Marine protected areas and managing fished ecosystems

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Summary

This paper provides a synthesis of the current literature on the potential of marine protected areas (MPAs) as a management tool to limit the ecosystem effects of fishing, including biological and socio-economic perspectives. There is sufficient evidence to show that fishing can indeed negatively impact ecosystems. Modelling and case studies show that the establishment of marine protected areas, especially for overexploited populations, can mitigate ecosystem effects. Although quantitative ecosystem modelling techniques incorporating MPAs are in their infancy, their role in exploring scenarios is considered crucial. Success in implementing MPAs will depend on how well the biological concern, and the socio-economic needs of the fishing community are reconciled.

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Approaches and goals in establishing marine protected areas[1]

Traditional living resource management includes the setting aside of areas from exploitation in both terrestrial and marine systems. Such areas are set aside to ensure the continuity of stocks for future generations and these practices are still being employed in developing countries throughout the world. The notion of setting aside protected natural areas solely for their scenic, natural or scientific values, however, is a relatively recent trend (MacEwen and MacEwen, 1982). Currently there are approximately 4,500 recognised protected areas (as per IUCN definitions) around the world. Of these, however, only about 850 include a coastal or marine component (Elder, 1993).

The first recorded attempts to establish marine protected areas (MPAs) were early this century. In 1906 an attempt at regulating the collection of marine organisms within three-quarters of a nautical mile of a recreation reserve at Green Island on the Great Barrier Reef, Australia, was reported (Morning Post, 1906). Fishers rejected the proposal then. It was not until 1937 that the island and the waters within one nautical mile of it were protected using the Fisheries and Oysters Act, which basically closed the area to all forms of fishing. The first marine protected area declared using dedicated legislation, including provisions for management of surrounding waters and their biota, was at Fort Jefferson National Monument, Florida, which was declared in 1935 (Randall, 1968). The legislation used to protect this area of the Dry Tortugas was primarily designed for terrestrial systems. It was not until the post-war era that more parks with significant marine areas were established (Bjorklund, 1974). These areas, however, were also primarily protected using terrestrial legislation. Indeed, even today few MPAs are declared using MPA-specific legislation (Alder, 1996).

The use of MPAs in managing marine resources such as those used for fishing was not widely applied until the 1970s. Although many nations recognised the economic potential of their marine environments, they did not perceive the exploitation of marine resources to be a threat to the sustainability of these coastal and marine areas. Their desire for MPAs was therefore based on the ideals of natural beauty, or scientific research, as in terrestrial protected areas. This trend continued until nations began to look more towards the sea for economic growth and new food sources, which resulted in heavy fishing pressure on the world's ecosystems, especially from distant water fleets (Bonfil *et al.*, 1998). One of the effects of this pressure was to galvanise political action worldwide, leading to the ratification of the Law of the Sea Convention in 1982, for instance. Once this occurred the role of MPAs became increasingly distinct from that of

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[1] It should be noted that in this paper, a marine protected area (MPA) refers to a management area in which usage is regulated by zoning for different activities. It includes marine reserves, which are strictly no-take areas.

terrestrial protected areas. Today, the development of MPAs within an Integrated Coastal Areas Management Plan or resources management strategy generally takes the form of a representative systems of MPAs aimed at contributing to the maintenance of biodiversity, ecological processes, and sustainable resource usage.

Although signs of overexploitation in most of the world's fisheries (Ludwig *et al.*, 1993; Safina, 1995) raise serious concerns about the efficacy of current fisheries management strategies, we still have to formally address the effects of fishing on entire ecosystems. Marine reserves, areas closed to exploitation, are seen as an additional management tool that could control fishing mortality (Bohnsack, 1996; Guénette *et al.*, 1998a) and thus hedge against the risk of fisheries collapse (Bohnsack, 1993; Clark, 1996; Guénette *et al.*, 1998a; Sumaila, 1998c). In tropical fisheries, where numerous species prevent managers from applying single-species stock assessment techniques, closed areas may be the only available tool (Roberts and Polunin, 1993a; Williams and Russ, 1995). Fishing throughout an ecosystem exposes us unnecessarily to the vagaries of uncertainty, and to the consequences of genuine management mistakes. In effect, such fishing practices deprive us of any insurance policy against fishery collapse (Clark, 1996; Lauck, 1996; Sumaila, 1998c).

In terms of socio-economics, the following narrative captures the issue at stake: A journalist once asked the Minister of Fisheries in Namibia how he planned to handle the tradeoffs between the needs to conserve Namibia's fishery resources and the need for maintaining high levels of employment in the fishing sector of the economy. The Minister countered (we believe rightly) that the question missed the point: The issue, according to the Minister, was not "conservation vs employment" but rather "employment today vs employment tomorrow" (Namibia Brief, 1994). Given the collapses of various fish stocks around the world (e.g. Atlantic cod off Newfoundland) and the scientific evidence gathered so far (see for instance, Safina, 1995; Pauly *et al.*, 1998), it is almost certain that, at current global fishing levels, we are unnecessarily sacrificing tomorrow's employment for today's.

In broad terms, this paper is made up of two main parts: a part that provides a synthesis of what the current literature says about how MPAs may be used to limit the ecosystem effects of fishing; and one which briefly presents a number of promising quantitative modelling methods (either current or being developed) for the assessment of marine reserves as ecosystem/fisheries management tools. Integrated in these two parts are issues addressing socio-economic effects of fishing practices and how these might change as MPAs are implemented. We end the paper by presenting some considerations about the establishment of MPAs with suggestions on how to move forward. It is beyond the scope of this paper to extensively review either the use of marine reserves in fisheries/ecosystem management or the effects of fishing on populations and ecosystems; instead, the objective is to focus sharply on how marine protected areas may be employed to mitigate against the effects of fishing. Comprehensive reviews have been published recently on both marine reserves and the effects of fishing. See, for instance, Hall (1999), Dayton *et al.* (1995), Roberts (1995a), Jones (1992) and Hutchings (1990) on the effects of fishing; and Guénette *et al.* (1998a), Attwood *et al.* (1997), Bohnsack (1996), Roberts (1995), Rowley (1994) and Dugan and Davis (1993) on marine reserves and MPAs. The reader is also referred to a forthcoming special issue of the *Bulletin of Marine Science*, which will contain selected papers presented at the 2nd Mote Symposium on Essential Fish Habitat and Marine Reserves, Sarasota, Florida, in November 1998.

Effects of fishing

The ecosystem effects of fishing may be classified into three broad groups, that is, if we include humans as part of the ecosystem. These are the effects on (i) the conservation of species, including maintaining fish populations above certain critical thresholds, enhancing the possibility of egg and larval exportation and adult dispersal, and hedging against natural and anthropogenic disasters and uncertainty; (ii) the conservation of marine habitats, protecting them from degradation resulting from fishing activities, and preserving marine biodiversity, healthy ecosystems and critical habitat; and (iii) the maintenance of sustainable employment and economic activity based on marine resources.

Conservation of species

Fisheries management has generally focussed on one single species at a time. It has aimed at maximising yields for the fishing industries while preserving the targeted species or stocks, and balancing the needs of different users while considering the social and economic imperatives (Hilborn and Walters, 1992). Various management reference points have been developed (Deriso, 1987; Sissenwine and Shepherd, 1987; Patterson, 1992; Mace and Sissenwine, 1993; Smith *et al.*, 1993; Mace, 1994; Myers *et al.*, 1994), but most of them still rely on accurate estimation of the stocks and adequate models, as well as efficient control of effort and catch. These strategies typically underestimate the importance of uncertainties in stock assessments, population dynamics and environmental processes, which often result in overfishing (Hilborn and Walters, 1992; Ludwig *et al.*, 1993; Rose, 1997; Lauck *et al.*, 1998). In addition, management schemes achieve only partial success in controlling effort and/or catch, in some cases inciting fishers to cheat by misreporting, discarding and upgrading (FRCC, 1996; Munro *et al.*, 1998). Reducing effective fishing effort is almost impossible in the face of improving technology (Hilborn and Walters, 1992; Parsons, 1992; Ludwig *et al.*, 1993; see also Pitcher, in press). Adequate stock assessments are often impossible because of changing spatial population distributions of fish that distort catch per unit effort data (Radovitch, 1979; Saville, 1980), sampling variance and misreporting of the catch (Larkin, 1977; Ludwig *et al.*, 1993). To be effective, the stock assessment has to be done quickly enough to be used in the quota setting process for the next year (using real time information) (Walters and Pearse, 1996). Unfortunately, there seems to be an inherent time lag between stock assessment and quota setting (Fahrig, 1993), increasing risks of overfishing in the case of variable recruitment. For all of these reasons, overexploitation is frequent, even in countries where large amounts of resources have been assigned to management science and stock assessment.

The effects of overexploitation on a species are well known: diminished biomass, decrease in mean body size and age at maturity, and an unbalanced sex-ratio in protogynous species (Heessen, 1988; Buxton, 1993b). As the stock is depleted, the age structure is truncated, which reduces the number of larger sizes and experienced spawners capable of producing more numerous and better quality eggs (Kjesbu, 1989; Solemdal, 1997; Marshall *et al.*, 1998). Truncated age structure may also influence the potential reproductive success by shortening the spawning season for both males (Trippel and Morgan, 1994) and females (Hutchings and Myers, 1993). In some species, a critical concentration of adults is necessary to ensure successful breeding (Rogers-Bennett *et al.*, 1995) or the survival of settling larvae (Tegner and Dayton, 1977; Davis, 1995). All of these make overexploitation even more dangerous. Although other factors such as climatic variations may have profound effects on fish populations (Cury and Roy, 1989; Kawasaki, 1992; Bakun, 1996; Klyashtorin, 1997; Springer and Speckman, 1997), fishing has been found to be a decisive factor in stock collapses in many cases (Pauly *et al.*, 1987; Heessen, 1988; Parsons, 1991; Hutchings and Myers, 1994; Myers *et al.*, 1996; Orensaz *et al.*, 1998).

Fishing for one species often implies catching other species which share the same habitat and are vulnerable to the same fishing gear (Brander, 1988; Alaska Sea Grant College Program, 1996). The problem may arise from the gear and methods used, the fishing season (Alderstein and Trumble, 1998), and/or the management regime (Crowder and Murawski, 1998). It is very difficult to find a set of regulations that would be practical and efficient in reducing such by-catch on multi-species fishing grounds. Single-species management, by using size-limits, mesh-size, quotas and by-catch limits, compels fishers to discard fish when one of these limits have been reached (Brander, 1988). The effects of by-catch on long-lived species, such as rays and sharks, are likely to be high as these species are affected by even a low fishing mortality rate (Brander, 1988; Pauly, 1988; Casey and Myers, 1998; Fogarty and Murawski, 1998). Similarly, catching the unwanted juveniles of a target species may be detrimental to both the population and the fishery by augmenting mortality of these juveniles (Reise, 1982; Riesen and Reise, 1982; Garcia and Demetropoulos, 1986; Myers *et al.*, 1997; Alderstein and Trumble, 1998).

Looking at only one species at a time, we often fail to realise the significance of serial depletion, of individual stocks and fishing grounds, as illustrated by fisheries in all parts of the world including the Gulf of Alaska (Orensaz *et al.*, 1998), the Cuban shelf (Claro, 1991), the Jamaican reef (Koslow *et al.*, 1988), the California Coast (Dugan and Davis, 1993), New Zealand (Ballantine, 1991), Lakes Victoria and Malawi (Craig, 1992), Georges Bank (Fogarty and Murawski, 1998), New England (Brailovskaya, 1998), the Gulf of Thailand (Pauly, 1988) and the North Sea (Daan, 1980; Heessen, 1988). These changes are not always conspicuous as the total yield may remain the same over time while the relative composition of the catch changes.

Many world fisheries, once targeting long-lived, high trophic level piscivorus fish, are now catching more invertebrates and short-lived pelagic planktivores (Fischer *et al.*, 1997b; Caddy and Rodhouse, 1998; Pauly *et al.*, 1998; Pitcher and Pauly, 1998). The resulting ecosystems are often economically less efficient since secondary species may have less value (Claro, 1991) and a larger proportion of the total catch comes from industrial fishing destined to the typically low-value production of fish meal (Robertson *et al.*, 1996; Fischer *et al.*, 1997b). Long-term effects on the ecosystem are often gradual and not formally documented, resulting in the absence of baselines needed to evaluate the seriousness of the situation (Pauly, 1995).

Fishing may also have an impact on community structure by altering predator-prey relationships. A good example would be the case of the cod and capelin (*Mallotus villosus*) relationship in the Barents Sea. Heavily fishing capelin, shrimp and herring led to reduced prey availability for cod, which showed decreasing growth and increasing cannibalism (Mehl, 1991; Tjemeland and Bogstad, 1993). Several studies are showing the impact of declining forage fish populations (often due to overfishing) on the survival of marine mammals (Hansen, 1997) and the breeding success of seabirds (Furness, 1982; Duffy, 1983; Anker-Nilssen *et al.*, 1997; Fischer *et al.*, 1997b; Hayes and Kuletz, 1997). The impact is not only restricted to the total abundance of prey but also its spatial distribution and the encounter rate between prey and predators (Furness, 1982; Robertson *et al.*, 1996; Furness and Tasker, 1997).

Fishing may even eliminate trophic groups or keystone species and result in a complete change to the overall community structure (Roberts and Polunin, 1991; Russ, 1991; Done, 1992; Roberts, 1995a; Jennings and Polunin, 1996; Goñi, 1998; Hall, 1999). For example, reef fishing mainly targets large predatory and herbivorous fish, among them triggerfish which feed on urchins, a keystone species of these ecosystems (Roberts, 1995a). Fishing finfish thus results in high concentrations of urchins, at the same time it controls algae (Hay and Taylor, 1985; McClanahan and Shafir, 1990; Jennings and Lock, 1996), and may even increase erosion of the coral reef substrate (McClanahan and Shafir, 1990; Roberts, 1995a). As urchins are more efficient than herbivorous fish, they may suppress the densities of these fish. Conversely, in Jamaica, in the absence of urchins, high fishing pressure on finfish still prevents the herbivorous fish population from recovering and thus helping to control algae (Hugues, 1994). Other examples of disturbance of top-down controls can be found in Botsford *et al.* (1997) and Parsons (Parsons, 1992). Once again, such ecological shifts may also be caused by a combination of environmental factors (e.g. McClanahan and Muthiga, 1998).

Conservation of habitats

Trawls and dredges may modify the sea bed by ploughing, scraping, resuspending sediments, and destroying non-target species (Jones, 1992; Goñi, 1998). Evidence that the use of dredges and bottom trawls is detrimental to demersal habitats and their fauna is however, difficult to gather because of an array of reasons. Often, studies are limited by the lack of unexploited habitats of similar type which can be used as controls (Jones, 1992; Kaiser, 1998). On top of this comes the lack of knowledge about the previous levels of fishing intensity on the studied grounds (Hutchings, 1990). Most studies are carried out over short periods of a few months and thus do not account for cumulative effects (Jones, 1992; Thrush *et al.*, 1995). Also, dredging may have less impact on high energy shallow grounds, which are regularly disturbed by storms, than on deeper-water fishing grounds which would be more likely to suffer long-lasting effects (Eleftheriou and Robertson, 1992; Jones, 1992). Clear impacts are also difficult to detect over long periods of time because the distribution of fishing effort is patchy, highly concentrated (Rijnsdorp *et al.*, 1996) and mobile (Allen and McGlade, 1986; Hutchings and Myers, 1994). This is further complicated by concomitant possible effects of pollution, eutrophication and variations in climate (Samoilys, 1988; Kaiser, 1998). Finally, impact studies are hampered by the lack of knowledge on these epibenthic communities, beginning with their taxonomy (Hutchings, 1990).

Despite these uncertainties, there are indications that the use of bottom gears may change the structure of the benthos and especially its species composition (Saxton, 1980; Bradstock and Gordon, 1983; Hutchings, 1990; Jones, 1992). It may also decrease bottom complexity by removing those macro-benthic organisms which provide shelter (Auster *et al.*, 1991; Sainsbury *et al.*, 1993; Auster and Malatesta, 1995; Auster *et al.*, 1996). A few dredges or bottom trawl passes are often sufficient to reduce habitat complexity (Auster, 1998; Watling and Norse, 1998), and kill or damage infaunal and epifaunal organisms, while sediments and small infauna such as polychaetes seem to recover after a few months (Peterson *et al.*, 1987; Eleftheriou and Robertson, 1992; Currie and Parry, 1996) or several years (Watling and Norse, 1998). However Poiner *et al.* (1998; 1998) found that each consecutive trawl removes 9-13% of the sessile and mobile benthic invertebrates, and fish communities. Repeated disturbance and mortality of large benthic organisms are likely to prevent any recovery of the vulnerable species, especially the long-lived ones (Dayton *et al.*, 1995), and the species associated with undisturbed highly structured bottoms (Watling and Norse, 1998). Fishing with mobile bottom gears has contributed to tremendous benthic changes in the Wadden Sea (Reise, 1982; Riesen and Reise, 1982). By modifying habitat structure and siltation processes (Jones, 1992; Rothschild *et al.*, 1994), or destroying seagrass habitat, mobile gears have been shown to hamper juvenile settlement for some species (Peterson *et al.*, 1987). Additional hints are provided by new fishing grounds in Australia (Saxton, 1980; Sainsbury *et al.*, 1993) and Arctic Canada (McAllister and Spiller, 1994) where trawls collected massive quantities of large epibenthic organisms that decreased rapidly with time.

In a few cases, the effect of dredging and the subsequent reduction in epibentic organisms has been linked to changes in relative fish community composition. For instance, Sainsbury (1993) showed that in trawled areas of the Northwest Shelf of Australia, *Nemipterus* and Sauridae were abundant while unfished areas were dominated by *Lutjanus* and *Lethrinus*, which preferred complex bottom structures for cover. Destruction of coral cover on reefs has also been linked to impoverished marine resources and fish stocks (Jennings and Lock, 1996; Vincent and Pajaro, 1997). Temperate demersal fish such as cod, which seek cover to reduce predation, may also be impacted by systematic decreases in bottom complexity (Lough *et al.*, 1989; Fraser *et al.*, 1996; Gregory and Anderson, 1997). Rao (1988) attributed the decline of a marine catfish (*Arius tenuispinis*) to the disappearance of its principal prey, a polychaete, due to incessant trawling of its feeding grounds.

Socio-economic considerations

If we consider fishing communities to be part of the ecosystem, then we can talk about the "socio-economic ecosystem effects of fishing". Many social scientists have convincing arguments to the effect that fishing communities ought to be seen as part of the ecosystem (see for instance, Coward *et al.*, in press). These scientists argue that the fact that fisheries are managed under multiple, usually conflicting objectives, should not be lost sight of. Apart from resource conservation and food supply, ecosystem management goals include generation of employment and economic wealth, income for fishers and the maintenance of viable fishing communities (Charles, 1989; Behnken, 1993).

Few studies have examined the socio-economic impacts of fishing, though a number of studies have quantified the cost of habitat changes on fisheries. However, the economic impacts of destructive fishing practices such as trawling, cyanide fishing and blasting are poorly understood. Cesar et al. (1997) studied the economic impact of destructive fishing practices, including poisoning and blast fishing, around Indonesian coral reefs. They found that the benefits to private individuals were high, but the social costs were much higher, up to 50 times larger in the case of blast fishing in tourist areas. Johannes and Riepen (1995) investigated the socio-economic implications of the live reef fish trade in Asia and the Western Pacific where cyanide is used extensively. The profits generated by this form of fishing were high for individual fishers, but only in the short-term. They noted the social costs of cyanide fishing to local communities but they did not put a dollar value on it.

The long term effects of fishing on the economic and social well-being of the fishing communities may be either negative or positive. They tend to be positive if the interaction between the fishing community and the fish is such that the ecological base of the resources remains intact through time; in other words, if sustainably managed. On the other hand, if this interaction degenerates into the destruction of the resource base, as it usually does, then the negative ecosystem effects of fishing hit hard on the community. This negative effect can result in huge dislocation in the economic and social life of the fishing community dependent on the resource. An often-cited modern example of this is the huge economic and social pain that followed the collapse of the North West Atlantic cod fishery off the coast of Newfoundland, Canada.

Several factors contributed to the fishery crises in Newfoundland, such as policy problems of the welfare state, socio-economic crisis of the fishing communities (Ommer, 1994), and inappropriate fisheries policies, resulting from overestimation of the stock (Steele *et al.*, 1992). A moratorium was imposed in 1992, in response to the overfishing situation of the northern cod stock. At that time, the fishing industry was already over-capitalised, both in vessels and in processing plants. It was suggested then that 19,000 fishers and plant workers plus 20,000 others would be directly affected (Steele *et al.*, 1992). This does not take into consideration, however, the effects on social and cultural identity and values of communities with such a long tradition of fishing.

Marine protected areas as a management tool

Ecological factors

From the single species point of view, a marine reserve would be expected to help control fishing mortality and by so doing restore, at least partially, pre-industrial exploitation patterns, when less efficient fishing techniques and lower boat power prevented the exploitation of portions of the fishing grounds. Such reserves would increase resilience against both overexploitation and uncertainties, and may even prevent resource collapses (Ballantine, 1989; Ballantine, 1995; Bohnsack, 1996; Guénette *et al.*, 1998a). Mistakes in stock assessment would have less impact in the presence of adequate protected areas. In the absence of exploitation, the spawner biomass is likely to increase, improving the reproductive potential, and eventually rebuilding the stocks. The presence of large individuals would also reduce the risk of sex imbalance in protogynous species (Buxton, 1993b).

Increases in density and biomass of various species and especially those targeted by the fishery have been reported in several reserves (Plan Development Team, 1990; Roberts and Polunin, 1991; Dugan and Davis, 1993; Roberts and Polunin, 1993a; Rowley, 1994; Bohnsack, 1996; Guénette *et al.*, 1998a) (see also Appendix 1). It should be noted, however, that the presence of even limited exploitation within the protected area diminishes expected benefits (ICES, 1994; Jennings *et al.*, 1996; Attwood *et al.*, 1997; Wantiez *et al.*, 1997; Goodridge *et al.*, in press). These benefits decrease rapidly after exploitation resumes in previously unfished reserves (Roberts, 1986; Alcala and Russ, 1990; Russell, 1997; Robertson, 1998). Generally, marine reserves have not been shown to swell the fish population in the unprotected parts of the habitat (Roberts and Polunin, 1993a; Schmidt, 1997; Guénette *et al.*, 1998a). However, in some cases reserves have been shown to sustain yield by adult migration into the neighbouring fishing grounds in the Philippines (Alcala and Russ, 1990; Russ *et al.*, 1992; Russ and Alcala, 1996a), South Africa (Bennett and Attwood, 1991) and Spain (Ramos-Espla and McNeill, 1994). In addition indirect evidence coming from modifications in fishers' behaviour should also be considered (Rowley, 1994). Reserves may also be a suitable tool for indirectly reducing by-catch, when it is possible to protect critical habitats of the species or age group at risk. For instance, spatial closures, both temporal and permanent, were successful in cases where juveniles migrate towards adult habitat, such as plaice (ICES, 1994) and red mullet (Garcia and Demetropoulos, 1986; Caddy, 1990). Such reserves would be more efficient than gear modifications, as well as easier to regulate and enforce than single-species oriented regulations, which can often be contradictory.

The effects of fishing on benthic structure and community structure underline the importance of creating permanent reserves. By eliminating mobile gear fishing, the bottom complexity as well as the benthos and fish species composition are likely to change from disturbed to mature ecosystems (Watling and Norse, 1998). Species vulnerable to fishing and perturbations are likely to increase while their prey may decrease. Similarly, long-lived species and those requiring highly structured habitat would be expected to thrive. However, we do not know if damage done to benthic communities is reversible, and if so, reconstruction could occur through switches of communities (Hall, 1994). In addition, responses of individual species may be dampened through competition (McClanahan and Obura, 1995) or global recruitment conditions (Jourde, 1985; Wantiez *et al.*, 1997). Evidence that closed areas may result in community structure modification have been shown in Kenya (McClanahan and Obura, 1995), California (Engel and Kvitek, 1998), Sicily (Pipitone et al. 1996 in Engel and Kvitek, 1998), and Zimbabwe (Sanyanga *et al.*, 1995). Since some epibenthic species are slow-growing and long-lived (around 100 years, Watling and Norse, 1998), rebuilding the habitat structure may be a long process.

Both larval dispersal and migration patterns will define the location, size and number of reserves necessary to protect a particular species (Carr and Reed, 1993; Quinn *et al.*, 1993; Attwood and Bennett, 1995; Allison *et al.*, 1998). The patterns of larval dispersal, the location of their settlement and the presence and contribution of neighbouring populations will be crucial to the efficacy of the reserve and its ability to sustain a population (Quinn *et al.*, 1993; Allison *et al.*, 1998). A few cases convincingly point out the importance of accounting for larval dispersal in sustaining or rebuilding fished patches (Tegner and Dayton, 1977; Tegner, 1992; Tegner, 1993; Rogers-Bennett *et al.*, 1995; Stoner and Ray, 1996; Dye *et al.*, 1997; Orensanz *et al.*, 1997). Although successful, some reserves would not be sufficient to sustain their own population. For example, in the Bahamas, the queen conch is thought to depend on unfished deep waters outside the reserve for a part of its recruitment (Stoner and Ray, 1996). Reserves would also be especially useful when adult density is an important factor for successful reproduction.

A fast rate of adult migration outside the reserve is likely to decrease the efficiency of the reserve since a large proportion of individuals would still be vulnerable to exploitation (Guénette *et al.*, 1998a). In consequence, the need for knowledge of home range and migration patterns becomes crucial, and this has already been addressed by several authors (Bennett and Attwood, 1993a; Holland *et al.*, 1993; Attwood and Bennett, 1994; Zeller, 1997). When the objective is to control fishing mortality for targeted species, it may be possible to design reserves that would help protect the stock when combined with other management measures. Possible solutions include permanent and/or temporal closures to include critical habitats such as nurseries, spawning and feeding grounds or to protect the stocks during crucial life history events such as migrations and spawning aggregations (Guénette *et al.*, 1998a). Some closed areas used as part of fishery management regimes (for single species) produced positive results for crabs (Yamasaki and Kuwahara, 1989), shrimps (Roberts, 1986), spiny lobster (Davis and Dodrill, 1989) and plaice (ICES, 1994). In other cases, poor results have been shown when the protected area is located in unfavourable habitats (Heslinga *et al.*, 1984; Tegner, 1993), or is not protecting a sufficient portion of critical habitats (Armstrong *et al.*, 1993; Shepherd and Brown, 1993; Cadrin *et al.*, 1995). In such situations, the establishment of marine reserves could lead to a false sense of security while antagonising fishers and other stakeholders (Carr and Reed, 1993; Dugan and Davis, 1993).

Based on the minimum spawning biomass that should be preserved in exploited stocks, the Plan Development Team (1990) suggested that 20% of the total habitat be protected. Modelling using species with different life histories suggested that a large proportion of the total habitat (up to 50%) should be included in reserves to efficiently protect both the habitat and the animals contained therein from the negative impacts of extractive use of the resources (Attwood and Bennett, 1995; Man *et al.*, 1995; Holland and Brazee, 1996; Sladek Nowlis and Roberts, 1997; Guénette and Pitcher, 1999). Compared to one single reserve, a network of reserves would increase their buffer function against environmental variation and local catastrophes (Ballantine, 1995; Ballantine, 1997). A network of reserves would also be more suited to species with a low site fidelity or with a poorly understood life history. A good example would be provided by a squid (*Loligo vulgaris reynaudii*), a species that sporadically uses the undisturbed spawning habitats within the Tsitsikamma National Park (South Africa), depending on environmental conditions (Sauer, 1995).

Socio-economic factors

Economic factors are generally not taken into account in the planning of MPAs (Tisdell, 1986), probably because MPAs are usually created either in anticipation of biological and ecological benefits, or in response to public pressure, in particular that from conservation groups. Arguments have been put forward for the inclusion of both social and economic variables in the decision to establish marine reserves (Sumaila, 1998c). Economic justification for establishing marine reserves usually takes two broad forms. First, it is argued that economic benefits may follow the establishment of marine reserves in the form of creating employment through non-consumptive activities such as tourism and recreation. Second, it is expected that marine reserve creation can protect future jobs by increasing the chances of managing the stocks sustainably.

Quantitative modelling for assessing marine reserves

Biological

Single species

Single-species modelling has been useful in showing how marine reserves could help rebuild over-exploited populations by increasing population abundance, survival and the numbers of older individuals, thus serving as a hedge against stochastic recruitment failure (see Guénette *et al.*, 1998a). Equilibrium models were useful to explore the influence of population dynamics and basic mechanisms behind marine reserves, such as the impact on fishing mortality, yield, body size, mean age, and the implications of high exchange rate between protected and unprotected areas (Polacheck, 1990; Die and Watson, 1992; Russ *et al.*, 1992; Daan, 1993; DeMartini, 1993; Watson *et al.*, 1993). The stage-based model built by Crouse *et al.* (1987) has shown how young adult mortality of loggerhead sea turtles (*Caretta caretta*) was more important for the population size and productivity of this species than were its nesting beaches. From this, it appears that the use of Turtle Excluder Devices in trawls (Crouse *et al.*, 1987) and more importantly, the reduction of turtle exploitation in Asia (Poiner *et al.*, 1990) would efficiently decrease the total mortality of adults. Using life tables, Walker (1996) showed how different species of skates are vulnerable to fishing at various degrees of intensity.

The addition of stock-recruitment relationship and reproductive potential led us to consider resilience to exploitation induced by the increase in the number of large spawners in closed areas (Quinn *et al.*, 1993; Man *et al.*, 1995; Holland and Brazee, 1996; Sladek Nowlis and Roberts, 1997; Guénette *et al.*, 1998a; Guénette and Pitcher, 1999; Sladek Nowlis and Roberts, 1999). The balance between stock rebuilding and yield improvement depends on the rate of biomass exchange between protected and unprotected areas. Also, larval dispersal is shown to be a possible mechanism for rebuilding the stock (Quinn *et al.*, 1993; Man *et al.*, 1995; Sladek Nowlis and Roberts, 1997; Sladek Nowlis and Roberts, 1999).

Spatial modelling

Since the marine environment is not homogenous, spatial structure of the species habitat should be included in modelling to help understand the influence of larval dispersal, adult migration and age-specific habitat needs. In addition, explicit spatial models summarise better the interaction between migration and the size and shape of the reserves. To date only a few spatial studies have incorporated marine reserves. Attwood and Bennett (1995) used simple spatial structure to compare three species with different life histories (longevity, reproduction,