

Spillover from marine reserves:  
A systematic literature review and  
population model for queen conch  
using Gladden Spit Marine Reserve,  
Belize, as a case study

Kirsty McGregor

Supervisor: E.J. Milner-Gulland

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## **Abstract**

Marine reserves have been used as a spatial form of fisheries management and conservation tool throughout the world. Central to the success of reserves is their ability to enhance catch in adjacent fished areas through ‘spillover’ of adult biomass. The volume of empirical and modelling literature on spillover has grown in recent decades and there has been debate over how much equivocal evidence there is for spillover. Here, I systematically review the empirical literature on spillover and adopt a case-study approach to examine the likelihood of spillover for queen conch (*Strombus gigas*) at Gladden Spit Marine Reserve, Belize. I review the literature on the effects of reserves on queen conch and use this information to develop an age-structured population model that includes density dependent migration between a protected and exploited population. By applying the model to Gladden Spit, I identify knowledge gaps for this case study that are essential in providing sound management advice. I conclude that there is empirical evidence for spillover in reef fish and invertebrates, but that all studies are lacking data on other confounding variables and a standardised sampling protocol should be adopted. Developing a model for conch highlights the absence of data on this species that are essential for its management, which include the lack of an empirical stock-recruitment relationship. Applying the model to a case study shows that specific data missing for Gladden Spit include fishing mortality rates, which are vital when estimating spillover.

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## Table of contents

<b>1 Introduction</b>	<b>1</b>
1.1 Marine reserves as a conservation tool	1
1.2 Belizean queen conch fishery	3
1.3 Gladden Spit Marine Reserve, Belize	4
1.4 Study aims	6
<b>2 Methods</b>	<b>6</b>
2.1 Systematic review of spillover and conch literature	6
2.2 The conceptual model	7
2.3 Model assumptions	8
2.4 The mathematical model	10
2.5 Model parameterisation	14
2.6 Sensitivity analysis	14
2.7 Applying the model to Gladden Spit	15
<b>3 Results</b>	<b>15</b>
3.1 Systematic review of empirical spillover literature	15
3.2 Studies on spillover	16
3.3 Conclusions from spillover literature	17
3.4 Problems for studying spillover	18
3.5 Conclusions and the future of spillover research	25
3.6 Review of queen conch literature	26
3.7 Life history	26
3.8 Queen conch conservation and management	39
3.9 Modelling queen conch populations	32
3.10 Model Results	32
3.11 Sensitivity to migration and fishing mortality	32
3.12 Spillover	32
3.13 The population mode applied to Gladden Spit	36
<b>4 Discussion</b>	<b>36</b>
4.1 Systematic review of spillover	36
4.2 Conch population model	37
4.3 Limitation of this study	37

4.4	Future work	38
4.5	Conclusions	39
	<b>References</b>	<b>40</b>
	<b>Appendix</b>	<b>56</b>

### List of Figures

Figure 1	Gladden Spit map	5
Figure 2	The conceptual model	9
Figure 3	Mortality rate-at-age curve	11
Figure 4	Tissue weight-at-age curve	13
Figure 5	Stock-recruitment curves	13
Figure 6	Population size varying migration and fishing mortality	33
Figure 7	Population sizes in reserve and non-reserve area	35
Figure 8	Spillover	35

### List of Tables

Table 1	List of model parameters and values	9
Table 2	Methods used to study spillover	19
Table 3	Summary of spillover studies	21
Table 4	Essential and desirable data for spillover	25
Table 5	von Bertalanffy parameters	28
Table 6	Mortality rate estimates	29
Table 7	Summary on studies of reserve effects on conch	30
Table 8	Summary of modelling studies on conch	31

## **1.0 Introduction**

### **1.1 Marine reserves as a conservation tool**

Marine reserves (or ‘marine protected areas’) are a spatial form of fishery management aimed at conserving biodiversity and restoring depleted fish stocks (Palumbi 2002). Conceptually, traditional fisheries management established refuges based on population numbers, whereas marine reserves provide a refuge in space (Bohnsack 1996). The term ‘marine reserves’ usually refers to areas that are closed to fishing (a ‘no-take zone’). However, in practice, many marine reserves have no-take areas inside a larger multiple use area, where some form of fishery regulation is enforced, such as gear, seasonal, or effort restrictions. For example, the Nabq Natural Resource Protected Area in the Egyptian Red Sea has small no-take areas where all fishing is forbidden, interspersed with areas open to artisanal fishing (Galal et al 2002). Mombasa Marine Park and Reserve in Kenya consists of a 10km<sup>2</sup> no-take area and an adjacent reserve where traditional fishing methods are permitted (McClanahan and Kaunda-Arara 1996). Marine reserves can also be used to regulate the impact of tourism, by restricting the number of visitors, tour operators and activities in an area.

Over the last two decades, interest in using marine reserves as a method for protecting fisheries in overexploited areas, particularly in developing countries, has grown. The subject has attracted marine ecologists, fisheries scientists and managers, policy makers, economists and modellers among many others. Consequently, a large body of literature now exists on the subject, which has been extensively reviewed elsewhere (e.g. Willis et al 2003; meta-analyses: Côté et al 2001; modelling studies: Roberts and Sargant 2002, Gell and Roberts 2003a, Gerber et al 2003, Micheli et al 2004; empirical studies: Rowley 1994, Roberts and Polunin 1991, Russ 2002, Halpern and Warner 2002, Palumbi 2004). The reason for the huge interest in marine reserves and the burgeoning literature is that traditional fisheries management (using catch and effort control) has failed to prevent massive overexploitation of fisheries worldwide (Russ 2002). Marine reserves could act as an insurance policy against such management failure, and provide potential to combine the conservation of marine ecosystems with sustainable exploitation for local communities (PDT 1990).

Some generalised effects of well-enforced marine reserves have been identified and are relatively well understood. An increase in total abundance and biomass of fish inside reserve boundaries has often been observed (Dugan and Davis

1993, Ferreira and Russ 1995, Wantiez et al 1997, Edgar and Barrett 1997, Côté et al 2001, Gell and Roberts 2003a, Palumbi 2004). This increase seems to occur independent of reserve size (Côté et al 2001, Halpern 2003). In some cases, rapid rates of abundance increases have been observed (Halpern and Warner 2002). There is usually a shift towards larger-sized individuals within marine reserves, which leads to an increased reproductive capacity of protected populations (Micheli et al 2004). Additionally, some reserves have enhanced habitat quality (Roberts and Polunin 1991), species diversity (e.g. Cole et al 1990, Russ and Alcala 1996), and increased community stability (Roberts and Polunin 1991, Dayton et al 1995). However, in other cases recovery has been slow, in the order of decades and effects are not always predictable (Russ and Alcala 2004). For example, species in different trophic groups respond differently to protection - an increase in the number of top carnivores can lead to a decreased abundance of prey species (Micheli et al 2004). Reserves are also unlikely to have benefits for highly mobile species (Hilborn et al 2004) and there is some disagreement about how much evidence there really is for increased fish density and size inside reserves (Willis et al 2003).

The effects *inside* reserves have led to the idea that marine reserves could enhance fisheries *outside* their boundaries, by larval export to fished areas (the 'recruitment effect'), or the export of adult biomass to adjacent fishing grounds (the 'spillover effect'). The recruitment effect is likely to be the most important benefit to fisheries, as a way of maintaining critical minimum spawning stock by larval export to overexploited fishing grounds. This benefit could be local or hundreds of kilometres away from the reserve itself, depending on the fate of larvae from the reserve. Attempts at measuring net export of eggs or larvae encounter huge logistical difficulties as larvae/eggs are hard to tag and track. The spatial scale is potentially tens to hundreds of kilometres, and the time scale of such studies perhaps 10-20 years (Russ 2002). A potential method for tracking the fate of larvae is to collect extensive genetic samples of fish populations to look for genetic patterns of isolation, that could provide a direct measure of larval dispersal (Palumbi 2001, 2003). The question of where larvae go is one of the most important in marine ecology, however the difficulties of measuring larval dispersal mean that it is still an open question (Dayton et al 1995).

Establishment of marine reserves in the developing world requires the support of local fishing communities that use the marine resource (e.g. Russ and Alcala 1999).

The promise of stock-wide increase through the recruitment effect that may benefit fisheries 10-100km away from the reserve may not be very attractive to local stakeholders. Any demonstration that a marine reserve will increase the fishery in local fishing grounds directly adjacent to the reserve through spillover could be critical to successful reserve establishment (Russ 2002). Designating a marine reserve effectively reduces the size of local fishing grounds. As a response to this fishers may move away from local grounds altogether, or leave fishing for alternate livelihoods. This happened in Kenya - when 65% of the fishing ground was lost to the Mombasa Marine Park and Reserve, approximately 65% of fishers left the area (McClanahan and Kaunda-Arara 1996). Consequently, the fishing pressure in fishing grounds adjacent to the reserve did not increase beyond pre-park levels. However, loss of fishing grounds could result in a higher fishing pressure in areas adjacent to a reserve, lead to poaching from the reserve, and to loss of livelihoods for fishers. Spillover from the reserve to fished areas could ameliorate the effects of reductions in fishing area, by increasing mean catch per unit effort (CPUE) in the fished area. Spillover is therefore a powerful political tool that can be used as evidence for the benefits of marine reserves to local fishing communities and gain local community support. The unequivocal demonstration of spillover is therefore of great importance to the establishment and success of marine reserves (Russ 2002).

## **1.2 Belizean Queen Conch Fishery**

The Queen Conch, *Strombus gigas*, is one of the most valuable fisheries resources in the Caribbean region. Consequently, most stocks are heavily exploited or over-harvested (Appeldoorn et al. 1987). In 1990, *S. gigas* was listed in Appendix II of the Convention of International Trade in Endangered Species (CITES), which includes a list of species that may become threatened with extinction without trade controls. The International Union for the Conservation of Nature (IUCN) categorised the species as commercially threatened on the 1994 Red List (Groombridge 1994).

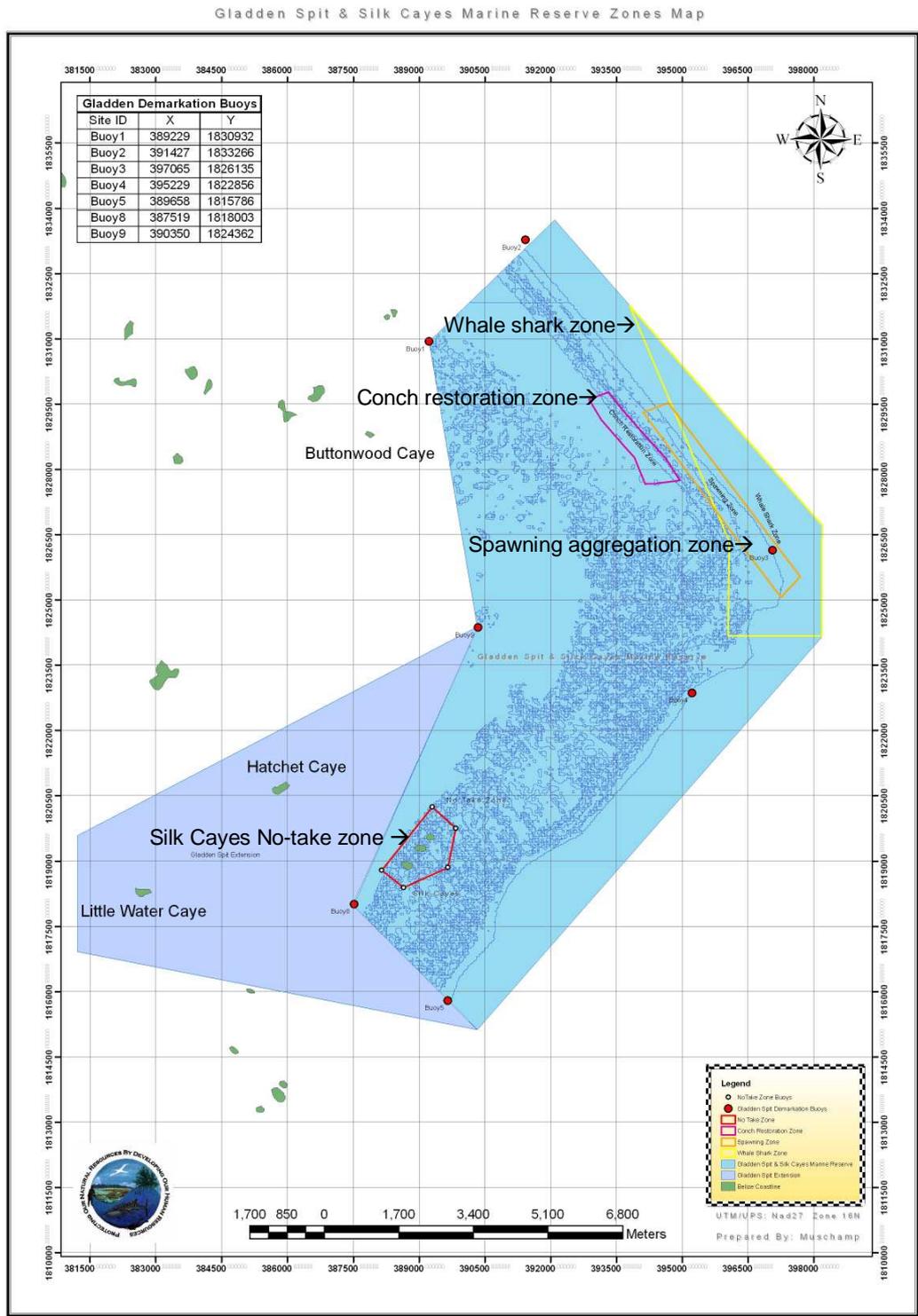
Belize is the seventh largest exporter of processed conch meat (Acosta 2006). The fishery is small scale and characterised by small boats called skiffs (Berks et al 2001). Queen conch account for approximately 20% of the earnings annually from exporting wild-caught marine produce (Belize Fisheries Department 2001). Fishing is concentrated in shallow water less than 10m deep, in seagrass meadows, sand-algal flats, and coral reefs. Maximum queen conch landings in Belize were 1,200 metric

tons in 1972, but landings declined rapidly after this period (Camillo 2004). Belizean fishery regulations include a minimum shell length of 178mm and a minimum processed meat weight of 85g. A closed season is enforced from July 1<sup>st</sup> to September 30<sup>th</sup> to coincide with the peak reproductive activity measured during early studies in Florida (D'Asaro 1965). However, it is likely that these measures are ineffective because size at maturity is very variable (Appeldoorn 1988a). In Belize, around 40% of the legally fishable population are immature - estimated mean adult weight is twice the legal limit of 85g (Acosta 2006). Additionally, the spawning season in the southern Caribbean has been recorded as early as May and as late as November, and could be all year round (Stoner et al 1992). Despite the Caribbean conch fishery being extremely valuable, little work has been published on the ability of marine reserves to enhance the fishery for this species through spillover.

### **1.3 Gladden Spit Marine Reserve, Belize**

Belize has a large section of barrier reef that extends from the northern border with Mexico south for about 260km to near the border with Guatemala (Pomeroy and Goetze 2003). The reef has an extensive and diverse coral reef ecosystem, and there are also mangrove and seagrass beds. Gladden Spit lies 36 km from the coast of Placencia (Figure 1) (16°32'43"N, 87°59'30"W) (Heyman 2001). The reef wall at Gladden Spit drops nearly vertically around the promontory to oceanic depth (Hayman 2001). The area is well known due to its annual spawning aggregations of at least 25 species of finfish, which migrate there to spawn, attracting whale sharks for 5-10 days around the time of full moons in April-June (Heyman and Graham 2000). Consequently, the area has become popular for commercial fishermen and tourist dive operators.

Gladden Spit Marine Reserve was officially established in May 2000 and has been co-managed by a small non-governmental organization called 'Friends of Nature' (FON) since 2002 (Friends of Nature Belize 2007). Co-management is the concept of sharing management responsibilities and authority between government and stakeholders (e.g. Berkes et al. 2001). Under its co-management agreement with the government, FON has control of zoning regulations, the behaviour of users and is authorized to police within the zones (Pomeroy and Goetze 2003). FON also works in the local community conducting socio-economic monitoring, education and outreach programmes in schools and villages (Friends of Nature Belize 2007).



**Figure 1.** Large map of Gladden Spit Marine Reserve showing the different zones. Produced by Friends of Nature, Belize (2007). Red= no-take zone, pink = conch restoration zone, orange = spawning zone, yellow = whale shark zone. Red circles indicate demarcation buoys.

The reserve covers approximately 10,523 ha of marine environment and encompasses the Silk Cayes that lie south of Gladden Entrance. There is a 526 ha no-

take conservation zone surrounding the Cayes and a special management area for whale sharks, within which access for fishers and divers is limited. Throughout the rest of the reserve motorboats are prohibited (Pomeroy and Goetze 2003). The central region of the barrier reef is continuous and well developed and runs northwest to southeast, ending at Gladden Spit (Pomeroy and Goetze 2003). The barrier reef has a particular form: (1) back reef, (2) reef crest, (3) inner fore reef with extensive spur and groove formation, and (4) an outer fore reef with a sand trough and coral ridge (Burke 1982). Durable and slow growing communities dominate, and shallow reefs are narrow and discontinuous (Burke 1982). Inside the barrier reef, northwest of the Spit, the lagoon area has a flat grassy bed that slopes slowly inland away from the reef (Pomeroy and Goetze 2003). Traditionally, this area has been a fishing ground for queen conch, but reports indicate that the population there has collapsed. A survey in 1996 at three sites at Gladden Spit indicated that the conch population was at a low level (Pomeroy and Goetze 2003). One transect running through the seagrass bed found only 3 legal sized conch ha<sup>-1</sup>. A transect through Gladden Entrance yielded only 34 conch ha<sup>-1</sup>.

#### **1.4 Study aims**

The first aim of this study is to conduct a systematic review of the empirical literature on spillover. The second aim of this study is to use a case study approach to examine the likelihood of spillover of queen conch from Gladden Spit Marine Reserve, Belize, including a review of the literature on conch biology. The third aim of this study is to use information from both systematic reviews to develop an age-structured model for conch that includes migration from a protected to an exploited population. The model has been used to estimate the potential spillover of conch from Gladden Spit under different levels of fishing mortality and migration conditions, and to assess the effects of unknown parameters, and identify areas where future empirical work is required.

### **2.0 Methods**

#### **2.1 Systematic review of spillover and conch literature**

Lack of systematic evaluation of the effectiveness of conservation practice has hindered advances in scientific management (Sutherland 2000). Recently, an ‘evidence-based framework’ for decision-making has been advocated as a solution

(Pullin and Knight 2001, 2003). Key features of this framework are the systematic review of evidence and the identification of knowledge gaps. The systematic review concept aims to summarise, appraise and communicate large amounts of empirical research to improve delivery of scientific evidence to the user-community (Pullin and Knight 2003). Systematic reviews are more powerful than a traditional literature review, as their methods are transparent and not purely descriptive. A set of guidelines have been developed (Stewart et al 2005) that include formulating a specific question, developing a review protocol, selecting relevant sources, assessing the quality of methodology, extracting data, and reporting the results. This enables identification of areas requiring future work. Systematic reviews of the empirical literature on spillover and both empirical and modelling work on conch were conducted by searching for published studies and relevant grey literature using internet search engines. Conch life history data gathered in the review were then used to parameterise the model.

## **2.2 The conceptual model**

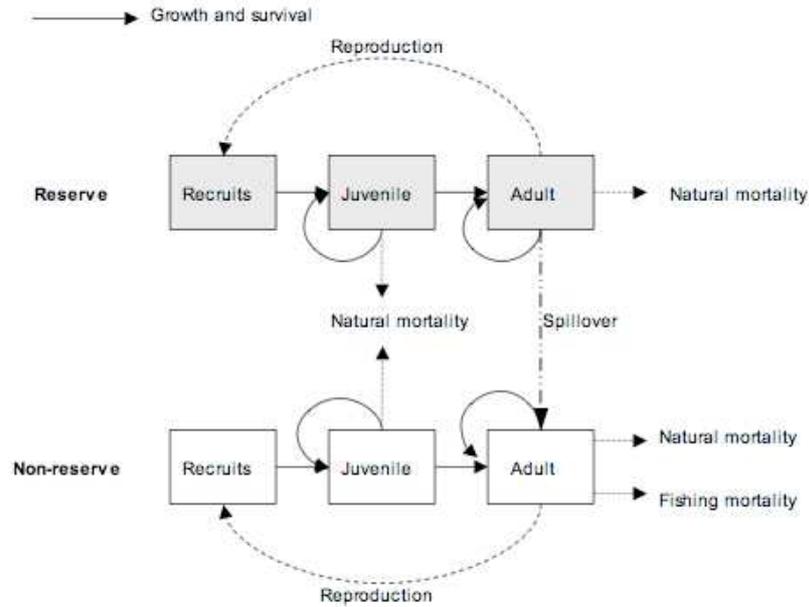
I developed a simple deterministic two-patch age-structured model (e.g. Polacheck 1990, DeMartini 1993) that progresses in time steps of one month (e.g. Pelletier and Magal 1996, Gu nette et al 2000). A reserve and non-reserve population are modelled - a conceptual version of the model is presented in Figure 2. An age-structured approach was chosen because an empirically derived weight-at-age function exists for conch (Table 7, Appeldoorn 1992). Density dependent size plasticity in conch means that a stage or size structured approach would be problematic. Monthly time steps were used because juveniles have age-dependent natural mortality rates that are best represented by recalculating mortality rate at short time intervals (Appeldoorn 1988a). Individuals are juveniles until sexual maturity at 3.6 years (Appeldoorn 1988a). Adults reproduce according to a Beverton-Holt stock-recruitment relationship (e.g. Attwood and Bennett 1995). Recruitment in each population is separate, therefore the populations are separate spawning stocks. Recruits enter the mobile population at 16 months as early post-settlement juveniles (see Stoner 2003). Early post-settlement juveniles are the most sedentary phase of the life history and density estimates of juveniles moving from nursery to adult habitat can be used to represent recruitment to the mobile population (Acosta 2002). Juveniles and adults in both populations suffer age-dependent natural mortality.

Adults in the non-reserve population also suffer fishing mortality. Adults can migrate (spillover) from the reserve to the non-reserve population; therefore migration is asymmetric (e.g. Holland and Brazee 1996). Spillover is dependent on the relative difference in the number of individuals in an age class between the reserve and non-reserve populations (e.g. Armstrong and Skonhøft 2006) and on the percentage migration allowed. The assumptions made about density dependent migration are key to the model results. In this model, the percentage migration allowed can be varied to simulate the mobility of the species. There is no information available on density-dependent migration in conch. This model assumes that as relatively sedentary molluscs, and the percentage that migrate at each time step likely to be small.

### **2.3 Model assumptions**

A simple age structured model has the following assumptions in addition to those already discussed, some of which are unrealistic or uncertain but necessary to keep the model simple:

- All individuals within an age class have identical ecological properties (i.e. growth and survivorship).
- There are no significant time delays in population processes.
- There is no seasonality, processes happen at a constant rate.
- Individuals' growth and survivorship are not density-dependent (though this is likely to be untrue in nature, and a density-dependent version of this model is a natural extension).
- There are no trophic or interspecific interactions. Individuals are not food limited and there is no predation or competition with other species for resources.
- Carrying capacity is set intrinsically by the stock-recruitment relationship parameter  $b$  (Table 1).
- There are no stochastic events (e.g. environmental variation, bonanza or catastrophe years), though this would be a logical extension to the model in the future.



**Figure 2.** The conceptual model: For simplicity, two boxes ('Juvenile' and 'Adult') represent numerous juvenile and adult age classes.

**Table 1.** Values of parameters used in the conch model

Parameter	Symbol (units)	Value and function	Source
Age at recruitment to the mobile population	$A_r$ (months)	16	Stoner (2003)
Age at reproductive maturity	$A_{mat}$ (months)	36	Appeldoorn (1988a)
Age class	$A$ (months)		
Beverton-Holt Parameters	$a$	15	Simulation
	$b$ ( $\text{ha}^{-1}$ )	120	Acosta (2002)
Biomass	$B$ ( $\text{kg ha}^{-1}$ )		
Fishing mortality	$F$ ( $\text{month}^{-1}$ )		
Maximum age class	$A_{max}$ (months)	360 (30 years)	Hoenig (1983)
Migration (total)	$m$		
Migration (in age class)	$m_A$		
Mortality rate constants	$w$	0.242	CFMC (1999)
	$x$	4.330	
Natural mortality rate at age	$M_A$ ( $\text{month}^{-1}$ )	$M_A = \frac{-w + x}{A} \min 0.1$	CFMC (1999)
Number of individuals	$N$ ( $\text{ha}^{-1}$ )		
Percentage migrating	$d$ (%)	Varied from 0 -1 (0-100%)	Simulation
Probability of survival at a given age	$S_A$	$S_{i,A} = e^{-M_A}$	-
Spawning stock biomass	$s$ ( $\text{kg ha}^{-1}$ )	$s_{i,t} = \sum_{a=A_{mat}}^{A_{max}} B_{i,a,t}$	
Tissue weight at age growth model	$T$ ( $\text{kg ha}^{-1}$ )	$T = y \cdot 10^{-5} e^{\left(1 - e^{-p \cdot A}\right)}$	Appeldoorn (1988b)
Tissue weight-at-age constants	$y$	1.263	Appeldoorn (1988b)
	$z$	17.44	
	$p$	1.126	

## 2.4 The mathematical model

The conceptual model (Figure. 2) was developed into a mathematical model (following the examples of Attwood and Bennett 1995, Holland and Brazee 1996, Guénette and Pitcher 1999). All parameters used in the mathematical model are listed in Table 1.  $N_1$  is the population inside a no-take marine reserve and  $N_2$  is the population in an area open to fishing that suffers fishing mortality ( $F$ ). The model is based on cohorts of individuals of the same age and size at a given age. Individuals within the same age class were treated as identical with respect to somatic growth pattern and mortality risk. The model was progressed in monthly time steps because juvenile mortality rate in conch is strongly dependent on age (Appeldoorn 1998b). Mortality can be calculated from the equation:

$$M_A = \frac{-w + x}{A} \quad (1)$$

where  $M_A$  is natural mortality rate for a given age class,  $A$  is age in months, parameters  $w$  and  $x$  are mortality rate equation constants (Table 1), and the minimum value for  $M_A$  is 0.1 (Figure 3). Monthly time steps allowed recalculation of mortality rate regularly. A survival function for a given age class in each population was calculated as,

$$S_{1,A} = e^{-M_A} \quad (2)$$

$$S_{2,A} = e^{-M_A + F} \quad (3)$$

where survival,  $S$ , in age class  $A$  in population 1 depends only on age specific natural mortality  $M_A$ , but in population 2,  $S$  also depends on fishing mortality  $F$ .  $F$  is only applied to sexually mature age classes.

The number of sexually immature individuals in a given age class can then be calculated. The projection equations for the model are:

$$N_{i,A+1,t+1} = N_{1,A,t} \cdot S_{i,A} \quad (4)$$

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TIFF (Uncompressed) decompressor  
are needed to see this picture.

**Figure 3.** Mortality rate-at-age curve used in the model, adapted from CFMC (1999).

Individuals then could grow and reproduce. Individuals were assumed to grow according to a tissue weight-at-age equation (Appeldoorn 1992),

$$T = y \cdot 10^{-5} e^{z(-e^{-pA})} \quad (5)$$

where  $T$  is tissue weight in (kg),  $A$  is age in months, and  $p$  and  $z$  are constants in the tissue-weight-at-age equation (Table 1) (Figure 4). Biomass in an age class was then calculated as:

$$B_{i,A,t} = N_{i,A,t} \cdot T \quad (6)$$

Sexually mature individuals can move out of the reserve into this fished area but not the other way, therefore migration is asymmetric. Migration for an age class,  $m_A$ , changes depending on the relative densities of the populations and on the percentage migration ( $d$ ),

$$m_A = (N_{1 \geq A_{mat}, t} - N_{2 \geq A_{mat}, t}) \cdot d \quad (7)$$

therefore, the total number of individuals migrating from the reserve in a month ( $m$ ) is,

$$m = \sum_{a=A_{mat}}^{A_{max}} m_a \quad (8)$$

The number of sexually mature individuals in the marine reserve population was then calculated as:

$$N_{1 \geq A_{mat} + 1, t} = N_{i \geq A_{mat}, t} \cdot S_{i,A} - m \quad (9)$$

and in the fished population as:

$$N_{2 \geq A_{mat} + 1, t} = N_{i \geq A_{mat}, t} \cdot S_{i,A} + m \quad (10)$$

The biomass of sexually mature individual, spawning stock biomass ( $s$ ), was then calculated as,

$$s_{i,t} = \sum_{a=A_{max}}^{A_{mat}} B_{i,a,t} \quad (11)$$

where  $A_{mat}$  is the age class at which sexual maturity is reached, and  $A_{max}$  is the maximum age an individual lives to. A Beverton-Holt stock-recruitment relationship was used to calculate monthly recruitment to the first age class:

$$N_{i,Ar,t} = \frac{a \cdot s}{1 + \left(\frac{a}{b}\right) \cdot s} \quad (12)$$

where  $a$  is a Beverton-Holt parameter that sets the steepness of the slope, and  $b$  is the recruitment asymptote (Figure 5). The mathematical model was then coded and run using R (R Development Core Team 2007) (Appendix A).

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are needed to see this picture.

**Figure 4.** Tissue weight-at-age curve used in the model, adapted from Appeldoorn (1992).

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are needed to see this picture.

**Figure 5.** Shape of the Beverton-Holt stock-recruitment relationship when  $b$  is 120 and parameter  $a$  is 15 (solid), 10 (dashed), 5 (dotted) and 1 (dot-dash). Recruitment and spawning stock biomass are values  $\text{ha}^{-1}$ . [figure legends need to go under the figure. Table legends in top of tables]

## 2.5 Model Parameterisation

Parameter values were taken from the literature when possible, and values for Belize specifically were used when there was a choice (Table 1). The value of the Beverton-Holt parameter  $a$  was fixed at a value of 15, which was chosen to give population densities at known values of  $F$  that matched those observed in the literature. As no stock-recruitment relationship for conch exists in the literature, this best estimate was accepted as a baseline parameter for the model. The consequences of varying  $a$  in the stock-recruitment relationship are shown in Figure 5.

## 2.6 Sensitivity Analysis

Sensitivity analysis is an important component of modelling. It highlights parameters that have the greatest influence on the model, which parameters should be measured most accurately and indicates the reliability of the model (McCarthy et al 1995). Sensitivity analysis is therefore useful for assessing management options (Possingham et al 1993). Analysing the effect of all parameter combinations (exhaustive approach) causes practical problems including large computational time and difficulty interpreting the large volume of results. If the outcome of interest is binary (e.g. population persistence or extinction), the logistic regression can be used to determine a 'line' (a multi-dimensional plane) of best fit for the relationship rather than exact values for points in parameter space (McCarthy et al 1995). However, the aim of this study was to develop a simple model for queen conch and then explore its limitations. Complex model analysis was not necessary; therefore simple sensitivity analysis varying only fishing mortality ( $F$ ) and percentage migration ( $d$ ) was conducted to explore model space.  $F$  and  $d$  were chosen because they are unknown, a key determinant of spillover, and could be modified or planned for when designing marine reserves.  $F$  is an issue that is key in marine reserve management and could be modified with management action. The percentage migration parameter  $d$  is important as it gives an indication of the amount of movement a species does, and is key designing reserves with a target species in mind. The parameter  $a$  in the stock-recruitment relationship was not varied (although the model was sensitive to this parameter) because the value of  $a$  is totally unknown, potentially over a large range and out of the control of management decisions. Including variation in  $a$  would have made model analysis complex and it was unnecessary. The issue of an unknown stock-recruitment relationship had already been highlighted and no further insights

could be gained by including variation in  $a$ . The aim of sensitivity analysis was also to check that the model worked in an intuitive way, and that the model responded to parameter change in the way I expected it to.

Sensitivity analysis was automated by building it into the R code (Appendix A). One parameter at a time was varied. Fishing mortality ( $F$ ) was selected at random from a uniform distribution from 0 to 3, at different values of the percentage migration parameter,  $d$ . Percentage migration ( $d$ ) was varied in steps of 0.02 from 0 to 1 (which is equivalent to 0 to 100% migration permitted). The model was run 30 times for each different  $d$  value. Each model run simulated 50 years of conch population dynamics. For both populations, total population size, total biomass, spawning stock biomass, and spillover was recorded for every model run. Spillover was measured in kilograms of tissue weight because tissue weight is ultimately what fishers sell at market. Measuring biomass rather than individuals was intended to allow the effects of density dependent growth to be included in the model in the future. Measuring spillover in number of individuals would have led to false conclusions – for example, many small individuals could have migrated, or just a few large ones, but the overall spillover biomass might be the same. Measuring biomass directly avoids such problems.

## **2.7 Applying the model to Gladden Spit**

The model was parameterised for Belize: fishing mortality ( $F$ ) was set at 0.8 based on the average fishing mortality recorded for adult conch in Belize (CFMC 1999), and the percentage migration ( $d$ ) was set at 4%, to reflect the sedentary nature of conch. The results were used to estimate population size and spillover that the proposed conch restoration zone could provide if fully protected.

## **3.0 Results**

### **3.1 Systematic review of empirical spillover literature**

The suggestion that there could be increased catches in fishing grounds adjacent to marine reserves was made by Roberts and Polunin (1991) and Rowley (1994). Spillover can be defined as the net export of adult (post-settlement) biomass from reserves to fished areas. Many studies use terms similar to ‘emigration of adults from reserves’ when they talk of the movement of fish from reserves to the surrounding

fished areas (e.g. Alcala and Russ 1990). However, there is a distinction between the terms ‘emigration’ and ‘net export’ - the latter requires that both emigration and immigration are measured.

The empirical evidence for spillover has been discussed before in reviews (e.g. Gell and Roberts 2003b), and in many studies’ introduction and discussion sections (e.g. Paddock and Estes 2000, Wilcox and Pomeroy 2003). However, empirical studies have not been the sole subject of a systematic review that critically evaluates the evidence to date for spillover. Previous reviews have generally focused on modelling studies (e.g. Gerber et al 2003).

### **3.2 Studies on spillover**

Studies on spillover can be divided broadly into four categories that use either (1) modelling, (2) tagging/movement analysis, (3) underwater visual census (UVC) of density gradients across reserve boundaries, (4) catch per unit effort (CPUE) or spatial fishing effort data, or a combination of these, to look for patterns consistent with spillover (see Table 2 for an explanation of the concepts and methods of each approach). I will only review the studies that have quantitatively measured spillover using UVC and CPUE analysis (Table 3), as comprehensive reviews are available for modelling (e.g. Gerber et al 2003) and tagging studies (e.g. Sánchez Lizaso et al 2000, Russ 2002).

Reliability of the various methods used to study spillover differs and all have their pros and cons (Table 2). In summary, the popular method of using UVC to monitor species abundance and diversity is unreliable. Firstly, because fish behaviour can be affected by the presence of divers, leading to biased counts. And secondly, because abundance data alone means little if it is not correlated with other variables, such as habitat quality and fishing effort. CPUE is often used to infer spillover by monitoring at landing sites. Change in CPUE after reserve establishment is a good indicator of spillover, however, it is often difficult to determine the spatial scale of spillover using this method. Monitoring CPUE onboard fishing boats or using logbook data may enable researchers to record the spatial extent of spillover more easily. Tag-recapture techniques are also extensively utilised. Traditional methods using visual tags do not allow researchers to directly observe the movements of fish, and home range size can only be inferred. Newer technologies like ultrasonic telemetry allow home range size to be directly measured, providing more insights into

fish behaviour around reserve boundaries. Researchers have begun to use experimental fishing to monitor spillover. This has the advantage that fishing effort is standardised, however, less catch data may be produced using this method than monitoring CPUE at ports. Finally, mathematical models of the effect of reserves on fish abundance and fisher behaviour have been widely applied. However, models can only ever be a simplified representation of reality, and cannot substitute for empirical data on spillover.

### **3.3 Conclusions from spillover literature**

The following list summarises the main findings to date on spillover that have good empirical support. A more detailed analysis of all studies is provided in Table 2.

- Higher CPUE and fish abundances have been recorded in fishing areas adjacent to no-take marine reserves (Table 3). Spillover may happen over relatively short distances of less than 300m for reef fish (Russ and Alcala 1996) and larger distances of 20km or more in temperate areas (Murawski et al 2004). However, patterns of abundance that suggest spillover of reef fish have been documented on the scale of 5km from a reserve boundary (Sluka et al 1997). In general tagging studies confirm that reef fish are likely to move distances of 100-500m and further for spawning aggregations or ontogenetic habitat shifts (e.g. Zeller and Russ 1998, Kelly et al 2002). Therefore, there is considerable potential for spillover from reserves over distances of less than 1km (Roberts and Polunin 1991, Cole et al 2000). The distance over which spillover could occur depends on a species home range size and pattern of migration (Palumbi 2004). Given these findings, it is surprising that many studies on marine reserves do not sample at small intervals within 500m of the reserve boundary as standard (Russ and Alcala 1996, Sluka et al 1997, Davidson 2001), thereby reducing their chances of finding patterns of fish abundance or CPUE that would suggest spillover.
- Spillover is more likely to occur from reserves that have a boundary onto continuously good reef habitat, isolated reserves are unlikely to export biomass (Kramer and Chapman 1999). The type and extent of habitats on the boundaries of a reserve will influence emigration (Chiappone and Sealey 2000). Sand cover is negatively correlated with fish abundance (Chapman and Kramer 1999),

suggesting that organisms may be unlikely to cross open sand flats to reach other reefs (Sale et al 1984, Ebeling et al 1985).

Spillover may take in the order of decades to occur, as the density of very slow growing fish could take a long time to sufficiently build up (Roberts et al 2001, Russ et al 2003). Roberts et al (2001) investigated spillover of record-sized fish to hook-and-line fisheries outside the Merritt Island no-take reserve. Spillover took nine, 27 and 31 years to develop for spotted sea trout, red drum and black drum respectively. These species have potential longevities of 15, 35, and 70 years respectively (Roberts et al 2001).

- A relatively short period of poaching from a reserve can reverse the build-up of biomass. An 18-month period of poaching resulted in a significant reduction in CPUE in adjacent fishing grounds. Mean CPUE at Sumilon Island fell from 1.98 kg man<sup>-1</sup>trap<sup>-1</sup> to just 0.99 kg man<sup>-1</sup>trap<sup>-1</sup> (Alcala and Russ 1990). Total fish abundance was also significantly lower after the 18-month period. Total yield fell by 54% from 36.90 metric t/km<sup>2</sup> (Alcala 1988) to 19.87 metric t/km<sup>2</sup> (Alcala and Russ 1990).
- The spatial distribution of fishing effort could obscure any patterns in fish abundance and negate any benefit to the wider fishing area. For example, trapping effort was higher within 2km of the Mombassa Marine Park and Reserve in Kenya, which could have prevented spillover further into the adjacent fishing grounds (McClanahan and Mangi 2000). Equally, spatial distribution of fishing pressure is an indicator of spillover and should be monitored (Wilcox and Pomoroy 2003)

### **3.4 Problems for studying spillover**

The major barrier to drawing generalized conclusions from studies on spillover is the lack of comparability amongst studies. The two main problems are *what* is sampled and *how* it is sampled. Studies considering a gradient or different CPUE or species abundances around marine reserves assume that the only ‘treatment’ effect is a reduction in fishing pressure inside the reserve (Murawski et al 2004). This may be true in some cases, but there could be other variables affecting CPUE or abundance. Studies on spillover would be strengthened by including as many of the desirable, and

all of the minimum points listed in Table 4. The following are among the most important variables that studies should try to account for

**Table 2.** Explanation of methods and concepts behind them that have been used to study marine reserves and spillover.

<b>Method</b>	<b>Approach</b>	<b>Pros and Cons</b>	<b>References</b>
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Modelling	Mathematical models are used to investigate the potential effects of marine reserves, usually on single species. Variables such as reserve size, fishing effort and biological parameters are used.	Modelling allows for scenarios and management options to be examined without manipulating the biological system. However, models are limited because they're often a very simplified representation of the system.	Reviews: Roberts and Polunin (1991), Roberts and Hawkins (2000), Gell and Roberts (2002), Russ (2002), Botsford et al (2003), Gerber et al (2003).
Tag-release-recapture/re-sight	Fish tagged inside the reserve are expected to move out into the fished area as density increases, due to inter- and intra-specific competition. Tags are attached to a large number of individuals. The location of any re-sighted/recaptured individuals is recorded.	Movement out of reserves can be demonstrated. Movement patterns between the point of tagging and the point of recapture/re-sight can only be inferred, and thousands of individuals may need to be tagged to get an informative number of re-sights/recaptures in some habitats.	e.g. Yamasaki and Kuwahara (1989), Atwood and Bennett (1994), Zeller and Russ (1998), Cole et al (2000), Kelly and MacDairmid (2003) Reviews: Roberts and Polunin (1991), Kramer and Chapman (1999), Davidson et al (2001), Russ (2002).
Ultrasonic Telemetry & GIS	A radio transmitter is attached to an individual, and movement can be monitored with receivers.	Home range sizes can be quantified for a species by tracking individuals implanted with a transmitter. The activity patterns of a target species will determine the likelihood of spillover from a given marine reserve. This is a relatively new technology, and the shrinking size of transmitters will facilitate the study of spillover in smaller reef fish in the future.	e.g. Zeller and Russ (1998), Eristhee and Oxenford (2001), Starr et al (2005).
Monitoring the spatial distribution of fishing effort around marine reserve without monitoring CPUE.	Relatively higher levels of fishing effort around the reserve boundary would indicate spillover, as fishers move to areas providing higher CPUE. The location of fishing boats or gear is analysed, but no measure of the resultant catch is taken (so no CPUE data is produced necessarily).	This method should be utilised more often to examine where effort is re-distributed to when fishers are displaced from fishing grounds when a reserve is established. May be impossible to disentangle effort and spillover.	e.g. McClanahan and Mangi (2000), Murawski et al (2000), Wilcox and Pomeroy (2003).

**Table 2 continued.** Explanation of methods and concepts behind them that have been used to study marine reserves and spillover.

Method	Approach	Pros and Cons	References
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Monitoring CPUE with observers at ports, on boats, or using logs	CPUE is monitored by observes at landing sites, on fishing vessels, or from logbooks. Relatively high CPUE adjacent to the reserve boundary would indicate spillover from the reserve. Increased CPUE in the area adjacent to a reserve after reserve establishment would indicate spillover.	A problem with monitoring CPUE at ports is that it may be impossible to assign a location to the catch that is precise enough to be used as evidence for spillover, because location is not directly observed. Observers on board boats could record GPS location and assign an exact location to the catch.	Yamasaki and Kuwahara (1989), Alcala and Russ (1990), McClanahan and Kaunda-Arara (1996), Rakitin and Kramer (1996), McClanahan and Mangi (2000), Roberts et al (2001), Galal et al (2002), Kelly et al (2002), Russ et al (2003), Murawski et al (2004), Russ et al (2004).
Experimental fishing to determine CPUE.	A gradient of reduced CPUE from reserve boundaries into fishing area would indicate spillover from the reserve. Investigators use a standard fishing gear at different locations and so quantify CPUE experimentally.	The amount of data collected could be limited, by time and success of the fishing technique. The advantage is that a standard fishing gear is used, and effort can be reliably quantified.	Yamasaki and Kuwahara (1989), McClanahan and Mangi (2000), Davidson (2001), Kaunda-Arara and Rose (2004)
UVC of species density.	Spillover is indicated if the density of target species declines along a gradient across the reserve boundary, into the fished area. This is accomplished by belt transects or point-counts conducted by a trained observer using SCUBA.	If no CPUE or habitat variability data is collected in conjunction with UVC data, observed abundance patterns could be due to these effects and there is no way to verify that the patterns are because of spillover. Fish can change their behaviour depending on how often they are exposed to divers, becoming diver neutral, leading to bias in sampling.	McClanahan and Kaunda-Arara (1996), Rakitin and Kramer (1996), Russ and Alcala (1996), Sluka et al (1997), Chapman and Kramer (1999), Davidson (2001), Roberts et al (2001), Davidson et al (2002), Gala et al (2002), Russ et al (2003), Ashworth and Ormond (2005), Russ et al (2004).

**Table 3.** Summary of empirical studies on spillover, their methods and main findings.

Location	Species	Method	Years of data	Spillover	Magnitude	Reference
Apo/Sumilon Island, the Philippines	Reef fish	CPUE	6	Yes	Fish trap yield from the whole area after management breakdown was significantly less than average yield from the non-reserve area alone before management breakdown.  Significantly higher biomass within 200m from the reserve, possible effects <500m.	Alcala and Russ (1990)
	178 reef fish species, <i>Naso vlamingii</i> , Acanthuridae & Carangidae	UVC, CPUE	7, 15	Yes		Russ and Alcala (1996), Russ et al (2003, 2004)
Barbados Marine Reserve	All reef fish encountered	UVC, Trapping	1	Borderline	Number of fish per trap decreased from 40 to 10, from 1-3km from reserve centre.	Rakitin and Kramer (1996)
	47 reef fish species	UVC, Habitat survey	1	No	None	Chapman and Kramer (1999)
Exuma Cayes Land & Sea Park, Bahamas	Nassau grouper	UVC	1	Yes	Biomass high within 5km of reserve boundary.	Sluka et al (1997)
Fiji	<i>Anadara spp.</i> (Clam)	Community size monitoring	~3	Yes	After 3 years of management clam abundance increased 13 times in the closed area and by 5 times in the fished area. CPUE increased.	Tawake et al (2001)

**Table 3 continued.** Summary of empirical studies on spillover, their methods and main findings.

Location	Species	Method	Years of data	Spillover	Magnitude	Reference
Kyoto Prefecture, Japan	<i>Chionoecetes opilio</i> (zuwai crab)	Trapping, CPUE, Tagging	5	Yes	10kg per trap more catch within 3 miles of reserve. Falling CPUE gradient from 1-4 miles from reserve.	Yamasaki and Kuwahara (1989)
Leigh Marine Reserve, New Zealand	<i>Jasus edwardsii</i> (spiny lobster)	CPUE	2	Yes	Overall CPUE was on average similar at all sites, but largest hauls were at reserve boundary at 7.9kg/trap/haul. Catch most variable around reserve. Lobsters caught around the reserve were significantly larger than elsewhere (averaged 3mm larger)	Kelly et al (2002)
Long Island-Kokomohua Marine Reserve, New Zealand	<i>Parapercis colias</i> (blue cod)	UVC, CPUE	9	No	None	Davidson (2001)
Merritt Island National Wildlife Refuge, Florida	Black drum, Red drum, Spotted seatrout	CPUE	40	Yes	Relatively high number of world record sized fish caught within 100km of reserve. This 13% of coast accounted for 60%, 54% and 50% of the records respectively.	Roberts et al (2001)
Tonga Island Marine Reserve, New Zealand	<i>Jasus edwardsii</i> (spiny lobster)	UVC, CPUE, tagging	2	No	No evidence from tagging for spillover. Abundance outside reserve boundaries declined.	Davidson et al (2002)

**Table 3 continued.** Summary of empirical studies on spillover, their methods and main findings.

Location	Species	Method	Years of data	Spillover	Magnitude	Reference
Mombasa Marine Park and Reserve, Kenya	Reef fish species	UVC, CPUE	7	Yes	CPUE of fishers higher in 0-2km of reserve boundary.	McClanahan and Kaunda-Arara (1996)
	Rabbitfish, emperors, surgeonfish.	CPUE Observing trapping effort	1 7	Yes	CPUE gradient evident up to 5km from reserve. Increase trapping effort 0-2km from reserve.	McClanahan and Mangi (2000)
Malindi & Watamu Marine Parks, Kenya	<i>Siganus sutor</i> (Whitespotted rabbitfish)	Trapping, CPUE model fit.	<1	Yes	Whitespotted rabbitfish showed spillover 0-4km away. Other species showed low spillover.	Kaunda-Arara and Rose (2004)
Nabq Natural Resource Protected Area, Egypt	Serranidae, Lethuridae, Lutjanidae Six families	UVC, CPUE	3	Yes	CPUE increased by 66% after 5 years' protection in adjacent areas <1km away.	Galal et al (2002)
	Serranidae, Lethuridae.	UVC	<1	Yes	A significant density gradient found at 1m depth, to <1.80km And at 3m depth to <1.8km	Ashworth and Ormond (2005)
New England, 4 reserves, USA	<i>Melanogrammus aelefinus</i> (Haddock)	CPUE (otter trawl survey data)	1	Yes	Spillover detected up to 20km	Murawski et al (2004)
Soufrière Marine Management Area, St. Lucia	Acanthuridae, Scaridae, Serranidae, Haemulidae, Lutjanidae.	UVC, CPUE	6	Yes	Biomass doubled in adjacent areas. Catches improved in adjacent areas in 5 years by 46-90%.	Roberts et al (2001)

- Environmental stochasticity and seasonal variation in community composition mean that it is desirable for time series data to be collected (Table 4).
- Habitat variables should be statistically analysed, but few studies have done this (though see Grigg 1994, Jennings et al 1996, Sluka et al 1997, Chapman and Kramer 1999, Paddock and Estes 2000). The paucity of studies controlling for habitat heterogeneity is puzzling, as the abundance of reef fish is known to correlate with variation in characteristics of reef habitat such as substrate topographic complexity (e.g. Luckhurst and Luckhurst 1978), and coral cover (e.g. Bell and Glazin 1984).
- It is desirable for data on actual (and not just assumed) fishing pressure to be included in the analysis (Table 4). Simply assuming that fishing pressure is zero inside the reserve is unsatisfactory, as a relatively short period of poaching can remove density gained over years of protection (Alcala and Russ 1990). This may be difficult in practice, as constant surveillance would be required.
- Concentration of fishing effort around the boundaries of marine reserves could reduce the reserves' effectiveness to enhance CPUE in the wider fishing area (McClanahan and Mangi 2000). This phenomenon has been observed at the Georges Banks using satellite monitoring (Murawski et al 2000), and in Kenya where the number and location of traps was recorded (McClanahan and Mangi 2000). Models have identified that the spatial distribution of fishing effort is one of the main determinants of reserve success, but also one of the least known (Walters 2000).

Whilst almost all studies have the minimum essential data required to detect spillover (Table 4), few have used standardised methods to collect these data. Many researchers use UVC or experimental fishing to record fish densities along transects (Table 3). However, the intervals sampled along each transect vary enormously between studies. Sampling at large intervals along transects will reduce the spatial resolution of data. For example, Russ et al (2003, 2004) were able to detect patterns in reef fish abundance over less than 250m, whereas Sluka et al (1997) could only detect changes over 5km distances. Each study also starts and ends sampling at different distances from the reserve boundary, from 200m-500m (Russ and Alcala

1996, Russ et al 2003, 2004), 0m-3.5km (Rakitin and Kramer 1999), to 0m-50km (Sluka et al 1997). In some papers, it is not made explicitly clear at what distance samples were taken (McClanahan and Kaunda-Arara 1996, Davidson et al 2002, Roberts et al 2001). It would be desirable for researchers to adopt a standardised approach to sampling that included sampling reef fish from the boundary at intervals of less than 50m, and sampling wider ranging species based on their home range sizes.

**Table 4.** Essential and desirable (non-essential) information for showing spillover.

<b>Essential</b>	<b>Example</b>
Snapshot at one time of CPUE/fish density along a gradient from the reserve into adjacent fishing grounds.	Rakitin and Kramer (1996), Sluka et al (1997), Chapman and Kramer (1999), McClanahan and Mangi (2000), Davidson et al (2002), Kaunda-Arara and Rose (2004), Murawski et al (2004), Ashworth and Ormond (2005)
If not using a gradient approach, demonstration of increasing CPUE/fish density in the area adjacent to reserve over time.	Alcala and Russ (1990), Roberts et al (2001).
Information on how well enforced the reserve really is.	Most studies though qualitatively
<b>Desirable</b>	<b>Example</b>
Time series data on CPUE/fish density along a gradient from the reserve into adjacent fishing grounds (preferably over the time scale of decades).	Yamasaki and Kuwahara (1989), McClanahan and Kaunda-Arara (1996), Russ and Alcala (1996), Davidson (2001), Galal et al (2002), Kelly et al (2002), Russ et al (2003, 2004)
Samples taken at spatial scales relevant to the species concerned (i.e. 50-100m for reef fish, 1-5km for wide-ranging temperate species)	Russ and Alcala (1996), Roberts et al (2001), Russ et al (2003, 2004), Murawski et al (2004), Ashworth and Ormond (2005).
Data on the spatial distribution and level of fishing effort around (and in) a reserve.	McClanahan and Mangi (2000), Wilcox and Pomeroy (2003)
Economic data from the area to monitor market prices and opportunity costs of fishers.	No examples to date
Statistically controlling for habitat characteristics (and larval supply).	Sluka et al (1997), Chapman and Kramer (1999)
Demonstration of individuals moving out of reserves using tagging studies.	e.g. Yamasaki and Kuwahara (1989), Zeller and Russ (1998), Davidson et al (2002).

### 3.5 Conclusion and the future of spillover research

Though studies on spillover began almost 20 years ago in the late 1980s, there are still only a handful of examples that convincingly demonstrate spillover from marine reserves (Table 3). Most evidence comes from tropical coral reef fish, with fewer examples for invertebrates and temperate species (Table 3). This is undoubtedly due to the difficulties of studying relatively large-scale patterns at sufficient spatial and temporal scales to detect significant trends. Future studies would be strengthened by including all of the minimum and as many of the desirable points listed in this review (Table 4). Of particular importance for future studies to include in order to strengthen the evidence for spillover, is sampling at scales relevant to the species under investigation, and statistically controlling for other variables, such as habitat, larval supply and fishing effort.

### **3.6 Systematic review of queen conch literature**

#### **3.7 Life History**

Regional populations of queen conch may be supplied with larvae from stocks in other parts of the Caribbean and most populations could be interdependent because of larval drift (see Stoner et al. 1997). However, there is disagreement over larval supply conditions. Regional differences in larval abundance appear to be associated with the size of local spawning stocks (Stoner and Davies 1997), supporting the idea of self-recruitment within the Belizean barrier reef ecosystem (Cowen et al 2006). However, no reliable stock-recruitment models for queen conch have been developed (Acosta 2006).

Larvae metamorphose into postlarvae within 14 days in field enclosures (Davis et al. 1996) but can stay in the water column for up to two months after reaching metamorphic competence if necessary (Noyes 1996). Growth rates are dependent on temperature and are sensitive to the amount and types of phytoplankton available for food in the water column (Davis and Stoner 1994). Populations are thought to be recruitment limited, not habitat limited, at the local scale (Stoner 1997). Transplant experiments indicate that most seagrass beds cannot support juvenile conch (see Stoner 1997). Juveniles strongly prefer nursery habitats with intermediate densities of seagrass (608 to 864 per m<sup>2</sup>) and at depths of 2-4 m (Stoner and Waite 1990). Maps of seagrass biomass (which is strongly correlated with shoot density) produced from satellite imagery and ground truth (Armstrong 1993) revealed that nurseries occur in specific locations within vast seagrass beds. In one case 80% of the

habitat deemed optimal was never occupied in more than 10 years of surveys and personal observations (Stoner 2003). Based on this incongruence in optimal nursery habitat and habitat occupancy, maps of seagrass cover incorporating numerous environmental variables could still hold poor predictive power for conch nursery distribution (Stoner 2003). This has implications for marine reserve design and stock management – it is crucial that the right areas of seagrass beds are protected from disturbances.

Conch populations typically have a sex ratio of 1:1, and fertilization is internal (Stoner and Ray-Culp 2000). Adult conch move onto homogeneous sand flats during spawning, where little or no feeding occurs during the spawning season (Stoner and Sandt 1992). Egg masses are up to 12 cm long, and spawning lasts for 24 – 36 hours (Stoner et al. 1992). An individual's fecundity is independent of age after maturity, because somatic growth stops after sexual maturity at about 4 years old, but is dependent on size at maturity, which is variable (Appeldoorn 1988a). Females can lay seven to nine egg masses in a warm reproductive season, each containing 300 000 eggs, which hatch after three to five days (Randall 1964, Davis et al. 1984).

Reproduction in conch is density dependent. At spawner densities below 56 conch  $\text{ha}^{-1}$  no spawning occurs, and at densities below 48 conch  $\text{ha}^{-1}$  no mating occurs because of depensation (Stoner and Ray-Culp 2000). Depensation may be the reason why heavily exploited populations in Florida failed to show recovery when protected from fishing (Stoner 1997). Reproduction reaches asymptotic level at 200 conch  $\text{ha}^{-1}$ , after which no further increases in reproduction are gained through increased numbers of conch  $\text{ha}^{-1}$  (Stoner and Ray-Culp 2000).

At sexual maturity, the flared shell lip of the adults is formed and further shell growth occurs only in lip thickening. Adult size can be reached in 3.2 years and age at first reproduction has been estimated at 3.6 years (Appeldoorn 1988a). Although growth in shell length ceases at sexual maturity, growth in tissue weight does not (Appeldoorn 1998b). Therefore, it cannot be assumed that length extrapolated to asymptotic length ( $L_{\infty}$ ) can be used to estimate asymptotic weight ( $W_{\infty}$ ), because weathering of the shell of old adults can actually reduce shell length. Despite this problem, many studies have used the von Bertalanffy growth model, based on asymptotic length, and many von Bertalanffy parameter estimates are available from published papers (Table 5). To overcome the problem using length based growth models, Appeldoorn (1992) combined growth in weight for juvenile and adults for an

average sized individual (24.5cm). Estimates of weight-at-age were fitted to a Gompertz model (a sigmoidal growth curve) resulting in equation 5.

**Table 5.** von Bertalanffy growth equation parameters compiled from conch literature.

Location	$L_{\infty}$	k	t0	Phi'	Source
Bahamas, Berry Inland	300	0.2	0.65	0.952	Iversen et al (1987)
Belize, Boca Chica	268	0.223	-0.05	0.967	Strasdine (1988)
Belize, Tres Cocos,	332	0.207	-0.33	0.997	Strasdine (1988)
Belize, Water Caye,	269	0.209		0.94	Strasdine (1988)
Columbia, San Bernardo	365	0.29		1.171	Gallo et al (1996)
Cuba, Cabo Cruz, Zone A	383.4	0.33	-0.05	1.241	Alcolado (1976)
Cuba, Cabo Cruz, Zone B,	380.6	0.287	-0.12	1.178	Alcolado (1976)
Cuba, Cayo Anclitas,	259.8	0.571	0.09	1.366	Alcolado (1976)
Cuba, Diego Perez, Zone A	232.7	0.429	-0.09	1.21	Alcolado (1976)
Cuba, Diego Perez, Zone B	207.6	0.442	-0.09	1.19	Alcolado (1976)
Cuba, Rada Inst. Oceanol.	334	0.36	0.13	1.239	Alcolado (1976)
Jamaica, Pedro Bank	221	0.58	0.155		Tewfik (1996)
Martinique, LFA	339	0.392			Rathier & Batteglya (1994)
Martinique, tagging	338.6	0.388			Rathier & Batteglya (1994)
Mexico, Quintana Roo,	341.7	0.58			Valle-Esquivel (1998)
Providencia & San Catalina	375	0.25		1.114	Marquez (1993)
Puerto Rico	54.9	0.3706	assumes 0		Appeldoorn (1988b)
Puerto Rico, La Parguera, LFA	340	0.437	0.462	1.328	Appeldoorn (1990)
Puerto Rico, La Parguera, Tagging	460	0.25	0.244	1.173	Appeldoorn (1990)
San Andres & Providencia	329.4	0.72		1.536	Garcia (1991)
San Andres & Providencia	350	0.27		1.127	Gallo et al (1996)
St. Croix, USVI	241.7	0.42		1.212	Berg (1976)
St. John, USVI	260.4	0.516		1.323	Berg (1976)
St. Kitts	331.9	0.347		1.221	Buckland (1989)
Turks & Caicos, Six Hill Cay,	256	0.563	-0.16	1.356	Appeldoorn et al (1987)

For most species, mortality rate stabilises at an early age, and mortality can be modelled with the assumption of constant mortality rate. This assumption is often used in fisheries models such as the yield-per-recruit model (Beverton and Holt 1957). However, for conch, the rate of instantaneous natural mortality ( $M$ ) decreases substantially with age until the onset of sexual maturity and can modelled using equation 1 (Appeldoorn 1988b). The value of  $M$  and total mortality ( $Z$ ) varies for conch of all ages with location (see Table 6) therefore equation 1 is not specific to Belize.

**Table 6.** Estimates of natural mortality rate ( $M$ ) and total mortality are ( $Z$ ) compiled from conch literature.

Parameter	Value	Age	Reference
$M$	0.52	<4.25 years	Appeldoorn (1988a)
	0.52	Adult	Appeldoorn (1987)
	1.05	Adult and juvenile	Appeldoorn (1987)
	2.12	Juvenile	Appeldoorn (1988b)
	0.84	Adults	Appeldoorn (1988b)
	1.86	Juveniles	Appeldoorn (1988b)
$Z$	0.28	20 years longevity	Hoenig (1983), CFMC (1999)
	0.2	30 years longevity	Hoenig (1983), CFMC (1999)
	1.66	First 1.75 years of adult life	Appeldoorn (1988b)

### 3.8 Queen conch conservation and management

To protect queen conch populations, high densities of breeding age individuals (over 56 conch ha<sup>-1</sup>) need to be maintained. There are two strategies that have been implemented to conserve conch populations:

- Depth refuges have been created throughout much of the Caribbean, including Belize, by banning scuba harvest and limiting fishing to free diving. Free divers cannot usually harvest below 10-15m deep. The maximum depth for conch in clear Caribbean waters is about 35-40 m, with a few rare observations at depths of 60 m (Stoner 1997). However, this management option is not ideal, because the vast majority of conch spend the first 2-3 years of their lives in shallow water. Young adults and adults that fail to migrate to deeper water might still be accessible to free divers, ultimately reducing the deep-water stocks (see Stoner and Ray 1996 and Stoner 1997 for discussions).
- Marine reserves where fishing is prohibited could maintain high densities of adult conch and protect all life stages. Table 7 summarises studies reporting the effects of marine reserves on conch densities and life history. General conclusions from these studies are that protection from fishing allows adult biomass to increase rapidly inside reserves (Stoner and Ray 1996, Acosta 2002). However, spillover depends on the ability of conch to migrate from the reserve, and barriers such as sand flats can prevent spillover (Tewfik and Béné 2003). If densities become high (over 300 conch ha<sup>-1</sup>), density-dependent growth results in individuals inside reserves having significantly smaller size than individuals outside the reserve at lower densities (Béné and Tewfick 2003). Therefore to maximise spillover,

reserves should have boundaries onto continuous conch habitat, allowing conch to disperse and grow to full size.

**Table 7.** Summary of studies reporting the effects of marine reserves on queen conch populations in the Caribbean.

Location	Method	Results	Reference
Glover's Reef, Belize	Ultrasonic telemetry used to track conch movements	Queen conch densities increased by a factor of 4.5 from 1997-2001. Individuals moved a daily average of 8.5m. 131 juveniles ha <sup>-1</sup> month <sup>-1</sup> were recruited into the adult population in the reserve.	Acosta (2002)
	UVC belt transect	Protection from fishing caused density to increase inside reserve for adults and large juveniles. Mean adult biomass increased from 4.8 to 36.7 kg/ha from 1997 to 2002. Exploitable biomass was six times greater in no-take area (506kg/ha) than in the fished area (85 kg ha <sup>-1</sup> ).	Acosta (2006)
Exuma Cays Land and Sea Park, Bahamas	UVC point counts	Conch density and biomass increased directly with increasing seagrass density (optimum 608-864 shoots/m <sup>2</sup> ).	Stoner and Waite (1990)
	Tethering experiment on juvenile conch	Conch in an aggregation experience lower predatory mortality than those not in aggregations. Weak negative correlation between mean conch size and log <sub>10</sub> density.	Stoner and Lally (1994)
	Depth stratified UVC belt transects, intrasite comparison of density, population age structure and larval densities recorded	Adult density varied over three orders of magnitude in the area, >31 times higher adult densities in reserve than fished area, partly due to high density of larvae >30 per 10m <sup>3</sup> in reserve compared to 2 per 10m <sup>3</sup> in fished area.	Stoner and Ray (1996)
	UVC point counts	Allee effects detected – mating never occurred at densities less than 56 conch/ha, spawning never occurred at densities below 48 conch ha <sup>-1</sup> . Reproductive activity increases rapidly from there and asymptotes at 200 conch/ha.	Stoner and Ray-Culp (2000)

**Table 7 continued.**

Location	Method	Results	Reference
East Harbour Lobster and Conch Reserve, Turks & Caicos	UVC belt transects	Adult density six times higher in reserve (277 conch ha <sup>-1</sup> ) than out (555 conch ha <sup>-1</sup> ). Crowding effects detected – adults in reserve have a mean siphonal length ~10mm shorter than individuals from fished areas.	Béné and Tewfick (2003)
	UVC belt transects & density gradient analysis	Presence of natural barriers such as sand bars and land masses limits spillover from the reserve.	Tewfik and Béné (2003)

**Table 8.** Summary of queen conch studies that use modelling.

Location	Model Type	Details	Results	Reference
Glover's Reef, Belize. Protected since 1998.	Spatially explicit logistic rate model. Constant larval recruitment assumed.	Designed to examine population dynamics and different spatial configurations of reserve by varying recruitment rates, movement behaviour, reserve size and boundary details. Movement behaviour modelled as a correlated random walk. Stock-recruitment and density dependence were not taken into consideration.	Model predicted the population would increase by 480% and reach equilibrium in 3-4 years. The magnitude of recruitment did not affect population trajectory. Increasing the refuge size by 50% and reducing absorbing boundary by 50% further increased the population size by 110%. Boundary conditions are important in determining equilibrium population sizes. The magnitude of recruitment did not affect equilibrium population size.	Acosta (2002)
East Harbour Lobster and Conch Reserve, Turks & Caicos	Theoretical model of distribution of species relative to reserve boundaries	Theoretical density patterns presented, modified from Rakitin and Kramer (1996), for scenarios of barriers to migration around the reserve. Tested these against observations.	Empirical density gradients matched theoretical ones, indicating the existence of sand plain barriers to conch dispersal.	Tewfik and Béné (2003)
	Spatially explicit agent-based model.	A pilot model using Landsat 7 ETM+ imagery to classify reserve into habitat types integrate with the Swarm model, Idrisi32 image processing and GIS.	None reported.	Rudd et al (2003)

### **3.9 Modeling queen conch populations**

There are very few published studies that model the population dynamics of queen conch (Table 8). Large increases in population densities inside reserves have been predicted using modelling (Acosta 2002), and empirical observations strongly support this conclusion (Table 7). Models that address the potential for spillover from reserves to adjacent areas are needed to assess the effectiveness of reserves at enhancing local fisheries.

### **3.10 Model Results**

#### **3.11 Sensitivity to migration and fishing mortality**

Viewing the reserve and non-reserve population dynamics together under different percentage migration (Figure 6), it becomes clear that the reserve population size begins to track the non-reserve population size when percentage migration is greater than 10% (Figure 6d). When percentage migration reached 30%, the reserve and non-reserve populations are almost identical at all levels of fishing mortality (Figure 6f). Similar patterns occur for biomass and spawning stock biomass. Therefore, no further analysis was conducted over 30% migration.

Increasing the percentage migration caused a decrease in total population size, biomass and spawning stock biomass in the reserve population (Figure 7). This reduction became larger as fishing mortality rate in the non-reserve population increased (Figure 7). When migration was 0% the fished population went extinct at fishing mortality rates over 2.5 (Figure 7b). The effect of increasing the percentage migration was interesting. For an example, 4% migration had a similar effect on total population size after 50 years as 30% migration at  $F < 2$ . When  $F$  was greater than two, 4% migration actually resulted in larger total population size after 50 years than 30% migration (Figure 7b). Similar patterns occur for biomass and spawning stock biomass.

#### **3.12 Spillover**

The amount of spillover (kg) at equilibrium conditions varies with the fishing mortality ( $F$ ) in the non-reserve population (Figure 8). When  $F < 0.5$ , the increase in spillover with fishing mortality rate is almost linear for migration below 10%. Then, when  $F > 0.5$ , the lines curve and become humped as both populations become depleted (Figure 8).

QuickTime™ and a  
TIFF (Uncompressed) decompressor  
are needed to see this picture.

**Figure 6.** Graphs showing the population size in the reserve (solid line) and non-reserve (dashed line) at different fishing mortalities under (a)  $d = 0$  (b)  $d = 0.02$  (c)  $d = 0.04$  (d)  $d = 0.10$  (e)  $d = 0.20$  (f)  $d = 0.30$ . All values are  $ha^{-1}$ .

QuickTime™ and a  
TIFF (Uncompressed) decompressor  
are needed to see this picture.

**Figure 6** continued.

QuickTime™ and a  
TIFF (Uncompressed) decompressor  
are needed to see this picture.

**Figure 7.** Graphs showing the equilibrium total population size at different fishing mortalities and values of  $d$ , (a) reserve and (b) non-reserve. All values are  $\text{ha}^{-1}$ .

QuickTime™ and a  
TIFF (Uncompressed) decompressor  
are needed to see this picture.

**Figure 8.** Graph showing spillover ( $\text{kg ha}^{-1}$ ) from the reserve at different fishing mortality and values of  $d$ , the percentage migration parameter.

High fishing mortality in the non-reserve population increases the difference in relative density, and at more than 10% migration, allows the two populations to homogenise (Figure 6f). As the populations homogenise, the relative difference between them decreases, and so there is less migration from the reserve to the fished area (Figure 8). When migration is less than 10% it is never enough to homogenise the populations, even when high  $F$  cause a very large difference in density, therefore spillover is maintained at a steady level (Figure 8).

### **3.13 The population model applied to Gladden Spit**

The number of conch Gladden Spit Marine Reserve could support in the absence of all fishing is estimated at  $632 \text{ ha}^{-1}$  under equilibrium conditions. With fishing outside the conch conservation zone at 0.8 and at 4% migration, equilibrium population size in the reserve is 522 and in the non-reserve is  $442 \text{ individuals ha}^{-1}$  and spillover is  $0.28 \text{ kg month}^{-1} \text{ ha}^{-1}$ .

## **4.0 Discussion**

### **4.1 Systematic review of spillover**

Systematically reviewing the literature on spillover from marine reserves showed that there are some convincing examples for reef fish and invertebrates (e.g. Russ et al 2004, Yamasaki and Kuwahara 1989). However, the evidence from many studies is equivocal due to the logistic difficulties of detecting large-scale patterns over sufficiently long time periods. Generalised results of empirical studies on spillover include higher CPUE adjacent to reserves, habitat effects on spillover, and a time-scale in the order of decades to detect spillover for long-lived species. Some work also suggests that a relatively short period of poaching can remove biomass gained over a long period of protection (Alcala and Russ 1990), and that the spatial distribution of fishing effort can both indicate and affect spillover (Wilcox and Pomoroy 2003). These results imply that to maximise the potential for spillover it is essential that reserves are well enforced and situated in areas of contiguous habitat. In order to make any predictions on the likelihood and magnitude of spillover; data on fishing effort, effort distribution and habitat characteristics around the reserve is essential. Demonstration of spillover is critical to the success of marine reserves and

identifying the conditions that promote optimal spillover for specific species is crucial for effective fisheries management.

#### **4.2 Conch population model**

This modelling study suggests that modelling queen conch populations using a simple age-structured model can produce realistic population sizes. Sensitivity analysis of the model showed that less than 10% migration from a reserve may be enough to ensure the survival of heavily exploited populations in adjacent areas. Although previous studies have modelled density-dependent migration from marine reserves (Gerber et al 2005, Armstrong and Skonhofs 2006), this is only the second study to do so for queen conch (the other being Acosta 2002). This model has been the first to investigate the likely range of spillover from marine reserves and found that a no-take area in Gladden Spit could support around 522 individuals  $\text{ha}^{-1}$  and provide 0.28 kg of spillover biomass  $\text{month}^{-1} \text{ha}^{-1}$ . It is not possible to put this figure into any context of the amount it would contribute to individual fishers catch, as no catch data are currently published for Gladden Spit. The model showed that the amount of spillover depends on fishing mortality outside the reserve. When a small amount of migration was allowed, high fishing mortality rates still affected the reserve population. This indicates that fishing effort outside the reserve may have to be monitored and reduced to maximise spillover in the long term.

#### **4.3 Limitations of this study**

Reviewing the literature on queen conch indicated that there is a large amount of information available on conch life history, due to an interest in stock enhancement using hatchery-reared conch several decades ago. However, there is a paucity of studies documenting the effects of reserves on life history traits because work in this area is relatively new (e.g. Béné and Tewfick 2003) and this affected model accuracy. For example, the model was limited by the lack of an empirical stock-recruitment relationship for conch. The model was very sensitive to a parameter in the stock-recruitment relationship that set the rate of approach to the recruitment asymptote, which had to be estimated by simulation for this study. Although logistically difficult, development of an accurate stock-recruitment relationship and more information of the effects of reserves on life history traits would greatly improve population models of queen conch. An additional limitation is this study was

highlighted when parameterising the model for Gladden Spit. It became clear that having no data on fishing mortality around the reserve was a major limiting factor in model precision, and no specific results could be drawn without such data.

#### **4.4 Future work**

Models that include density-dependent migration have found that the nature of migration (symmetric or asymmetric) and fish behaviour influence the effects of protected areas on adjacent fisheries (Gerber et al 2005, Armstrong and Skonhøft 2006). Although some data on individual conch movements are available (Acosta 2002), the effect of increased density on movement has only recently been investigated (Tewfick and Béné 2003) and is an area worthy of future empirical study.

However, migration is not the only density-dependent process occurring in some populations and the importance of density-dependence in protected populations has been recognised and reviewed (Sánchez Lizaaso et al 2000). Recently, modelling studies have examined the effects of density-dependent body growth on the ability of marine reserves to enhance yield (St. Mary et al 2000, Gårdmark et al 2006). This work has shown that if density-dependent somatic effects are important, a general increase in yield biomass cannot be exacted (Gårdmark et al 2006) and that the probability of population extinction is sensitive to the presence and form of density-dependence (e.g. Ginzburg et al 1990). Density-dependence can be difficult to estimate, therefore it is important to explore how different forms and strengths of density-dependence can influence population models (Yearsley et al 2003) and to validate models with empirical data.

Conch are known to show reduced size at maturity when at high densities and reach maturity at a younger age (Béné and Tewfick 2003). Beverton and Holt (1957) showed that density-dependent growth mediated by competition for food is expected to affect asymptotic size ( $L_{\infty}$ ), but not the growth rate ( $k$ ) at which this size is approached. Subsequent work has provided further theoretical and empirical support for this result (e.g. Lorenzen 1996). The accuracy of the current model was potentially limited by not including density-dependent somatic growth of conch. However, the model could be developed to include density-dependent growth in the future. A simple equation, where asymptotic length is defined as a linear function of population biomass density, could be used to model density-dependent growth in conch (Lorenzen 1996, Lorenzen and Enberg 2000). Alternatively, the tissue-weight-

at-age equation used in this study (equation 5, Figure 3 and Appeldoorn 1992) could be developed to include density-dependent effects.

More information on conch response to density would be valuable for future modelling work in this area, and the development of an empirical equation describing this should be a goal. The current model could be developed following the framework of previous modelling studies to include density-dependent effects (e.g. Gerber et al 2005). The current modelling work could also be developed to include depensation below 56 conch  $\text{ha}^{-1}$ , for which a modified stock-recruitment relationship has been developed (Stoner and Ray-Culp 2000, Gascoigne and Lipcius 2004). This addition would make the model more realistic and allow investigation of population recovery after overexploitation. An additional extension of this work could include modelling the effects of natural barriers to conch dispersal. Habitat features such as sand flats are known to prevent conch dispersal to adjacent reef habitats and can create a crowding effect (Tewfick and Béné 2003). Barriers could be included in a spatially explicit individual based model, together with density-dependent growth, to better estimate spillover. Finally, once the biology was more accurately represented by a model, stochastic environmental events such as hurricanes could be simulated to explore their affects on conch populations.

#### **4.5 Conclusions**

This study has shown that there is some evidence for spillover from marine reserves in tropical and temperate environments. Further studies on spillover are needed that include data on habitat and fishing effort variables, preferably over a timescale of decades. Reviewing the literature on queen conch indicated that this species can show large increases in population size inside reserves, however, little work is available that addresses the potential for spillover. This model is the first to directly quantify spillover of conch. The model included no density-dependent processes other than for migration, and produced an estimate of 0.28kg of spillover biomass  $\text{ha}^{-1}$  from Gladden Spit reserve in Belize. The effects of protection on life history traits such as growth and mortality may affect spillover in this species. Developing spatially explicit models that incorporate habitat characteristics, density-dependent growth and migration, and depensation could give more accurate predictions. The main finding of this study was that there is a lack of empirical data for stock-recruitment assessment in conch and no data on fishing effort in Gladden Spit reserve. With more complete

data and further development of the model, well-informed management decisions are possible for this species at Gladden Spit and beyond.

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## Appendix – R code for population model

```
allResults<-data.frame(0,0,0,0,0,0,0,0,0)
colnames(allResults)<-
c("mm","FF","totfish1","totfish2","bio1","bio2","ssb1","ssb2","spillover")
# Loop to run model specified number of times:
for (numModelRuns in 1:10)
{
maxConchAge<-30*12
ageAtRecruitment<-16
juvenileRecruitsPerMonth<-120
# Beverton-Holt parameters for stock-recruitment:
a<-15
b<-120
# Fishing mortality is selected from a uniform distribution each mode run:
F<-runif(1,min=0,max=3)
ageAtMaturity<-3*12
numberOfAgeClasses<-maxConchAge-ageAtRecruitment
# Each population has its own survival function:
survivalFunction<-function(ageInMonths)
{
  M<- max(0.1, -0.242+4.330/(ageInMonths/12))
  survivalProb<-exp(-M/12)
  survivalProb
}
survivalFunctionWithFishing<-function(ageInMonths)
{
  M<- max(0.1, -0.242+4.330/(ageInMonths/12))

  if ( ageInMonths > ageAtMaturity )
  {
    M <- M + F
  }
  survivalProb<-exp(-M/12)
  survivalProb
}
# Both population use one stock-recruitment relationship:
stockRecruitmentRelationship<-function(SSB)
{
  (a*SSB)/(1+(a/b)*SSB)
}
# Growth equation from Appeldoorn (1992a)
tissueWeight<-function(ageInMonths)
{
  0.00001263*(exp(17.44*(1-exp(-1.126*(ageInMonths/12)))))/1000
}
numYearsToRun<-50
# Set up age class vector for patch 1 with 120 juveniles
ageClassVector1<- seq(0,0,length=numberOfAgeClasses)
ageClassVector1[1] <- 120
```

```

# Set up age class vector for patch 2 with 120 juveniles
ageClassVector2 <- seq(0,0,length=numberOfAgeClasses)
ageClassVector2[1] <- 120
TotalNumFishAtDate1<-seq(0,0,length=numYearsToRun*12)
SSBAtDate1<-seq(0,0,length=numYearsToRun*12)
Biomass1<-seq(0,0,length=numYearsToRun*12)
TotalNumFishAtDate2<-seq(0,0,length=numYearsToRun*12)
SSBAtDate2<-seq(0,0,length=numYearsToRun*12)
Biomass2<-seq(0,0,length=numYearsToRun*12)
SpilloverBiomass<-seq(0,0,length=numYearsToRun*12)
#The loop that runs the population model:
for (date in 1:(numYearsToRun*12))
{
totalBiomass1<-0
SSB1<-0
totalIndividuals1<-0
totalBiomass2<-0
SSB2<-0
totalIndividuals2<-0
totalBiomassMoved<-0
m<-0
for(i in numberOfAgeClasses:2)
{
ageInMonths<-ageAtRecruitment+i
# Progress age classes in patch 1
ageClassVector1[i]<-ageClassVector1[i]*survivalFunction(ageInMonths-1)
# Progress age classes in patch 2
ageClassVector2[i]<-
ageClassVector2[i]*survivalFunctionWithFishing(ageInMonths-1)
# Move mature adults from patch 1 to patch 2
if(ageInMonths>=ageAtMaturity)
{
numToMoveInThisAgeClass <- (ageClassVector1[i] - ageClassVector2[i]) * m
if ( numToMoveInThisAgeClass > 0 )
{
ageClassVector1[i] <- ageClassVector1[i] - numToMoveInThisAgeClass
ageClassVector2[i] <- ageClassVector2[i] + numToMoveInThisAgeClass
totalBiomassMoved <- totalBiomassMoved +
(numToMoveInThisAgeClass*tissueWeight(ageInMonths))
}
}
}
# Calculate total individuals, total biomass and SSB for use (and viewing) later
totalIndividuals1<-totalIndividuals1+ageClassVector1[i]
totalBiomass1<-totalBiomass1+ageClassVector1[i]*tissueWeight(ageInMonths)
totalIndividuals2<-totalIndividuals2+ageClassVector2[i]
totalBiomass2<-totalBiomass2+ageClassVector2[i]*tissueWeight(ageInMonths)
if(ageInMonths>=ageAtMaturity)
{
SSB1<-SSB1+ageClassVector1[i]*tissueWeight(ageInMonths)
SSB2<-SSB2+ageClassVector2[i]*tissueWeight(ageInMonths)
}
}
}

```

```

}
}
if(date>ageAtMaturity)
{
ageClassVector1[1]<-stockRecruitmentRelationship(SSBAtDate1[date-
ageAtMaturity])
ageClassVector2[1]<-stockRecruitmentRelationship(SSBAtDate2[date-
ageAtMaturity])
}
else
{
    ageClassVector1[1]<-0
    ageClassVector2[1]<-0
}

# These are the results that you get and can plot
totalIndividuals1<-totalIndividuals1+ageClassVector1[1]
totalBiomass1<-totalBiomass1+ageClassVector1[1]*tissueWeight(ageAtRecruitment)
TotalNumFishAtDate1[date]<-totalIndividuals1
SSBAtDate1[date]<-SSB1
Biomass1[date]<-totalBiomass1

totalIndividuals2<-totalIndividuals2+ageClassVector2[1]
totalBiomass2<-totalBiomass2+ageClassVector2[1]*tissueWeight(ageAtRecruitment)
TotalNumFishAtDate2[date]<-totalIndividuals2
SSBAtDate2[date]<-SSB2
Biomass2[date]<-totalBiomass2

SpilloverBiomass[date]<-totalBiomassMoved

year <- floor(date/12)
monthInYear <- date %% 12

# This will set how the numbers are output in the R window - so in the R window it
will print all this out, you can check that the model is working.
cat("Year",year, "Month",monthInYear,"\n",
"Population1", "Individuals",totalIndividuals1, "Total
Biomass:",totalBiomass1,"kg", "SSB",SSB1,"kg\n",
"Population
2", "Individuals",totalIndividuals2, "TotalBiomass:",totalBiomass2,"kg", "SSB",SSB2,"
kg\n",
"Spillover", totalBiomassMoved, "kg\n")
}

# Want to make it write a single row containing the values of N1,N2, SSB1, SSB2,
B1, B2, Spillover of month 600
modelResults<-data.frame(m, F, TotalNumFishAtDate1[date=600],
TotalNumFishAtDate2[date=600],Biomass1[date=600]
,Biomass2[date=600],SSBAtDate1[date=600], SSBAtDate2[date=600],

```

```
SpilloverBiomass[date=600])
colnames(modelResults)<-
c("mm","FF","totfish1","totfish2","bio1","bio2","ssb1","ssb2","spillover")
allResults<-rbind(allResults,modelResults)
write.table(allResults,file="/Users/Kirsty/Desktop/Results/M0.txt",sep= "\t" )

}
# Remove the first row of results that contain only zeros:
allResults<-allResults[-1,]
write.table(allResults,file="/Users/Kirsty/Desktop/Results/M0.txt",sep= "\t" )
```