of the map and to have unrestricted access to all cells in the grid, at equal cost. When fishing starts in the model, a single fisher is operating. On each day this fisher travels to the place where they will get the maximum financial return for their trip, harvests a proportion of the most valuable resource (largest fish first) and returns. The fish caught are realised as revenue (for a fixed price per unit weight) and the fisher's bank balance is credited with the obtained sale revenue. Finally the fisher's cost of living (or opportunity cost) is subtracted from their bank balance and the day ends.

At regular intervals, should the average revenue per fisher in the fishery rise above the opportunity cost of fishing, new fishers will be introduced into the model and start fishing alongside the first. When multiple fishers are present in the model, each one goes fishing in turn in an order that is randomised on each day. Each fisher is assumed (rather unrealistically - but adequately for the purposes of the model) to finish harvesting before the next fisher is given the opportunity to start, and hence that the next fisher sees the fish distribution as already diminished by the activities of the fisher(s) that have gone before him on that day. This simple rule allows the inclusion of equal competition for fishing locations amongst fishers into the simulation.

### 3.3.1.2 Relaxation of the ideal free assumptions

In order to investigate the effects of differing behaviour on the dynamics of the simulation, a number of aspects of more realistic behaviour can be activated:

The first of these relaxes the assumption of uniform cost access to resources by introducing a cost to fishers depending upon the distance travelled. All fishers are assumed to depart from the same point in space, and trips to areas that are further away from that point will result in a greater cost (equivalent to
fuel costs on a boat) than those nearer. It is expected that this will affect the spatial distribution of fishers, the number of fishers operating in the reserve and the distribution (and perhaps total magnitude) of biomass within the reserve (with further areas and less mobile species being better protected).

The second allows the relaxation of both the assumption that fishers are all indistinguishable and homogeneous and the assumption that fishers have full knowledge of the distribution of the fish in the reserve. This latter assumption is realised through some new behaviour that requires further explanation:

### 3.3.1.3 Risk, exploration and memory

Under this more realistic scenario, the fishers have no indirect, remote knowledge of the distribution of fish in the reserve. The only information they have access to is that obtained through their own fishing experiences and that of other fishers who choose to communicate with them. In order to find out about new areas as existing known areas become depleted, it is important for fishers to try new areas speculatively. Moreover when returning to a place from memory, fishers may not be able to find the exact location but will return to roughly the same area (within a few grid cells) One of the sources of heterogeneity between fishers is in how they choose to balance the frequency with which they choose to fish at existing known good locations versus the frequency with which they try new locations.

To realise this behaviour, each fisher retains a memory of a small number of the best locations (and gear types) used for fishing. This memory is represented by a list of locations and gear types and the moving average catch taken from each location over time, as illustrated in figure 3.3 on the facing page (In each row the first column represents the average revenue gained over time from a particular location, the second row the species caught and the third the coordinates of the location).
an ordered list of the 5 best catch locations and
gear choices
The revenue associated with a particular location is a moving average of the revenue from the last 5 fishing attempts, weighted towards the last catch

| $\$ 10$ |  |  |  |
| :--- | :--- | :--- | :--- |
| $\$ 8$ | $\$ 12$ | $\$ 6$ | $\$ 6$ |


| $\$ 9$ | $L$ | $(12,14)$ |
| :---: | :---: | :---: |
| $\$ 8$ | $C$ | $(8,6)$ |
| $\$ 5$ | $L$ | $(30,2)$ |
| $\$ 5$ | $L$ | $(19,12)$ |
| $\$ 4$ | $C$ | $(2,2)$ | $\$ 9=(10 / 2)+((8+12+6+6) / 4) / 2$

Figure 3.3: An example of a fisher memory

On each day, depending upon their relationship with risk, each fisher will either choose an existing location from memory, biased towards the locations with the better catches, or a new location chosen randomly nearby an existing location. If a catch at a new location results in a greater return than that from one or more of the locations in memory, the new location will be remembered and an existing location displaced as shown in figure 3.4 .


Figure 3.4: Remembering a new fishing location

Should a fisher choose to try a location from memory, the moving average revenue for that location will be updated with the newly realised revenue as shown in figure 3.5 on the following page.


Figure 3.5: Updating the revenue for a known fishing location

In combination this behaviour allows a more realistic model of fisher exploration behaviour to be evaluated and to allow the implications on catch and biomass levels to be explored.

### 3.3.1.4 Communication

As well as being able to discover new fishing locations by exploration, fishers are also able to communicate with one another. Such communication may occur between two fishers, with each choosing a location from memory at random and offering it to the other. In each case, should a received location be better than an existing location, the receiver will incorporate it into their own memory using the procedure outlined in figure 3.4 on the previous page. Each fisher has their sociability determined by a constant which can vary between zero and one and which signifies both the number of other fishers
that they trust (and hence will exchange information with) and the frequency with which they will exchange such information.

### 3.3.1.5 Fisher heterogeneity and adaptation

When a fisher enters the fishery (for the first time or after previously having left), there are four characteristics defining that fisher that can be chosen at random from a distribution. These are: the probability of trying totally new locations (risk/exploration), the average memory size of the fisher, the degree of communication that fisher engages in and the degree of local exploration a fisher will engage in around a remembered location. As the fishery evolves it is anticipated that the less successful fishers will leave the fishery and the more successful will stay in gradually altering the distribution of fisher characteristics within the fishery.

### 3.3.2 Fishing restrictions

### 3.3.2.1 Marine reserves (no-take zones)

The model supports the establishment of circular and square marine reserves of arbitrary width at any time during the simulation. When a reserve is established, fishers are no longer able to fish within its bounds and those who have locations within the reserve in their memories are required to discard them and explore elsewhere. Thus as well as often reducing the number of fishers supported by the fishery, reserve establishment will often cause the less resilient fishers (whether disinclined to explore, or whether infrequent communicators) to go out of business before they are able to establish new fishing grounds.

As well as the two aforementioned configurations, the model is capable of generating reserves with random geometry, and in particular with both random area and boundary length. This is accomplished through a process of successively closing overlapping rectangles of random size and shape
until a particular area was reached and then measuring the boundary length achieved. By tuning how the rectangles were chosen it was possible to achieve a combination of reserves with a reasonably uniform spread through area and boundary length space. By generating a large number of random reserves the model allows the effects of changing reserve boundary length and area on spillover and hence management outcomes to be explored.

### 3.3.2.2 Other restrictions

As well as controlling harvesting by initiating marine reserves, the model also allows restrictions to be placed on the minimum catch age (and hence catch size) of fish, the maximum per capita catch per fisher and the maximum number of active fishers. It is also possible to entirely close one of the two fisheries in order to compare and contrast results with single-species outcomes.

### 3.3.3 Cheating

As mentioned in section 2.4, fishing restrictions are rarely followed by all. In order to investigate the implications of cheating, the model can be configured to allow a chosen proportion of fishers to ignore the reserve restrictions and to fish within the no-take zone.

### 3.4 Simulation timescales

The basic simulation timestep is a single day. However many simulation processes happen less frequently. The basic simulation steps taken each day are outlined below (in the order in which they occur):

1. Economics and fisher behaviour
(a) Randomise the visit order of fishers.
(b) Allow each fisher in turn to:
i. If no longer active, but the average fishery catch is above the opportunity cost of fishing and no-one has re-entered recently, re-enter the fishery.
ii. Choose a fishing location and fishing gear based on memory and risk/exploration behaviour.
iii. Catch fish at the location.
iv. Update memory based on catch revenue.
v. If appropriate based on communication characteristics exchange a fishing location with another fisher.
2. Biology
(a) If enough time has passed for another move to occur (respecting the species movement rate), move fish in each cell according to the algorithm chosen (random or density-dependent).
(b) If a new quarter has begun, advance the fish through each age class.
(c) If a new month has begun, apply natural mortality and add new recruits into age class one.
(d) If heterogeneous habitat is enabled and the appropriate amount of time has passed, regenerate the habitat suitability map.

### 3.5 Model parameters

In the following tables are three sets of model parameters that can be varied from simulation to simulation to explore different fisheries outcomes. Table 3.1 on the following page shows parameters that affect the model at a high level. Table 3.2 on the next page shows parameters that affect the biological component of the model and table 3.3 on page 47 the parameters
that affect the economic and fisher behaviour component of the model. Each parameter is also accompanied by the default value it takes in simulations (unless otherwise stated). Where a fisher behaviour parameter specifies a range, for each fisher that parameter will be randomly drawn (using a uniform distribution) from that range ensuring a fishery with a considerable mix of different fisher strategies.

Table 3.1: General model parameters

| Parameter Name | Default value | Description |
| :---: | :---: | :--- |
| fishingStartYear | 30 years | The year (after the model starts) at which fishing <br> begins. |
| reserveStartYear | 60 years | The year that a reserve is put in place. |
| numYearsToSimulate | 90 years | The number of years the simulation will be run. |
| useFractalTerrain | No | Whether the underlying habitat will be <br> homogeneous or heterogeneous. |
| terrainRebuildInterval | 1000000 days | If heterogeneous habitat is in use and is to vary <br> over time, the interval between each change. |

Table 3.2: Biology model parameters (see table 2.3 on page 30 for sources)

| Parameter name | Default value | Description |
| :---: | :---: | :--- |
| lobsterAgeAtRecruitment | 12 months | Lobster age at recruitment into the model. |
| conchAgeAtRecruitment | 16 months | Conch age at recruitment into the model. |
| lobsterRecruitmentPerHaPerMonth | $3 / \mathrm{ha} / \mathrm{month}$ | Lobster recruitment per hectare per month. |
| conchRecruitmentPerHaPerMonth | $63.6 / \mathrm{ha} / \mathrm{month}$ | Conch recruitment per hectare per month. |
| lobsterMaxMoveDistancePerDay | 61 m | The maximum distance a lobster can move per day. |
| conchMaxMoveDistancePerDay | 9 m | The maximum distance a conch can move per day. |
| movesAreDensityDep | Yes | Whether movement behaviour is density <br> dependent. |
| useSeasonalRecruitment | Yes | Recruitment intensity into the model is not uniform <br> throughout the year but varies seasonally. |

Table 3.3: Fisher behaviour model parameters

| Parameter name | Default value | Description | Source |
| :---: | :---: | :---: | :---: |
| maxNumFishers | 8000 | The maximum number of fishers in the model. | - |
| allowedGearTypes | Conch <br> and <br> lobster | Which species the fishers are able to exploit. | - |
| fishersHaveFull-KnowledgeOfFishDensities | No | Whether fishers have full knowledge of fish densities. | - |
| fisherRiskRange | 0-1.0 | The range over which fisher risk taking behaviour can vary. | - |
| fisherInfoSharingRange | 0-1.0 | The range over which fisher information behaviour can vary. | - |
| fisherPerturbRange | 0-5.0 cells | The range over which fisher local exploration can occur. | - |
| fisherMemorySizeRange | 0-9 | The range over which the number of locations a fisher can remember can occur. | - |
| fisherCostOfLivingRange | 6.0-6.0\$ | The range over which fisher cost of living/opportunity cost of fishing varies. | Hargreaves-Allen <br> 2007) |
| numFisherFriends | 10 | The maximum number of friends a fisher can have. | - |
| numDaysBetween- <br> FisherReentry | 30 days | The minimum interval between two fishers re-entering the fishery. | - |
| maxFractionFishers- <br> FishingIllegally | 0.0 | The maximum fraction of fishers fishing illegally within the reserve. | - |
| reserveType | Square | The default reserve shape. | - |
| reserveWidthAs- <br> FractionOfModel- <br> Width | 0.85 | The reserve width as a fraction of model width. | - |
| minDaysBetween- <br> FisherInfo- Sharing | 3.0 | The minimum number of days between fisher information sharing. | - |
| travelCostMultiplier | 0 \$/km | The cost of travel per kilometre travelled. | - |
| conchCatchableAge | $25$ <br> months | Conch age at recruitment into the fishery. | (CFMC 1999) |
| lobsterCatchableAge | $\begin{gathered} 30 \\ \text { months } \end{gathered}$ | Lobster age at recruitment into the fishery. | (CFMC 1999) |
| conchSalePricePerGramme | 2.48 \$/kg | The sale price of conch per kilogramme. | Hargreaves-Allen <br> 2007) |
| lobsterSalePrice- <br> PerGramme | 2.29 \$/kg | The sale price of lobster per kilogramme. | (Hargreaves-Allen <br> 2007) |

### 3.6 Model implementation

The model was written in the C++ programming language (Stroustrup, 1991) using the Boost libraries (Boost, 2007) and the Intel Math Kernel libraries (Intel, 2007b) and compiled using the GNU C ++ compiler (GSF, 2007a) and the Intel Linux optimising compiler (Intel, 2007a). Debugging and optimisation were performed using GDB ( $\overline{\mathrm{GSF}}, 2$ 2007b) and Valgrind (Valgrind, 2007). The model controller was written using the Python language (van Rossum, 2007) and implemented for a Linux multiprocessor system (Burbridge \& Harvey, 2007) using the PBS batch scheduling system (Altair, 2007).

### 3.7 Running the model

The model developed for this study is a dynamic simulation model. However in most cases the study is interested in the model state after an equilibrium has been reached. Thus a typical model run involves setting a simulation running until a steady-state has been reached (typically about 30 years), then similarly waiting for a stability to be reached after making each exploratory change. An default simulation run would be of the form:

Table 3.4: Default model run

| Year | Procedure |
| :---: | :---: |
| $0-29$ | Allow fish population to develop to a natural <br> equilibrium |
| $30-59$ | Allow fishing to start and fish and fisher numbers to <br> develop to a stable level |
| $60-89$ | Establish reserve and allow fish and fisher numbers to <br> settle to a stable level |

In order to characterise the effects of varying model parameters on reserve outcomes, it is necessary to run the model many times. Each model run can take between ten and thirty minutes on a modern desktop computer, and
several thousand runs are required to explore an interesting set of parameter variations. Consequently the model has been adapted to run on the Imperial College High Performance Computing Service, where many instances with varying simulation parameters can be run simultaneously (Burbridge \& Harvey, 2007). By using this it is possible to run the model between twenty and forty times faster and hence there is much greater scope for experimentation.

### 3.8 Data analysis

Data analysis and graph generation were performed using GNU R (The GNU foundation, 2007). As well as simple x-y scatter plots and histograms, results were also presented using contour plots and regression trees.

Contour plots allow the change of a variable to be represented in response to a change in two explanatory variables, representing the value of the response variable using colours and delineating areas of equal value using contour lines.

Regression trees allow the display of the response of a continuous variable to changes in many explanatory variables. These are particularly useful for data with features which interact in complex non-linear ways. Regression tree analysis iteratively identifies the explanatory variable which most contributes to changes in the response variable and partitions the data into two ranges, with a particular value of the explanatory variable determining the split between these two ranges. This splitting is repeated recursively until the remaining ranges of data are insufficiently different (measured using analysis of variance) to merit further partitioning. Splits which have the most significant effect in partitioning the response variable data are represented with longer lines in the displayed tree, and the final leaf nodes of the tree are labelled with the mean value of the explanatory variables that have been partitioned via that path. Thus the most important variables explaining the variation in a response variable are identified and the effect (on the response variable) of different combinations of explanatory variable ranges is displayed.

## Chapter 4

## Results

In this chapter, the model is used to characterise the response of the simulated area to a number of different biological, economic and management scenarios. Unless otherwise stated, the model parameters were the defaults mentioned in section 3.5 , and the procedure for running the model that described in section 3.7, with the full behavioural fishing model, density-dependent movement and no underlying terrain heterogeneities. By default any reserve established was square in shape and illegal fishing was not permitted within (unless otherwise specified).

### 4.1 Model verification

Before using a model for carrying out any research, it is first important to verify that under simple operation it behaves both as expected and in agreement with any previous studies upon which it is based (Milner-Gulland \& Rowcliffe, 2007). Moreover when there is uncertainty in any of the fundamental underlying parameters, it is important to confirm that varying these parameters within their feasible range does not alter the overall behaviour of the model in a way that might compromise further experimentation. As mentioned earlier, the artisanal conch and lobster fishery operating in coastal Belize has been the subject of few comprehensive studies. As a result a number of the parameters
chosen as defaults for this study have a high associated degree of uncertainty and were therefore identified as important candidates for model verification. The response variables of most interest for this study were:

- The equilibrium number of fishers supported by the fishery
- The equilibrium biomass of the conch and lobster populations averaged over the whole area covered by the model.

The most fundamental parameters underlying the basic bio-economic model were:

- The number of juvenile conch and lobster recruited into the model each month
- The age of conch and lobster recruitment into the fishery
- The mean movement distance of conch and lobster per day
- The sale price (per unit weight) of conch and lobster meat
- The natural mortality rate of conch and lobster
- The relationship between the age and the weight of conch and lobster


### 4.1.1 Sensitivity analysis

The verification experiment consisted of studying the change in the response variables as each of the aforementioned chosen response variables was varied in turn over a set range ( $\pm 40 \%$ ), whilst keeping all other parameters at their default values. The results of this are outlined in tables 4.1 on the next page and 4.2 on page 54 (including the $R^{2}$ value of a linear regression calculated on the data and the percentage change in the response variables in response to a ten percent change in each explanatory variable):

Table 4.1: Results of varying Conch model parameters

|  | Number of fishers | Response to <br> a $10 \%$ <br> increase in <br> explanatory <br> parameter | $R^{2}$ | Spawning stock biomass | Response to <br> a $10 \%$ <br> increase in <br> explanatory <br> parameter | $R^{2}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Number of new juvenile recruits entering model per month | Increases <br> with increasing number of recruits | 10.1\% | 0.99 | Increases <br> with increasing number of recruits | 9.0\% | 0.99 |
| Age of recruitment into fishery | Decreases with increasing age of recruitment | -7.6\% | 0.91 | Increases with increasing age of recruitment | 2.7\% | 0.97 |
| Mean movement distance | Increases <br> marginally with increasing movement, but data very noisy | 1.0\% | 0.32 | Decreases with increased movement, but data noisy | -0.1\% | 0.47 |
| Sale price of meat | Increases <br> with increasing sale price | 9.4\% | 0.99 | Decreases with increasing sale price | -1.5\% | 0.98 |
| Natural mortality | Decreases <br> with increasing mortality, slight curvature | -25.5\% | 0.87 | Decreases with increasing mortality, quite strong curvature. | -30.9\% | 0.79 |
| Age-to- weight relationship | Increases as <br> weight <br> increases <br> with age | 10.2\% | 0.98 | Increases as <br> weight <br> increases with age | 8.5\% | 0.99 |

Table 4.2: Results of varying Lobster model parameters

|  | Number of fishers | Response to <br> a 10\% <br> increase in <br> explanatory <br> parameter | $R^{2}$ | Spawning stock biomass | Response to <br> a $10 \%$ <br> increase in <br> explanatory <br> parameter | $R^{2}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Number of new juvenile recruits entering model per month | Increases with increasing number of recruits | 8.5\% | 0.97 | Increases with increasing number of recruits | 9.4\% | 0.99 |
| Age of recruitment into fishery | No obvious relationship | 0.4\% | 0.12 | Increases with increasing age of recruitment | 2.5\% | 0.96 |
| Mean movement distance | No obvious relationship | 0.5\% | 0.15 | Decreases with increased movement | -0.5\% | 0.87 |
| Sale price of meat | Increases <br> with increasing sale price | 6.9\% | 0.96 | Decreases <br> with increasing sale price | -2.1\% | 0.96 |
| Natural mortality | Decreases with increasing mortality | -11.6\% | 0.98 | Decreases with increasing mortality, slight curvature | -17.2\% | 0.93 |
| Age-to- weight relationship | Increases as weight increases with age | 7\% | 0.97 | Increases as <br> weight <br> increases with age | 8.0\% | 0.99 |

Biomass and number of fishers for fisheries for both species responded either linearly or were largely uninfluenced by variation in each of the explanatory variables, showing that the model did not experience any qualitative change in response within the range of uncertainty of each parameter.

For each species an increase in both the number of new monthly recruits and the age to weight relationship caused an approximately proportionate increase in fish biomass, and in the number of fishers supported. Similarly a decrease in natural mortality also increased biomass and the number of fishers, but at a greater rate than any of the previous explanatory variables. Given that mortality was not density-dependent, that the biomass in the model was a simple function of the number of fish multiplied by their weight and that these three parameters directly controlled either the number of fish in the reserve or the relative weight per fish - these results were entirely as anticipated. Similarly since the opportunity cost of fishing was the same for each fisher and fishers were free to enter the fishery to take advantage of extra biomass - the consequent increase in number of fishers was also as anticipated.

For both species an increase in the age of recruitment resulted in an increase in biomass. For lobster the number of fishers did not vary significantly with changes in age of recruitment but for conch the number of fishers decreased slightly. The increase in biomass reflected a simple increase in the number of age classes protected and was as anticipated. The change in the number of fishers is explained with reference to the conch and lobster total population biomass at age curves (figures 2.1 on page 23 and 2.2 on page 23) - and reflects the fact that conch biomass decreases as age of recruitment is increased beyond the default value, whereas for lobster there is a slight increase in biomass as minimum catch age increases but not sufficient to result in any significant increase in number of fishers.

An increase in fish sale price caused a significant linear increase in the number of fishers, and a small decrease in the average biomass levels for each species. As anticipated, an increase in the sale price of a given weight of fish allowed the modelled area to support a proportionate extra number of fishers. However an increase in the sale price not only increased the revenue from each
fishing trip but also decreased the minimum level of biomass worth fishing, and hence increased the fishing pressure, reducing average biomass levels.

Finally an increase in movement was not associated with any significant changes in either biomass or the number of fishers, reflecting the model's relative insensitivity to small changes in this parameter.

In summary, for both species the most important determinants of the number of fishers were (in descending order): the natural mortality of the fish, the age to weight relationship, the number of juvenile recruits and the sale price of the meat. For biomass the list and order were the same, but excepting sale price which proved less significant.

The above observations confirm that the model responded in a predictable and measured way to changes in individual parameters, and also confirm that the model was behaving in line with expectations.

### 4.2 Scenario testing procedure

In a number of the experiments fishing effort was varied in order to study how model behaviour responded. As fishing effort is managed endogenously by the economic component of the model, it could not be set explicitly. As a result, effort was increased indirectly by simultaneously decreasing the opportunity cost of fishing and by increasing the maximum proportion of fish that a fisher could catch in any given location. The effect on the biomass of fish within the fishery was then measured and processed in order to give an estimation of ' F ', a measure of the fishing mortality should the model have included a simple constant-effort fishing model (as described in section 2.3.2). This allowed the results in this study to be compared with other studies in the literature which frame their results in terms of F .

### 4.3 Reserves and space

In the following section a number of scenarios were simulated to shed light on how model response variables varied over space and how the model responded to changes in the geometry and spatial characteristics of reserves.

### 4.3.1 Spillover and biomass transects

Biomass transect measurements were carried out for the model for two circular reserves, one of 8.5 km diameter ( $56 \%$ of the total model area) and one of 2 km diameter ( $3 \%$ of the total model area). For each reserve size, the model was run several times with high and low fishing effort and for conch and lobster single-species fisheries. In each case the biomass was measured at regular intervals from the centre of the reserve. The results of these simulations are shown in figures 4.1 on the next page and 4.2 on page 59. In each figure the vertical line marks the location of the reserve boundary and the horizontal lines the biomass as equilibrium is reached at sufficient distance from the reserve.

In all cases, biomass within the reserve was lowered by fishing activity outside. For the larger of the two reserves, the conch population had largely recovered to unfished levels by about 1.5km inside the reserve, but the lobster population was only approaching unfished levels by the centre of the reserve, approximately 4 km from the boundary. This confirmed the general hypothesis that fish with greater daily movement distances require larger reserves to offer equivalent levels of protection. Within the smaller of the two reserves, neither the conch nor the lobster were able to reach unfished biomass levels as the protection offered was inadequate relative to their daily movement distances.

For both reserve sizes, higher fishing pressures lowered the average biomass seen outside the reserve, and also increased the distance within the reserve over which populations were depleted relative to an unfished level. Table 4.3


Figure 4.1: Conch and lobster biomass transects for a circular reserve of 8.5 km diameter


Figure 4.2: Conch and lobster biomass transects for a circular reserve of 2 km diameter

Table 4.3: Biomass export for several reserve configurations (kg/day)

|  | 8.5 km , low F | 8.5 km , high F | 2 km , low F | 2 km , high F |
| :---: | :---: | :---: | :---: | :---: |
| Conch | $0.3 \mathrm{~kg} /$ day | $0.4 \mathrm{~kg} /$ day | $0.05 \mathrm{~kg} /$ day | $0.08 \mathrm{~kg} /$ day |
| Lobster | $2.1 \mathrm{~kg} /$ day | $3.5 \mathrm{~kg} /$ day | $0.21 \mathrm{~kg} /$ day | $0.25 \mathrm{~kg} /$ day |

shows the biomass exported from each reserve configuration for each level of fishing effort.

As might be intuitively expected, the larger reserves, as well as providing greater protection also exported greater levels of biomass (as a result of having both longer boundary lengths and larger populations). Moreover, it was seen that the degree of fishing pressure outside a reserve also affected the biomass flow out of the reserve as density-dependent export was increased as the density gradient over the reserve boundary increased.

For the larger reserve configuration, the distance over which spillover occurred was not hugely different between the two species, being between about 500 m and 1000 m . However the density of lobster compared with that at some distance away from the reserve was proportionately higher than the similar ratio for conch. Thus although the lobster did travel considerably further on average than the conch, the spillover distances observed for the two species were not a good indication of the relative biomass export of each. For the smaller reserve configuration the spillover distance was again similar for conch at both levels of fishing effort and lobster at high fishing effort. However, increased density occurred at greater distances from the reserve for lobster at low fishing effort.

Clearly then, the magnitude of spillover and the distance over which it is experienced is influenced by fisher behaviour as well as fish behaviour. Figures 4.3 on the next page and 4.4 on page 62 show the frequency of fishing visits at increasing distance from the reserve boundary. Fishing effort was considerably higher in all cases around the boundary of the reserve (confirming the presence of so-called 'fishing the line', observed in the literature (Kellner et al., 2007)) and this contrast between fishing levels close to the boundary and further from the boundary was much higher for higher fishing effort levels. These higher effort levels prevented spillover from occurring at


Figure 4.3: Fisher visit frequency transects for 8.5 km reserve configurations
greater distances from the reserve by catching exported fish before they had a chance to travel any great distance. In the case of the lobster fishery at low F and the smaller reserve, the fishing pressure was considerably less elevated at the boundary than in the other lobster fishery examples and it is perhaps this phenomenon that explains the greater spillover distances for this scenario.

### 4.3.2 Changing reserve size

To explore further the effect of reserve size and movement distance, the model was run multiple times for a conch population, and the daily move distance of the conch was varied between 0 m and 300 m (somewhat unrealistically - but in order to detach the effect of move distance from fish biology) whilst the reserve area was simultaneously varied from $0 \%$ to $90 \%$ of the total model area.


Figure 4.4: Fisher visit frequency transects for 2 km reserve configurations


Figure 4.5: How number of fishers varies with reserve area and conch movement distance


Figure 4.6: How average conch SSB (kg/ha) varies with reserve area and conch movement distance

The dominant effect on the number of fishers, shown in figure 4.5 on the preceding page, was the reserve area. When the fish were immobile the number of fishers was proportional to the area remaining outside of the reserve. At low reserve sizes, the move distance of the fish was not a significant determinant of the number of fishers supported. However as the reserve area increased, increasing fish movement rates increased the number of fishers supported. For a reserve covering $80 \%$ of the modelled area, the effect on fisher numbers of increasing the average daily movement distance from 0 to $300 \mathrm{~m} /$ day was equivalent to the effect seen by reducing the reserve area to $60 \%$ of the modelled area with no movement.

An inverse relationship was seen for fish biomass (figure 4.6), with biomass levels at very low movement distances being largely determined by and increasing linearly with reserve area. Similarly at larger reserve sizes, the movement distance of the fish became more important, with greater daily movement distances resulting in a decrease in model biomass. In line with the observations above, for an $80 \%$ reserve the effect of increasing the movement distance from 0 to $300 \mathrm{~m} /$ day was equivalent to the effect seen when reducing the reserve area to $60 \%$ with no movement.

The most significant effects of this move distance change were felt when the move distance was between 0 and $100 \mathrm{~m} /$ day. This range encompassed the move distances of the two species under investigation and shows that to maintain a particular percentage of pristine biomass levels the appropriate area of a square reserve is likely to be different for each species. Thus to offer adequate protection for both may require overprotecting one at the expense of the productivity of its fishery. Alternatively it may be that different reserve geometries are able to protect both adequately and this is explored further in section 5.1.2.2.

### 4.3.3 Varying area and boundary length

Reserve outlines rarely follow simple geometric shapes, but often follow habitat gradients, coastlines or are determined by political considerations. As a result not only can the area of a reserve vary but also its boundary length. In order to investigate the effects on a fishery, one thousand random reserves were generated of varying area and boundary length. The simulation was run for each to characterise the effect of different physical geometries. It was run for high and low fishing efforts and with and without protection of juveniles within the fishery to see whether there were any qualitative differences in the response. Note that in the following figures, each 'cell' in the reserve is equivalent to about 9 hectares of modelled area. Thus the reserve area was varying from about $20 \%$ to about $85 \%$ of total modelled area.

Figure 4.7 on the next page shows that for low fishing effort, the total number of fishers decreased with reserve area (as observed earlier) but increased with increasing boundary length. This is largely to be expected as a longer boundary length exposes a greater proportion of the contained biomass to the fished areas (confirming the results shown in Acosta (2002)).

Similarly figure 4.8 on the facing page shows that as the number of boundary cells increased, the average biomass per hectare in the model decreased.

However for high levels of fishing effort, the number of supported fishers varied in a more interesting way. Whilst still predominantly decreasing with


Figure 4.7: How number of fishers varies with varying reserve area and boundary length (low fishing effort)


Figure 4.8: How lobster biomass varies with varying reserve area and boundary length (low fishing effort)


Figure 4.9: How number of fishers varies with varying reserve area and boundary length (high fishing effort)
reserve area, the relationship between boundary length was more complicated. As shown in figure 4.9, at low values of boundary length an increase resulted in an increase in the number of fishers. However this relationship did not continue as the boundary length continued to increase. Instead, the number of fishers peaked at a given length and then started to fall. This effect occurred at higher boundary lengths as the reserve size increased but was still clearly apparent.

Examining the average biomass for the high effort scenario (figure 4.10 on the facing page), it can be seen that the relationship was similar to that under low effort, with biomass increasing with reserve area and decreasing with increasing boundary length. Hence by varying the reserve parameters it was possible for a given number of fishers to be supported with a variety of different average levels of biomass in the reserve.

This effect is illustrated in figure 4.11 on page 68, showing the range of possible combinations of biomass and number of fishers obtainable when able to vary both area and boundary length. The results show that for an equivalent number of fishers the levels of average biomass can vary by up to a factor of five (when fisher levels were at about 250, biomass levels varied


Figure 4.10: How lobster biomass varies with varying reserve area and boundary length (high fishing effort)
between about 2 and $10 \mathrm{~kg} / \mathrm{ha}$ ), and that the best degree of stock protection for a particular fishery is obtained when reserve boundary lengths are kept to a minimum.

### 4.3.4 Characterising the biological contributors to spillover

As mentioned in section 2.2.1, it is thought that there are a strictly limited combination of circumstances under which marine reserve establishment results in an increase in both stock biomass and in the number of fishers and/or the fishery catch. A number of the parameters thought likely to influence the size of any spillover were identified with help from the literature, plausible ranges were chosen for each and the model was run three thousand times with the parameters in each case drawn randomly from appropriate distributions. For each run the main response variable was the log ratio of the number of fishers after versus before reserve establishment. A positive value of this variable indicated an increase in the proportionate number of fishers, and a negative value a decrease.

Figures 4.12 on the following page and 4.13 on page 69 confirm that for both


Figure 4.11: Variation in number of fishers and lobster SSB for a variety of reserve geometries


Figure 4.12: Frequency of change in fishers after reserve establishment in lobster fishery


Figure 4.13: Frequency of change in fishers after reserve establishment in conch fishery
conch and lobster, the circumstance where the number of fishers decreased outweighs the circumstances where they increased by a considerable degree (about seven to one). However there were a number of model runs where an increase was seen in both the biomass and the number of fishers supported.

Figures 4.14 on the following page and 4.15 on page 71 seek to highlight any relationships between the chosen explanatory parameters and the occurrence of increasing number of fishers. As can be seen, the relationships between the change in number of fishers and each of the parameters was not always a well-formed normally distributed linear function. Nevertheless regression line and significance levels for the associated slope were calculated and are shown in tables 4.4 on page 72 and 4.5 on page 72 . Thus it was possible to make some general observations about when fisher numbers were observed to increase (and hence the log ratio was positive).

For lobster, an increase in number of fishers occurred when fishing mortality was either low (although this could just have been explained by high variance at low mortalities) or relatively high (between 10 and 15) with the instances of fisher increases occurring more frequently and of greater magnitude as $F$ increased in the latter case. An increase in the number of fishers was


Figure 4.14: Looking for relationships between lobster model parameters and a post-reserve increase in fishers


Figure 4.15: Looking for relationships between conch model parameters and a post-reserve increase in fishers
also seen to occur more frequently and with greater magnitude as lobster move distances increased. Therefore at realistic move distances of about 60 $\mathrm{m} /$ day,opportunities for increases in yields were predicted.

Such increases were both more prevalent and of greater magnitude when younger fish were being caught outside the reserve, and increases occurred predominantly at lower reserve sizes - between about $50 \%$ and $85 \%$ of model area and decreasing with increasing model area.

For conch an increase in the number of fishers occurred primarily at low

Table 4.4: Regression statistics for conch spillover parameters

|  | Regression line | $R^{2}$ | F value (slope) |
| :---: | :---: | :---: | :---: |
| Fishing mortality | $y=0.045 \cdot x-0.536$ | 0.261 | $F_{1,896}=319, p<0.001$ |
| Maximum move distance | $y=0.002 \cdot x-0.391$ | 0.05 | $F_{1,896}=48, p<0.001$ |
| Age at recruitment | $y=-0.006 \cdot x-0.153$ | 0.01 | $F_{1,896}=10, p<0.005$ |
| Reserve width | $y=-1.237 \cdot x-0.622$ | 0.365 | $F_{1,896}=516, p<0.001$ |

Table 4.5: Regression statistics for conch spillover parameters

|  | Regression line | $R^{2}$ | F value (slope) |
| :---: | :---: | :---: | :---: |
| Fishing mortality | $y=0.0421 \cdot x-0.333$ | 0.085 | $F_{1,831}=79, p<0.001$ |
| Maximum move distance | $y=0.002 \cdot x-0.319$ | 0.034 | $F_{1,831}=30, p<0.001$ |
| Age at recruitment | $y=0.003 \cdot x-0.294$ | 0.002 | $F_{1,831}=2.7, p>0.05$ |
| Reserve width | $y=-1.177 \cdot x+0.616$ | 0.380 | $F_{1,831}=511, p<0.001$ |

fishing mortality ( $\mathrm{F}<5$ ) although there were also a few increases at very high effort levels ( $\mathrm{F}>10$ ). Maximum move distance seemed to be less correlated with an increase in the number of fishers when compared with lobster, but with the greatest benefits occurring for move distances between 30 and 90 $\mathrm{m} /$ day. At realistic conch move distances of about $9 \mathrm{~m} /$ day there were still a few data points where the number of fishers increased, but considerably fewer than for the lobster.

No statistically significant relationship was apparent between conch age at recruitment and the change in the number of fishers. Finally conch reserve yield increases occurred most frequently and with greatest effect for smaller reserves than optimal for lobster, producing benefits at between $40 \%$ and $75 \%$ of total model area with a discernible peak at about $65 \%$.

Such results as outlined above are largely qualitative but they do illustrate the range of circumstances under which double benefits can occur and could hopefully provide structure for future research (whether empirical or through modelling) on this effect.

### 4.4 Comparing reserves to traditional management

When considering the establishment of a marine reserve, it is instructive to compare the possible effects of the reserve with those caused by other possible fishing restrictions. Combining control of the number of fishers that can fish in a particular area with a minimum catch age is a common management technique used in small scale fisheries (McClanahan \& Castilla, 2006). In order to contrast this method with reserve establishment, the model was run multiple times in two different modes. In the first no reserve was present but the maximum permitted number of fishers and the minimum catch age of the fish were varied and the effects on number of fishers and biomass were observed. In the second mode, a reserve was present and its size and the minimum catch age of fish were varied simultaneously and the same two response variables observed. Figures 4.16 on the following page and 4.17 on the next page show the results of these experiments for a conch fishery. The traditional method responded with an increase in the number of fishers supported as conch age at recruitment into the fishery decreased, and by increasing the number of fishers to carrying capacity for the available biomass as more were allowed into the reserve.

As also could be expected, biomass increased as permissible catch age increased and as number of fishers was decreased (figure 4.17 on the following page). A similar pattern was apparent when marine reserves were used, with fisher numbers increasing as permissible catch age declined and decreasing as reserve size increased.

The pattern for number of fishers for a lobster fishery for the two types of restriction is shown in figures 4.18 on page 75 and 4.19 on page 76 . The notable difference between these and the conch fishery was that initially as lobster age at recruitment into the fishery increased, for both methods of protection the total number of fishers increased to a peak at about 30 months of age.

Moreover in the case with the reserve the number of fishers remained roughly


Figure 4.16: How number of fishers varies in a conch fishery as max number of fishers and conch catchable age are varied


Figure 4.17: How conch biomass varies in a conch fishery as max number of fishers and conch catchable age are varied


Figure 4.18: How number of fishers varies in a lobster fishery as max number of fishers and lobster catchable age are varied
constant at this point until the reserve width increased beyond about $30 \%$ of the model area showing the potential for double benefits from the establishment of a small reserve along with catch age restrictions in adjacent fishing grounds. Beyond this age further increases caused the number of supported fishers to decline.

These two methods effected different levels of average biomass and number of fishers within the modelled area. The available combinations found for conch and lobster are shown in figures 4.20 on the next page and 4.21 on page 77.

It is clear from these figures that, except for small differences, all of the combinations of average biomass and number of fishers supported by limiting entry to the fishery were also supported through the establishment of marine reserves. However there is the added complication when protecting multiple species with reserves, that the optimal reserve size may differ for each and thus to protect all may involve over-protecting some at the expense of the associated fishery.

As outlined in earlier chapters, traditional management often fails through scientific uncertainty or as a result of political or enforcement issues. In the


Figure 4.19: How number of fishers varies in a lobster fishery as reserve width and lobster catchable age are varied


Figure 4.20: Comparing the number of fishers and lobster biomass supported by two management methods in a lobster fishery


Figure 4.21: Comparing the number of fishers and lobster biomass supported by two management methods in a lobster fishery, high effort
context of marine reserves additionally providing both ecosystem protection and greater larval export through substantially increased biomass within the reserve, this result seems to support the case for reserves.

### 4.5 Inter-species interactions

Although the conch and lobster populations do not interact directly in the model, it is likely that changes to one population may result indirectly in changes to the other through the modulation of fisher behaviour, or that changes in economic or management regimes might influence one species more than the other. In this section two possible sources of such interactions are investigated.

### 4.5.1 Technical interactions

The first investigation involved exploring a possible relationship between varying the recruitment and then sale price of one species on the abundance


Figure 4.22: How the number of fishers supported varies with the magnitude of conch and lobster juvenile recruitment into model
of the other. In order to investigate this, the model was run with both conch and lobster populations and a multi-gear fishery. Multiple simulations were run with the levels of both conch and lobster juvenile recruitment (into the model) varied simultaneously and the effect on the stable number of fishers and the stable conch and lobster average biomass were observed.

Figure 4.22 shows the effect on the number of fishers of varying conch and lobster recruitment. As might be expected (and confirming the result in section 4.1.1), an increase in the level of recruitment of either and both species resulted in an increased number of fishers supported.

Figures 4.23 on the facing page and 4.24 on page 80 show the effects of varying recruitment on the average biomass of the conch and lobster populations. As expected, in both cases increasing the recruitment of the measured species increased its equilibrium average spawning stock biomass. However both also showed a strong response to an increase in the companion species recruitment - with biomass of the first declining in response to an increase in recruitment of the companion species.

This was particularly apparent when the companion species recruitment was at low levels and some fishers concentrating primarily on it had occasionally


Figure 4.23: How conch biomass (kg) varies with the magnitude of conch and lobster juvenile recruitment into model
to fish the main species as companion species biomass varied throughout the year. The lobster population was also observed to be more influenced by variations in conch recruitment than vice-versa. This was likely to be an artifact of the range of recruitment levels studied, as in this range the conch fishery was economically dominant.

A similar investigation was then carried out varying conch and lobster meat sale price (instead of recruitment). The results were very similar to those described above, with an increase in the sale price of one species causing a decrease in the biomass of the other. As before (and for the same reason) the effect was more pronounced in the lobster fishery as conch sale price increased than vice-versa.

### 4.5.2 The differential effects of different reserve configurations

The second investigation involved studying the differential effect of varying reserve geometry on the two species populations. In order to carry out this study a variety of random reserve geometries were created using the method


Figure 4.24: How lobster biomass (kg) varies with the magnitude of conch and lobster juvenile recruitment into model
described in section 4.3.3. The model was run as before, but with a two species multi-gear fishery without juvenile protection and the log ratio of conch to lobster biomass was measured at high and low fishing effort.

As can be seen in figures 4.25 on the facing page and 4.26 on the next page, for both effort levels an increase in reserve area led to a relative increase in average lobster biomass relative to average conch biomass. At first glance this result seems surprising as it might be expected that large reserves would offer preferential protection to the slower moving conch. However lobster natural mortality is considerably lower at higher age classes than conch and thus this result reflected the greater upper levels of biomass to which the lobster population could grow when offered a degree of protection.

As reserve boundary length increased an opposite relationship was seen with lobster biomass decreasing relative to conch biomass as more of the protected populations became exposed to adjacent fishing grounds.

Although the general trend was the same between the two effort levels, in the high effort scenario (figure 4.26 on the facing page), the lobster population biomass was considerably more depleted relative to the conch biomass as a steeper biomass gradient across the reserve boundary significantly increased


Figure 4.25: How log ratio of conch biomass : lobster biomass varies with reserve area and boundary length at low effort


Figure 4.26: How log ratio of conch biomass : lobster biomass varies with reserve area and boundary length at high effort


Figure 4.27: How average lobster catch per hectare varies as fishing effort increases with juvenile protection
lobster biomass export whilst affecting conch biomass export less (as confirmed by the results seen in figure 4.3 on page 61 earlier). It would have been interesting to see whether this relationship also held for fisheries with juvenile protection, but unfortunately limited time did not permit.

### 4.6 Fisher effort and juvenile protection

As fisher effort and levels of juvenile protection play such an important part in determining the outcome of many of the scenarios explored, in this section the effect of varying fisher effort (F) was investigated to help shed light on earlier results. To this end a number of simulations were run for a lobster fishery, with and without juvenile protection and with fisher effort varying over an appropriate range by (as mentioned previously) modifying fisher living costs. The average daily per hectare lobster catch was recorded and is shown in figures 4.27 and 4.28 on the next page.

In the scenario with juvenile protection daily catch rose quickly from zero as effort increased, reaching a peak at about $\mathrm{F} \sim 2$. Then as F increased


Figure 4.28: How average lobster catch per hectare varies as fishing effort increases with no juvenile protection
further the daily catch fell a small amount before levelling out at about 90\% of the maximum value achieved. For the scenario with no juvenile protection, catches built much more quickly to a peak, by about F $\sim 1$, of about half that reached with protection. Further increases in effort then reduced catches sharply before they eventually started to level out at under half those seen at the peak. This differing relationship between effort and fishery catch with and without juvenile protection illustrates why, in the latter scenarios it is possible for reserves to increase fisher take despite closing large areas to fishing: even though closed areas do not export huge amounts of biomass by spillover, they are still able to compensate for the lost area when fisheries are very depleted.

Figures 4.29 on the following page and 4.30 on page 85 respectively illustrate how the number of fishers and the biomass in the model varied as reserve width and fishing effort were changed (with no juvenile protection). Biomass varied predictably with higher values of F resulting in lower biomass, and larger reserves offsetting this loss and increasing biomass.

In figure 4.30 on page 85 the relationship for number of fishers supported was rather more complicated (as could be expected having analysed figure 4.28). At low values of fishing effort, increased reserve area decreased the number


Figure 4.29: How the average biomass per hectare a lobster fishery varies as reserve size and fishing effort increase
of fishers. However at larger values of F the relationship was no longer linear, with the number of fishers increasing as reserve size increased from zero before levelling out and decreasing as reserve sizes increased beyond about $50 \%$ of total model size.

### 4.7 Fisher behaviour

The scenarios explored in this section investigate the effect of different fisher behaviour on the number of fishers supported by a fishery and the biomass of the stocks therein.

### 4.7.1 Limited fisher knowledge compared to IFD

In this scenario the effects of different reserve sizes on fisheries exploited by fishers both with and without full knowledge of fish locations were explored. Figure 4.31 on page 86 shows that as common sense might suggest, when fishers have full knowledge of fish distributions, a fishery is able to support


Figure 4.30: How number of fishers supported by a lobster fishery varies as reserve size and fishing effort increases
more participants but that as reserve size increases so the difference narrows as there are fewer locations for the fishers to explore.

Figures 4.32 on the next page and 4.33 on page 87 show the variation in conch and lobster biomass at different reserve sizes. Fishers without full knowledge were less able to exploit the conch fishery fully when compared to the lobster fishery. This is likely to be because the lower daily movement rates of conch allowed unexploited areas to remain at high biomass for longer without being depleted through movement whereas for lobster, the higher movement rates quickly averaged out local peaks in biomass levels and reduced the advantage of knowing exact fish distributions.

### 4.7.2 The relative importance of different components of the fisher model to the size of the active fishing population

Although it is valuable of itself to know that a more realistic model of fisher behaviour leads to fewer fishers being supported by a fishery and a lower


Figure 4.31: How fisher knowledge affects the number of fishers a fishery can support


Figure 4.32: How conch SSB is influenced by fisher knowledge


Figure 4.33: How lobster SSB is influenced by fisher knowledge
utilisation of the resource, it is also interesting to know how the components of this behaviour contribute towards fishery outcomes - to break the behaviour down and investigate how each component contributes to increasing or decreasing the number of fishers supported. Furthermore it is also interesting to see whether different behaviours are appropriate for different situations. In particular whether different strategies prosper more in stable fisheries, in fisheries where fish distributions vary significantly over time, in fisheries with reserves and during the transient period immediately following reserve establishment.

Four components of fisher behaviour were chosen to be investigated, and for each two possible modes of operation identified - one in which the component behaviour was fixed and simple and one in which it was allowed to vary and hence induce more complex behaviour. Those components and their modes of operation are described in table 4.6 on the next page.

The model was run ten times for each of every possible combination of these individual modes (excepting a few that didn't make sense, e.g. communication with no memory) and for each set of runs of each combination, the average number of fishers at three time periods of interest (each averaged over a whole year) was recorded. This was done for a conch fishery (as conch

Table 4.6: Components of fisher behaviour under investigation

|  | Abbrev | Component description | Mode 0 | Outcome | Mode 1 | Outcome |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Risk taking | risk | Deterimines  <br> how fre- <br> quently  <br> fisher will visit  <br> a known loca-  <br> tion compared  <br> to trying a  <br> distant new <br> location  | 1.0 | Fishers always try new locations and never any from memory. | 0.0-1.0 | Levels of risk taking vary uniformly throughout the fisher population. |
| Communication | comms | Determines how many friends a fisher has, and how frequently they will share catch locations. | 0.0 | Fishers never communicate | 0.0-1.0 | Levels of communication vary uniformly through the fisher population. |
| Memory size | memsize | Determines how many catch locations a fisher is able to remember. | 0.0 | Fishers never remember any locations. | 0.0-1.0 | The number of remembered locations varys uniformly from 0 to 10 throughoutout the fisher population. |
| Perturbation | perturb | Determines how close to a remembered location a fisher will fish. | 0.0 | Fishers only ever visit the exact location remembered. | 0.0-5.0 | Exploration distances amongst fishers vary uniformly from a radius of 0 to 5 cells around a remembered location. |



Figure 4.34: Effect of fisher behavioural characteristics just before reserve establishment
fisheries were shown in section 4.7.1 to have the greater difference in number of fishers when compared to a fishery with IFD behaviour) both with normal homogeneous habitat and an artificial fishery with significant and shifting spatial heterogeneity. The latter was chosen to simulate a fishery where fish distributions were less homogeneous and varied over time, hence requiring greater exploration and increasing the value of locations once found.

The results of these scenarios are presented using tree regression plots (section 3.8) and are as follows: Figure 4.34 shows how the different fisher behaviours determined the number of fishers in an equilibrium model before reserve establishment. Figure 4.35 on the next page shows the effect of different behaviours in the first year following reserve establishment and figure 4.36 on page 91 shows the effects of the different behaviours thirty years after reserve establishment when the fisheries had again reached an equilibrium.

In the equilibrium fisheries before reserve establishment, the fisheries with homogeneous habitat were most affected by variation in fisher communication and fisher memory, with significantly more fishers being supported when there was no communication, and slightly more still when no fishing locations were being remembered. In the heterogeneous habitat fisheries the same


Figure 4.35: Effect of fisher behavioural characteristics in first year of reserve establishment
two components were significant, but although communication still reduced the number of supported fishers, remembering good fishing locations was a significantly better strategy than random choice. This reflected the difficulty involved in finding good fishing grounds at random with significantly inhomogeneous fish distributions, and the importance of remembering them once found. Thus despite differences in the usefulness of memory, in both cases the benefits of learning about known good fishing locations from another fisher are outweighed by the potential disbenefits from telling them about a location that may currently be being relied on for the first fisher's own livelihood.

During the first year of reserve establishment the heterogeneous habitat fisheries did best under the same combination of behaviours although the presence or absence of memory made less difference than before, and the importance of not communicating became even more important: presumably because sharing good fishing locations as fishing became less viable was even more likely to jeopardise a fisher's livelihood.

In the homogeneous habitat fisheries, communication was still harmful, but the importance or otherwise of remembering good locations had been displaced in importance by the perturbation characteristic. Hence in these


Figure 4.36: Effect of fisher behaviour characteristics as equilibrium is established, post reserve
fisheries, as the reserve was established, competition for fish increased and a new equilibrium number of fishers was sought. For fishers it became most important to be continuously exploring a range of locations in the remaining fishing grounds to try to maximise catch and avoid being one of the newly bankrupt.

After a further twenty nine years, stability was reached and the optimal strategies in both types of fishery had shifted again. The greatest difference was in the homogeneous habitat fishery where there was no longer any great differentiation in the success of the different strategies reflecting low levels of competition in a stable fishery. For the heterogeneous habitat fisheries, memory remained the most important determinant of success, but communication no longer seemed of significance, again likely reflecting the lower levels of competition gained through stability. In the absence of memory, a benefit was gained by being able to explore more widely.


Figure 4.37: How number of fishers varies with reserve area and proportion of cheaters, low effort

### 4.7.3 Illegal fishing

In this section the effect of illegal fishing on fishery outcomes was explored. The first scenario investigated the effect of allowing a varying proportion of fishers to cheat and fish inside the reserve area. Simulations were run for a lobster fishery with and without juvenile protection, simultaneously varying reserve widths and the proportion of illegal fishers, at high and low fishing effort (in these scenarios an individual fisher is either honest or a cheat and the proportion represents the number of active cheats rather than the alternative of representing the probability of an fisher cheating on any given day).

For both scenarios with juvenile protection and also for the low effort scenario without, the number of supported fishers decreased as reserve area increased and increased as cheating increased, as shown in figure 4.37. Conversely biomass increased as reserve area increased, and decreased as cheating increased, as shown in figure 4.38 on the facing page.

In the high effort scenario without juvenile protection biomass responded qualitatively as with the other scenarios, but the level of biomass was much


Figure 4.38: How lobster biomass varies with reserve area and number of cheaters, low effort
more quickly depleted as cheating increased, being lowered to the level present in an unprotected fishery when cheating had reached about $1 \%$ of the total population (figure 4.39 on the next page).

In this scenario at zero levels of cheating (figure 4.40 on the following page), the number of fishers decreased as the reserve size increased, although at a lower rate than in the low effort scenario, as biomass export from the reserve offsets the catch lost from out-of-bounds fishing grounds. However as cheating increased from zero the initial effect was a drop in the number of fishers supported. This was presumably as a result of the few fishers cheating getting rich fishing in the reserve whilst causing significant stock depletion, in turn reducing the level of spillover and the level of the legal fishing population that could be supported. Beyond about 2\% cheating, the fisher population started to increase again as the number of prospering cheats offset the decline in law-abiding fishers.


Figure 4.39: How lobster biomass varies with reserve area and number of cheaters, high effort


Figure 4.40: How number of fishers varies with reserve area and proportion of cheaters, high effort

### 4.8 Random movement behaviour

A significant difficulty was found when trying to compare the effects of the model with random movement against the model with density-dependent movement: It was not obvious how random movement should be implemented, (should all fish move on each relevant timestep, or should only a fraction move and if so, how would that fraction be chosen?) The outcomes of the modelling were extremely sensitive to these decisions, with some choices producing considerably lower spillover rates than for density-dependent movement whereas others produced considerably higher spillover rates. Having not been able to resolve this problem, it was decided not to include random movement results as under the aforementioned circumstances they could prove largely meaningless.

## Chapter 5

## Discussion

This chapter is divided into three sections. In the first, the results from the previous section are summarised and placed in their wider context; in the second, limitations of the study are highlighted along with their implications, and suggestions presented for further research; and in the final section the implications of this study for Gladden Spit marine reserve are explored and recommendations presented.

### 5.1 Wide context

As mentioned at the beginning of this study, the current deteriorating state of fish stocks worldwide and the failures of conventional management procedures have rekindled interest in marine reserves as a method for conserving fish stocks. Marine reserves have been considered in the literature to be equivalent to traditional management procedures in their protection of fish stocks (Beverton \& Holt, 1957), but are now perceived as having a number of additional benefits attributed to them, namely: the protection of habitat and ecosystems as well as individual stocks, easier enforcement, more precautionary protection, the potential for spillover and a significant increase in larval export ( $\mathrm{Russ}, 2002$ ). As well as framing the results of this study in a broader context, the following sections will attempt to use these results to
examine critically a number of these suggested benefits and to assess whether they can be supported by this work. The three broad issues to follow are: management, spillover and fisher behaviour and sustainable livelihoods.

### 5.1.1 Management

This study confirms the consensus in the literature that marine reserves are in many respects equivalent to traditional management methods. Comparing the effects of a range of limits on the number of fishers allowed with the establishment of differing reserves predicted that for every optimal combination of number of fishers and average biomass achieved by conventional management, there is also a reserve that can achieve the same outcome. Furthermore three additional areas of interest for reserve management are highlighted:

### 5.1.1.1 Life history, growth and fishing effort

This study has shown the importance for all forms of management of having full knowledge about the life history and growth of a species, and to a lesser extent the level of fishing effort in a fishery. For a sink population such the one focused on in this study, the population total biomass at age curve is the most important determinant of conservation outcomes. Many of the most interesting results of this study have come about because a particular scenario shifted the level of the maximum age achieved in a fishery either side of the peak of this curve, in turn modifying the maximum sustainable level of biomass accessible for harvest.

Of particular importance was the age at which peak population biomass is achieved, whether fishing age restrictions allow fish younger than this age to be caught and whether levels of fishing effort are high enough to make it (temporarily) economically viable to catch fish below the peak population biomass. Benefits for both conservation and fisheries occurred when a population which was fished to significantly below the age at which maximum
biomass yield could be achieved and was allowed to increase in maximum age to this point once more. This was shown to be achieved with both reserves and limits on the number of fishers when combined with restrictions on minimum catch age. However in reality the exact age at which to place the limit is often not known, and fishing gear is often not sufficiently selective to meet a precise minimum age/size limit (MacLennan, 1992) and hence there are considerable risks associated with traditional management techniques. But for marine reserves, these considerations are of much lesser importance especially as a proportion of the population is always protected and hence they offer a more precautionary way of providing essential juvenile protection (Lauck et al., 1998).

### 5.1.1.2 Enforcement

The exploration of the effects on fishery outcomes of illegal fishing is of particular interest in the context of attempted marine reserve enforcement. With the growing interest in the idea that marine reserves may be easier to enforce than conventional management methods and with the knowledge that enforcement of any restriction is rarely ever perfect (?), it is interesting to discover the implications of a variety of levels of illegal fishing on marine reserve outcomes.

This study predicts that under most circumstances the low levels of illegal fishing likely under a reasonable enforcement regime ( $<5 \%$ of fishers cheating) are unlikely to have a disastrous effect on the number of fishers supported or on the average biomass present in a fishery. However when a fishery with high levels of effort combined with poor protection of juveniles is being managed with a reserve, the conclusions drawn are rather different: Under these circumstances only $2 \%$ of fishers need to cheat before the levels of biomass are depleted back to the levels seen with no reserve whatsoever. Moreover with this level of cheating, the total number of fishers supported by the fishery also decreases because their law-abiding colleagues outside the reserve lose the benefits from spillover since the excess biomass is harvested by the cheats. Such an outcome is bad for both conservation and fisher livelihoods and
casts doubt on the wisdom of using reserves under such circumstances unless enforcement will be very effective. It also highlights the need to evaluate carefully the level of policing needed and the sensitivity (with respect to reserve outcomes) of the management regime to transgressions before choosing a marine reserve as a tool for management.

### 5.1.1.3 Multi-species effects

The study predicts two complications for reserves involving multi-species fisheries: Firstly reserves offer different levels of protection to species with different movement behaviour (elaborated in section 5.1.2.2). Secondly changes in the abundance of one species or the economics of harvesting in a multi-species multi-gear fishery may have implications for the level of fishing effort on, and hence biomass of its companion species. The model predicts that increases in abundance or sale price of one particular species may increase the level of effort on a companion species and hence reduce their biomass levels. Thus increasing levels of demand for one species, whether as a result of changes in market conditions or fisheries management may end up resulting in an increase in effort on all species. Moreover should authorities seek to shift effort from one species to another by subsidising a particular type of gear, they should consider that this might have a similar economic effect to increasing the sale price of that species and hence that there may be unanticipated increases in levels of effort on companion species.

### 5.1.2 Spillover

With respect to spillover, this study confirms a number of broad results and expectations found in the marine reserve literature: That species with higher movement rates both increase the export of biomass from reserves and require larger reserves for full protection (Russ, 2002); that the export of biomass is generally low compared to the catch opportunities lost from restricting fishing in reserve areas, except under specific limited conditions (Russ, 2002); and that where reserves are able to increase catches as well as providing
conservation benefits, fishing pressure in the absence of a reserve must be sufficiently high that the average age of the fish stocks is lower than that at which maximum yield can be achieved (Apostolaki et al., 2002). This confirms previous results that movement rates, life history, minimum catch age restrictions (and how well they are implemented) and fishing pressure must all be known in order to predict the outcomes of reserve establishment. Thus by explicitly including space and fish movement behaviour, this study has been able to draw a number of additional conclusions about reserves and spillover.

### 5.1.2.1 Transects

Transects measuring the average fish densities and fisher visit frequencies over a range of distances show a number of interesting results. Firstly that fishers visit areas close to the reserve more frequently than more distant areas (fishing the line) and that this behaviour occurs even with a model of fisher behaviour where catch choice is informed solely by previous catch abundance (fishers have no prior knowledge that there are likely to be increased densities near the reserve, and neither do they have full knowledge of fish distributions). In order for this to happen, biomass densities adjacent to the reserve must be consistently and appreciably higher than at other points in the reserve. This is confirmed by transects of fish biomass densities at different distances from the reserve.

In addition these transects show that the distance from the reserve boundary over which densities are raised is not significantly different between two species with considerably different movement rates and different biomass export levels. Instead spillover distance appears to be at least as strongly determined by fisher behaviour as it is by fish behaviour. Thus spillover distances cannot be reliably used as a proxy for estimating the levels of biomass exported from a reserve.

Furthermore, fish movement rates and fishing effort have a significant and measurable effect on the levels of biomass within the reserve. At sufficient
distances from the inside edge of the reserve, biomass of both conch and lobster approached the equilibrium levels achieved in the model before fishing began but as the reserve boundary was approached biomass levels decreased. This effect was felt at considerably greater distances into the reserve for lobster as a result of its higher relative mobility. At all fishing effort levels biomass inside the reserve boundary was reduced but as effort levels increased so both the magnitude of reduction and the distance over which it was felt were considerably increased. This result is important in three ways: Firstly it implies that spillover can be detected by measuring not only elevated levels of fish densities just outside a reserve boundaries, but also the distance into a reserve over which a change in fish densities can be observed. Secondly, if one of the purposes of a reserve is to build maximal levels of biomass within (for instance for the purposes of maximising larval export) then in reserves of insufficient size, high fish mobility or high fishing effort may compromise that objective. Thirdly for a fishery with a species whose movements are influenced by density gradients, fishing the line will not only take advantage of the natural export from the reserve but by sustaining a high gradient across the reserve boundary and into its body may significantly increase the level of spillover experienced.

### 5.1.2.2 Reserve geometry

The explicit inclusion of space also allowed the implications of different reserve geometries to be explored; in particular the effects of trialing reserves with different boundary lengths as well as different areas. Increasing reserve area and decreasing boundary length increased the levels of biomass within the modelled area, and in most cases was found to decrease the number of fishers. However in the case of a high effort lobster fishery with no juvenile protection, boundary length increased the number of fishers slightly and further increases subsequently lowered the number of fishers once more. In this situation, fishing effort was sufficiently high and all areas of the reserve sufficiently close to fished areas to negate the protective effect of the reserve. As a result of investigating changes in reserve geometry the model predicted that a given number of fishers can be achieved with a number of different
average levels of biomass within the reserve. This result shows that in some circumstances a reserve of lower boundary length for a given area is a considerably better way of achieving conservation outcomes. Although in practical circumstances a single reserve with an extremely long boundary length would never be considered, several smaller reserves protecting a particular total area are often used and in these circumstance total boundary length could become sufficiently high that such effects may become relevant. Thus this study suggests that in general a large reserve may well meet conservation objectives where several small reserves would not. It also suggests that in order to provide precautionary protection, care must be taken to ensure that the focus of reserve establishment is not only on the amount of area protected, but its geometry is also taken into consideration - especially in fisheries with very high levels of effort.

### 5.1.3 Fisher behaviour and sustainable livelihoods

Using the broad measures of average equilibrium fish biomass and number of supported fishers, the bio-economic behavioural fisher simulations confirmed the general conclusions from the literature that more realistic fisher behaviour predicts lower fishing effort and higher equilibrium biomass than simple constant-effort models (Smith \& Wilen, 2003). In the model presented in this study, fishing effort adjusted dynamically to the amount of available biomass, meaning that the number of fishers at equilibrium was always approximately proportional to the available biomass as a result of fisher entry and exit to and from the fishery. Thus the high levels of overfishing predicted by simple reserve models were not seen. When incorporating the full behavioural fishing model, in which fish distributions were known only imperfectly, fishing effort and the number of fishers fell still further, reflecting the inability of the fishers to exploit the resource fully, even within the bounds of the economic constraints.

The difference between the equilibrium number of fishers with and without full knowledge of fish distributions was greatest for a conch fishery with no reserve. In a lobster fishery, relatively higher movement rates ensured that
any areas of high biomass quickly faded as the fish within moved swiftly to fished areas of lower density. However conch, with their considerably lower movement rates were less able to smooth out variations in biomass density. Hence small areas of high biomass built up which the modelled fishers found difficult to discover and exploit.

Further investigations into the appropriateness of the various fishing strategies under different circumstances revealed that the simple behavioural model was relatively robust to a number of different fishery scenarios but that different aspects of behaviour were relevant in different situations. Retaining a memory of fishing locations was seen to be important in maximising the number of fishers in a fishery with a significant degree of fish distribution heterogeneity. On the other hand for a homogeneous fishery, reliance on remembered locations reduced the number of fishers supported, probably because it reduced the level of exploration and inappropriately focused exploitation on a small number of areas without sufficient biomass to support such frequent visits.

In the first year after reserve establishment local exploration significantly improved outcomes in the homogeneous habitat fishery as fishers ejected from the reserve struggled to find new fishing grounds. However perhaps the most surprising outcome of the fisher behaviour investigation was that communication decreased the viable number of fishers supported by any given fishery. Given that this result contradicts the empirical literature (although not the modelling literature (Little \& McDonald, 2007)), it is likely that this is a consequence of this model's particular combination of fisher behaviour and resource distribution dynamics: In the fishery simulated, even with heterogeneous fish distributions, few locations are sufficiently productive to support several fishers and thus the value of a good location in which to fish was substantially diluted by sharing it with others.

Moreover in real fisheries, because communication does occur and has not been found to prejudice the livelihood of those who practise it, such information sharing is likely to occur less freely, be less indiscriminate and be more informed by the levels of catch available at a particular location.

Despite not mirroring empirically determined data with regard to fisher com-
munication, this model of fisher behaviour does highlight the implications of heterogeneity in fisher populations when change takes place. It is well known that differences in fishing ability and economic means can leave some groups more vulnerable than others (Salas \& Gaertner, 2004b). This study predicts additionally that different fishing strategies may also make some groups of fishers more vulnerable to change than others. Incorporating increasing realism may allow a future model to predict which groups (distinguished by strategy) within a fishery would be particularly vulnerable to reserve establishment in order to provide appropriate assistance, training or the opportunity to diversify into alternative livelihoods.

Finally, the dearth of circumstances under which reserve establishment benefits both local fishers and the ecosystem highlights the fact that adult spillover is far from the whole story. The literature suggests that in many cases the major benefits from a reserve are obtained as a result of greater biomass increasing larval export (Pelletier \& Mahevas, 2005). In a fishery such as the one modelled, none of this benefit is felt locally. Consequently with little promise of increased catches and hence little incentive for conservation, local fishers would be unlikely to assent to reserve establishment and putative downstream sink areas would suffer reduced larval flux leading to lower catches.

This impasse might be resolved if the part of the increased catch revenues enabled by increased larval flux to a source area could be shared by the beneficiary sink in order to compensate for the revenues lost through the establishment of a reserve.

### 5.2 Limitations and future work

Many simplifications and assumptions were made in the course of this study, and many interesting avenues of exploration became apparent as it progressed but were ultimately outside the scope of a project of this duration. Perhaps the most significant issue was the lack of real empirical data against which
to verify the model. This notwithstanding, a number of the other more interesting areas for future work are outlined below:

The response of fishers to reserve establishment varied considerably from model run to model run. Under most circumstances the number of fishers decreased gradually to an equilibrium level in the first few years after reserve establishment. However under some circumstances the number of fishers dropped considerably more quickly, often undershooting the eventual stable value. Moreover on other occasions the average characteristics of the fishers in the fisher population changed substantially after reserve establishment. In some circumstances fishers who engaged in high levels of communication were those predominantly leaving the fishery. In other circumstances fishers who engaged in less exploration suffered similarly. Should these behaviours be mirrored in a real fishery, they could have serious consequences either for the fisher population or for certain subsections of the fisher population and ultimately for the acceptability of reserves. Thus further research into fisher resilience, such transient behaviour and how to mitigate it could well be valuable.

It would also be instructive to refine the fisher behavioural model especially in conjunction with a specific empirical study. The prediction made in this study that communication jeopardises the livelihood of fishers is in contradiction with outcomes in real fisheries, and this is perhaps because the assumption that fishers communicate regularly with their friends without taking into consideration any impact on their own livelihoods is rather unrealistic. A refined model of communication and exploration would be valuable for furthering the understanding of the implications of management procedures and their impacts on fisheries.

A number of empirical studies have shown that for some species, fish growth is restricted in regions of high density - and queen conch is such a species (Bene \& Tewfik, 2003). Moreover in some species fecundity rises at a greater than linear rate and hence at the same level of biomass, a small number of large adults produce many times more larvae than a larger number of smaller adults (Gardmark et al., 2006). In that connection it has been hypothesised that such an effect may significantly reduce any spillover from a reserve, especially for
more sedentary species (Bene \& Tewfik, 2003). Studies have even suggested that under such circumstance rotating reserves, in which protected areas are occasionally harvested to stimulate further growth may be needed to maintain spillover and high levels of larval export (Gardmark et al., 2006). Moreover in the current model, no differentiation is made between adults and juveniles when considering movement rates. As juveniles are generally less mobile than adults this simplification is likely to have resulted in an underestimate of the protection offered by a reserve and of the potential levels of spillover. As both of these opposing effects can be of significant magnitude it would be valuable to establish what effect they might have on fisheries outcomes, and also to consider the effects of a degree of self-recruitment within such a population.

In this study habitat heterogeneity has been ignored when considering reserve placement. However studies have shown that protecting appropriate habitat, particularly nurseries and high productivity areas can significantly improve fishery outcomes. Investigating habitat heterogeneity and reserve placement in a geometry aware, spatially explicit model such as this may throw further light on the importance of these considerations for management.

Under some circumstances seasonality in the levels of fish stocks seemed to affect the extent of interaction between species through fishing effort. It would be interesting to see if this is a significant effect and whether such cyclical variability enhanced or reduced the levels of coupling of effort.

Finally, given that much of the benefit of establishing a reserve in a metapopulations is often through increased larval export which does not produce local benefits, it would be particularly interesting to investigate whether there may be financially sustainable ways in which fishing communities benefiting from larvae from other areas might be able to encourage reserve establishment in those source areas by compensating the distant fishers for catch lost from the reserve area (in recruitment-limited areas, potentially through increases in source catch revenues).

### 5.3 Recommendations for Gladden Spit marine reserve

The parameters upon which most of the results of this study have been founded are based around those expected for Gladden Spit marine reserve. However there is considerable uncertainty in a number of these, which although not compromising the general conclusions of the study do mean that considerable caution must be exercised when making recommendations for that specific region. The parameters that need to be known with the most certainty are those that could contribute to a qualitative shift in fishery dynamics. The most likely candidates for this are: the effectiveness of current levels of juvenile protection, the current level of fishing effort within the reserve and whether or not the population is self-recruiting. Under all circumstances the marine life within the Gladden Spit area is likely to benefit from the inclusion of a no take zone, although the degree of protection for each species will be affected by the size, geometry and placement of the zone. Thus the existing $1 \mathrm{~km}^{2}$ no take zone will offer some protection to both the conch and lobster populations (although the latter to a lesser degree), and larger reserves would only improve the situation.

The impacts on the fisher community are less certain. Reports suggest that both lobster and conch density levels are significantly lower than in the recent past, and that the sizes of individuals of both species arriving at markets throughout Belize are decreasing (CFMC, 1999). Hence if this is the case, and if juvenile protection is inadequate (perhaps because juveniles are being taken for home consumption and the practise is therefore difficult to prevent) then it may be possible that instigating a larger reserve would produce benefits for both fish and fishers, provided it was enforced adequately. If a decision be taken to protect the marine life regardless of the impact on the fishery, then this study suggests that it is imperative to identify the most vulnerable sections of the fisher community and to provide them with the opportunity to shift to an alternative livelihood if they are forced to leave the fishery. However, given the aforementioned uncertainties in the data, and the potential impact on the fisher community if such a reserve is put in place and the modelling
assumptions were to be proved wrong, the predominant conclusion must be that the first recommendation is for further study of the reserve area, starting with the three most important parameters identified.

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