ISRS BRIEFING PAPER 1

MARINE PROTECTED AREAS (MPAS) IN MANAGEMENT OF CORAL REEFS[1]

SYNOPSIS

Marine protected areas (MPAs) may stop all extractive uses, protect particular species or locally prohibit specific kinds of fishing. These areas may be established for reasons of conservation, tourism or fisheries management. This briefing paper discusses the potential uses of MPAs, factors that have affected their success and the conditions under which they are likely to be effective.

- MPAs are often established as a conservation tool, allowing protection of species sensitive to fishing and thus preserving intact ecosystems, their processes and biodiversity and ultimately their resilience to perturbations.
- Increases in charismatic species such as large groupers in MPAs combined with the perception that the reefs there are relatively pristine mean that MPAs can play a significant role in tourism.
- By reducing fishing mortality, effective MPAs have positive effects locally on abundances, biomass, sizes and reproductive outputs of many exploitable site-attached reef species.
- Because high biomass of focal species is sought but this is quickly depleted and is slow to recover, poaching is a problem in most reef MPAs.
- Target-species 'spillover' into fishing areas is likely occurring close to the MPA boundaries and benefits will often be related to MPA size. Evidence for MPAs acting as a source of larval export remains weak.
- The science of MPAs is at an early stage of its development and MPAs will rarely suffice alone to address the main objectives of fisheries management; concomitant control of effort and other measures are needed to reduce fishery impacts, sustain yields or help stocks to recover.
- The design and enforcement of MPAs often differs between wealthy and poorer nations, in the latter people often being much more dependent on resource exploitation.
- In most situations community involvement and support during MPA establishment are essential to MPA success.
- The design of MPAs must increasingly be adapted to the specific purpose or purposes set for reef management and this will be feasible with more improved scientific understanding of the recovery processes, their implications for fisheries and broader conservation, including the social and economic values.

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INTRODUCTION

The establishment of marine protected areas (MPAs) on coral reefs has increasingly been considered a useful option for management of these systems (Clark *et al.* 1989, Jennings 2001). The general idea of MPAs is to locally stop all extractive uses, however some may protect only particular species or locally prohibit specific kinds of fishing (Bohnsack 1996). In this paper we are primarily referring to fully protected areas, often referred to as no-take marine reserves. The motivations for establishing these protected areas vary, but high on the list are economic benefits of tourism, maintenance of fisheries, conservation of coral reef ecosystems, and protection of traditional use (Clark *et al.* 1989). The use of MPAs as a traditional management technique in regions such as Southeast Asia and the Pacific dates back centuries in some cases (Johannes 1998) and despite increased external pressures, their use are increasing in many areas (Johannes 2002). Although the objectives of MPAs may work in synergy, MPAs are often established with certain goals, for example increased tourism revenue, in mind. This has wide connotations for the design of the areas, including placement, optimum size, habitats and enforcement (Roberts *et al.* 2003). Compliance with the rules of MPA management is widely a problem (Russ 2002) and in the majority of cases, the support and involvement of local fishing communities in particular is considered to be essential (Francis *et al.* 2002).

This briefing paper addresses the uses and issues surrounding the application of MPAs in the management of coral reefs. The paper first assesses the issues that MPAs might address on reefs and how these conflict or complement each other. The factors which have affected the success of MPAs are then reviewed, covering issues such as mobility of fish, enforcement, economic development and ecological control of the ecosystem. The paper concludes by discussing conditions under which MPAs are likely to be effective.

ISSUES ADDRESSED BY MPAS

Conservation

An important function of MPAs is that they protect species that are very sensitive to fishing. For example, MPAs can protect fragile benthic habitat-forming organisms, such as gorgonians, from the direct physical impacts of fishing (Polunin 2002) and thus generally improve habitat quality within the area protected (Rodwell *et al.* 2003).

Improved habitat quality may enhance overall reef biodiversity. They will also protect slow growing species of fish and invertebrates that are particularly susceptible to overfishing due to their life history characteristics. Indeed, MPAs serve to protect the full diversity of species and maintain species that would not do well under any sort of fisheries management system. With build up of piscivorous target species within MPAs, reduction in abundance of some prey species is expected (Graham *et al.* 2003), but patterns can be expected to be complex and take 20 or more years to reach equilibrium (Pinnegar & Polunin 2004). Build up of herbivorous grazers within MPAs may be expected to control macro-algal overgrowth and increase ecosystem resilience in the face of perturbations such as hurricanes, crown-of-thorns starfish outbreaks and mass bleaching events that often result in 'phase shifts' on reefs (Williams *et al.* 2001; Hughes *et al.* 2003; West & Salm 2003). Due to such large-scale impacts on reefs, reducing at least some anthropogenic stressors, is reason enough for MPA establishment in some locations. Given these benefits from MPAs, a primary focus of many established areas, particularly nationally established protected areas, is to preserve intact ecosystems, their processes and biodiversity. In doing so, they also provide useful controls for scientific study into understanding the human effects on these ecosystems.

Tourism

Many MPAs are established to attract tourists and the economic benefits of this may far outweigh those gained from fishing (Polunin 2002). Increases in abundance, size and diversity of reef-associated fishes in reef MPAs can be more valued by divers than the condition of the reef itself (Williams & Polunin 2000). Many dive operators in the Caribbean conduct most of their diving within MPAs (Green & Donnelly 2003). Only 25% of the MPAs charge an entry fee, generating annual revenue of approximately US$1-2million, and this might be greatly enhanced (Green & Donnelly 2003). In the Seychelles very few tourists express an unwillingness to pay entrance fees, and the majority are willing to pay a fee of US$12 (Mathieu *et al.* 2003). In most situations this revenue will scarcely reach the local communities involved (Polunin 2002), however if this were changed, MPAs should help alleviate fishing pressure in surrounding areas through compensation or providing alternative sources of income.

Fisheries

There are seven main benefits hoped to be derived from an MPA for fisheries, five within the MPA (lower fishing mortality, higher density of target species, higher mean size and age of target species, higher biomass of target species and higher production of propagules of target species) and two outside the MPA (export of adult fishes to fished areas [spillover] and export of eggs and larvae to fished areas [recruitment effect]) (Russ 2002). It is therefore hoped that MPAs will promote recovery of stocks and ecosystem functioning within the area and provide for sustainable yield through spillover and larval export outside of it. Although these expectations are widely discussed (e.g. Roberts & Polunin 1991; Bohnsack 1996; Roberts 1998; Polunin 2002; Russ 2002; Gell & Roberts 2003; Halpern 2003), at this time there are relatively few good empirical studies of the actual functioning of MPAs, and these studies are often poorly designed (Russ 2002; Willis et al. 2003).

Reducing or eliminating fishing mortality in MPAs is the most important aim if the other objectives are to be achieved. The biomass of target species may take a long time to build up to unexploited levels within MPAs, yet it can be fished down very rapidly (Fig. 1) (Russ & Alcala 1999) and this is an argument against rotational closure in the absence of other controls on effort. Despite this, there have been few measurements of fishing mortality in relation to MPA function and affective enforcement appears to be the exception rather than the rule, even for well developed MPA systems in more developed countries (Russ 2002). Increases in density, biomass and mean body size of site-attached target species have been

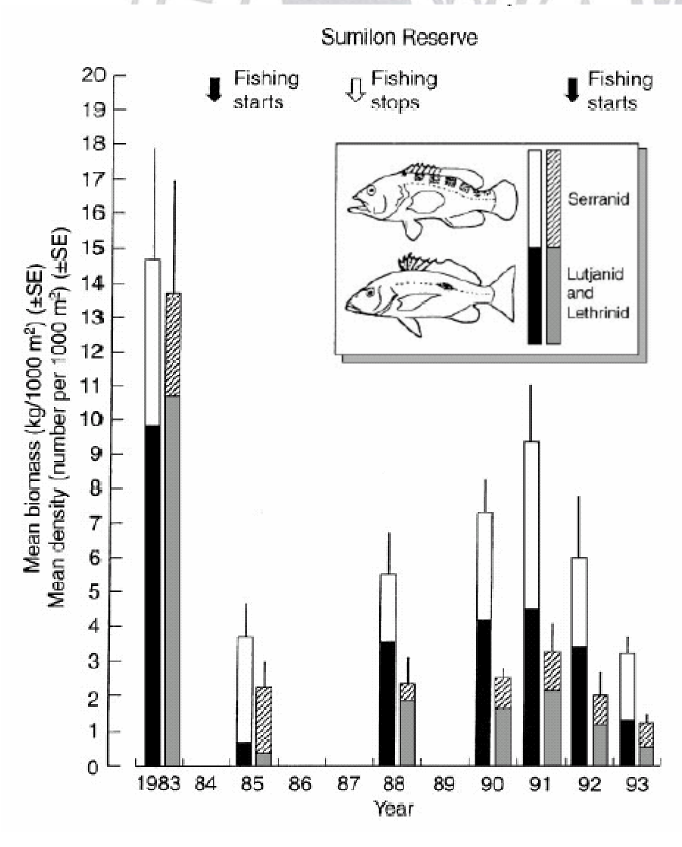

Figure 1. *Mean number (left columns) and mean biomass (right columns) of large predatory reef fish per 1000 m2 in the Sumilon MPA, Philippines, from 1983-1993. From Russ & Alcala 1999.*

documented from MPAs in many regions of the world including East Africa (McClanahan & Shafir 1990; McClanahan 1994; Watson & Ormond 1994), the Red Sea (Galal *et al.* 2002), Florida (Clark et al. 1989), the Caribbean (Koslow et al. 1988; Polunin & Roberts 1993; Roberts 1995; Roberts *et al.* 2001), the Seychelles (Jennings et al. 1995, 1996), Hawaii (Friedlander *et al.* 2003), the Philippines (Russ & Alcala 1996a, 1999, 2004) and the Great Barrier Reef (Craik 1981; Evans & Russ in press). Early increases may be rapid (Halpern & Warner 2002), however full recovery can take decades for most fishery target species, which have 'slow' life history characteristics (Russ & Alcala 2004). These studies showing such effects within MPAs are relatively few however, and the majority are comparisons at one point in time and often only one site whereas before/after evidence with replicated sites are needed (Russ 2002). The strongest biomass effects are recorded when species data are aggregated in to taxanomic (e.g. family) or other groupings. Species-level data may not show an MPA effect, because of variability inherent in both the populations and the measurements. Empirical evidence for a higher production of propagules is nearly non-existent (Russ 2002). Tropical invertebrates may show increasing reproductive output (Dugan & Davis 1993), however the evidence for coral reef fish is mainly based on theoretical predictions from increases in fish density and size (Russ 2002).

Evidence in support of the spillover and recruitment effects outside of effective MPAs is very sparse. Movement of juvenile and adult fish occurs across the boundaries of effective MPAs (Alcala & Russ 1990; Russ & Alcala 1996b; McClanahan & Mangi 2000; Roberts *et al.* 2001), however this is confined to areas very close to MPA boundaries (Fig. 2)(Russ & Alcala 1996b, McClanahan & Mangi 2000), probably due to the limited movement of most reef fishes which are site-attached (Chapman & Kramer 2000). Evidence of this spillover enhancing yield in fished areas is inconsistent. Some studies suggest enhanced catches despite the loss of fishing ground area due to establishment of MPAs (e.g. Russ & Alcala 1996b; Roberts et al. 2001), while others report an overall reduction in yield attributable to the area lost to fishing (e.g. McClanahan & Kaunda-Arara 1995). This may be linked to the size of the MPA; smaller MPAs provide more 'edge' per area for fishers to benefit from spillover (McClanahan & Kaunda-Arara 1995). There has been little effective research on the recruitment effect of MPAs, as it is so difficult to tag and quantitatively trace larval fish. Increased spawning stock biomass within effective MPAs should lead to net export of recruits to fished areas. Models of this dispersal (e.g. Roberts 1997) have suffered from not accounting for the abilities of larval fish to swim and orientate towards reefs in response to stimuli (Leis & McCormick 2002). There is also increasing evidence of moderate to high levels of self recruitment to natal reefs (Jones *et al*. 1999; Swearer *et al*. 1999).

FACTORS WHICH HAVE AFFECTED MPA SUCCESS

Poaching, perception, benefits, and governance

One of the greatest constraints on the performance of MPAs is poaching through lack of effective enforcement or compliance. Poaching may emerge from inside the local community, or from outsiders fishing in the area, but is often a result of perceptions of MPAs, lack of management will and resources, and/or lack of involvement of the local community. In most situations, particularly in poorer nations where inhabitants are more dependant on the resources involved, community involvement and support of MPA establishment are essential to MPA success (Russ & Alcala 1999; Elliott *et al.* 2001; Francis *et al.* 2002; White *et al.* 2002). In some nations, for example the Philippines and Fiji, major policy shifts are favouring the co-management or devolution of authority for management of natural resources to local governments and communities (Russ & Alcala 1999; White *et al.* 2002). Benefits of MPAs to local fishing communities are likely to be delayed. As fishers will be displaced from a portion of their grounds and the stocks are often already overexploited, a programme of education, other fisheries management techniques and development of alternative livelihoods is necessary to complement MPAs (Polunin 2002).

Given the disparity in resource needs of users it is expected that methods of MPA establishment and management will differ between poor and wealthy countries. Although the high level of community involvement needed in MPA establishment may be greater in poor countries, wealthy countries have fast realised the need for public consultation in the design and establishment of new MPA networks (see www.gbrmpa.gov.au for the methods of re-zoning the Great Barrier Reef). However the decisions are often much more ‘top-down’ and the scientific deliverables can often be much better thought out and incorporated into design. MPAs in wealthy countries can be much larger in area than in poor nations, with less resource dependence, less division of user area and the specific outputs of MPAs often aimed at conservation and tourism benefits rather than local increases in fish yields. Large MPAs established by governments in poorer nations can come into greater conflict with resource users (Elliott *et al.* 2001) than small MPAs established with community support (Russ & Alcala 1999).

Biology of species to be protected

Another important consideration when establishing MPAs is the mobility of the organisms it is hoped to protect. Many coral reef fishes and invertebrates are relatively site attached, however larger targeted species of fish may be expected to move greater distances. Target reef fishes may display large intra-reefal movements, but there is little movement between reefs across channels (Davies 1995; Chapman & Kramer 2000). Even apparently transient fish such as the blue trevally show strong site fidelity (Holland *et al.* 1996). This has huge implications for MPA design. If the objective is to enhance adjacent fisheries production through spillover of post-settlement fish, MPAs encompassing sections of reefs or islands would be preferable to whole reefs or islands; fishery benefits through spillover are most likely to occur within 500m of MPA boundaries (Fig. 2) (Russ 2002). Although many species such as coral trout move large distances within reefs (Davies 1995; Kramer & Chapman 1999), evidence is available for increases in densities of such predators within MPAs that only protect part of an island (Russ & Alcala 1996a; Evans & Russ in press). Furthermore, although home range size may be large, a number of smaller locations may be preferred within that range (Zeller 1997). Conversely, MPAs established for conservation and/or larval export objectives will be likely to produce the best results through protection of whole reefs and/or small islands as units. The use of MPAs to

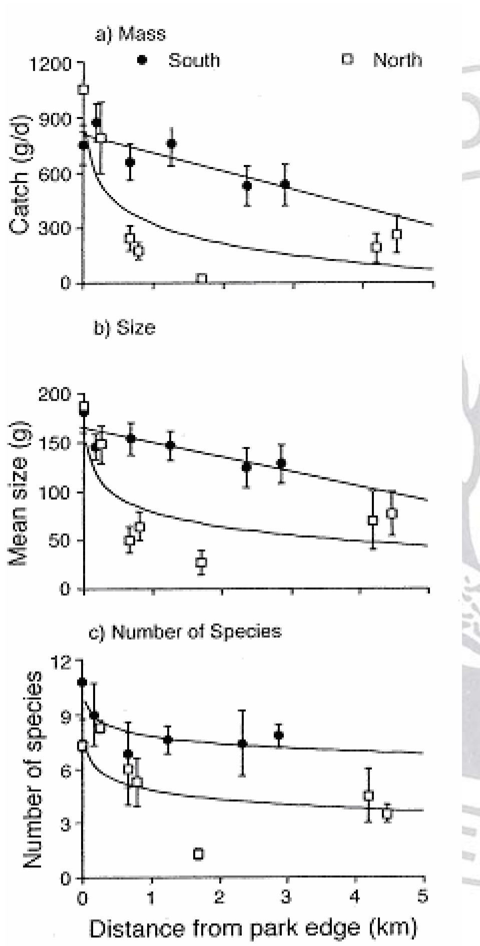

Figure 2. *a) total fish catch by mass, b) mean size of fish, and c) number of species as a function of distance away from the park border on both the southern and northern sides of the Mombasa Marine Park, Kenya. From McClanahan & Mangi 2000.*

manage species that migrate large distances is also receiving renewed attention with the protection of areas known to be used by a small portion of the population of certain species thought to have high site fidelity (Gell & Roberts 2003). Beyond movement of adults, many reef fish species utilise different habitats, such as seagrass beds, estuaries and mangrove swamps, during different life history stages (Nagelkerken *et al.* 2002; Mumby *et al.* 2004) and networks of MPAs protecting a range of these 'representative' areas may prove useful for management purposes (see www.gbrmpa.gov.au).

Ecological linkages

A long-standing debate in coral reef ecology is fuelled by whether the ecosystem is controlled by 'bottom-up' processes such as variable recruitment (Doherty & Williams 1988) or 'top-down' processes through predation (Grigg *et al.* 1984). Highly variable recruitment has been shown in some coral reef fish populations (Newman *et al.* 1996; Meekan *et al.* 2001), and if common across a wide range of species, may have profound impacts on the ecosystem. Predatory control of sea urchins has been well documented on East African reefs (McClanahan & Muthiga 1989) and is indicated in coral reef fish assemblages (Graham *et al.* 2003; Dulvy *et al.* 2004a, but see Jennings & Polunin 1997). Overall, it is likely that both recruitment and predation affect reef fish abundances and assemblage structure. Large-scale oceanic events, such as storms, can have significant impacts on recruitment and thus small MPAs (Polunin 2002). Predation on the other hand may serve to control outbreaking species such as crown-of-thorns starfish (Dulvy *et al.* 2004b), MPA size potentially influencing the ability of a MPA on part of an island or reef to control such outbreaks.

Design of effective MPAs

MPAs should encompass large proportions of fishing grounds if they are to benefit fisheries, particularly at the scale of whole stocks (Roberts *et al.* 2003). Furthermore, small MPAs may be more vulnerable to the negative impacts of large environmental perturbations such as storms, diseases and pests (Polunin 2002). However, in the majority of cases, particularly in poorer nations, small MPAs are more feasible, are often community led, improving scope for compliance, and often demonstrate measurable benefits (Russ & Alcala 1999). One of the greatest issues is the displacement of fishers from large portions of their fishing grounds. As highlighted above, in some cases displacement is expected to be compensated through increased yields, as indicated by modelling (Nowlis & Roberts 1999) and empirical data (Russ & Alcala 1996b; Roberts et al. 2001), but in other cases yield has decreased (McClanahan & Kaunda-Arara 1995). These differences may be influenced by MPA size when related to adult species spillover; however, the larval export role of MPAs may prove the greater source of benefit from protection (Russ 2002). MPA site selection based on ecological before sociological criteria has been advocated (Roberts *et al.* 2003), yet in many cases communities may only wish to place MPAs in unproductive fishing grounds and this placement may be integral to effective compliance. Criteria that would enable MPAs to be designed to optimise multiple objectives would be ideal and networks of MPAs to link source and sink populations of larval replenishment should ensure the widest benefits (Roberts *et al.* 2003). It is important to highlight the importance of other habitats to life history stages of many species (Nagelkerken *et al.* 2002; Mumby *et al.* 2004). The Great Barrier Reef is currently being rezoned to this affect; a suite of 'representative areas' included in the new network of fully protected areas (www.gbrmpa.gov.au).

CONCLUSIONS AND FUTURE USE OF MPAS IN CORAL REEF MANAGEMENT

Given the number of well-designed empirical studies is few, particularly for the benefits outside MPAs, continued research in these areas should be a priority (Russ 2002). This lack of scientific knowledge, should not, however, delay establishment of MPAs (Russ 2002). The use of protected areas in tourism development and thus as a source of alternative livelihoods should not be overlooked. Research on diver perceptions and tourism related benefits are sorely needed. Although MPAs are a useful management option, they should not be used in isolation. Reducing fishing effort, greater education and alternative livelihoods will all play key roles in the success of a management system. The design of MPAs should take into account the specific objectives, socioeconomics of the resource users and the ecological characteristics of the specific locations. Although larger areas may be preferential, smaller MPAs will often be more practical and prove useful in many situations where users are heavily dependant on the resource. Involvement of local communities in planning, design, establishment and management of MPAs should improve chances of success in the long term.

REFERENCES

Alcala AC, Russ GR (1990) A direct test of the effects of protective management on abundance and yield of tropical marine resources. *Journal du Conseil International pour l'Exploration de la Mer* 46: 40-47

Bohnsack JA (1996) Maintenance and recovery of reef fishery productivity. In Polunin NVC, Roberts CM (eds) *Reef fisheries*. Chapman & Hall, London. pp: 283-313

Chapman MR, Kramer DL (2000) Movement of fishes within and among fringing coral reefs in Barbados. *Environmental Biology of Fishes* 57:11-24

Clark JR, Causey B, Bohnsack JA (1989) Benefits from coral reef protection: Looe Key Reef, Florida. In: Magoon OT, Converse H, Miner D, Tobin LT, Clark D (eds) *Coastal Zone '89*. pp: 3076-3086

Craik GJS (1981) Underwater survey of coral trout *Plectropomus leopardus* (Serranidae) populations in the Capricornia section of the Great Barrier Reef Marine Park. Proceedings of the Fourth International Coral Reef Symposium, Manila. Vol. 1:53-58

Davies CR (1995) Patterns of movement of three species of coral reef fish on the Great Barrier Reef. Ph.D. diss., James Cook University of North Queensland, Townsville, Australia. 212p

Doherty PJ, Williams DM (1988) The replenishment of coral-reef fish populations. *Oceanography and Marine Biology* 26: 487-551

Dugan JE, Davis GE (1993) Applications of marine refugia to coastal fisheries management. *Canadian Journal of Fisheries and Aquatic Science* 50: 2029-2042

Dulvy NK, Polunin NVC, Mill AC, Graham NAJ (2004a) Size structural change in lightly exploited coral reef fish communities: evidence for weak ecological release. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 466-475

Dulvy NKD, Freckleton RP, Polunin NVC (2004b) Coral reef cascades and the indirect effects of predator removal by exploitation. *Ecology Letters* 7: 410-416

Elliott G, Mitchell B, Wiltshire B, Manan IA, Wismer S (2001) Community participation in marine protected area management: Wakatobi National Park, Sulawesi, Indonesia. *Coastal Managament* 29: 295-316

Evans RD, Russ GR (in press) Larger biomass of targeted reef fish in no-take marine reserves on the Great Barrier Reef. *Aquatic Conservation: Marine and Freshwater Ecosystems*

Francis J, Nilsson A, Waruinge D (2002) Marine protected areas in the eastern African region: How successful are they? *Ambio* 31:503-511

Friedlander AM, Brown EK, Jokiel PL, Smith WR, Rodgers KS (2003) Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs* 22: 291-305

Galal N, Ormond RFG, Hassan O (2002) Effect of a network of no-take reserves in increasing catch per unit effort and stocks of exploited reef fish at Nabq, South Sinai, Egypt. *Marine and Freshwater Research* 53: 199-205

Gell FR, Roberts CM (2003) Benefits beyond boundaries: the fishery effects of marine reserves. *Trends in Ecology and Evolution* 18: 448-455

Graham NAJ, Evans R, Russ GR (2003) The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. *Environmental Conservation* 30: 200-208

Grigg RW, Polovina JJ, Atkinson MJ (1984) Model of a coral reef ecosystem III. Resource limitation, community regulation, fisheries yield and resource management. *Coral Reefs* 3: 23-27

Green E, Donnelly R (2003) Recreational scuba diving in Caribbean marine protected areas: Do the users pay? *Ambio* 32: 140-144

Halpern BS (2003) The impact of marine reserves: do reserves work and does reserve size matter? *Ecological Applications* 13: S117-S137

Halpern BS, Warner RR (2002) Marine reserves have rapid and lasting effects. *Ecology Letters* 5: 361-366

Holland KN, Lowe CG, Bradley M, Wetherbee BM (1996) Movements and dispersal patterns of blue trevally (*Caranx melampygus*) in a fisheries conservation zone. *Fisheries Research* 25: 279-292

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nyström M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* 301: 929-933

Jennings S, Polunin NVC (1997) Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities. *Coral Reefs* 16: 71-82

Jennings S, Grandcourt EM, Polunin NVC (1995) The effects of fishing on the diversity, biomass and trophic structure of Seychelles' reef fish communities. *Coral Reefs* 14: 225-235

Jennings S, Marshall SS, Polunin NVC (1996) Seychelles' marine protected areas: comparative structure and status of reef fish communities. *Biological Conservation* 75: 201-209

Johannes RE (1998) The case for data-less marine resource management: examples from tropical nearshore finfisheries. *Trends in Ecology and Evolution* 13: 243-246

Johannes RE (2002) The renaissance of community-based marine resource management in Oceania. *Annual Review of Ecology and Systematics* 33: 317-340

Jones GP, Milicich MJ, Emslie MJ, Lunow C (1999) Self-recruitment in a coral reef fish population. *Nature* 402: 802-804

Koslow JA, Hanley F, Wicklund R (1988) Effects of fishing on reef fish communities at Pedro bank and Port Royal Cays, Jamaica. *Marine Ecology Progress Series* 43: 201-212

Kramer DL, Chapman MR (1999) Implications of fish home range size and relocation for marine reserve function. *Environmental Biology of Fishes* 55: 65-79

Leis JM, McCormick MI (2002) The biology, behaviour, and ecology of the pelagic larval stage of coral reef fishes. In: Sale PF (ed) *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*, Academic Press, San Diego. pp: 171-199

McClanahan TR (1994) Kenyan coral reef lagoon fish: effects of fishing, substrate complexity, and sea urchins. *Coral Reefs* 13: 231-241

McClanahan TR, Kaunda-Arara B (1996) Fishery recovery in a coral-reef marine park and its effect on the adjacent fishery. *Conservation Biology* 10:1187-1199

McClanahan TR, Mangi S (2000) Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecological Applications* 10: 1792-1805

McClanahan TR, Muthiga NA (1989) Patterns of predation on a sea urchin, *Echinometra mathaei* (de Blainville), on Kenyan coral reefs. *Journal of Experimental Marine Biology & Ecology* 126: 77-94

McClanahan TR, Shafir SH (1990) Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. *Oecologia* 83: 362-370

Meekan MG, Ackerman JL, Wellington GM (2001) Demography and age structures of coral reef damselfishes in the tropical eastern Pacific Ocean. *Marine Ecology Progress Series* 212: 223-232

Mumby PJ, Edwards AJ, Arias-Ganzalez JE, Lindeman KC, Blackwell PG, Gall A, Gorczynska MI, Harborne AR, Pescod CL, Renken H, Wabnitz CCC, Llewellyn G (2004) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* 427: 533-536

Nagelkerken I, Roberts CM, van der Velde G, Dorenbosch M, van Riel MC, de la Morinere EC, Nienhuis PH (2002) How important are mangroves and seagrass beds for coral-reef fish? The nursery hypothesis tested on an island scale. *Marine Ecology Progress Series* 244: 299-305

Newman SJ, Williams D.McB, Russ GR (1996) Age validation, growth, and mortality rates of the tropical snappers (Pisces: Lutjanidae) *Lutjanus adetii* (Castelnau, 1873) and *L. quinquelineatus* (Bloch, 1790) from the central Great Barrier Reef. *Fishery Bulletin* 94:313-329

Nowlis JS, Roberts CM (1999) Fisheries benefits and optimal design of marine reserves. *Fishery Bulletin* 97: 604-616

Pinnegar JK, Polunin NVC (2004) Predicting indirect effects of fishing in Mediterranean rocky littoral communities using a dynamic simulation model. *Ecological Modelling* 172: 249-267

Polunin NVC (2002) Marine protected areas, fish and fisheries. In: Hart PJB, Reynolds JC (eds) *Handbook of Fish and Fisheries*, Volume II, Blackwell, Oxford. pp: 293-318

Polunin NVC, Roberts CM (1993) Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Marine Ecology Progress Series* 100: 167-176

Roberts CM (1995) Rapid buildup of fish biomass in a Caribbean marine reserve. *Conservation Biology* 9: 815-826

Roberts CM (1997) Connectivity and management of Caribbean coral reefs. *Science* 278: 1454-1457

Roberts CM (1998) Sources, sinks, and the design of marine reserve networks. *Fisheries* 17: 16-19

Roberts CM, Polunin NVC (1991) Are marine reserves effective in management of reef fisheries? *Review in Fish Biology and Fisheries* 1: 65-91

Roberts CM, Bohnsack JA, Gell F, Hawkins JP, Goodridge R (2001) Effects of marine reserves on adjacent fisheries. *Science* 294: 1920-1923

Roberts CM, Branch G, Bustamante RH, Castilla JC, Dugan J, Halpern BS, Lafferty KD, Leslie H, Lubchenco J, McArdle D, Ruckelshaus M, Warner RR (2003) Application of ecological criteria in selecting marine reserves and developing reserve networks. *Ecological Applications* 13: S215-S228

Rodwell LD, Barbier EB, Roberts CM, McClanahan TR (2003) The importance of habitat quality for marine reserve fishery linkages. *Canadian Journal of Fisheries and Aquatic Science* 60: 171-181

Russ GR (2002) Yet another review of marine reserves as reef fisheries management tools. In: Sale PF (ed) *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*, Academic Press, San Diego. pp: 421-443

Russ GR, Alcala AC (1996a) Marine reserves: rates and patterns of recovery and decline of large predatory fish. *Ecological Applications* 6: 947-961

Russ GR, Alcala AC (1996b) Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Marine Ecology Progress Series* 132: 1-9

Russ GR, Alcala AC (1999) Management histories of Sumilon and Apo marine reserves, Philippines, and their influence on national marine resource policy. *Coral Reefs* 18: 307-319

Russ GR, Alcala AC (2004) Marine reserves: long-term protection is required for full recovery of predatory fish populations. *Oecologia* 138: 622-627

Swearer SE, Caselle JE, Lea DW, Warner RR (1999) Larval retention and recruitment in an island population of a coral reef fish. *Nature* 402: 799-802

Watson M, Ormond RFG (1994) Effect of an artisanal fishery on the fish and urchin populations of a Kenyan coral reef. *Marine Ecology Progress Series* 109: 115-129

West JM, Salm RV (2003) Resistance and resilience to coral bleaching: Implications for coral reef conservation and management. *Conservation Biology* 17: 956-967

White AT, Courtney CA, Salamanca A (2002) Experience with marine protected area planning and management in the Philippines. *Coastal Management* 30: 1-26

Williams ID, Polunin NVC (2000) Differences between protected and unprotected reefs of the western Caribbean in attributes preferred by dive tourists. *Environmental Conservation* 27: 382-391

Williams ID, Polunin NVC, Hendrick VJ (2001) Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. *Marine Ecology Progress Series* 222: 187-196

Willis TJ, Millar RB, Babcock RC, Tolimieri N (2003) Burdens of evidence and the benefits of marine reserves: putting Descartes before des horse? *Environmental Conservation* 30: 97-103

Zeller DC (1997) Home range and activity patterns of the coral trout *Plectropomus leopardus* (Serranidae). *Marine Ecology Progress Series* 154: 65-77