Economic Implications of Fully-Protected Marine Reserves for Coral Reef Fisheries

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ABSTRACT

Overexploitation of coral reefs causes species loss, stock collapses and habitat degradation and remains a major challenge for fisheries scientists and managers alike. To counter these, fully-protected marine reserves, areas closed to fishing and other harmful human activities represent an essential component of coral reef fisheries management. They overcome many of the management complexities of coral reefs, such as lack of data and enforcement, and provide vital opportunities for unhindered growth of fish stocks and protection of coral communities. Their role in conserving biodiversity and protecting habitat is undisputed. The degree to which fully-protected marine reserves can benefit fisheries, however, remains uncertain. A number of bioeconomic studies have attempted to assess the contribution of these marine reserves to fish biomass, catch levels and the present value of the fishery. They suggest that fishery enhancement by reserves will be significant. Habitat protection by reserves makes a vital, but as yet poorly appreciated contribution to fishery enhancement. We argue that this protection has many positive effects on habitat that will lead to increased standing stocks and productivity of reef fishes. Such effects are rarely considered in economic models but could have overriding importance for long-term fishery production. Fully-protected reserves have many benefits beyond fisheries that can also help compensate for the costs of establishment. We conclude that fishery sustainability for coral reef fisheries cannot be attained without the contribution of fully-protected marine reserves.

1. INTRODUCTION

There are now well over 1300 marine protected areas in the world (Kelleher et al. 1995) and new ones are being established faster than ever before. However, there is a growing recognition that many of them fail to provide adequate protection against one of the key threats to marine biodiversity: fishing (NRC 1995; McArdle 1997; Roberts 1998a). Studies of the effects of fishing on marine ecosystems reveal that it has a profound and far reaching impact at all levels, from the largest predators through to the most humble mud-dwelling invertebrates (Roberts 1995; Safina 1998). For this reason, there has been a blossoming of interest in a particular class of protected area — the fully-protected marine reserve — an area closed to all forms of fishing and other extractive and harmful uses (Ballantine 1995).

The complexity of coral reef fisheries has defied some of the best efforts to manage them using conventional approaches of limitations on catch or effort (Munro 1996). The theoretical construct of 'optimal' fishery management, management that holds fish stocks at their supposed maximum level of production, is impossible to achieve on coral reefs (or elsewhere) due to ecological and fishery complexity, and a lack of information and enforcement powers. Fully-protected reserves represent a promising alternative that overcomes many of the problems of managing multispecies, coral reef fisheries. They

also seem capable of providing many other benefits beyond fisheries, including tourism, education and research, and ecosystem services.

Effective protection of marine resources requires management, which in turn requires money. Finance is often the most crucial constraint upon protection, the degree of local co-operation and, therefore, the success of reserve creation. Economic theory is often employed in natural resource decision-making as a guide to management. Whilst economic valuation techniques have been applied to numerous terrestrial protected areas (Dixon & Sherman 1990), applications to marine protected areas are still limited (Hoagland et al. 1995). However, recently there has been an attempt to value their potential economic benefits, concentrating on effects on fishery production and other sources of revenues such as tourism (Dixon et al. 1993).

The focus on 'fully-protected' marine reserves is critical since there are few benefits to be gained from reserves, which are open to exploitation. These often end up being nothing more than 'paper-parks'. Marine reserves that are closed to fishing are also referred to in the literature as no-take zones, harvest refugia, fishery reserves, and protected marine reserves. Less protected areas are often described using the terms sanctuaries, reserves, or parks and may imply certain restrictions on gears or seasonal closures. Unless otherwise stated, the marine reserves referred to here are fully-protected.

In this paper we explore the effects of fully-protected marine reserves on coral reef fisheries whilst acknowledging that other benefits can accrue. In section 2, we turn our attention to the ecological consequences of full protection on coral reefs, summarising the findings of ecological studies to date. Section 3 reviews the findings and assumptions of the existing bioeconomic models, which link marine reserves and fisheries. We focus our discussion, in section 4, on the importance of habitat protection for coral reef fisheries, the question of fisheries sustainability and the other benefits and costs associated with protection.

2. EFFECTS OF FULLY-PROTECTED MARINE RESERVES ON CORAL REEFS

The earliest fully-protected marine reserves were established in the late, 1970s in the tropics and warm-temperate regions. These reserves have had remarkable effects on coral reef ecosystems wherever they have been established. Closure to fishing has led to build up in both the abundance and average size of previously exploited fish species, typically doubling biomass in 3 to 5 years (e.g. Polunin & Roberts 1993; Russ & Alcala 1996a,b; Wantiez et al. 1997). Together with a recovery in numbers, there are usually increases in number of species, with species reappearing in reserves that are virtually absent from fishing grounds (Clark et al. 1989; Roberts & Polunin 1993a).

Studies of these fully-protected reserves have also suggested that closing an area to fishing might actually benefit rather than harm adjacent fisheries (PDT 1990). In the Philippines (Russ 1985), New Zealand (Ballantine 1991), and Florida (Clark et al. 1989) for example, closure to fishing resulted in rapid rebuilding of exploited stocks. The biomass of commercially important species increased quickly in these cases, as did the numbers of species present. Data from a fully-protected reserve in Sumilon island, Philippines, suggested the reserve actually supported catches in an adjacent area (Alcala 1989).

Theorists propose that adjacent fisheries can be enhanced by two processes: adult and juvenile 'spillover' and 'larval transport'. As stocks in reserves build up, conditions in the reserve become more crowded, leading to a net emigration of adults and juveniles to fishing grounds. This is now commonly known as 'spillover' (Bohnsack 1996). More importantly, they realised that reserves could contribute to fisheries by producing offspring at a far higher rate than in adjacent fishing areas. Egg production by larger stocks of bigger fish inside reserves can be many times, sometimes orders of magnitude greater than by exploited stocks. Larvae are then transported to fishing grounds by ocean currents.

Fully-protected reserves have also had important effects on coral reef habitat, although there has been much less study than on fish. For example, in East Africa

McClanahan & Shafir (1990) found that sea urchins were 100 times more common in fished areas than in the reserves. The high densities of urchins outside reserves led to increased bioerosion of the reef, lower coral cover, reduced structural complexity, and a diminished capacity to support fishery production (McClanahan & Shafir 1990). Urchin densities in fully-protected reserves were controlled by predatory fish, such as triggerfish, that had been decimated by fishing outside reserves.

In the Caribbean, the opposite problem occurs. The black-spine sea urchin, *Diadema antillarum*, was once a major herbivore on Caribbean reefs but suffered a 99% reduction in densities due to a pathogen that swept the region in, 1983/84 (Lessios 1988). This led to coral reefs becoming overgrown with algae in places where herbivorous fish populations had been heavily overexploited (Hughes 1994). Algal overgrowth reduces coral cover, structural complexity, diversity of bottom-living organisms and damages the structural integrity of the reef framework itself (Birkeland 1997). It has been suggested that fully-protected reserves, by rebuilding stocks of herbivorous fish, can hold back or reverse algal overgrowth. Evidence for this is limited but tests are now underway. In a large network of Caribbean coral reef monitoring sites, the only places where coral cover was increasing were those places with fully-protected reserves (J. C. Ogden, pers. comm.). There is also some experimental evidence for fish populations controlling algal growth in St. Lucian fully-protected reserves (C. M. Roberts et al., unpublished data).

In recent years there has been a prolific number of studies on the effects of protection on fish stocks and to a lesser extent habitat. We summarise some of the main findings of these studies in table 1 (on next page).

3. FISHERY ENHANCEMENT AND FULLY-PROTECTED MARINE RESERVES

While the biological effects of fully-protected reserves have been well-established in the field, fishery effects have been better studied through modelling. It is the fishery functions of reserves that have caught the atten-

tion of most economists. A number of recent bio-economic models have aimed to test the effectiveness of marine reserve creation on fishery production. This research has been partly driven by the fishery sector's generally strong opposition to reserve creation. They argue that reserve establishment comes at the cost of fishery revenues. However, as noted above, fishery production may be enhanced through 'spillover' and larval transport from the protected region to the fishery grounds.

Bioeconomic models build on the work of Polacheck (1990), DeMartini (1993), Beverton & Holt (1957) and Sladek Nowlis & Roberts (1997) who concentrated on biological effects of reserve creation on measures such as yield per recruit and spawning stock biomass. Their general conclusions were that yield per recruit (catch) may increase under certain circumstances, such as low spillover (adult migration) rates from reserve and high mortality in the fishing ground. Sladek Nowlis & Roberts (1999) argued that the main fishery benefit is likely to be an increase in egg production due to increase in the average size and numbers of fish.

Ideally a model which aims to describe the effectiveness of a fully-protected coral reef marine reserves on fishery enhancement would incorporate coral reef fishery characteristics such as: open access (possibly regulated gear use), explicit wide larval dispersal, limited adult spillover, multiple species, spatial heterogeneity and age-structured dynamics. However, a model with all these elements would be too complex to provide any meaningful results. Although this book focuses on coral reefs, we also consider temperate models because they have many features that could be adapted and provide useful insight into potential effects of fully-protected reserves on coral reefs.

The diversity in modelling approaches makes the task of classifying them a difficult one. We, therefore, simply group the bioeconomic models of fully-protected marine reserves into two classes based on the dispersal characteristics assumed for adults of the species examined. Coral reef species tend to be sedentary as adults while dispersing widely as larvae (Polunin & Roberts 1996) though there are many reef species that make more lim-

Table 1. Summary of Findings of Ecological Studies of Marine Reserves in Reef Areas.

Reserve name and location	Years of protection	Effects reported
Mayotte Island, Indian Ocean	3	Total species richness did not differ between protected and unprotected areas. However most large carnivores were more diverse and abundant in the reserve. The mean biomass of commercial species was 202g/m^2 in the reserve compared to 79g/m^2 outside (Letourneur 1996).
Looe Key, Florida, USA	2	15 species that were targeted by spear fishers increased in abundance after spearfishing was banned: snappers by 93%, grunts by 439% (Clark et al. 1989).
Cousin Island, Seychelles	15+	Groupers, emperors and snappers were more abundant and diverse within the reserve than in fished sites (Jenning 1998).
Sainte Anne, Seychelles	11	Despite the fact that a few families retain fishing rights and poaching is fairly common in this reserve, the diversity of target species and total fish biomass were both higher than in heavily fished areas. The biomass of prey did not increase when predators were removed by fishing (Jennings et al. 1995, 1996).
Kisite Marine National Park, Kenya	5	Snappers, emperors and groupers were more abundant in the park and appear to be spilling over into fishing grounds. Protection did not affect species number or diversity (Watson et al. 1996).
Barbados Marine Reserve	11	Large, trappable fish were approximately twice as abundant in the protected area, and 18 of 24 species were bigger (Rakitin & Kramer 1996; Chapman & Kramer 1998).
Exuma Cays Land and Sea Park, Bahamas	not reported	The reproductive output of Nassau grouper (*Epinephelus striatus*) was 6 times greater in the reserve (Sluka et al. 1997).
Hawaii Marine Life Conservation Districts	not reported	Fishes were 63% more abundant in areas protected from fishing (Grigg 1994).
Saba Marine Park, Saba, Netherlands Antilles	4	In the no-take zone the biomass of target species was over twice that in fishing grounds (Polunin & Roberts 1993).
Hol Chan Marine Reserve, Belize	4	Biomass of target species in the reserve was on average almost double that in fishing grounds, while in certain parts of the reserve it was ten times greater (Polunin & Roberts 1993; Roberts & Polunin 1994).
Anse Chastanet Reserve, St Lucia	2	Total biomass of commercially important species was more than double that in fishing grounds and the reserve contained three easily caught species found nowhere else (Roberts & Hawkins 1997).
Ras Mohammed Marine Park, Egypt	15	Mean biomass of fish was 1.2 times greater on protected reefs, while differences for seven target species were much greater. Individuals of the lunartail grouper (*Variola louti*) were three times larger in the reserve (Roberts & Polunin 1993a, 1993b).
Three Kenyan Marine Parks: Malindi Watamu Kisite	20+ 20+ 10+	Of the 110 species recorded on protected reefs, 52, were not found in fished areas (McClanahan 1994). However in Malindi and Watumu commercially important species were no more abundant than in fishing grounds (Watson et al. 1997).
South Lagoon Marine Park, New Caledonia	5	Within protected areas the species richness of fish populations increased by 67%, density by 160%, and biomass by 246%, but the average size of most species did not increase (Wantiez et al. 1997).
Sumilon Island Reserve, The Philippines	10	Eighteen months after fishing was resumed in the reserve, catch per unit effort fell by a half, and the total yield of fish was 54% less, despite a greater area available for fishing (Alcala & Russ 1990).
Apo Island Reserve, The Philippines	10	The biomass of large predators increased 8-fold in the reserve. In fishing grounds mean density and species richness of large predators also increased (Russ & Alcala 1996a, 1996b).

ited migrations such as snappers (*Lutjanidae*) and grunts (*Haemulidae*) (Appeldoorn et al. 1997). By contrast, many non-reef species tend to move further or migrate as adults, as well as dispersing widely as larvae. Some models discuss migrating biomass making no distinction between the movement patterns of adults, juveniles and larvae. Therefore, potential benefits could be derived from both 'spillover' and larval transport. The transfer mechanisms may be either a density-dependent or uni-directional i.e. source and sink. Density-dependence biomass transfer implies a 'spillover' effect from the protected region. Uni-directional (source-sink) transfer, on the other hand, may suggest larval transport from a spawning aggregation for example.

For the existing bioeconomic models we discuss the assumptions, results and the applicability to coral reef environments in the two following subsections.

3.1 Models with Low Adult Dispersal

These models are most applicable to non-migratory fish species. In this case, fully-protected areas are likely to benefit coral reef fisheries mainly through larval transport to adjacent fishing grounds and low adult 'spillover'. Where adult migration is assumed to be zero the 'spillover' effect is underestimated. The use of either single cohorts or multiple age classes can go some way to explain differing results. See table 2-A on next page for an overview of the existing literature.

Holland & Brazee (1996) built and analysed an age-based dynamic model of marine reserves applicable to inshore fisheries, adding an economic dimension to the work of Polacheck (1990). The model provides information on equilibrium conditions and the paths to equilibrium for red snapper (*Lutjanus campechanus*) in the Gulf of Mexico. They assume that adults have a high fidelity to base locations but eggs and larvae disperse uniformly.

The use of a stock recruitment and multiple age class functions enabled Holland and Brazee to investigate explicitly the effects of changing population size and age structure on recruitment and catch over time. Under the criteria of maximising present value of catch, they conclude that reserves would significantly benefit moderately or heavily fished fisheries but less so lightly fished areas. In contrast, Polacheck (1990) and DeMartini (1993) who employ yield per recruit analyses, found that only small increases in overall catches can be achieved and only in previously heavily overexploited regions. Since the Polacheck (1990) and DeMartini (1993) models follow only a single cohort, they are limited in their ability to predict how reproductive potential can effect future catches. Sladek Nowlis & Roberts (1997) use a size-classified model, which may explain the similar conclusions to Holland & Brazee (1996).

Unlike many bioeconomic modelling attempts, Holland & Brazee (1996) do not analyse open access conditions of the fishery but instead assume that fishing effort is constant i.e. redistributed to the remaining fishing ground once the reserve is created. In fact, if effort increased after reserve creation, the estimated economic gains may be negligible. If effort were to fall after reserve creation, the value of the reserves may actually be greater than the simulation estimated. Holland & Brazee (1996) also stress that the optimal reserve size is inversely dependent on the discount rate employed. High interest rates decrease the optimal size of the reserve since it becomes more profitable to exploit the fish population early. This takes little account of the long-term sustainability of a fishery and clearly has important implications for management and marine reserve establishment if the objective is to maximise present value of catch.

Brown & Roughgarden (1997) provide a 'spatially-explicit' metapopulation model, which does not directly examine reserve effects but is undeniably related to the dynamics of marine reserve-fishery linkages. A larval pool acts as a common property providing recruits to all local sites. The species modelled, barnacles, has a two-phase life cycle: open water larvae and bottom-living adults — characteristics common to many coastal marine populations such as lobsters, clams, shrimp, scallops and crabs. The adult population size is assumed to be limited by space — density-dependent — but larval population is not. The common larval pool described has no direct commercial value but influences the population of marketable adults. Fishing takes place at all

Table 2-A. Summary Table of Bioeconomic Models of Marine Reserve-Fishery Linkages (Low Adult Dispersal)

Reference	Species	Location	Model Characteristics			Criteria of success	Main results
			Adult and Larval Movement	Distinguishing characteristics	Other Features		
Holland & Brazee (1996)	Red Snapper	Gulf of Mexico	High fidelity of adults to base locations – limited feeding range; Uniform dispersal of eggs and larvae	Stock recruitment relationship Age class matrices	Deterministic Discrete time Reserve size considered Dynamic path considered Fixed effort	Optimal reserve size determined by maximising present value of catch	• Reserves provide benefits for moderately to highly fished areas • Optimal reserve size is dependent on the discount rate
Brown & Roughgarden (1997)	Barnacles	None specified	Density-dependent population size; Common larval pool – injecting biomass into exploited sites	Metapopulation model Increasing biological returns – larval pool acts as a multiplier in catch function	Two stage life cycle – larval and adult Deterministic Continuous time	Maximising discounted net benefits of catch	• Optimal catch attained when exploiting only one subpopulation – the site with 'comparative advantage' in catch
Pezzey et al. (in press)	Reef species	Jamaica Belize St Lucia	No adult migration; High uniform larval dispersal – implicit in growth function	Modified Logistic Growth function in Schaefer Gordon Function	Deterministic Continuous time Open Access Stability analysis Reserve size considered	Increase in catch Optimal reserve size	• Catch increases if Stock Carrying Capacity <1:2 • Optimal Reserve Size tends to _ as Stock Carrying Capacity tends to 0
Tuck & Possingham (in press)	Example: abalone or reef fish	None specified	Sedentary adults Larvae disperse widely	Consider different classifications: • relative exporters/ importers • relative source/ sinks • uni-directional transfer Some loss in larvae from system	Discrete time Deterministic Impact of protecting source or sink on spawning stock abundance Focus on contribution of larval transfer parameter	Maximisation of present value – modelled in terms of optimal escapement not catch!	• For unidirectional larval transfer – optimal escapement is independent of transfer parameters • Sink not source populations should be exploited for maximum catch and conservation benefits but not maximum SSA • Loss in yields from reserve may be countered by potential environmental and economic benefits of reserves

local sites where the adult population is commercially valuable. The fishing objective is to maximise discounted net benefits.

The intriguing finding of this study is that the most profitable fishing strategy required the exploitation of only one sub-population while the other sub-populations were closed to fishing and conserved as nurseries. This result stems from the biological productivity of the common larval pool. Unlike many economic models, increasing returns are common to biological structures. The common larval pool acts as a multiplier in the formula for optimal catch. Therefore anything which abates the enhancement of this pool will result in a decline in catch. The result is analogous to the economic theory of comparative advantage where only the site (country) with comparative advantage in catch exploits its stock. The catch is maximised by exploiting until there are no adults remaining in that site. This is possible due to the biological common pool constantly inputting exploitable biomass. This model has very interesting implications for studies of coral reef marine reserves that may be thought equivalent to the nursery sites generating the larval pool.

The model presented by Pezzey et al. (2000) contrasts with other bioeconomic models in that it implicitly assumes the dispersal of larvae and sedentary nature of adult coral reef fish through a modified logistic growth function in a Schaefer-Gordon model. This allows for age-dependent dispersal and analytical simplicity. They also examine the optimal size of reserve.

Pezzey et al. (2000) examine the economic effects of reserve creation in a coral reef environment with open access to the fishing ground. Catch price and unit cost of effort are assumed to be constant. Fishing effort adjusts according to Smith's (1968) assumption that effort is a function of profit levels — unlike Holland & Brazee (1996). Following Sladek Nowlis & Roberts' (1997) conclusion that the principal benefit of fully-protected reserves on coral reefs will be from larval dispersal, adult migration is assumed to be zero for simplicity.

Pezzey et al. (2000) applied their model to reef fisheries of Jamaica, Belize and St. Lucia. Since coral reef fisheries are always multispecies, they approximated the different growth characteristics of stocks subject to different fishing intensities by adjusting population growth rate. Heavily exploited stocks tend to be dominated by smaller faster growing species than less exploited stocks and so are assumed to have a higher growth rate. Based on the initial ratio of exploited to unexploited stock size prevailing in these countries at the time of reserve creation, they conclude that reserves covering 21%, 36% and 40% of the management area would maximise catches in Belize, St. Lucia and Jamaica, respectively. They found that a reserve would increase the equilibrium catch when the pre-reserve ratio of stock to carrying capacity is less than a half — reflecting heavy exploitation. This is a common situation on coral reefs, where fisheries have been intensifying as human populations expand (McManus 1996). Reserve size that maximised catches increased as fishing intensity in the exploited area increased, rising to 50% of the fishing area at the highest levels of exploitation. Overall they estimated that coral reef reserves worldwide could yield one billion dollars per year in fishery benefits alone.

Tuck & Possingham (in press) consider the exploitation of a single species local population, which is connected to a protected population solely through the transfer of larvae like Pezzey et al. (2000). The main focus of this model is on the contribution of the larval transfer parameters to the optimal fishing strategy.

Tuck & Possingham (in press) assume that a single managing authority is able to selectively exploit the local populations and aims to maximise discounted net revenues. They examine in some detail the relationship between the larval transfer, fishing policies and the choice of reserve location — source or sink. The model is set up to find the optimal escapement of the exploited population i.e. the level of stock-less-catch, which maximises returns. They find that for the special case of uni-directional larval transfer the optimal escapement is independent of the transfer parameters — however, catch could be greater through the transfer of 'bonuses' from the reserve population.

In addition, Tuck & Possingham (in press) analyse the implications of protecting either a source or sink popu-

lation for the spawning stock abundance. In a numerical example they discover that since the source population is smaller than the sink population exploiting it results in a higher spawning stock abundance. Exploiting the larger sink population would lead to increased catch levels and lower spawning stock abundance. There are, however, negative implications for conservation and catch if the sink were to be exploited. Spawning stock abundance will always be greater with a reserve whether in a sink or source.

Like Polacheck (1990), DeMartini (1993), Sanchirico & Wilen (1998) and Guénette & Pitcher (1999), Tuck & Possingham (in press) find that high transfer rates reduce the benefits of reserves since they reduce the reproductive capacity through a decrease in adult stock in the reserve. In the examples used, the exploitation of the whole metapopulation produces the greatest catches. However, they note that the economic loss resulting from reduced yields after reserve creation may be countered by the potential environmental and economic benefits of the reserve — through increased habitat quality and tourism revenues for example. The degree of loss in yield revenues due to protection depends on the source and sink properties. Models with more explicit age structure (Beverton & Holt 1957; Polacheck 1990; Russ et al. 1992; De Martini 1993; Quinn et al. 1993; Guénette & Pitcher 1999) have found an increase in yield per recruit can be attained under high levels of exploitation dependent on reserve size and transfer rates.

Tuck & Possingham (in press) also conclude that sink rather than source populations should be exploited in order to avoid local population collapse. This is an intuitive conclusion supported fully by Sanchirico & Wilen (1996). However, while this is theoretically attractive, the means to identify sink and source populations have yet to be developed by ecologists. Furthermore, some doubt the practicality of such an approach, arguing that sources and sinks will vary widely among species (Roberts 1998b). Since species can not be targeted separately in coral reef fisheries, neither can source-sink dynamics be used as a basis for management.

3.2 Models With High Adult Dispersal

These models are associated mainly with mobile temperate species. In general, the assumption of mobile adults will overestimate the adult migration or 'spillover' effects for coral reef fish species. However, these models can be applied to some coral reef species with limited adult movement such as some snappers, groupers (*Serranidae*) and jacks (*Carangidae*). These models will underestimate the benefits from larval transport for coral reef species since mobile adults do not have the same opportunities for unimpeded growth and egg production as sedentary adults in a protected region. Migration is described as either density dependent or uni-directional. A summary of the literature is given in table 2-B.

Table 2-B. Summary Table of Bioeconomic Models of Marine Reserve-Fishery Linkages (High Adult Dispersal)

Reference	Species	Location	Model Characteristics			Criteria of Success	Main results
			Adult and Larval Movement	**Distinguishing characteristics**	**Other Features**		
Conrad (1997)	Halibut	North Pacific	Density-dependent biomass migration No explicit larval dispersal function	Regulated Open Access Model – Fishery regulated by season length Rents dissipated in each time period	Deterministic and Stochastic analyses Discrete time Stability analysis about the long run equilibrium –2D	Long run equilibrium: Increase in biomass Increase in catch	• Higher biomass levels in both reserve and fishing ground • Lower, less variable catches overall

Reference	Species	Location	Model Characteristics			Criteria of Success	Main results
			Adult and Larval Movement	Distinguishing characteristics	Other Features		
Hannesson (1998)	None specified	None specified	Density-dependent stock migration High-zero simulations No explicit larval dispersal function	Optimal fishing defined as maximum rent per year – no discounting Comparison of open access to total area/open access to area outside reserve and optimal fishing	Continuous and discrete time Deterministic Stability considered – 2D Reserve size considered Season length considered	Which system yields the highest: catch? revenue? conservation benefit?	• Marine reserves can hedge against stock collapses if accompanied by restraints on fishing effort and capacity • On their own reserves result in increased fishing costs and overcapitalisation, shorter season lengths • Minimal conservation benefits for highly migratory stocks
Sumaila (1998)	Cod	Barents Sea	Proportion of biomass migrates No explicit larval dispersal function	Focus on uncertainty Influence of a shock to the system – recruitment failure	Discrete time Deterministic Variety of recruitment failure scenarios All common property problems eliminated	Optimal size of reserve with respect to economic rent, catch and standing stock (biomass)	• Reserves are beneficial only when transfer rates are high and reserves large • Reserves can hedge against biological losses
Sanchirico & Wilen (1996)	None specified	None specified	Proportion of source biomass migrating to sink No explicit larval dispersal function	Uni-directional proportion of biomass flow to sink population	Continuous time Deterministic Open Access Modified Schaefer production function Dynamic path considered	Long run equilibrium: Increase in biomass Increase in catch Increase in transitional rents	• Biomass increased in both protected and unprotected patches • Catch increases if $E_{postreserve} > E_{prereserve}$ and available biomass > pre-reserve intrinsic growth in both patches • Transitional rents can also be generated
Sanchirico & Wilen (1999)	None specified	None specified	Migrating biomass No explicit larval dispersal function	Various systems considered: • closed • source-sink • density-dependent Spatial heterogeneity	Continuous time Deterministic Open Access Modified Schaefer production function	Long run equilibrium: Increase in biomass Increase in catch	• Biomass always increases with protection • In closed systems and protected sink reserves catch will fall • 'Double dividend' in 'source' reserve and 'density-dependent' reserve cases – if biomass migration increase > catch lost from prereserve source patch – in overfished areas

3.2.1 DENSITY-DEPENDENT MIGRATION MODELS

Conrad (1997) extends a model of regulated open access analysed by Homans & Wilen (1997). The model focuses on the North Pacific halibut (*Hippoglossus stenolepis*) fishery. Fish catches are targeted and restricted by season lengths rather than subject to a complete ban — though the simulation includes one case of full protection. Biomass diffusion between reserve and fishing ground is assumed to be density — dependent.

Conrad (1997) assesses reserve success on subsequent increases in biomass and catch levels. Assuming profits to be dissipated in each time period, Conrad solves the remaining two dimensional system. He predicts that reserve creation will lead to higher biomass levels in both the reserve and the fishing grounds but lower, although less variable, catches overall. In the case of the fully-protected reserve scenario, the total catch from the management area (reserve and fishing ground), fell by 40%. The model shows increases in biomass and lower catch variability — both important benefits to any fishery. Lower catch variability is a significant benefit because fishery managers should in time be able to better predict future catch levels, perhaps helping reduce over-capacity problems in the fishery.

Though developed for temperate regions, the framework of Conrad's (1997) model can apply to coral reef environments in which biomass spillover is expected to be a significant factor. A useful adaptation to make this more applicable to coral reef environments would be the incorporation of a 'spillover' limit and a more explicit larval dispersal function. Regulated open access is also relevant to coral reef fisheries though the regulation is likely to be based more on gear restrictions than seasonal closures.

Hannesson (1998) investigates the response of fishing effort and capacity to reserve establishment and how reserve efficacy depends on the migration rate of fish using deterministic equilibrium models. A density-dependent migration of stock between a reserve and the fishing ground — much like that of Conrad (1997) — is assumed.

Hannesson (1998) compares three management regimes: open access to the entire area, open access to the area outside the reserve and optimum fishing in the entire area. The optimal fishing policy is defined as that which maximises sustainable rent each year — ignoring discounting of future. He develops both a discrete time and a continuous time model allowing season length to be considered. The sensitivity of results to changes in reserve size is also explored.

Stock size and catch levels are found to be remarkably similar under the two open access regimes: 'with-reserve' and 'without-reserve'. 'With-reserve' stock size exceeds 'without-reserve' at all levels of cost. Catch levels are generally larger in the 'with-reserve' scenario, however, Hannesson claims that any increases in catch would be negated by increasing costs. He favours the 'optimal fishing policy' claiming that a marine reserve would have to be 70–80% of the original fishing ground to achieve the same yields and conservation benefits. In reality, however, 'optimal fishing' is difficult, if not impossible, to achieve due to the open access nature of the resource and imperfect knowledge surrounding the dynamics of populations.

Hannesson's (1998) simulations for a zero migration rate should be viewed with caution since the situation described is one of a closed system — where no interaction at all occurs between the protected and unprotected populations. This is entirely unrealistic for both temperate and tropical ecosystems alike. In a closed system clearly the fishery can not benefit (Sanchirico & Wilen 1998). Hannesson concludes that reserve creation can act as a hedge against stock collapses but only when accompanied by measures, which control effort and capacity. His main argument is that marine reserves will simply result in increased fishing costs and overcapitalisation, shorter season lengths and — for highly migratory stocks — marginal conservation benefit compared with optimum fishing in the entire area.

3.2.2 UNI-DIRECTIONAL MIGRATION MODELS

Sumaila (1998) uses a dynamic bioeconomic model to determine the optimal size of a fully protected marine reserve for the Barents Sea cod fishery with respect to

economic rent, catches and standing stock. He assumes that a proportion of biomass migrates between the reserve and fishing ground.

Sumaila (1998) adds another dimension to previous modelling attempts by considering the impact of a major shock to the system — recruitment failure — to the outcomes of 'with-reserve' and 'without-reserve' scenarios. The management objective is to maximise discounted economic rents over a 28 year time horizon. He examines different periods of recruitment failure — the most drastic being for a ten-year period. The model is based on the assumption that the two fishing 'agents' Norway and Russia co-operate eliminating all common property problems, which are usually associated with marine management. This also implies there is complete and perfect information about the fishery and the exact amount of fishing effort can be employed to maximise the discounted net revenues. Though this is quite realistic for Barents Sea cod the results are not so applicable to coral reefs situations.

Sumaila (1998) finds that high net transfer rates between protected and unprotected regions are necessary to ensure minimal losses in catch. He tests this by comparing results with an 'experimental' scenario — no marine reserve with a shock — and a 'control' scenario — no marine reserve with no shock. Results suggest that reserves will only be bioeconomically beneficial when both transfer rates are high and the reserves are large. However, reserves increased biomass under all circumstances. Sumaila (1998) fully supports the findings of Lauck et al. (1998) that reserves hedge against biological losses.

A major shortcoming of this model is the assumption that the transfer rate — on which the results hinge — is assumed to be proportional to the size of the stock (like Sanchirico & Wilen 1996). No consideration of the influence of reserve size on transfer rate is made. Furthermore, the model is developed in a way, which suggests that the productivity of the stock increases with the size of the reserve. This may explain why it concludes that large reserves are necessary.

Sanchirico & Wilen (1996, 1998) develop two models of marine reserve-fishery linkages. They first develop a simple model (Sanchirico & Wilen 1996) to illustrate the effects of establishing a marine reserve in a source-sink system with uni-directional biomass movement. A proportion of the source population biomass is assumed to migrate to the sink.

Sanchirico & Wilen (1996) assess the success of reserve establishment on three criteria: increase in (i) biomass, (ii) catch and (iii) transitional rents — bearing in mind that in open access equilibrium rents are driven to zero. The fishing industry dynamics are governed by the Smith/Gordon (Gordon 1954; Smith 1968) model of entry/exit behaviour. The standard Schaefer production function is adjusted to account for the catchability of the migrating biomass from larvae to the most vulnerable adults. With and without reserve scenarios are examined in the contexts of both the steady state and transitional dynamics.

Creating a reserve in the source patch allows the recovery of an overexploited stock and increased the aggregate population size. In this simplified case of source and sink, the population in the reserve patch (source) grows and, in turn, enhances the sink population. Aggregate biomass also increases. Sanchirico & Wilen (1996) show that reserve creation can increase aggregate catches if effort after protection is greater than before and the available biomass is greater than the sum of intrinsic growth in both pre-reserve patches. Transitional rents can also be generated — initially falling and then rising as the sink benefits from the migration of source biomass.

The model predicts that the fishery will not necessarily incur a loss as a result of reserve establishment, especially in the case where the reserve provides a source of larvae to the neighbouring fishery. The simple case of source and sink is likely to be the most flattering to reserve creation and so explains the more favourable outcome compared to bi-directional models. The formulation generates different results to density-dependent migration because biomass continues to flow between patches even after each population reaches its equilibrium.

Sanchirico & Wilen (1998) extend their simple model to investigate the effects of reserve creation on aggregate biomass and catch in a variety of ecological systems: closed, source-sink and density-dependent. The standard open access conditions are maintained whilst the theoretical model is developed to describe multiple patches which experience various inter-dispersal scenarios emphasising the heterogeneity of these patches i.e. different intrinsic growth rates as well as economic characteristics such as cost/price ratios and effort. The model is discrete in space but continuous in time.

Sanchirico & Wilen (1998) assess under what circumstances a marine reserve can provide the most benefits to an existing fishery in terms of increased catch and biomass. They use a two patch example for simplicity. In the case of a closed system — with no interaction between the two populations — the result of closing an area to fishing resulted in an increase in aggregate biomass but a reduction in aggregate catch — as one might expect. This was also the case when a sink area was protected. However, in the cases of source reserved areas and density-dependent systems they found circumstances under which both biomass and catch could be increased i.e. a 'double dividend'.

Protecting a source population creates a 'double-dividend' if the gain in dispersal resulting from protection outweighs the loss of catch from pre-reserve source patch. This is more likely to occur if the cost/price ratio in this area is low prior to protection meaning that it is attractive to exploit the area and the equilibrium pre-reserve biomass is low. This also indicates that the opportunity cost of protecting this area is low and likely benefits of protection high. The biological conditions conducive to a 'double-dividend' are that neither the dispersal rate nor the intrinsic growth rate of the reserve should be too high or too low. High dispersal would mean little would stay in the reserve to benefit from protection. Low dispersal would mean that the open fishing ground would not benefit from an injection of biomass.

In a density-dependent system, the 'double-dividend' is likely to occur when the patch to be closed is at a low biomass level. The reserve will always increase biomass and catch will also increase if the increase in dispersal compensates foregone catch from reserve. Sanchirico & Wilen (1998) also found that catch could be increased in the cases where the characteristics of the patches were alike. If, for example, there is a high cost/price ratio in the pre-reserve but low in the open area, the biomass in the pre-reserve is likely to be high — reflecting low exploitation. Protecting this population will do little good since no-one wants to exploit it anyway! If the low cost/price area were to be protected the density gradient between the two is such that this area acts as a sink for dispersing biomass from the fishing ground. As they already found, protecting a sink results in reduced catch. Furthermore, the intrinsic growth rate of a pre-reserve area would mean a high opportunity cost resulting from protection. This high cost is less likely to be overcome by the increase in dispersal. Protecting an area with very low growth rate is not likely to reap the benefits of protection either. It is unlikely to reach a biomass level where it can produce a density gradient in favour of injecting biomass into the open fishing ground.

Sanchirico & Wilen (1998) thoroughly examine conditions under which marine reserves can satisfy the desires of both conservationists and fishers. They confirm other findings that the best policy is to protect previously overexploited populations (Holland & Brazee 1996; Sladek Nowlis & Roberts 1997; Pezzey et al. 2000). However, they also point out that the conclusions of simple biological analyses that areas of high productivity should be protected actually flies in the face of the opportunity for a 'double-dividend' of increased biomass and catch!

3.3 Related Model

A quite different approach to marine reserve-fishery linkages was taken by Lauck et al. (1998) who were the first to use modelling to directly address the question of uncertainty and sustainability in fisheries management. They use a simple model to explore the probability of

maintaining a population level equalling at least 60% of the carrying capacity i.e. a population in the 'Optimal Sustainable Population' region[1] under various scenarios of reserve size, levels of protection and catch rates. Their results are quite startling. Assuming that the initial stock size is at the carrying capacity, they find that the chances of successfully maintaining 60% of this carrying capacity fall dramatically when the total area available for exploitation exceeds 30%. An alternative to the reserve scenario would be to reduce catch rates to 10% of the stock level. They find that reserve protection can simultaneously achieve stock protection and a higher level of catch by intensifying fishing in the smaller fishing ground, but only at high levels of protection. They recommend fully-protected reserves as a hedge against the prevailing uncertainties of both biological, management and economic systems.

3.4 General Findings

The models described above aim to provide some insight into the effects of marine reserves on fishery production in coral reef and temperate regions. The temperate models can be directly applied to some migratory or more mobile coral reef species or adapted through consideration of more explicit larval dispersal and more limited adult movement. There appears to be consensus that marine reserves will result in an increase in aggregate biomass inside and outside reserves despite varying adult migration assumptions. However, the conclusions regarding the effect of protection on catch are less consistent and often hinge on the combination of circumstances and assumptions described.

4. DISCUSSION

The data and models we have reviewed in this paper make it clear that fully-protected marine reserves could make a major contribution to improving the manage-

ment of coral reefs and their fisheries. As yet there have been few field tests of the effects of reserves on fisheries, but bioeconomic models suggest that expectations of fishery enhancement are realistic. Although models greatly simplify reality, the diversity of approaches taken, and the convergence of many of the predictions made by widely different models, lend confidence to those predictions. Reinforcing this, empirical evidence already supports many of those preconditions for fishery enhancement, such as increased overall stock biomass after reserve creation, and spillover of animals across reserve boundaries.

Though many models touch on the impact on performance of reserve size and location, design, shape and networking have not been included. Research on biological consequences of these factors is ongoing. Most recent work indicates that reserves will have to be established in large-scale networks covering significant fractions of marine ecosystems (10–20% and upwards) in order to achieve their full potential (both from biodiversity and fishery standpoints) (Ballantine 1995; Allison et al. 1998; Roberts et al., in press a, b). However, these considerations have not yet filtered through to bioeconomic modelling.

4.1 Sustainability

What is missing from most bioeconomic studies discussed is the question of sustainability of the fishery. Evidence suggests that marine reserves can perform the crucial role of helping to maintain the extended age-structure of long-lived species (Bohnsack 1996). Under all circumstances on reefs they would also increase aggregate fish biomass. Both features will lead to a reduced likelihood of fishery collapse in variable environments (Lauck et al. 1998), and to a lower probability of species loss. This implies reserves will increase the sustainability of future catches.

Reduced uncertainty surrounding future fish populations and possible fishery collapses must certainly be weighed as a benefit against economic predictions of possible short-term decreases in fishery catches due to protection (Lauck et al. 1998).

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[1]'Optimal Sustainable Population' region -This is cited in legislation such as: US Marine Mammal Protection Act, 1972, Magnuson Fishery Management and Conservation Act – Sustainable Fisheries Act

4.2 Habitat Protection

A critical aspect for the sustainability of any fishery, including those of coral reefs is the maintenance and protection of habitat. What remains absent from any modelling attempts so far is the impact of habitat on the productivity of a fishery.

Employing a *change in productivity* approach, the habitat quality provided by fully-protected marine reserves can be taken as input into the production function of a fishery and changes in fishery output can be determined. Barbier & Strand (1998) employ a dynamic approach to production function analysis to value the role of mangroves as a breeding and nursery habitat supporting a shrimp fishery. A similar approach can be taken with habitats protected in marine reserves. The distinguishing feature in the production function is that the establishment of a reserve reduces the size of fishing grounds. However, both marine reserve habitats and mangrove areas can be thought of as an input to fisheries. This method requires the comparison of output with and without the reserve to determine their net benefit.

Habitat protection in reserves can be valued using this approach, for example the role reserves could play in preventing phase shift from coral (high production, high value) to algal domination (low production, low value). Where migratory fish stocks move through reserves they might benefit from increased food production and higher survival rates that could also be valued using the change in productivity approach.

4.3 Other implications of fully-protected marine reserves

Though the use of reserves for fishery enhancement has recently become a popular research topic there are several other implications of protection. We summarise potential benefits and costs of fully-protected marine reserves in table 3.

The legal designation of a marine reserve alone will not guarantee successful implementation. Strong management must accompany it. User fees and permits may help to control access to potentially overused resources. These measures can be applied to both tourists and local residents. Ideally, pricing techniques would be employed to raise revenue which may in turn finance the management and maintenance of the reserve, as noted earlier for Bonaire. In some places, compensation payments might be made to those who have lost access to fishing grounds. In St. Lucia, after problems with gaining compliance for a new series of marine reserves, the Government provided monthly compensation payments for a period of a year to fishermen who were displaced. These payments increased compliance and helped to offset short-term losses during the early phase of reserve establishment. User fees might also be applied to the restoration of damaged or degraded areas. There is a critical need to design policies to both protect marine resources and ensure local communities benefit. Designing marine reserves to capture financial benefits through user fees is one possible way to achieve this.

One principle that might be adopted in decision-making regarding the protection of a marine area is the Safe Minimum Standard (SMS). Since we are uncertain of the costs involved in *not* protecting an area — unless the costs of establishing a reserve area are 'unacceptably' large (left to the discretion of the decision-maker) — the reserve should be established. This approach aims to avoid loss of species, habitat degradation, or possible fishery collapses by accepting a known cost today to prevent larger costs in the future. There is still little direct evidence to evaluate the full economic consequences of marine reserve establishment. However, the consequences of not extending protection to the marine environment are becoming clearer by the day.

Economists may question whether fully-protected marine reserves can be described as the first or even second best policy option for fisheries management. In theory, if all management options were available to us and we had complete knowledge of both environmental and economic factors, a sustainable and efficient fishing policy could be attained through quotas, taxes, restricted effort and gear. This might then constitute the first best option. Fully-protected marine reserves may, in this case, be a desirable but not essential part of coral reef management (although from a conservation perspective they are

Table 3. Fully-Protected Marine Reserves: Major Categories of Benefits and Costs.

Benefits	Costs
Fishery Enhancement – There may be some time lag before benefits accrue but the results of protection are larger, more valuable and variable fish species within the reserve, with transfer of benefits to fishing areas through adult spillover, and the export of larvae. Habitat protection may also increase production in reserves. Stock protection is expected to reduce the likelihood of fishery collapse, provide more predictable (and therefore more easily managed) catches, and provide a buffer against management failure.	Opportunity Costs – include the loss of potential earnings such as: • short term fishery revenues; • revenues from other activities in region – e.g. coral and shell extraction; • industrial development involving shipping and waste disposal in the protected area.
Biodiversity Conservation – Reserve protection leads to the recovery of exploited species in reserves, increased species diversity and improvements in habitat. These changes are expected to lead to greater resilience of populations to environmental perturbations, reducing the likelihood of local extinctions.	Direct Costs – including costs of: • establishment; • administration; • employment; • monitoring and enforcement.
Tourism and Recreation – Enhanced opportunities for tourism and recreation is a major objective of many protected areas. Enhancement of fish stocks in reserves and associated habitat protection are expected to increase appeal for tourism. This will create employment opportunities directly linked to the reserve (e.g. tour guides, wardens) and could stimulate a multiplier effect through the local economy (e.g. hotels, restaurants, infrastructure, taxi services etc.).	Indirect Costs – this may include compensation payments to those adversely affected by the decision to establish the reserve – for example: fishers and processors in the short-term. Alternative employment packages. Infrastructure costs for increasing tourism.
Ecosystem Services – Other than fishing, protection of reefs could provide protection against storms and coastal erosion, and increase assimilative capacity for pollutants, for example.	
Education and Research – reserves provide opportunities to learn about natural processes from 'undisturbed' regions.	
Non-market Benefits. Option, bequest, existence, aesthetic and spiritual.	

clearly essential). In practice, however, we are oblivious to what nature has in-store for us and policy options such as quotas and taxes are infeasible, particularly in tropical — often developing — countries. The first best policy option is therefore unattainable. Can we then turn to fully-protected reserves as our second best option?

The ability of fully-protected marine reserves to act as a buffer against environmental uncertainties makes them an essential tool in attaining the second best fishery management solution. However, persistent overexploitation and habitat degradation beyond the boundaries of

marine reserves must also be halted to fully achieve this goal. An effective coral reef fisheries management program will combine the virtues of both fully-protected marine reserves with fishing regulation outside the reserves to control catches.

Fishery enhancement is only one of many potential benefits of fully-protected marine reserves. Their role in biodiversity conservation, tourism and recreation, education and research, and ecosystem stability already make a strong economic and environmental case for their careful establishment and management worldwide.

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