

SPATIAL ECOSYSTEM SIMULATION OF NO-TAKE HUMAN-MADE REEFS IN MARINE PROTECTED AREAS: FORECASTING THE COSTS AND BENEFITS IN HONG KONG

Tony J. Pitcher¹, Eny A. Buchary and Ussif Rashid Sumalia

Fisheries Centre, University of British Columbia, Vancouver, Canada

Abstract

This paper demonstrates the use of ECOSPACE, a spatially-explicit simulation model of whole ecosystem dynamics, as a policy evaluation tool for forecasting resource and fishery responses to no-take marine protected areas deployed with human-made reefs. Our case study is based on a recent initiative to establish these devices in Hong Kong waters.

Our mass-balance ecosystem model comprised 37 functional ecosystem groups and seven sectors of the Hong Kong fishery, which was assumed to increase its aggregate catching power by 3% per year. Parameters for the fishery and habitats were obtained from recent surveys and fisheries assessment work in Hong Kong. Additional model parameters were obtained from meta-analyses and other literature on fishes of the South China Sea. Separate ecosystem groups were associated with reef and non-reef habitats and the assignation of more than 250 fish species to reef and non-reef habitats was performed with the help of an expert consultation.

First, Ecospace was used to compare the relative gains in biomass and catch of no-take reef areas in the Hong Kong ecosystem. Results suggest that, for reef fishes, both biomass and catch rise with MPA size, with the exception of valuable larger reef fish, which show a peak catch when between 8% and 15% of the area is closed.

Secondly, the modelling system was used to evaluate returns to the fishery outside the closed area from a range of MPA/AR complexes in which size, perimeter and corridors were designed using biogeographical theory. Results suggest that a no-take area split into 3 reefs performs better than the same area as one reef. Benefits that might be deliberately foregone by allowing fishers to exploit designated artificial reefs may enhance consent and cooperation among these groups.

Thirdly, five specific policy scenarios were evaluated using a spatial map of Hong Kong waters. Gains and losses to different fishery sectors are tracked, along with shifts in the species composition of the catches. Human-made reefs with no protection will do little to avert an impending conservation disaster that may see many of Hong Kong animal groups become locally extinct in the next 25 years, despite the continuation of a profitable fishery whose major player is prawn trawling. Overall, a planned deployment of human-made reefs within 5 major and 4 minor no-take areas, comprising about 16% of Hong Kong's waters, is forecast to perform well in comparison with other scenarios. Conservation benefits would be increased by banning trawling or by bringing Hong Kong's expanding fish catching power under control. Economic valuation of the various policy scenarios indicate that while different fishery sectors prefer different policy options, overall, the scenario with ARs deployed within MPAs with no trawling permitted, delivered the best economic results.

Simulated results are sensitive to uncertainties in many of the model parameters, and further work on the trophic relationships and dispersion patterns of Hong Kong fishes is advised. The use of the ECOSPACE modelling system in the adaptive management of AR/MPA system is discussed.

Introduction

This paper aims to demonstrate a new policy evaluation tool, performing spatial simulation of whole ecosystems (*Ecospace*: Walters et al. 1998), that can forecast resource and fishery responses to artificial reefs deployed within no-take marine protected areas. Our case study is based on an initiative to establish artificial reefs (ARs) as part of no-take marine protected areas (MPAs) in Hong Kong (Wilson and Cook 1998; Pitcher et al. 2000)², which is a brave attempt, in one region, to turn the tide of world-wide fisheries depletions that are so serious that many fear complete shifts in the nature of life in the oceans (Pitcher 2001).

The marine ecosystem of the South China Sea has been heavily affected by fishing (Silvestre & Pauly 1997, Pauly et al. 1996) so that species composition has shifted towards low-value short-lived pelagic fish, a dismal example of "fishing down the food web" (Pauly et al. 1998b) that is also reported from the nearby East China Sea (Chen et al. 1997). In Hong Kong, where fisheries

¹ 2204 Main Mall, University of British Columbia, Vancouver, V6T 1Z4 Canada. E-mail: t.pitcher@fisheries.ubc.ca

² The deployment of the first phase received final government approval in July 2001 (Keith Wilson, Pers. Comm.).

have been assessed quantitatively, trawling has had large impacts on benthic structure and fauna (Gomez et al. 1990, Wu 1988, Leung & Lee 1987), fishery catches have fallen (Cook et al. 1997, Richards 1985, Richards et al. 1985) and assessment has revealed high fishing mortality rates (Pitcher et al. 1998). Trawling has large effects (Valente et al. 1996): for example in Tolo harbour each square meter may be trawled three times a day (K. Wilson, pers. comm.). Consequently, the biomass of long-lived high-value demersal fish species has been almost eliminated from many areas of Hong Kong. The chances of reversing this depressing state appear low (Heinke 1996), as data concerning and management of capture fisheries has been almost absent (Lai et al. 1995).

In Hong Kong, human-made reefs (= artificial reefs: Pitcher and Seaman 2000) aim to increase depleted biomass, so if they were to remain open to uncontrolled fishing this aim would be prejudiced. Hence, including them within a no-take area makes sense (Bohnsack 1996, 1993): here we refer to them as AR/MPA systems. A major issue in AR/MPA deployment has pivoted on how to forecast responses (see Seaman 2000): there has been a debate between those who fear that ARs aggregate existing resources, making them more vulnerable to catch (e.g. Romero 1996; Polovina 1989), and those who see AR/MPAs as providing a lasting enhancement by rebuilding depleted resources. Increases in total biomass can be regarded as a hedge against overfishing and mistakes in fishery management (Bortone 1998; Bohnsack et al. 1997). But, there remains uncertainty about the conditions under which AR/MPAs can increase fishery catches (Sumaila et al. 2000; Russ and Alcalá 1996).

The debate has been largely centred around the responses of single species. Ecospace simulations, by mapping the biomass fluxes of all of the components of an ecosystem, including predation, competition and fishery extractions, have the potential to transcend this debate. Both recruitment and aggregation responses are implicit in the model, which conserves total ecosystem biomass while allocating different proportions of the biomass pools to different taxa in different habitats. This new modelling system provides an average picture of biomass responses, spatially mapped onto an surrogate of the actual location. In this paper, we explore the use of Ecospace to evaluate a range of policy options and designs for the Hong Kong AR/MPA system.

Methods

Spatial simulations were based upon a mass-balance Ecopath model for the Hong Kong marine ecosystem, structured around reef-associated functional groups of organisms and including seven sectors of the Hong Kong fishery. Spatial ecosystem simulations aimed to investigate first, catches and biomass recovery for a range of sizes and design options for the AR/MPA complex; and secondly, forecast biomass and catch from scenarios resembling likely actual deployments of AR/MPA complexes in Hong Kong waters. Finally, economic analysis of the different policy scenarios are performed.

Ecopath model of Hong Kong structured for reef resources

The Hong Kong marine ecosystem model comprised 37 functional groups (Table 1), updated from on a previous Ecopath model with 15 groups (Pitcher et al. 1999): two primary producer groups, twelve invertebrate groups, one marine reptile group (turtles), fourteen fish groups, four elasmobranch groups, two seabird groups, one marine mammal group and one detritus group. Fish species were taken from a Hong Kong survey and catch database (Pitcher et al. 1998). For most fish in the database, reef indices prepared by expert consultation were used to divide fishes into reef-associated and non-reef groups (for details see Pitcher et al. 1999). The model also includes reef-associated prawns, cephalopods and benthic molluscs. Using Hong Kong survey data, meta-analyses (e.g. Palomares and Pauly 1998; Pauly et al. 1993) and databases for the South China Sea such as Fishbase (Froese and Pauly 1998), growth, mortality, consumption and diet data were assembled for groups of small, medium and large reef-associated fish and pelagic fish, where the size categories were determined by asymptotic length. Parameters were obtained for over 250 species from the Hong Kong survey database. Parameter values for functional groups were obtained from averages of the species included, weighted to increase or decrease by size category where necessary. The biomass pools for large fish were split into juveniles and adults, as suggested by Walters et al. (1997). Full details of parameters used in the model are available elsewhere (Buchary et al. 2001).

Seven sectors of the Hong Kong fishery were modelled: stern, hang, pair and shrimp trawlers, purse seiners, and two small-scale artisanal sectors "P4/7" vessels and "miscellaneous", which employ a wide range of nets, traps and hook gear. The catch composition of each sector obtained from the survey database was mapped onto the 37

Ecopath groups. Landing data entered in previous Ecopath models of Hong Kong waters were based on the revised catch estimates outlined in Buchary et al. (2001). Discard data previously omitted were derived using information from an inshore survey (Chong 1984). Landing and discard records for sea turtles, dolphins and certain other functional groups not officially documented in the statistics but reported anecdotally were also taken into account (see Buchary et al. 2001 for full details).

Mass-balance of the model was achieved in the usual way by adjusting biomass, diet matrix and consumption and mortality parameters (Christensen and Pauly 1992). Input and output parameters for the balanced model are listed in Table 2. Full details of sources and estimations for the parameters are presented elsewhere (Buchary et al. 2001).

Ecospace simulations for reef resources

The mass-balanced Ecopath model is used as the starting point for dynamic Ecospace simulations, which are structured on biomass pools, linked by trophic fluxes, that migrate among a grid of cells. An intermediate stage sets up a non-spatial simulation of the biomass pools Ecosim, which takes account of predator-prey interactions, recruitment and trophic ontogeny, and changes in diet with relative abundance. To mimic a more realistic trophic flow control in the ecosystem, the predator-prey vulnerability parameter of each functional group was adjusted to be proportional to their Ecopath estimated trophic level (Cheung et al., 2001, in prep.). Trophic ontogeny parameters were obtained from the literature. We also represented a non-feeding interaction (i.e., mediation) of protection effects (Christensen et al., 2000), between corals and reef-associated groups and between living bottom structure and its associated fish. Our simulated fisheries experienced a 3% increase in catching power per year, an average figure from fleet changes between 1950 and 1996 (Cheung 2001). Further details of Ecosim parameters are given in Buchary et al. (2001).

In Ecospace, movements are driven by relative foraging success, avoidance of predation, and intrinsic dispersal rates linked to specified habitats. Fishers in the model act to maximise their catches (or the value of their catch) according to the 'gravity' model (Hilborn and Walters 1987; Caddy 1975), since most evidence suggest that this closely mimics how fishers behave (Walters et al. 1999). Simulations are made tractable for PC-based software using

innovative integration routines that take account of different time scales (Walters et al. 1998).

Our Ecospace model for Hong Kong mapped four habitat types: natural reefs, human-made reefs, non-reef areas with marine mammals and non-reef areas without marine mammals (see Figure 2). Higher primary productivity (20%) in the Pearl River estuary was also simulated. Robust default parameters for dispersal, foraging and predator avoidance by habitat, based on life histories, are built into the Ecospace software (Walters et al 1998). We adjusted these values for strongly reef-associated groups such as the reef fish. According to the scenario, each of the seven fishery sectors was set to fish in defined habitats delineated on the map.

Baseline simulations, with no areas protected from the fishery, suggested that several functional ecosystem groups become extinct after a period of 10-15 years. Accordingly, for comparison among scenarios, Ecospace simulations were carried out over 25 years. Each scenario was initialized using the 'status quo' map, which was replaced by map of the scenario to be investigated after two time steps (half a simulated year) (C. Walters, pers. comm.).

Scenarios for AR/MPA Design

AR/MPA complexes following the principles of design reported in Pitcher et al. (2000) were investigated in a series of Ecospace scenarios.

The vast majority of work on protected areas agrees that the single most important factor, determining rebuilding of resource biomass, and any enhancement of fishery catches, is size relative to the total area used by the resource (see Guénette et al. 1998). Hence this is the first factor we investigated with the Hong Kong Ecospace simulations. Single no-take ARs were set up in the model with ten sizes ranging from 0.2% to 64% of the total area .

Secondly, biogeographic theory suggests that, for a given amount of reef or protected area, species survival will be greater when maximizing area in relation to perimeter (Boecklen 1997; Hart and Horowitz 1991; Bohnsack 1991; Soulé et al. 1992). This means that, in general, taking purely geographic factors into account, one reef should be more effective than splitting the same amount of reef into two or more. However, the statistical needs of replication are required to maximize the discriminating power of monitoring. Moreover, replication also acts as a hedge against local accidents. Protected corridors (Gilbert et al. 1998) joining pairs of reef can aid initial colonization,

rebuilding after accidents and facilitate the foraging movements of large mobile reef predators. So, taking trophic, colonizing and statistical factors into account, several reefs may be better than one. A third set of factors affecting AR/MPA complex design is social. It has been suggested that to encourage compliance with regulations, a buy-in to the AR/MPA scheme and self-enforcement, some reefs might be fished, in a regulated fashion by sectors of the fishing industry (Pitcher et al. 1999; Sumaila et al. 2000, Beaumont 1997).

Accordingly, we have designed a series of Ecospace scenarios to investigate the trade-offs among these design factors. For a given amount of artificial reef embedded in a Hong Kong-like marine area, scenarios were designed to investigate single, double and triple ARs within MPA buffer zones that provide protected corridors of non-reef habitat between reefs. In addition, a scenario examined the impact of allowing one of three ARs in the AR/MPA system to be fished by the small-scale fishery (Figure 1).

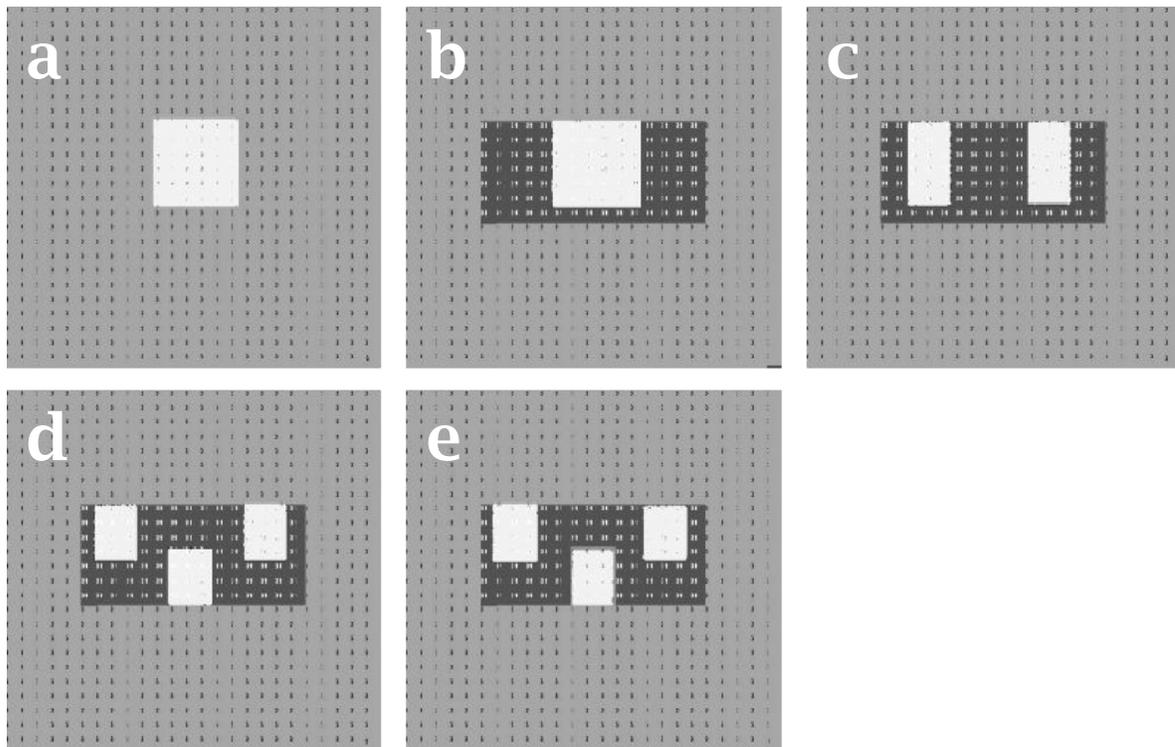


Figure 1. Map scenarios used to investigate alternative designs of MPA/AR complexes. Light areas represent human-made reefs (ARs); dark areas are surrounding no-take zones. Five scenarios are shown with with 36 cells of AR: a, with no protection; b, c, and d with one, two and three ARs inside a 105 cell no-take MPA; e, bottom right with one fishable 12-cell AR and two 12 cell ARs inside a 93 cell MPA). For details see text.

Hong Kong scenarios

The Hong Kong map used in the spatial simulations is drawn on a on grid of 25 by 25 approx 4km squares, and is based on Hong Kong survey data used to plan the deployment sites for AR/MPA complexes (ERM 1997, 1999). For the ecosystem simulations reported in this paper (Figure 2), 351 cells represent the marine ecosystem, 10 cells represent one of the planned deployments of artificial reefs, 2 cells represent

remaining natural reefs in Hong Kong (Figure 2, top), and 59 cells in 9 areas (16% of the area) represent the approximate locations of planned no-take areas (Figure 2, bottom) (Wilson and Cook 1998). For the purposes of the simulations reported here, all of these areas were assumed closed to all fishing, whereas in practice some fishery sectors will be allowed in three different types of protected area (see Buchary et al. 2001 for full details).

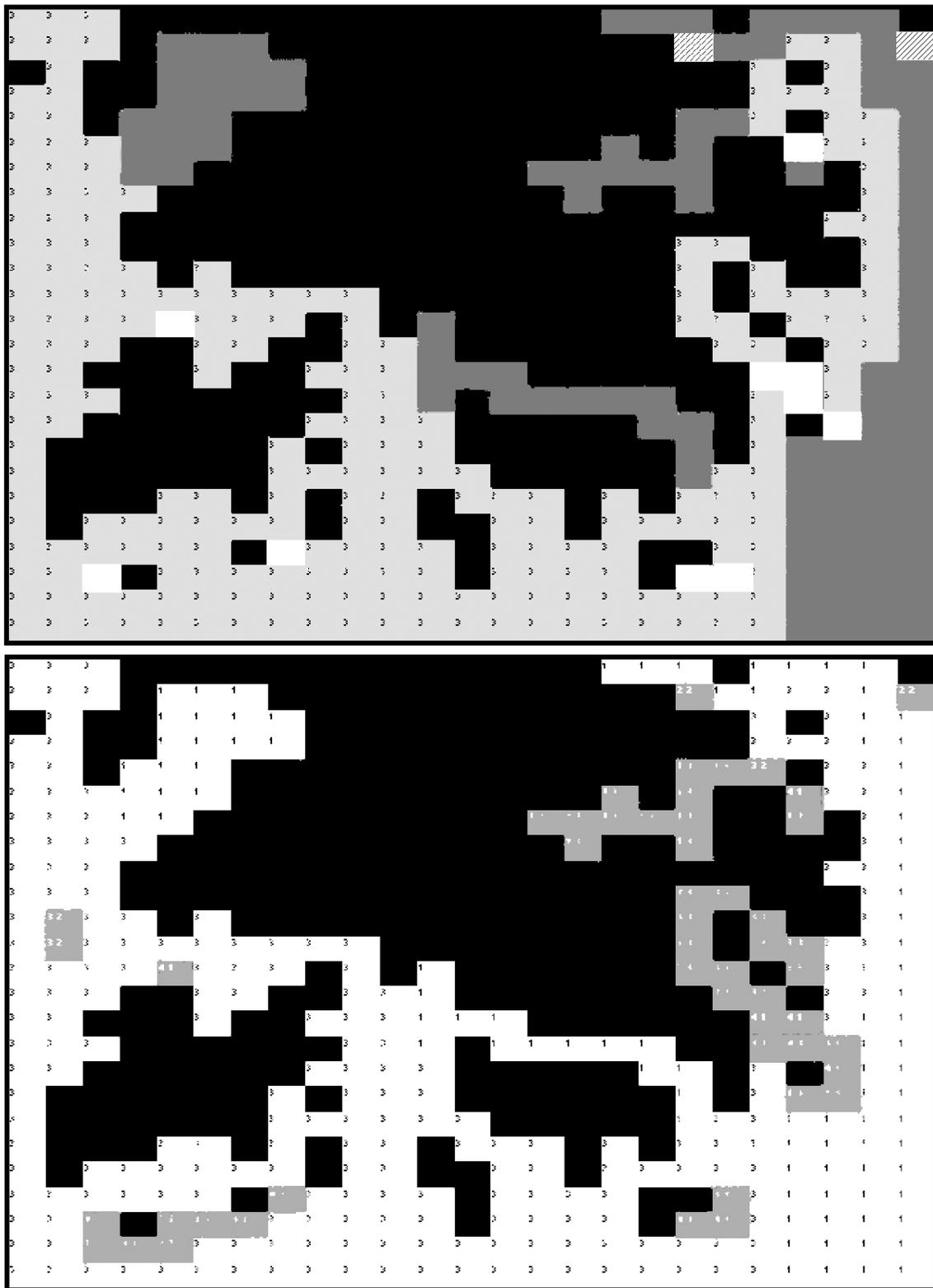


Figure 2. Four-km grid maps of Hong Kong used in the spatial ecosystem simulations. Upper map: Habitats. Black area is Hong Kong land areas; white areas are proposed deployment of artificial reefs; hatched areas are natural reef; light grey: marine mammal habitat; dark grey other marine areas. Lower map: grey shows no-take protected areas. Simplified from planned implementation designs 2001 (see Buchary et al. 2001). Note: small numbers, not legible here, indicate habitats and no-take zones in the Ecospace interface.

Five scenarios were compared using the same map described above. In the baseline scenario, ARs were deployed but no fishery protection was provided. In the second scenario, only the 12 reef cells were no-take MPAs. In the third scenario similar to one of the actual planned deployments for Hong Kong, no-take areas surrounded the ARs (and another area near the airport). Scenario four is the same as scenario three with the addition of a ban on all trawling, leaving only three fishery sectors in operation (small scale miscellaneous, licensed P4/7 boats and purse seiners). Scenario 5 was the same as scenario three with the addition of a control of fishing effort to the current level, instead of increasing each year.

Economic valuation of the ecological outcomes under the above five scenarios has been carried out. Predicted catches under the five scenarios are captured and valued economically by applying appropriate price and cost data (see Table 5). In this way, market values are computed to help us determine the economic impacts of the different policy options.

Results

Depletion under no protection

Baseline simulations of the Hong Kong ecosystem and its fishery with no protected areas, even with human-made reefs (ARs but no MPAs), suggest a future with even more depletion. In a 25 year simulation, 6 of the 37 Ecopath groups were reduced almost less than 1.5% of their initial biomass to zero by year 10, and 17 groups, or 46%, were depleted to this level by year 25. One group became extinct after ten years, and eleven groups after 25 years. Groups representing low trophic level organisms increase in biomass at the expense of larger more valuable resources. Figure 3 illustrates changes in catch and biomass for nine important groups of resource organisms, pooled from 15 groups in the simulation model. In general, it is clear that the biomass and catch of valuable demersal and pelagic fish is drastically reduced. Catches of small pelagic fish increase after ten simulated years, but even they are reduced after 25 years. Prawn, crustacean and jellyfish biomasses increase up to 60%, while prawn and crustacean catches double, a worrying prediction of fishing down the food web while economically viable fisheries continue. The picture depicted in Figure 3 is reproduced exactly when economic rents are plotted. This is because for the same fish group we have made an assumption of constant price and cost over time.

Size of AR/MPA

Figure 4 shows the biomass and catch of reef fish from simulations in which the size of the AR/MPA complex was varied from 0.2% to 64% of the total area. As might be expected, all biomasses exhibit a progressive increase as the size of the protected area increases. The model suggests that with a very large AR/MPA, large reef fish biomass after 25 years can approach 3 tonnes per km² in Hong Kong waters, with medium and small reef fish biomass approaching 100 tonnes per km².

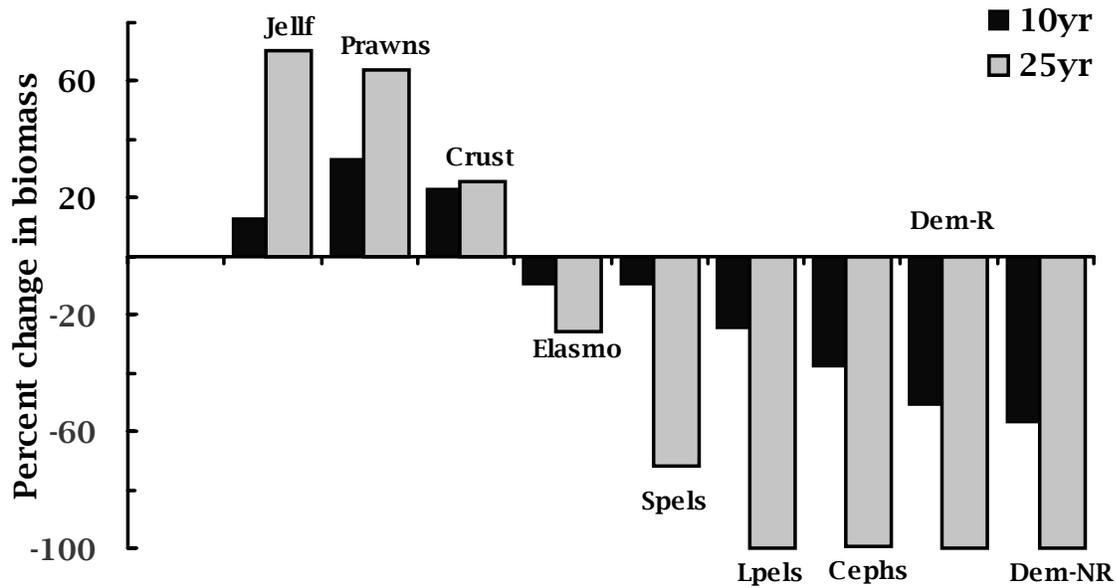
Catches, however, present a different story. With a small AR/MPA catches of the valuable large reef fish immediately increase, but then fall gradually. The highest catches of large reef fish can be expected from something in the region of 10%. Catches of medium and small reef fish, however, rise monotonically from small to large AR/MPAs so total reef catch will increase with MPA size. The result probably comes from a trophic cascade within the protected areas as large reef fish increase in numbers.

Comparison of AR/MPA design options

Figure 5 illustrates percentage changes in reef fish biomass and catch after 25 years of deployment of the AR/MPA system in a Hong Kong-like marine ecosystem. Results for the design scenarios described above are shown. The baseline scenario for comparisons was ARs of the same size deployed with no protection, and hence fished in the model by the two small scale fishing sectors, P4/7 and miscellaneous. No-take MPAs bring significant increases in both biomass and catch of medium and large reef fish, while catch of small reef fish is about the same.

Compared to the same area in one no-take AR, splitting the AR area into two or three equal elements increases the biomass and catch of medium and large reef fish (Figure 4) although biomass of small fish decreases, probably due to predation. Catches of large reef fish are dramatically larger with 3 ARs than with 2. Hence, the model suggests that the benefits of replication and protected corridors can accompany gains to catch and biomass of reef fish. Figure 4 shows that the small scale fishery sectors gain most.

Base case changes in HK biomass



Base case changes in HK fishery catches

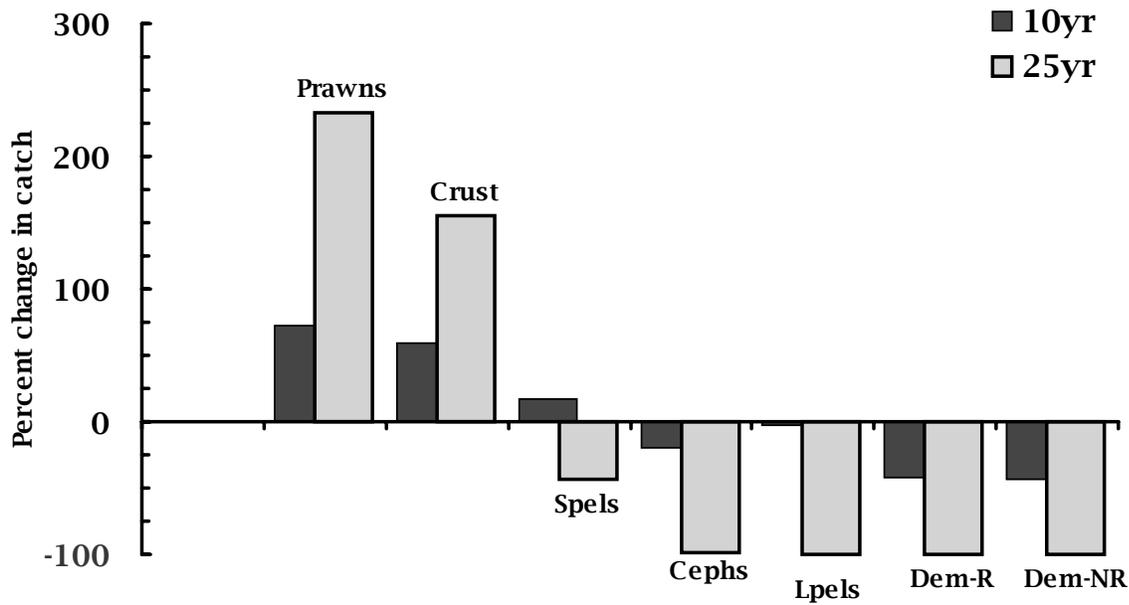


Figure 3. Changes in biomass (top), and catch (bottom), as forecast by Ecosim for nine resource groups (pooled from 15 functional model groups) in Hong Kong, under a scenario with no changes to the existing fishery regime and no fishery protection for deployed human-made reefs. Dark bars: 10 year simulation; light bars: 25 year simulation. Jellf = jellyfish; Crust = benthic crustaceans; Prawns = non-reef associated penaeid prawns; Elasmos = large and small sharks, rays and skates; Spels = small pelagic fish; Lpels = adult and juvenile large pelagic fish; Cephs = non-reef associated cephalopods; Dem-NR = non-reef associated juvenile and adult large, and medium demersal fish; Dem-R = reef associated juvenile and adult large, and medium demersal fish.

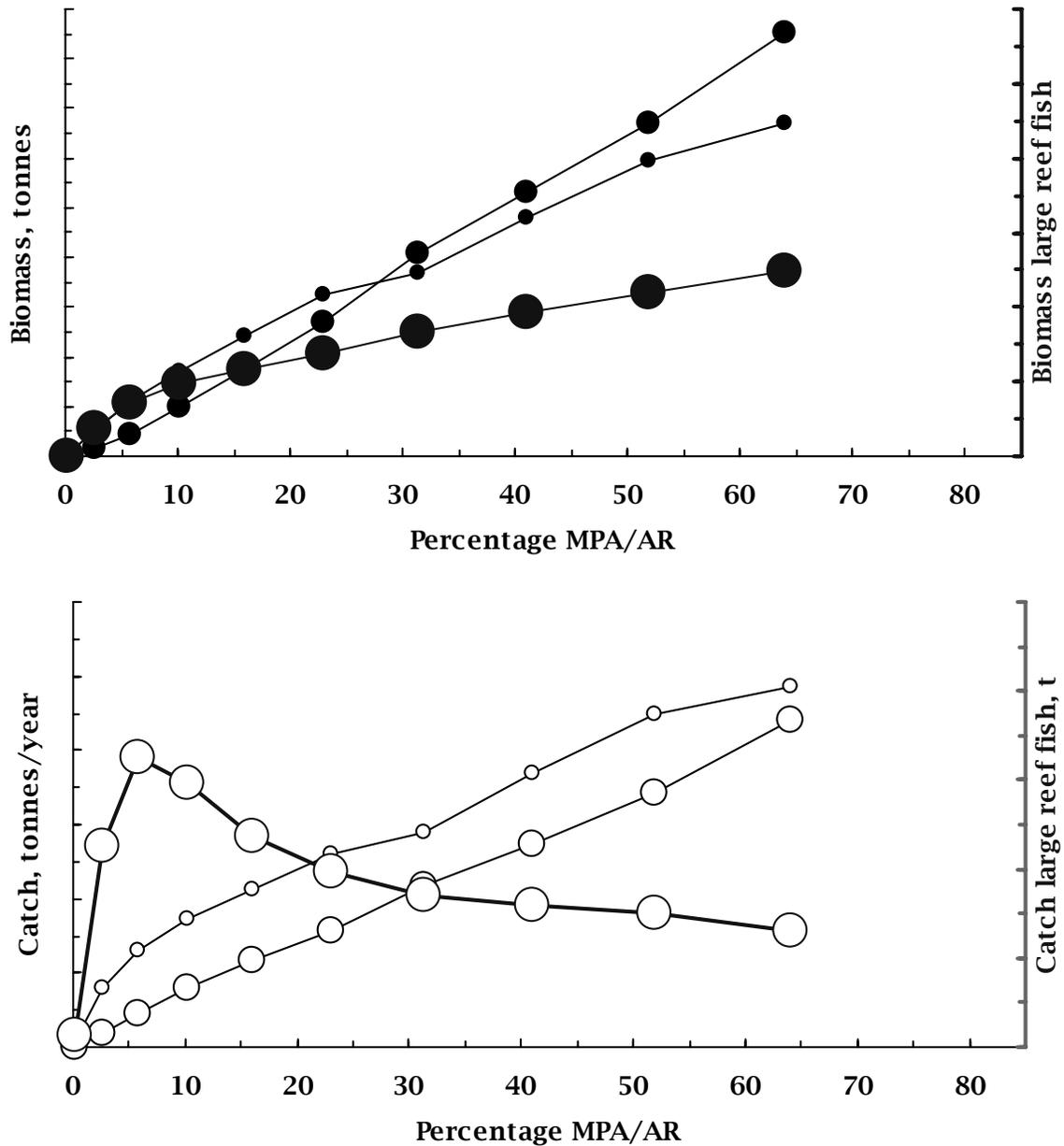
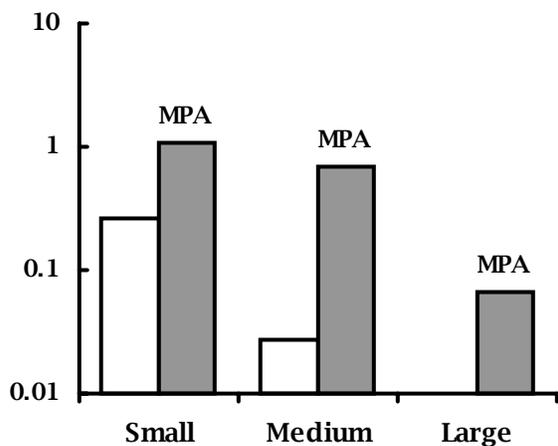
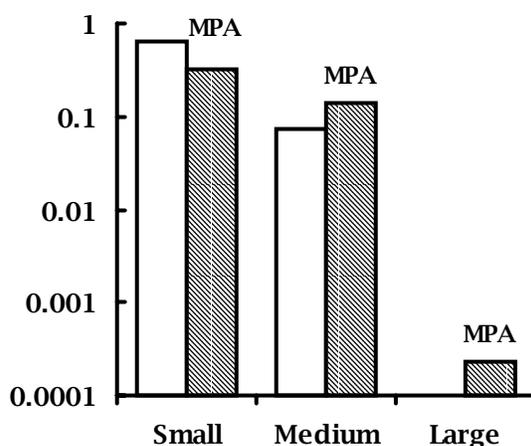


Figure 4. Biomass of three size categories of reef fish (top), and catch (bottom), as forecast by Ecospace simulations for the Hong Kong ecosystem over ten relative sizes of AR/MPA, as indicated on the x-axis. Three size class of demersal reef fish are shown: large circles = large fish with $L_{\infty} > 50\text{cm}$ (plotted on right-hand Y-axis); medium circles = medium fish with $L_{\infty} > 25$ and $< 50\text{cm}$; small circles = small fish with $L_{\infty} < 25\text{cm}$.

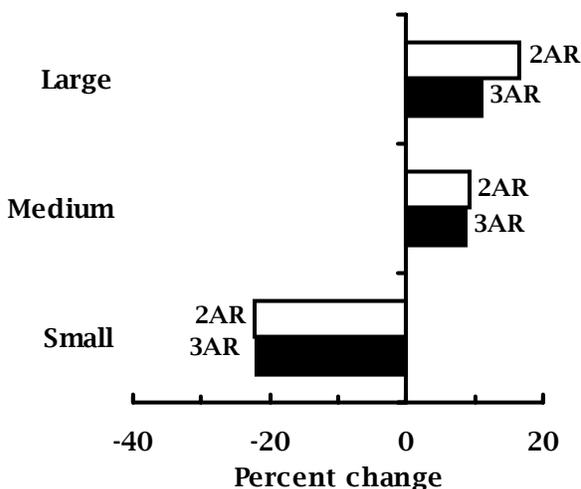
Reef fish biomass with MPA



Reef fish catch with MPA



Reef fish biomass change



Reef fish catch change

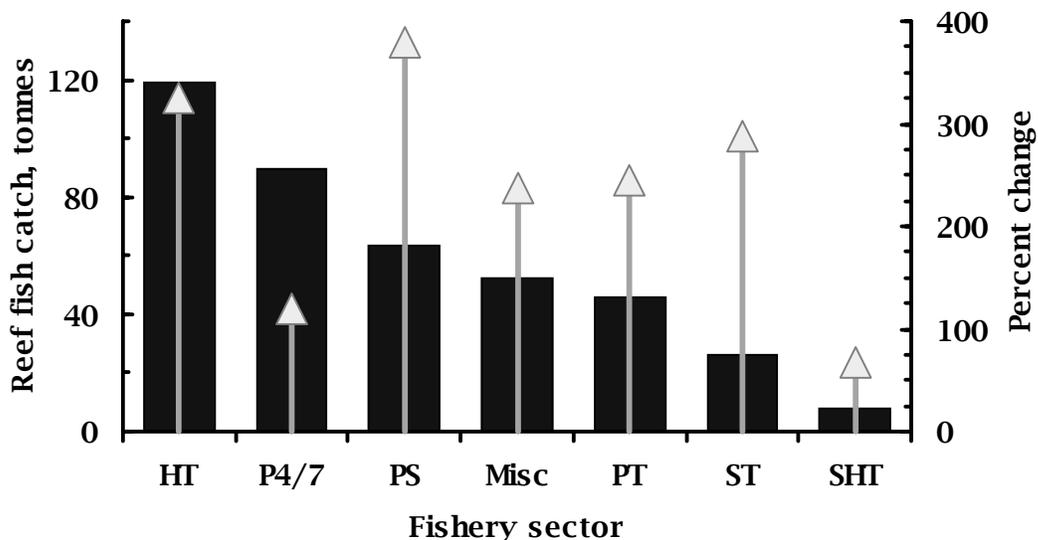
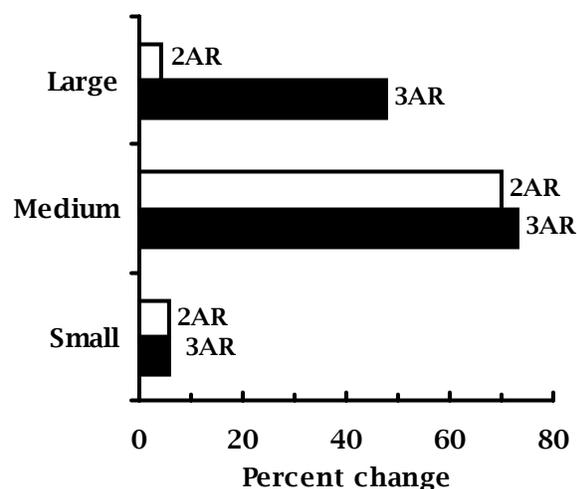


Figure 5. A (top). Reef fish biomass (left) and catch (right) with AR and AR-MPA. B (centre). Percentage changes in reef fish biomass (left) and catch (right) from 1AR to 3 ARs of the same area inside an MPA. C (left bottom). Percentage changes in reef fish catch and biomass comparing 3ARs inside MPA with a scenario in which one AR is fishable. D (bottom). Bars show catches of large and medium reef fish catch by sector for the 3AR scenario. Arrows (right hand scale) show percentage changes from catches in the unprotected 1AR scenario.

Figure 6 illustrates the cost of having a fishable reef. When one of three ARs is fished by the two small-scale sectors, the biomass of large and medium reef fish is reduced by 30-40% compared to the unfished 3-AR/MPA scenario. Catches of large fish follow suit, but catches of medium fish increase slightly. Small reef fish catch increases

greatly. Figure 6 also illustrates approximately two-fold gains in catch of large and medium reef fish made by the two small-scale fishery sectors. Evidently a trade-off policy that sacrifices some ARs to fishing may well be worth the increased risk if it brings greater compliance and support for the scheme from the small-scale sector, who tend to live adjacent to the resource.

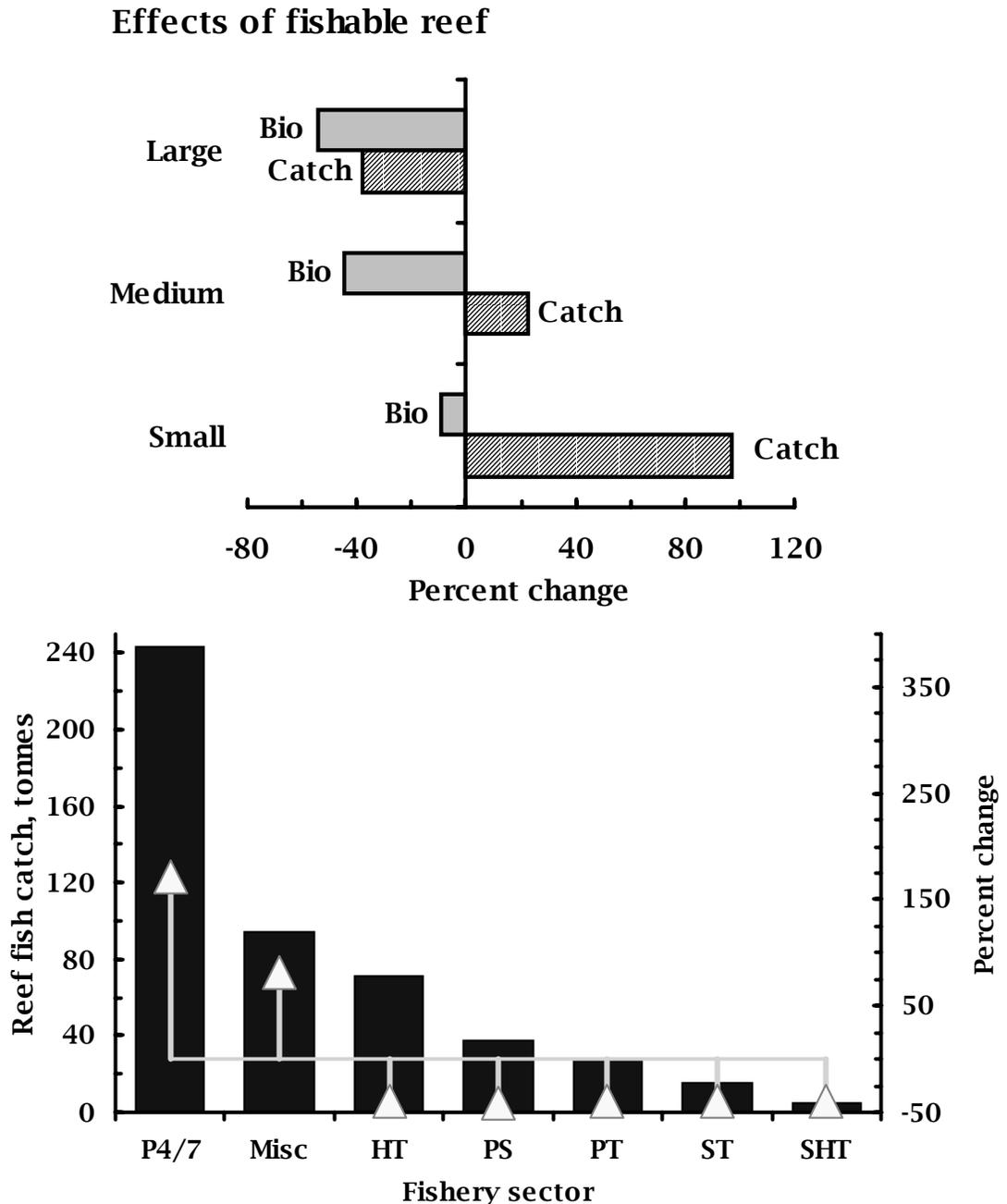


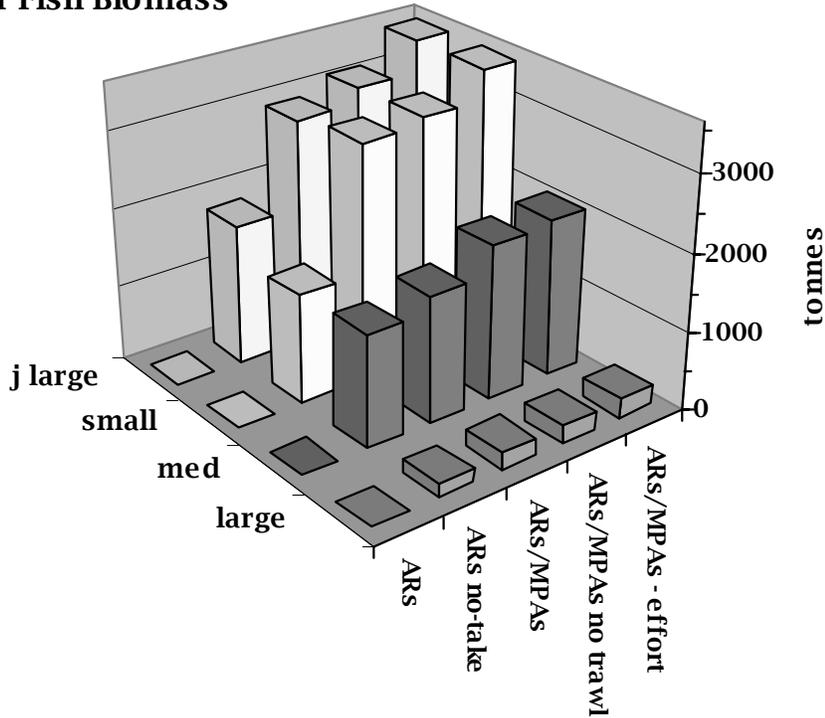
Figure 6. Effects of a fishable reef in the 3AR design. Top: percentage change in the catch and biomass of large, medium and small reef fish. Bottom: Catch by fishery sector in the fishable reef scenario (dark bars), and percentage change in catch compared to the 3Ar/MPA scenario (arrows).

Forecast effects of deployment of AR/MPAs in Hong Kong

Simulated annual catch and biomass after 25 years of four functional groups of reef fish, extracted from the full ecosystem simulation results, for the five scenarios are compared in Figure 7. First, it is clear that no protection for the

reefs results in very low reef fish biomass and almost zero catch. Significant gains in biomass of all reef fish groups are seen when ARs are no-take, more when surrounded by no-take MPAs, and more again with a ban on trawling or with fishing effort control.

Reef Fish Biomass



Reef Fish Catch

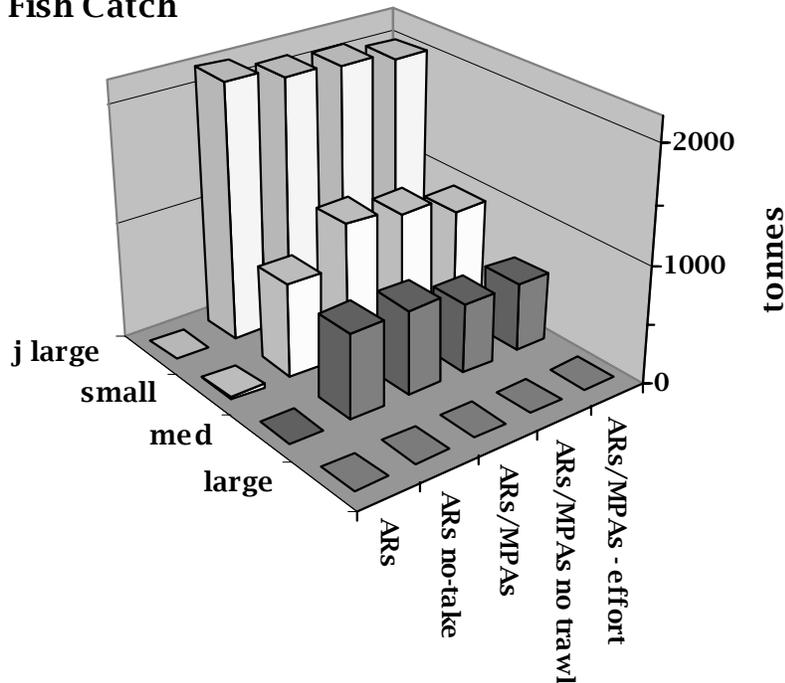


Figure 7. Simulated Hong Kong reef fish biomass and catch after 25 years under five scenarios. The four functional groups used in the model are shown .

The highest catches of small, medium and adult large reef fish are in scenario 3, the closest to the actual deployment, while the highest catch of juvenile large fish is in scenario 2 when only the reefs themselves are protected. Prawns and cephalopods are also caught on reefs, and the highest catch of these invertebrates is in the

unprotected scenario 1 (Figure 8), whereas the highest total catch of reef fish is in scenario 3 with no-take MPAs. But the differences among all except scenario 1 are small, and it is therefore clear that catch of reef fish alone is not sufficient to choose among the alternative scenarios.

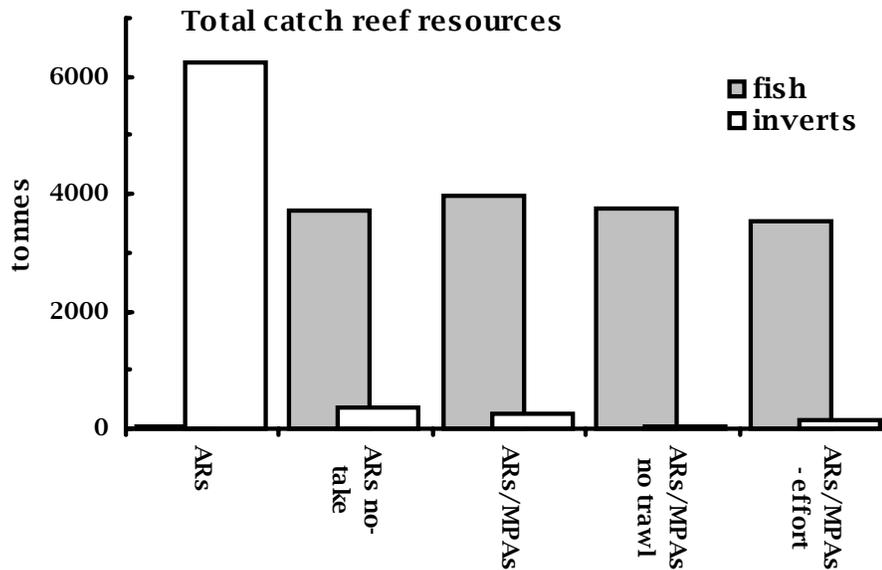


Figure 8. Forecast total catch of Hong Kong reef resources after 25 year spatial ecosystem simulation under five scenarios. Fish include small, medium, large and juvenile larger reef fish. Invertebrates include reef-associated prawns and cephalopods.

Figure 9a shows the catch in year 25 for each of the seven fishery sectors in Hong Kong under each of the five scenarios. In terms of catch, in general the beneficiaries of the AR and MPA deployment are the two small-scale fishery sectors and the purse seines. However, most trawlers do reasonably well under scenarios 2 and 3. Although shrimp trawlers have their highest catches by far with no controls, their next best catches are under scenarios 2 and 3. Figure 9b was plotted for the economic rents to be derived by the various sectors. The general patterns are similar but there are some differences. For instance, the ST sector catches more fish under scenario 3 (ARs/MPAs), but they would economically prefer scenario 5 (ARs/MPAs – effort) because they make higher economic rent.

A simple non-economic way of determining the best policy option among the competing fishery sectors is to assign ranks to catches within each gear sector across the scenarios. Table 3 shows that when we do this, the sum of the ranks places scenario 3 clearly as the best, followed by scenario 5 (effort control) and no-take ARS, with no trawling in third place. Despite large catches for the prawn trawlers, scenario 1 is so poor for the

other sectors that it lies in last place. How does the non-economic approach compare with the results from an economic evaluation? Based on the total current value of economic rent under the different scenarios, we determine that scenario 4 (no-take ARS, with no trawling) does best, followed by scenario 5 (effort control), with the third place taken by scenario 1.

From a conservation perspective, biomass of the fish resources and of non-exploited components of the marine ecosystem should be considered in policy choice. Accordingly Figures 10 illustrates the biomass responses of nine categories of organisms (pooled from 25 functional groups in the ecosystem simulation model).

Jelly fish, organisms of considerable concern (Pitcher 2001), are highest in depleted scenarios (scenario 1), and lowest with effort control or the cessation of trawling (scenario 5). Prawns, valuable resources, also have the highest biomass with no controls. Reef fish resources highest biomass with effort control or no trawling, but biomass under scenario 3 is within 15% of these values, while they are almost completely eliminated under scenario 1. Pelagic fish do best

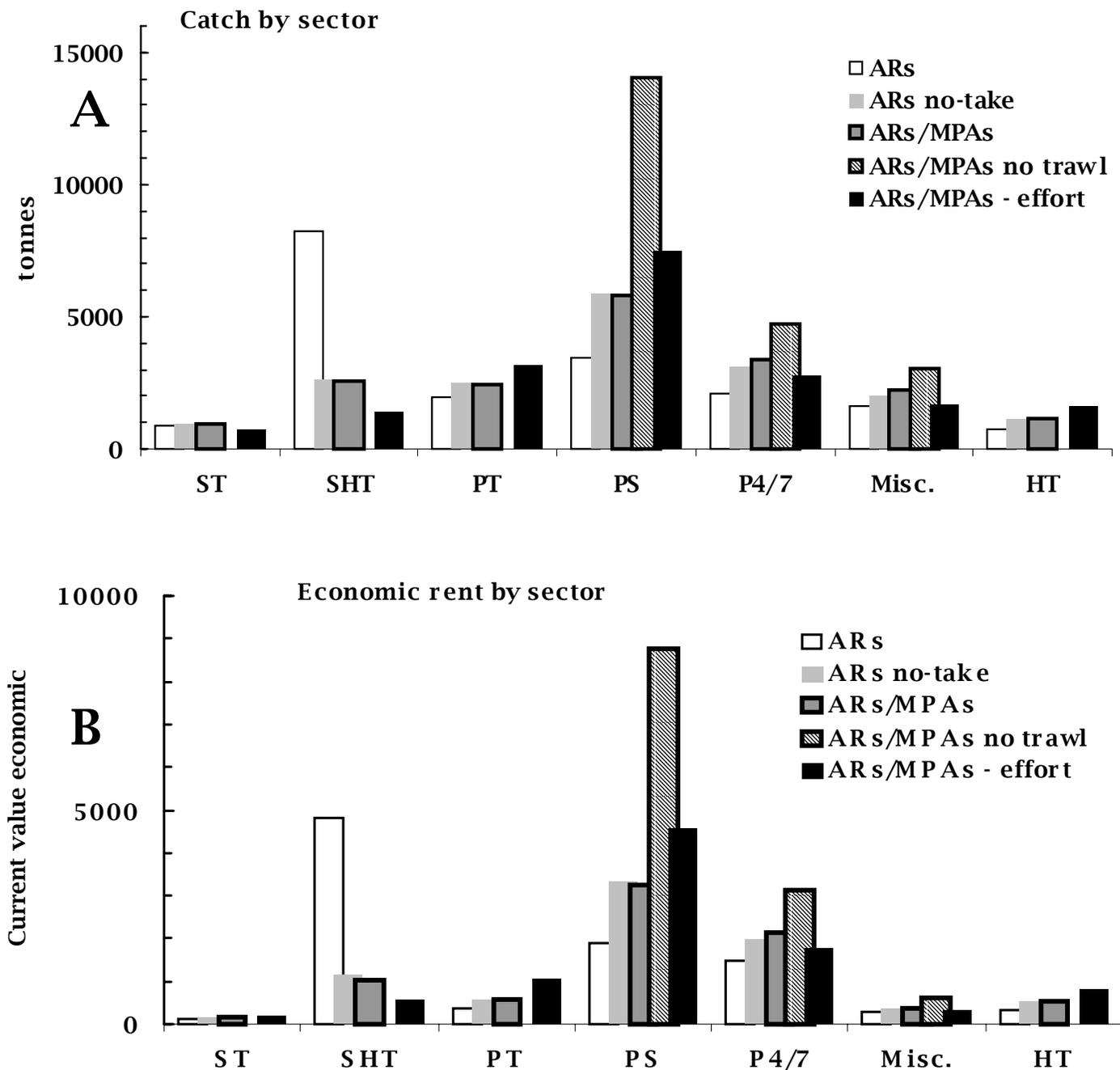


Figure 9. A. Forecast catches of seven gear sectors of Hong Kong fisheries under five scenarios (shadings as shown in key) after a 25 year simulation of the Hong Kong marine ecosystem. B. Calculated economic rent to each sector.

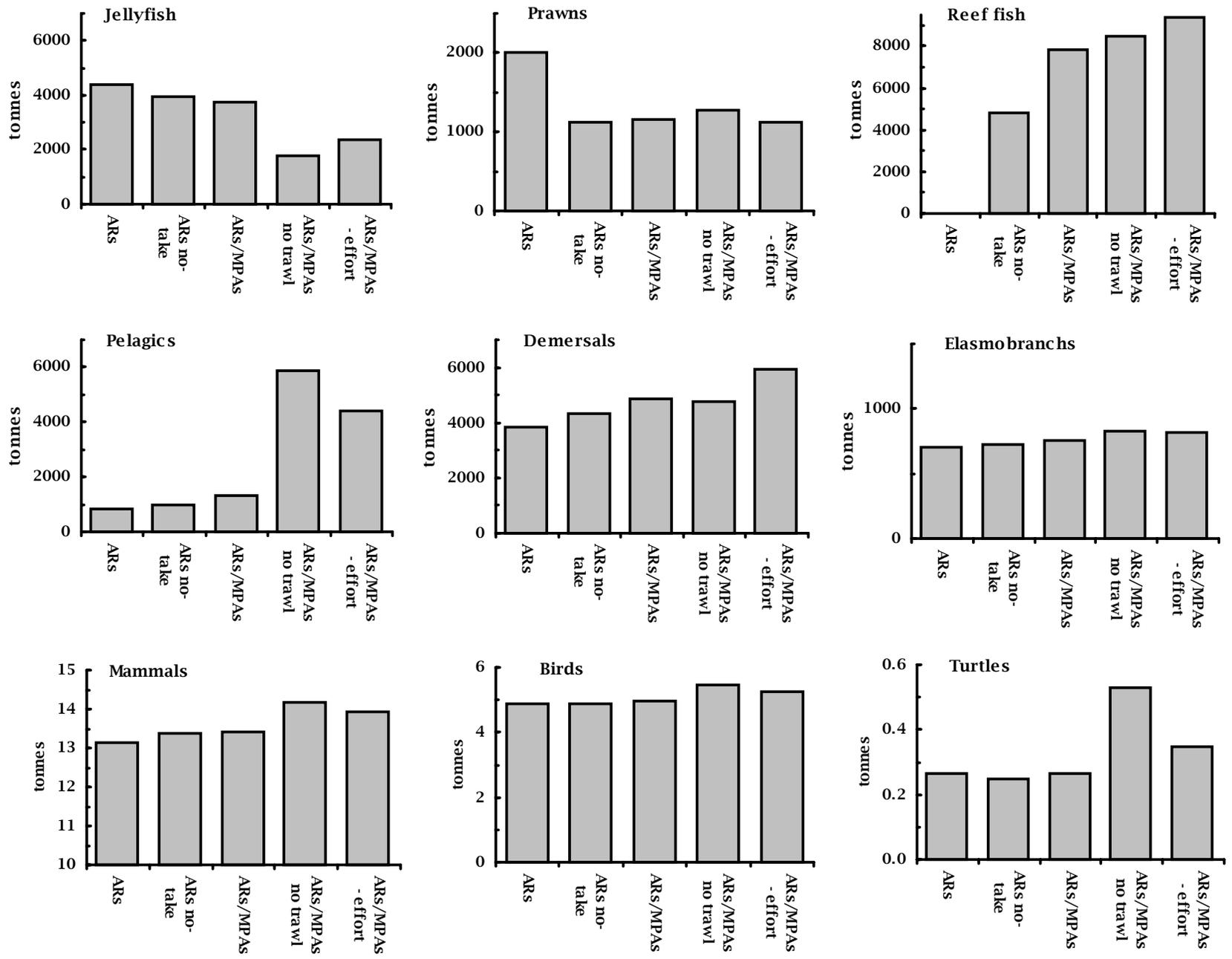


Figure 10. Biomass of nine selected components of the Hong Kong ecosystem, pooled from 25 model functional groups, after a 25 year simulation under 5 scenarios.

under the no-trawling and effort control scenarios, probably because most of Hong Kong's waters are less than 20m deep and many pelagic fish are caught in the trawls. Demersal fish as a group do quite well under all scenarios, although this conceals a shift from large to small species with depletion. Peak demersal biomass is with effort control of scenario 5, followed closely by the AR/MPA scenario 3. Elasmobranchs as a group also show few differences across the scenarios, but large sharks only do well under lower fishing scenarios 3, 4 and 5. Marine mammals and bird show a similar pattern, with biomasses about 10% higher under the no trawling scenario 4. Turtles, on the other hand, show about 40% increase with the cessation of trawling under scenario 4.

Figure 10 shows the biomass responses of groups of conservation concern, but we need an objective way to conflate all these factors when trying to choose the best policy. Using the same type of ranking analysis as for the fishery sectors above, Table 4 shows that the AR/MPA no-trawl option, scenario 4, ranks highest, closely followed by scenario 5 (AR/MPA with effort control). The last desirable scenario is 1 (no controls), and then are large gaps in the total scores to scenario 2 (ARs only no-take) and scenario 3 (AR/MPA).

Discussion

The results illustrate the use of this new spatial ecosystem modelling tool, Ecospace, to compare policy options related to artificial reef complex design and deployment, no-take areas and buffer zones, and the regulation of a multi-species, multi-sector fishery. Forecasts comprise changes in biomass, catches and economic rent by resource group and fishery sector. Simulations of the various scenarios may be performed over a number of years, and long and short-term benefits evaluated.

The model paints an alarming picture of massive depletion and local extinction of species if nothing is done to control fishing on the deployed human-made reefs. It is instructive to note that that this doomsday scenario has considerable fishery benefits as most sectors catch alternative high turn-over species and a massive prawn trawl fishery thrives.

Consideration of reef fish resources alone shows that, although catches of large valuable fish are highest under scenario 3, there are only small differences in total catch of reef fish among the four no-take scenarios. If we wish to attempt to

take the broader concerns of all the sectors of the fishing industry into account, analysis of the catch suggests that existing plans may be a reasonable compromise among the seven Hong Kong fishery gear sectors.

In most stock assessment or survey work it is not easy to make forecasts for all of the components of marine ecosystems. For the first time, this ecosystem modelling technique enables the responses of animals, fish, turtles and birds of conservation concern to various policy scenarios to be quantified alongside extractive resources. Hence, when biomass conservation is considered, policy options that include effort control or a trawl ban begin to look more attractive for the Hong Kong marine ecosystem.

Another attractive feature of the modelling system is the ability to examine and evaluate trade-offs, in this case between biomass recovery, fishery catch and economic rent, for example by encouraging compliance with no-take MPAs through a greater buy-in and learning by fishers and the public. Sacrificing some artificial reefs to fishing by the numerous small-scale sector may be worth it if biomass recovery is not prejudiced too much. Models of this kind allows this trade-off to be quantified.

The principal question, as with any simulation modelling, is of course, what confidence can we have in the model forecasts? Ultimately, the only answer to this will come from comparison with actual biomass and catch trajectories from protected AR deployments. To date, the new modelling system has been used in very few situations where the simulations can be challenged by actual data and it would clearly be unwise to put great reliance on the actual numerical results. However, Walters et al. (1998) suggest that comparisons among scenarios should be robust enough to at least screen a number of policy options.

Our model in its present state does not take account of uncertainty. There are a large number of estimation errors in the parameters for the basic Ecopath mass-balance ecosystem model. These may be addressed using Monte Carlo simulation, as represented by a facility ('ecoranger' – Christensen and Pauly 1992) in the Ecopath software that outputs a subset of balanced models from a large number of possibilities of random samples from prior error distributions on the input parameters. These uncertainties could then translate into a set of spatial simulations each based on one of the balanced ecosystem models. In practice, the

process error in simulating the natural ecosystems is likely to be far larger than estimation errors, and, at present, we are more likely to be able to deal with this robustly through scenario comparisons.

The problems of parameter estimation for Ecospace are less well understood, although it appears that results are relatively insensitive to small changes to parameters in the dispersal sub-model. In our work, many heuristic improvements to parameter values have derived from iterated runs of the model using and comparisons with actual ecosystem biomasses and fishery catches from the Hong Kong survey and fishery assessments. Improvements to parameter values can come in future from monitoring of the Hong Kong human-made reef system as it is deployed.

In the long term, large positive or negative changes in ecosystem components may be so great that major structural changes to the ecosystem are likely. For example sessile vegetation like kelp beds or mangroves or benthic organisms like sponges can provide (increase in biomass) or remove (loss of biomass) physical cover from predators for juveniles of commercially important species. Similar effects on cover and structure can occur through selective predation and some predator species can act as keystone species in this way (e.g. sea otters). Changes like this have been mimicked in our model through the mediation interface, but precise parameter values would again have to await monitoring of real system recovery. One unrealistic assumption we have had to make is that human-made reefs act as though they were natural reefs from the day of deployment. In present version of Ecospace the defined habitats do not change with time, whereas with human-made reefs and some other habitats, including this feature would be helpful

Since the ecosystem model is grounded in trophic interactions and movements, it is not surprising that it is quite good at showing trophic cascades. We found a number of scenarios in which we were initially surprised by large forecast gains to the fisheries when the reef and non-reef portions of the MPA were separated in space. This was evidently caused by the development of such a strong cascade within the MPA that large fish significantly reduced the biomass of their prey, and hence reduced catches of these resources by the fishery. When reef MPA and non-reef MPA were separated, fishing at the edge of the MPA sucked large fish out from the edge of the protected areas (see Walters et al. 1998), thus reducing the

severity of the cascade and hence increasing the combined fishery catch. In effect, the trophic cascade expropriated resources that might otherwise be caught in the fishery.

It is important to realize that the spatial results generated by the Ecospace model are average responses, and are not intended to mimic closely actual transitional dynamics and migrations in small (a few km) scales of space and time. Nor is the mapped biomass dynamics intended to mimic closely actual places in the real world, especially on as small a scale as the Hong Kong map. Moreover, in the real world there are far too many fractal and chaotic process affecting fish responses at a particular small-scale place and time to be forecast by any modelling system.

There are two general implications of this work for the Hong Kong marine ecosystem.

First, it is clear that, in a system so depleted as Hong Kong, any of these measures will provide some help in the form of biomass recovery and increased future catches and economic rent from valuable reef resources. Even unprotected ARs delay the collapse of resources and a dismal prospect of 'fishing down the food web' that will surely occur if no action is taken. Model results suggest, however, that protection of reef fish biomass recovery through no-take MPAs vastly increases the benefits and, for reasonably-sized protected areas, should avert ultimate resource collapse.

Secondly, our results show the value of enhancing compliance with fishery regulations and closed areas through careful design of the ARs and their associated MPAs. The trade-offs necessary to do this may be quantified using this approach.

Previous non-spatial ecosystem simulation of this system (Pitcher et al. 2000), and some preliminary spatial work with a much simpler ecosystem model (Pitcher et al. 2001) provided broadly similar, but much less specific and detailed results. So, in conclusion, the new modelling tool appears to help evaluate and design policy scenarios for artificial reefs and their associated protected areas.

Acknowledgements

We gratefully acknowledge permission to use data and analyses belonging to the Agriculture and Fisheries Department of the Hong Kong Special Administrative Region Government, and in particular helpful discussions with Keith Wilson and Albert Leung. Much of the survey and analysis work in Hong Kong was carried out and reported by ERM (Hong Kong) Ltd., and we acknowledge their help, especially Robin Kennish and Shelley Clark. The original Ecopath model for Hong Kong was built by Reg Watson and Tony Courtney with help from Daniel Pauly. Sylvie Guenette drew up the reef index analysis, with help from Dave Cook, Keith Wilson and Nick Polunin. Reef design scenarios were discussed with Robin Kennish, Nigel Haggan and Keith Wilson. We are most grateful to Villy Christensen and Carl Walters at the Fisheries Centre for advice in setting up the Ecospace simulations. The work reported in this paper was supported by the Fisheries Centre, while a related but wider range of simulated scenarios were sponsored by the AFCD of Hong Kong.

References

- Beaumont, J. (1997). Community participation in the establishment and management of marine protected areas: a review of selected international experience. *S. Afr. J. Mar. Sci.* 18: 333-340.
- Boecklen, W. J. (1997). Nestedness, biogeographic theory and the design of nature reserves. *Oecologia* 112: 123-142.
- Bohnsack, J.A. (1991). Habitat Diversity and the design of artificial reefs. Pages 412-426 in Bell, S.S., McCoy, E.D. and Mushinsky, H.R. (eds) *Habitat Structure: the physical arrangement of objects in space*. Chapman & Hall, London, UK, 437pp.
- Bohnsack, J.A. (1993). Marine reserves. They enhance fisheries, reduce conflicts, and protect resources. *Oceanus* 36: 63-71.
- Bohnsack, J.A. (1996). Marine reserves, zoning, and the future of fishery management. *Fisheries* 21 (9) : 14-16.
- Bohnsack, J.A., Ecklund, A-M. and Szimant, A.M. (1997). Artificial reef research: is there more than the attraction-production issue? *Fisheries* 22: 14-16.
- Bortone, S.A. (1998). Resolving the attraction-production dilemma in artificial reef research: some yeas and nays. *Fisheries* 23(3) 6-11.
- Buchary, E., Pitcher, T.J., Sumaila, U.R. and Haggan, N (2001). Spatial Simulations of Hong Kong's Marine Ecosystem: Ecological and Economic Forecasting of Marine Protected Areas with Artificial Reefs. Fisheries Centre Research Reports (in prep.).
- Caddy, J.F. (1975). Spatial model for an exploited shellfish population, and its application to the Georges Bank scallop fishery. *J. Fish. Res. Bd. Canada* 32: 1305-1328.
- Chen, W.Z., Zheng, Y.Z., Chen, Y.Q. and Mathews, C.P. (1997). An assessment of fishery yields from the East China Sea Ecosystem. *Marine Fisheries Review* 59(4) 1-7.
- Chong, C. K. (1984). The demersal fishery resources in Hong Kong waters. MRRD/WP/1/85. Agriculture and Fisheries Department, Hong Kong. 56p.
- Cheung, W.L. (2001). Changes in Hong Kong's Capture Fisheries during the 20th Century and Reconstruction of the Marine Ecosystem of Local Inshore Waters in the 1950s. M.Phil. Thesis. The University of Hong Kong, Hong Kong. 186 pp.
- Cheung, W.L., R. Watson, and T.J. Pitcher (2001). Policy Simulation of Fisheries on the Hong Kong Marine Ecosystem. In Cochrane, K. (ed) *FAO/UBC Fisheries Centre Workshop - The Use of Ecosystem Models to Investigate Multispecies Management Strategies for Capture Fisheries*. University of British Columbia, Canada. 14-20 July, 2000. Fisheries Centre Research Reports (in press).
- Christensen, V. and Pauly, D. (1992). The ECOPATH II - a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling* 61: 169-185.
- Christensen, V., C.J. Walters, and D. Pauly (2000). *Ecopath with Ecosim: A User's Guide*. Univ. of British Columbia, Fisheries Centre, Vancouver, Canada and ICLARM, Penang, Malaysia. 125p.
- Cook, D. C., Chan, A.L., Fok, K.C.C. and Wilson, K.D.P. (1997). A fisheries resource profile prior to artificial reef deployment in Hong Kong. In *PACON 97, Symposium on Resource Development - Environmental Issues and Sustainable Development of Coastal Waters, Hong Kong*.
- ERM Ltd (1997). *Artificial Reef Deployment Study: Technical Paper 2 - AR Deployment and Management Strategy*. ERM Ltd, Chatham Road, Kowloon, Hong Kong. 152 pp.
- ERM Ltd (1999). *Artificial Reef Deployment Study: Final Report*. ERM Ltd, Chatham Road, Kowloon, Hong Kong. 114 pp.
- Froese and D. Pauly (Editors). 1998. *FishBase 98: Concepts, Design and Data Sources*. ICLARM, Manila, 293 pp.
- Gilbert, F., Gonzalez, A. and Evans-Freke, I. (1998). Corridors maintain species richness in the fragmented landscapes of a microecosystem. *Proc. Roy Soc. (Lond.) B*: 265: 577-582
- Gomez, E.D. Deocadiz, E., Hungspreugs, M., Jothy, A.A., Kuan, Kwee Jee, Soegiarto, A. and Wu, R.S.S. (1990). State of the marine environment in the East Asian Seas Region. United Nations Environment Program, Regional Seas Reports and Studies 126: 69 pp.
- Guénette, S., Lauck, T. and Clark, C. (1998). Marine Reserves: from Beverton and Holt to the present. *Rev Fish Biol Fish.* 8(3): 251-272.
- Hart, D.D. and Horowitz, R.J. (1991). Habitat diversity and the species area relationship: alternative models and tests. Pages 47-68 in Bell, S.S., McCoy, E.D. and Mushinsky, H.R. (eds) *Habitat Structure: the physical arrangement of objects in space*. Chapman & Hall, London, UK, 437pp.
- Heinke, G.W. (1996). South China Sea: coastal ecosystem management. *Proceedings of Eco Informa '96*. Global Networks for Environmental Information, Environmental Research Institute of Michigan, Ann Arbor, USA, *Erim* 11: 805-812.
- Hilborn, R. and Walters, C.J. (1987). A general model for the simulation of stock and fleet dynamics in spatially heterogenous environments. *Can. J. Fish. Aquat. Sci.* 44: 1366-1369.
- Lai, L. W.C. And Yu, B.T. (1995). The Hong Kong solution to the overfishing problem: a study of the cultured fish industry in Hong Kong. *Manage. Decis. Econ.* 16(5) 525-535.
- Leung, A.W.Y. and Lee, C.K.C. (1987). On the application of catch and effort information from the Hong Kong trawl fishery, and associated problems. *IPFC Symp. on the Exploitation and Management of Marine Fishery Resources in Southeast Asia, Darwin (Australia)*. *FAO Reg. Off. for Asia and the Pacific, Bangkok Thailand* 1987. 10: 306-323.

- Palomares, M.L.D. and Pauly, D. (1998). Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. *Mar. Freshwater Res.* 49: 447-453.
- Pauly, D., Soriano-Bartz, M.L. and M.L.D. Palomares (1993). Improved construction, parametrization and interpretation of steady-state ecosystem models. Pages 1-13 in V. Christensen and D. Pauly (eds.) *Trophic models of aquatic ecosystems*. ICLARM Conf. Proc. 26.
- Pauly, D., Martosubroto, P. and J. Saeger (1996). The *Mutiara 4* surveys in the Java and Southern South China Seas, November 1974 to July 1976. Pages 47-54 in D. Pauly and P. Martosubroto (eds) *Baselines studies in biodiversity: the fish resources of western Indonesia*. ICLARM Studies and Reviews 23, Manila, 312pp.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. Jnr (1998a). Fishing down marine food webs. *Science* 279: 860-863.
- Pitcher T.J. (2001). Fisheries Managed to Rebuild Ecosystems: Reconstructing the Past to Salvage The Future. *Ecological Applications* 11(2): 601-617.
- Pitcher, T.J. and Seaman W. Jr. (2000). Petrarch's Principle: how protected human-made reefs can help the reconstruction of fisheries and marine ecosystems. *Fish and Fisheries* 1: 73-81.
- Pitcher, T.J., Buchary, A. and Hutton. T. (2001). Forecasting the Benefits of No-take Artificial Reefs Using Spatial Ecosystem Simulation. *ICES J. Mar. Sci.* (*in press*).
- Pitcher, T.J., Watson, R., Courtney, A.M., and Pauly D. (1998). Assessment of Hong Kong's Inshore Fishery Resources. *Fisheries Centre Research Reports* 6 (1): 1-168.
- Pitcher, T.J., Watson, R., Haggan, N., Guénette, S., Kennish, R., Sumaila, R., Cook, D., Wilson, K. and Leung, A. (2000). Marine Reserves and the Restoration of Fisheries and Marine Ecosystems in the South China Sea. *Bulletin of Marine Science* 66(3): 530-566.
- Polovina, J.J. (1989). Artificial reefs: nothing more than benthic fish aggregators. *CalCOFI Reports* 30: 32-37.
- Richards, J. (1985). *Fisheries Production in Hong Kong Waters*. Agriculture and Fisheries Department, Hong Kong Government. Manuscript Report. 9pp.
- Richards, J., Chong, C.K., Mak, P. and Leung, A.W.Y. (1985). Country report: Hong Kong. The demersal fish resources of the northern shelf of the South China Sea. *FAO/SEAFDEC Workshop on Shared Stocks in Southeast Asia, Bangkok (Thailand)*. *FAO FISH. REP. FAO FIRM* 337: 63-71.
- Romero, F.G. (1996). Artificial reefs: bane or boon to Philippine fisheries. *Marine Life* 2(2): 4-7.
- Russ, G.R. and Alcala, A.C. (1996a). Do marine reserves export adult fish biomass? *Mar. Ecol. Prog. Ser.* 132: 1-9.
- Seaman, W. Jr. (ed.) (2000). *Artificial reef evaluation: with application to natural marine habitats*. CRC Press, London.
- Silvestre, G. and Pauly, D. (1997). Management of Tropical Coastal fisheries in Asia: an overview of the key challenges and opportunities. Pages 8-25 in Silvestre, G. and Pauly, D. (eds) *Status and management of tropical coastal fisheries in Asia*. ICLARM Conf. Proc. 53: 208pp.
- Soulé, M.E., Alberts, A.C. and Bolger, D.T. (1992). The effects of habitat fragmentation on chaparral plants and vertebrates. *Oikos* 63(1): 39-47.
- Sumaila, U.R., S. Guénette, J. Alder and R. Chuenpagdee (2000). Addressing the ecosystem effects of fishing using marine protected areas. *ICES J. Mar. Sci.* 57: 752-760.
- Valente, R.M., Evans, N.C., and Whiteside, P.G.D. (1996). Environmental monitoring in Hong Kong using the REMOTS seabed camera. *Coast. Manage. Trop. Asia* (6): 26-29.
- Walters, C., Christensen, V. and Pauly, D. (1997). Structuring Dynamic Models of Exploited Ecosystems from Trophic Mass-Balance Assessments. *Rev. Fish Biol. Fish.* 7: 139-172.
- Walters, C., Pauly, D. and Christensen, V. (1998). Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems with emphasis on the impacts of marine protected areas. *ICES CM* 1998/S:4 20pp.
- Walters, C., Pauly, D. and Christensen, V. (1999). Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems* 2: 539-554.
- Watson, R. and Walters, C.J. (1998). Ecosim and MPAs: a quasi spatial use of Ecosim. *Fisheries Centre Research Reports* 6(2): 15-18.
- Watson, R., Alder, J. and Walters, C.J. (2000). A dynamic mass-balance model for marine protected areas. *Fish and Fisheries* 1: 94-98.
- Wilson, K.D.P. and Cook, D.C. (1998). Artificial reef development: a marine protected area approach. Pages 529-539 in Morton, B. (ed.) *Proceedings of the Third International Conference on the Marine Biology of the South China Sea*. Hong Kong University Press.
- Wu, R.S.S. (1988). Marine pollution in Hong Kong. *Asian Mar. Biol.* 5: 1-23.

Table 1. Species composition of the 37 functional groups of the Hong Kong marine Ecopath model.

No.	Functional groups	Trophic level	Group description
1	Benthic producers	1	Marine algae (epilithic algae, endolithic algae, reef turf algae, benthic fleshy algae, macroalgae, and benthic algae) and spermatophytes (sea grass)
2	Phytoplankton	1	Diatoms and dinoflagellates
3	Corals	1.5	All hermatypic corals in Hong Kong
4	Zooplankton	2	Copepods, ostracods, bivalve larvae, cirripedia larvae, cladocerans, echinoderm larvae, larvacea, other mollusk larvae, and larvacea; mysids, sergestids, euphausiids, amphipodes, luciferidae, and other decapod larvae; chaetognaths, annelids and ichthyoplankton
5	Sea turtles	2.5	Mostly <i>Chelonia mydas</i>
6	Jellyfish	3	Includes Cnidarians (hydrozoa and scyphozoa)
7	Living bottom structure (LBS)	2.1	Sponges (<i>Poterion</i> spp.), gorgonians (sea fans and sea whips), soft corals, sea pens, sea squirts and sea anemones
8	Small zoobenthos	2.1	Includes all burrowing benthos of the size less than 1.0 mm. These include polychaetes, mollusks, echinoderms, crustaceans, sipunculans, and benthic stage larvae of other larger organisms
9	Macrozoobenthos	2.4	Includes all mollusks and echinoderms larger than 1.0 mm, such as conch, oysters, scallops, clams, cockles, mussels, sea urchins, sea cucumbers, and sea stars
10	Benthic Crustaceans, non-reef associated	3.2	Portunidae (<i>Charybdis</i> spp., <i>Portunus</i> spp., and <i>Scylla serrata</i>), Solenoceridae, Squillidae, Decapoda, and Tachypleidae
11	Benthic Crustaceans, reef associated	3	Palinuridae (<i>Panulirus versicolor</i>) and Portunidae (<i>Portunus pelagicus</i>)
12	Penaeid prawns, non-reef associated	2.7	Penaeidae (<i>Parapenaeopsis</i> spp., <i>Penaeus</i> spp. and <i>Trachypenaeus</i> spp.)
13	Penaeid prawns, reef associated	2.5	Penaeidae (<i>Metapenaeopsis</i> spp. and <i>Metapenaeus</i> spp.)
14	Cephalopods, non-reef associated	3.8	<i>Loligo</i> spp., <i>Sepioteuthis</i> spp., <i>Octopus indicus</i> , <i>O. indicus</i> , <i>O. aegini</i> , <i>O. dofleini</i> , <i>O. dollfusi</i> and <i>O. membranaceus</i>
15	Cephalopods, reef associated	3.6	<i>Octopus cyaneus</i> , <i>O. vulgaris</i> , <i>Sepia</i> spp, <i>Sepiella</i> spp. and <i>Euprymna mosei</i>
16	LBS-associated fish Juvenile	3.1	Juvenile stage of fishes predominantly associated

Table 1. Species composition of the 37 functional groups of the Hong Kong marine Ecopath model.

No.	Functional groups	Trophic level	Group description
			with LBS including Carangidae, Lethrinidae, Lutjanidae, Polynemidae and Sphraenidae
17	LBS-associated fish Adult	4.1	Adult stage of fishes listed in group 16
18	Small demersal reef associated fish	2.7	Demersal reef fishes with less than 30 cm total length including Apogonidae, Cirrhitidae, Gerreidae, Haemulidae, Holocentridae, Kyphosidae, Labridae, Lutjanidae, Monacanthidae, Nemipteridae, Pempheridae, Pomacanthidae, Pomacentridae, Scorpaenidae, Sebastidae, Serranidae, Zanclidae, Antennariidae, Priacanthidae, Syngnathidae and Synanceiidae
19	Small demersal non-reef associated fish	2.9	Demersal fishes associated in non-reef area (<i>e.g.</i> , muddy and sandy area) with less than 30 cm total length, including Ambassidae, Blennidae, Callionymidae, Carangidae, Chaetodontidae, Cynoglossidae, Gerreidae, Gobiidae, Haemulidae, Leiognathidae, Microdesmidae, Monacanthidae, Monodactylidae, Mugilidae, Mullidae, Nemipteridae, Platycephalidae, Plotosidae, Polynemidae, Sciaenidae, Scorpaenidae, Sillaginidae, Sparidae, Stromateidae, Synodontidae, Terapontidae, Tetraodontidae, Aploactinidae, Ariidae, Bothidae, Eleotridae, Paralichthyidae, Rhyacichthyidae, Soleidae, Synanceiidae, Triacanthidae and Triglidae
20	Medium demersal reef associated fish	3.2	Demersal reef fishes with 30-60 cm total length, including Acanthuridae, Apogonidae, Blennidae, Carangidae, Chaetodontidae, Haemulidae, Labridae, Lethrinidae, Lutjanidae, Muraenidae, Pomacanthidae, Scorpaenidae, Serranidae and Sparidae
21	Medium demersal non-reef associated fish	3.3	Demersal non-reef fishes with 30-60 cm total length, including Carangidae, Cynoglossidae, Dasyatidae, Labridae, Malacanthidae, Mugilidae, Platycephalidae, Scaridae, Scatophagidae, Sciaenidae, Synodontidae, Tetraodontidae and Syngnathidae
22	Large demersal reef associated fish Juvenile	2.7	Juvenile stage of the demersal reef fishes with more than 60 cm total length, including Carangidae, Chaetodontidae, Fistularidae, Labridae, Lethrinidae, Lutjanidae, Percichthyidae, Serranidae, Sparidae, and Ophichthidae
23	Large demersal reef associated fish Adult	3.6	Adult stage of the fishes listed in group 22
24	Large demersal non-reef associated fish Juvenile	2.9	Juvenile stage of demersal non-reef fishes with more than 60 cm total length, including Carangidae, Centropomidae, Fistularidae, Kyphosidae, Mugilidae, Muraenesocidae, Paralichthyidae, Platycephalidae, Rachycentridae, Sciaenidae, Serranidae, Congridae, and Ophichthidae
25	Large demersal non-reef associated fish Adult	3.5	Adult stage of fishes listed in group 24
26	Small pelagic fish	2.9	Pelagic fishes with less than 30 cm total length, including Atherinidae, Bregmacerotidae,

Table 1. Species composition of the 37 functional groups of the Hong Kong marine Ecopath model.

No.	Functional groups	Trophic level	Group description
			Carangidae, Centrolphidae, Clupeidae, Engraulidae, Mugilidae, Synodontidae, Terapontidae and Hemiramphidae
27	Medium pelagic fish	3.3	Pelagic fishes with 30 - 60 cm total length, including Carangidae, Carangidae, Cheilodactylidae, Clupeidae, Lacteridae, Scombridae and Sphyraenidae
28	Large pelagic fish Juvenile	2.9	Juvenile stage of pelagic fishes with more than 60 cm total length, including Carangidae, Lobotidae, Scombridae and Trichiuridae
29	Large pelagic fish Adult	3.9	Adult stage of fishes listed in group 28
30	Rays and skates	3.8	Dasyatidae, Gymnuridae, Myliobatidae and Rajidae
31	Small sharks	3.9	Sharks below 100 cm total length including Carcharhinidae, Hemiscylliidae and Orectolobidae
32	Large sharks Juvenile	3.9	Juvenile stage of large sharks over 100 cm total length including Carcharhinidae
33	Large sharks Adult	4.3	Adult stage of large sharks group
34	Fish-eating seabirds	3.9	Sea and shore birds with fish dominates in their diet, including Ardeidae, Gaviidae, Laridae, Pelecanidae and Treskiornithidae
35	Invertebrate-eating seabirds	3.2	Sea and shore birds with invertebrates dominate in their diet, including Anatidae, Charadriidae, Gaviidae, Jacanidae, Laridae, Recurvirostridae and Scolopacidae
36	Marine mammals	4.1	Comprised of Indo-Pacific Hump-backed dolphins (<i>Sousa chinensis</i>) and Finless porpoises (<i>Neophocaena phocaenoides</i>)
37	Detritus	1	Comprised of particulate and dissolved organic matters

Table 2: Input and output (in brackets) parameters of the Ecopath model of Hong Kong marine ecosystem in 1990s.

No.	Group name	Trophic level	Biomass (t/km ²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE	P/Q
1	Benthic Producers	(1)	153	11.885	-	(0.00855)	-
2	Phytoplankton	(1)	13	231	-	(0.76861)	-
3	Corals	(1.5)	(0.33993)	1.09	9	0.99	(0.12111)
4	Zooplankton	(2)	14.7	32	192	(0.16749)	(0.16667)
5	Sea Turtles	(2.5)	0.0002	0.1	2.5	(0.95072)	(0.04)
6	Jellyfish	(3)	1.52879	5.011	25.05	(0.25716)	(0.20004)
7	LBS	(2.1)	0.0042	0.25	0.5	(0.77896)	(0.5)
8	Sm. zoobenthos	(2.1)	70.37	6.57	27.4	(0.41763)	(0.23978)
9	Macrozoobenthos	(2.4)	(1.76869)	3	12.5	0.95	(0.24)
10	Bent. Crus. NRA	(3.2)	0.35813	5.65	26.9	(0.69435)	(0.21004)
11	Bent. Crus. RA	(3)	0.8036	1.85	8.35	(0.77353)	(0.22156)
12	Pen. prawns NRA	(2.7)	0.06126	4.8	16.352	(0.94872)	(0.29354)
13	Pen. prawns RA	(2.5)	0.33181	7.6	41.537	(0.9028)	(0.18297)
14	Cephalopods NRA	(3.8)	0.39529	3.1	11.97	(0.65109)	(0.25898)
15	Cephalopods RA	(3.6)	0.18669	3.1	11.97	(0.2188)	(0.25898)
16	LBS-assoc. fish Juv	(3.1)	0.0953	2.5	10.89	(0.9171)	(0.22957)
17	LBS-assoc. fish Ad	(4.1)	0.00762	1.5	6.64	(0.93306)	(0.2259)
18	Sm. Dem. RA	(2.7)	0.96475	3	10.47	(0.94776)	(0.28653)
19	Sm. Dem. NRA	(2.9)	2.49592	3	10.89	(0.98118)	(0.27548)
20	Med. Dem. RA	(3.2)	0.31412	2	8.63	(0.84526)	(0.23175)
21	Med. Dem. NRA	(3.3)	0.34583	2.2	8.63	(0.9693)	(0.25492)
22	Lg. Dem. RA. Juv	(2.7)	0.18308	4.18	15	(0.996)	(0.27867)
23	Lg. Dem. RA. Ad	(3.6)	0.00578	0.6	5.11	(0.99801)	(0.11742)
24	Lg. Dem. NRA. Juv	(2.9)	0.327	3	10.89	(0.99577)	(0.27548)
25	Lg. Dem. NRA. Ad	(3.5)	0.05	0.92	4.53	(0.9798)	(0.20309)
26	Sm. Pelagics	(2.9)	2.09076	4	11	(0.89123)	(0.36364)
27	Med. Pelagics	(3.3)	0.21449	2	7.59	(0.98126)	(0.2635)
28	Lg. Pelagics Juv	(2.9)	0.21195	3	10.81	(0.88698)	(0.27752)
29	Lg. Pelagics Ad	(3.9)	0.04579	1.2	5.9	(0.78447)	(0.20339)
30	Rays and Skates	(3.8)	0.12649	0.5	6.35	(0.00834)	(0.07874)
31	Small Sharks	(3.9)	0.12742	0.4	6.83	(0.0126)	(0.05857)
32	Large Sharks Juv.	(3.9)	0.05	0.4	6.83	(0.03212)	(0.05857)
33	Large Sharks Ad.	(4.3)	0.005	0.2	4.13	(0.1147)	(0.04843)
34	Fish-eating Seabirds	(3.9)	0.00076	0.06	61.28029	(0)	(0.00098)
35	Invertebrate-eating Seabirds	(3.2)	0.00229	0.06	72.76378	(0)	(0.00082)
36	Marine Mammals	(4.1)	0.009	0.045	14.7682	(0.96845)	(0.00305)
37	Detritus	(1)	200	-	-	(0.49014)	-

Table 3. Simulation scenarios ranked in order of catch for each Hong Kong fishery sector.

Gear sector	Scenario				
	AR	AR no take	AR/MPA	AR/MPA no trawl	AR/MPA - effort
Stern trawls	3	2	1	5	4
Shrimp trawls	1	3	2	5	4
Pair trawls	4	3	2	5	1
Purse seines	5	4	3	1	2
Small-scale P4/7	5	3	2	1	4
Small-scale Misc	4	3	2	1	5
Hang trawls	4	3	2	5	1
Scenario rank totals	26	21	14	23	19
Scenario rank order	5	3	1	4	2

Table 4. Simulation scenarios ranked in order of biomass for nine major types of organism pooled from 25 functional ecosystem groups. Order for jelly fish and prawns was reversed.

	jellyfish	reef fish	prawns	pelagics	demersals	elasmn	mannm	seabirds	turtles	SUM	OVERALL RANK
AR	5	5	5	5	5	5	5	4	3	42	5
AR no-take	4	4	1	4	4	4	4	5	5	35	4
AR/MPA	3	3	3	3	2	3	3	3	3	26	3
AR/MPA no trawl	1	2	4	1	3	1	1	1	1	15	1
AR/MPA -effort	2	1	2	2	1	2	2	2	2	16	2

Table 5: Economic data

- A. Computed prices by functional groups. A blank by a species group implies no price quoted for that group. Original prices per commercial species were supplied by AFCD.

Ecopath Functional group	Price (HK\$/ton)
Benthic Producers	
Phytoplankton	
Corals	
Zooplankton	
Sea Turtles	
Jellyfish	
LBS	
Sm. zoobenthos	
Macrozoobenthos	14,721
Bent. Crus. NRA	14,721
Bent. Crus. RA	14,721
Pen. prawns NRA	62,895
Pen. prawns RA	27,917
Cephalopods NRA	13,574
Cephalopods RA	13,186
LBS-assoc. fish Juv	11,963
LBS-assoc. fish Ad	27,915
Sm. Dem. RA	11,101
Sm. Dem. NRA	9,309
Med. Dem. RA	15,331
Med. Dem. NRA	16,111
Lg. Dem. RA. Juv	11,735
Lg. Dem. RA. Ad	27,382
Lg. Dem. NRA. Juv	8,872
Lg. Dem. NRA. Ad	20,701
Sm. Pelagics	13,054
Med. Pelagics	14,774
Lg. Pelagics Juv	13,567
Lg. Pelagics Ad	31,657
Rays and Skates	
Small Sharks	9,913
Large Sharks Juv.	7,435
Large Sharks Ad.	17,348
Fish-eating Seabirds	
Invertebrate-eating Seabirds	
Marine Mammals	
Detritus	

B. Harvesting cost data by vessel type supplied by AFCD

Boat	Weighting	Capital (HK\$)	Catch (Tons)	Revenue (HK\$)	Fuel (HK\$)	Wages (HK\$)	Ice (HK\$)	Repairs (HK\$)	Depreciation (HK\$)	Fixed cost (HK\$)	Variable cost (HK\$)	Total cost (HK\$)	Profits (HK\$)	Profit%
Pair Trawler	0.11	2,034,324	142	1,493,481	505,285	152,704	161,048	167,744	101,716	269,460	819,037	1,088,497	404,984	27.1
Stern Trawler	0.04	1,045,182	91	924,632	349,486	68,300	118,296	124,591	52,259	176,850	536,082	712,932	211,700	22.9
Shrimp Trawler	0.1	885,758	13	523,271	146,773	43,675	88,738	80,184	44,288	124,472	279,186	403,658	119,613	22.9
Long Liner	0.05	1,040,909	34	885,570	155,126	72,268	204,372	193,167	52,045	245,212	431,766	676,978	208,592	23.6
Gill Netter	0.1	191,824	9	231,595	42,771	16,204	42,577	41,366	9,591	50,957	101,552	152,509	79,086	34.1
Purse Seiner	0.03	358,571	42	585,817	57,600	68,570	101,048	48,217	17,929	66,146	227,218	293,364	292,453	49.9
Hang Trawler	0.01	3,771,429	77	1,571,361	401,470	139,371	138,516	123,143	188,571	311,714	679,357	991,071	580,290	36.9
Hand Liner	0.02	1,857,909	24	1,659,965	269,037	570,584	169,154	235,888	92,895	328,783	1,008,775	1,337,558	322,407	19.4
P4/7	0.55	26,700	3	78,727	17,215	0	6,570	10,944	1,335	12,279	23,785	36,064	42,663	54.2

Note:

- 1) Data were obtained from fishing vessel interviews and the number of vessels sampled represented about 3 to 5% of the local fishing fleet.
- 2) Wages of P4/7 was absorbed into profit as fishing activities were only performed by owner himself.
- 3) Weighting is based on the ratio of vessel number: particular vessel number/total vessel number (including those fish outside Hong Kong waters)
- 4) All data are for 1997

ESTIMATING THE FISHERY BENEFITS OF FULLY-PROTECTED MARINE RESERVES: WHY HABITAT AND BEHAVIOUR ARE IMPORTANT

Callum M. Roberts and Helen Sargent¹

Environment Dept, University of York, York, YO10 5DD, UK. Email: cr10@york.ac.uk ;

Abstract

Fully-protected marine reserves, areas that are closed to all fishing, have attracted great interest for their potential to benefit fisheries. A wide range of models suggest reserves will be most effective for species that are relatively sedentary as adults, but produce offspring that disperse widely. Adult spawning stocks will be secure from capture in reserves, while their offspring disperse freely into fishing grounds. Such species include animals like reef fish, molluscs and echinoderms, and models typically indicate that when they are overfished, catches will be higher with reserves than without. By contrast, the same models suggest that reserves will be ineffective for animals that are mobile as adults - species like cod, tuna or sharks. They remain vulnerable to fishing whenever they move outside reserves. Unfortunately, most models lack sufficient realism to effectively gauge reserve effects on migratory species. They usually assume that individuals are homogeneously distributed in a uniform sea and move randomly. They also assume that fishers hunt at random. Neither is true. For centuries, fishers have targeted places and times when their quarry are most vulnerable to capture. Protecting these sites could have disproportionately large effects on stocks. Furthermore, models rarely take into account possible benefits from improvements in habitat within reserves. Such changes, like increased biomass and complexity of bottom-living organisms, could alter fish movement patterns and reduce natural mortality rates in ways that enhance reserve benefits. We present a simple model of reserve effects on a migratory fish species. The model incorporates spatial variation in vulnerability to capture and shows that strategically placed reserves can offer benefits in the form of increased spawning stock and catch, especially when fishing intensities are high. We need to develop a new generation of models that incorporate habitat and behaviour to better explore the utility of reserves for mobile species.

Migratory behaviour does not preclude reserves from benefitting a species, but it demands that we apply different principles in designing them. We must identify critical sites to species and develop reserve networks that focus protection on those places.

Introduction

Fully-protected marine reserves are areas that are closed to all fishing and other extractive or harmful human uses. Such areas have been attracting a great deal of attention as possible tools for managing fisheries more effectively (Roberts 1997, Allison et al. 1998, Bohnsack 1998, Hastings and Botsford 1999, Murray et al. 1999). Much effort has been invested recently in developing the theoretical underpinning for the use of reserves. This work suggests that reserves could help support fisheries offering benefits such as increased spawning stocks, sustained or increased yields, reduced variability in catches from year to year, reduced risk of management failure and simplified management (Bohnsack 1998, Sladek Nowlis and Roberts 1999, Pezzey et al. 2000).

Much of our expectations of marine reserve performance come from modeling work (e.g. Holland and Brazee 1996, Guenette and Pitcher 1999, Mangel 2000). This is because there are still very few fully-protected reserves established at sufficiently large scales to gather empirical data on how they impact upon fisheries. The shortage is especially acute in temperate regions. Additionally, most of those reserves that do exist have only been around for a short-time and their effects have yet to develop completely. There have been two typical modeling approaches used for investigating reserve effects. The first owes its inspiration to many of the earliest reserves which were established on coral reefs. Such models usually consist of two simulated populations, those on the reserve and fishing grounds, and in which adults are sessile but there is a shared larval pool. Eggs and larvae from each population enter the common pool and there is assumed to be complete larval mixing with subsequent recruitment shared between reserve and fishing grounds in direct proportion to their areal coverage. These models usually include multiple fish cohorts and are run over many iterations until equilibrium population sizes are reached for given levels of natural and fishing mortality. Examples include Holland and Brazee (1996), Sladek Nowlis and Roberts (1997, 1999), Sladek Nowlis and Yoklavich (1998), and Pezzey et al. (2000).

The second modeling approach has been based more on temperate fish stocks. Such models are often based on yield-per-recruit

¹Present address: Flat 3 Raynes Court, Claremont Road, Cricklewood, London, NW2 1EW, UK

analyses or surplus-yield functions and follow a single fish cohort through time (e.g. Polacheck 1990, Daan 1993, Conrad 1999, Hanneson 1999). While the models are still based on two patches, reserve and fishing grounds, they allow movement of adults from one to the other, often over a range of simulated transfer rates. Such models, although they look at changes in spawning stock biomass, rarely consider the possible contribution of increases in spawning stock to recruitment rates. Of course, there have been many variations on these models created over the years. Some include elements of both approaches (e.g. Pezzey et al. 2000), while others incorporate refinements such as multiple populations (Quinn et al. 1993, Mangel in press), metapopulations (Man et al. 1995), stochasticity (Lauck et al. 1998), or source-sink dynamics (Sanchirico and Wilen 1996, 1998). However, the basic templates on which they are built remain similar (Gerber et al. in press).

Both classes of model greatly simplify reality. For example, in many coral reef fisheries there is likely to be significant spillover of adults and juveniles from reserves to fishing grounds (e.g. McClanahan and Kaunda-Arara 1996, Russ and Alcala 1996), as well as larval export. In temperate regions, increased spawning stock size could well contribute to increased recruitment. Both classes of model ignore effects of habitat on fish stocks, assuming instead that habitats are homogeneous and always sufficient to support production. Neither do they incorporate any heterogeneity in fishing patterns or stock vulnerability (catch-per-unit-effort, CPUE).

Models must, by necessity, simplify reality in order to be tractable. These basic models have offered us many useful insights into how reserves could perform, either as primary fishery management tools, or as one of a suite of measures. A key conclusion emerging from them is that reserve benefits are greatest for species that are sessile as adults and have widely dispersing offspring. As adult mobility increases, reserve benefits diminish. At high rates of adult transfer between reserves and fishing grounds, reserves become ineffective. Incorporating stochasticity into recruitment or fishing effort increases the long-term benefits of reserves to stock protection, but does not greatly alter this conclusion.

These findings have led to a growing perception among scientists and fishery managers that reserves will not be helpful in managing stocks of migratory species. In this paper I argue that this view is misplaced. The models from which we reach this conclusion are too simple to properly capture the dynamics of migratory fish stocks. The critical missing elements centre upon

the interactions between fish and their habitats, and between fish and fishers. To provide a realistic assessment of whether reserves could be useful for managing migratory fishes, we must incorporate the effects of habitat and behaviour into our models.

Why are the effects of habitat and behaviour important?

Fish populations are heterogeneously distributed in time and space

Most models consider fish to be particles that are distributed and fished at random within homogeneous seas. The reality is very different. Fish are associated with different habitats to greater or lesser extents. Those habitat associations may change throughout development or with the time of year. There are two main forms of fish migration, ontogenetic and adult migrations. Ontogenetic migrations involve the use of, and movement between, different kinds of habitat at different developmental stages. Many fishes that are commonly considered site-attached as adults undergo ontogenetic migrations. For example, several species of tropical grunts (Haemulidae) settle into nearshore mangrove and seagrass beds and move progressively offshore into coral reef habitats as they grow (Appeldoorn et al. 1997). Adult migrations involve the regular movements of mature fish from place to place, often to take advantage of site-specific conditions for feeding and breeding (Harden Jones 1968).

Both kinds of migration take advantage of habitat heterogeneity. Migration has evolved because being in particular places at particular times increases fitness (Dodson 1997). For example, juveniles may use nursery habitats where there is less predation pressure or greater food availability (Tupper and Boutilier 1995, Szedlmayer and Howe 1997). They move to other habitats as they grow in size, and their diet and predation risks change. For other species, aggregation breeding at particular sites offers advantages over other reproductive strategies. For example, tropical snappers and groupers are well known to form spectacular spawning aggregations of up to tens of thousands of fish, often around reef promontories (Johannes 1998, Heyman et al. in press).

For millennia, fishers have recognised that the sea is heterogeneous and that there are better places and times for fishing than others. Their fishing patterns have become attuned to the migration patterns of the species they hunt. For example, herring roe fisheries are closely linked to the times and places of herring spawning in nearshore gravel habitats. Tuna fisheries often

target aggregation sites such as seamounts or coastal narrows as the tuna arrive from their cross ocean migrations (Cushing 1988, Holland et al. 1998). For many species, seasonal patterns of aggregation and dispersal mean that there is a large difference in catchability over the course of a year. Fishers target sites and times that offer the greatest catch rates. For example, in the Gulf of California, around the beginning of the 20th century, fisheries developed for the Totoaba (*Totoaba macdonaldi*), a giant species of croaker (Sciaenidae). Before their populations were decimated by overfishing and habitat change (Roberts and Hawkins 1999), these fish undertook a mass annual migration from deep water, following close to the coasts to spawn near the mouth of the Colorado River. A fishery soon developed for their swim bladders which were exported to the Far East. During the first half of the century, migration runs were so prolific that fishers could literally wade into the shallows and fork fish onto the shore from their thrashing spawning aggregations (Kira 2000).

If fishers can take advantage of differences in catchability, marine reserves could be placed strategically in areas of greatest vulnerability. Targetting such areas of high CPUE could offer much greater benefits than if CPUE was homogeneous over the entire fishing grounds (Roberts in press). To assess the potential benefits of reserves for migratory species, models must explore the effects of heterogeneity in CPUE and fishing effort.

Habitat quality is important to fish

The assumption made in most models (and in much on the ground management!) is that habitats will always be sufficient to support fish production (although see Mangel in press). Furthermore, no account is taken of differences in habitat quality among locations and how they might affect fish stocks. Such differences may be important. Furthermore, by offering protection from fishing, reserves can be expected to change habitat quality through the reduction of damage to the bottom by fishing gear (Auster and Malatesta 1995, Auster and Langton 1999, Jennings and Kaiser 1998).

Mobile fishing gears, such as trawls and dredges, reduce habitat structural complexity by removing and killing bottom living animals and plants, and smoothing out structures such as tidal ripples or depressions (Auster and Langton 1999, Jennings and Kaiser 1998). A reduction in habitat complexity can affect population processes in important ways. Juvenile fish are often subject to lower predation rates in structurally complex habitats than in simple ones because they offer more refuges from predators (Szedlmayer and

Howe 1997, Goteceitas et al. 1995, 1997, Lindholm et al. 1999). Reductions in habitat complexity by fishing could reduce recruitment to fisheries by increasing predation rates on young fish (Auster and Malatesta 1995).

However, reserves also increase the biomass of predators (e.g. Russ and Alcala 1996). Yet structurally complex habitats could offer enhanced feeding conditions, for prey and predators alike, because they support a higher biomass and diversity of fish and other life (e.g. Roberts and Ormond 1987; Szedlmayer and Able 1996). In other words, there may be a double dividend, with larger prey fish populations supported by greater food and refuge availability, and greater prey encounter rates for predators. Protection of habitat in reserves could increase the availability of high quality habitat for both juvenile and adult fishes. Furthermore, establishing reserves, and so creating patches of greater habitat complexity within large areas of lower relief, could alter patterns of habitat use by fish, especially of migratory species whose movements enable them to sample large areas of habitat. Migratory predators may spend more time in reserves, benefitting from better feeding conditions and, consequentially, greater protection from fishing. Today's reserve models fail to recognize the possible stock protection benefits of such shifts in habitat use.

Marine reserves might also enhance recruitment to a fishery by reducing mortality rates on juvenile fish. Lower mortality may be a combination of reduced predation risk in complex habitats and increased growth rates. Large juvenile cod have greater overwinter survival than small, so placing a premium on rapid growth (Goteceitas et al. 1999). Reserves could also increase recruitment by creating more nursery habitat. For example, the red hake (*Urophycis chuss*) settles as larvae into scallop beds off the north-east coast of North America (Kramer et al. 1997). The larvae enter adult scallops where they metamorphose and develop as juveniles. They leave the scallops when they grow too large or winter temperatures reach 4°C. Recent closures to trawl fishing in New England led to massive increases in abundance and size of scallops in reserves (Murawski et al. in press). Such an effect could both increase numbers and size of recruiting red hake. Similarly, juvenile silver hake (*Merluccius bilinearis*) require sand-silt bottoms with some cover of amphipod tubes (Auster et al. 1997). These delicate structures are destroyed by trawling but could develop in reserves.

Juvenile fish are also often subjected to massive by-catch mortality on nursery grounds. Yield-per-recruit models consistently indicate that reserves could increase fishery yields by

reducing by-catch mortality (Horwood et al. 1998).

To summarize the above, strategically placed marine reserves could benefit migratory species in several ways: (1) reducing adult mortality in migration bottlenecks, areas that have exceptionally high CPUE and are intensively targeted by fishers; (2) reducing juvenile mortality by decreasing predation rates and increasing growth rates in reserves; (3) increasing the quality and/or area of nursery grounds; (4) protecting juvenile fish from by-catch mortality; and (5) through improved habitat quality increasing the time spent by mobile fish in reserves. In the following section, we develop a model of reserve impacts on a migratory species that incorporates two of these effects: spatial variation in CPUE and juvenile by-catch mortality on nursery grounds.

A model of marine reserve effects on a migratory species

Model specification

A discrete, size-specific, model of a hypothetical migratory fish species was created and programmed in STELLA (HPS Inc. 1997). A Leslie matrix approach was taken (see Williamson 1974) to model the dynamics of a size structured population with 12 size classes. Natural and fishing mortality and egg production were defined by size class (Table 1). Natural mortality for the first size class was assumed to be density-dependent and was controlled according to a Beverton-Holt recruitment relationship (Equation 1).

$$R = \frac{1}{\alpha + (\beta / S)} \quad [1]$$

R = recruitment, S = spawning stock, α was set to 0.00001 and β to 0.1.

The second size class was subjected to annual natural mortality of 30% (as they are prey to other fishes) and all the other size classes (3-12) suffered 20% natural losses per year. Fish did not mature and produce eggs until they entered the second size class and egg production increased exponentially with size class, using an equation based on that used by Gu enette and Pitcher (1999).

The migratory population was conceived as four linked units in space and time: a feeding area, a migration route to a spawning area, a spawning area, and a migration route back to the feeding area (Figure 1). The population moved from one place to the next in an annual cycle (Figure 1) so capturing the spatial and temporal dimensions of a typical migratory stock. They spent five months per year on the feeding grounds, two months travelling to the spawning aggregation site, one month on the spawning aggregation site and four months on the return route to the feeding grounds. Within each area, fish were exposed to natural and fishing mortality. Fish stocks and catches were calculated on a monthly basis. Fish in the model were programmed to reproduce once per year while on the spawning grounds. The fish 'grew', i.e. the fish were moved up to the next size class, in the flow from the feeding grounds to the spawning area. The largest fish (size class 12) were removed from the model at this point.

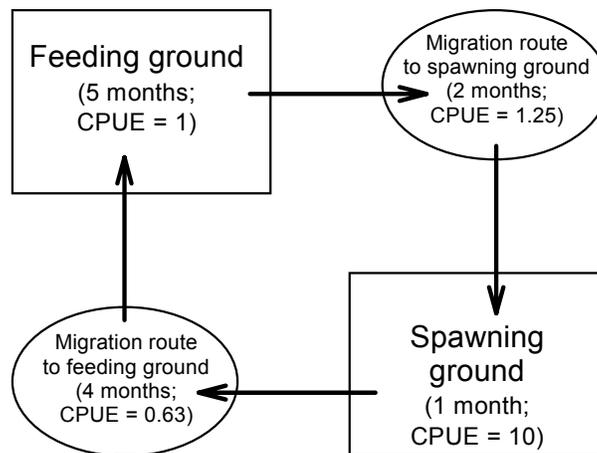


Figure 1: Diagrammatic representation of the model of a migratory fish species. The annual migration cycle was represented as a series of flows connecting four areas: the feeding grounds (which also constitutes nursery habitat for juvenile fish), the migration route from feeding grounds to spawning area, the spawning area, and the migration route back to the feeding grounds. The amount of time fish spend in each area, and their vulnerability to fishing (catch per unit effort, CPUE) are denoted on the figure.

Once the natural mortality and egg production were determined, three separate versions of the model were made with light, moderate and heavy fishing regimes. Under the light regime an average of 10% of the fish were caught every year, compared to 30% under the moderate and 50% for the heavy regime. Under each regime the catchability of fish was related to size class (Table 1), with larger fish being more vulnerable to capture than small. Catchability was also related to the area the stock was in at the time. The fish were assumed to be most aggregated in the spawning area and most dispersed in the feeding area. Catchability was similar on the migration routes to that in the feeding area. These patterns of aggregation and dispersion corresponded to relative levels of CPUE of 1 in the feeding area, 1.25 in the migration route from the feeding to spawning area, 10 in the spawning area, and 0.63 in the migration route from the spawning to feeding area (Figure 1). The initial stock size was set at the equilibrium the model achieved after 100 years with light fishing and no reserve (Table 1).

In a second version of the model, juvenile fish of size class 1 were subjected to by-catch mortality in the feeding area for a period of four months after the settlement event. The by-catch model was designed to simulate the effect of a fishery for another species on juveniles of the stock. This is common in fisheries. For example, around Britain, there are high levels of by-catch of juvenile cod and hake in beam trawl fisheries targeting plaice. By-catch mortality was arbitrarily set at the average mortality level for the rest of the stock under each fishing regime (Table 1).

The model was firstly run with no reserves and open access. Then three different reserve scenarios were simulated by setting fishing effort to zero in (1) the feeding area (which also stopped by-catch), (2) the spawning area, and (3) the migration route and spawning ground (effort set to zero in both areas). In the present model, protection could not be defined by amount of area protected (eg the size of reserve in km²) as the spatial dimension of the model was implied rather than explicit. The model was run for 100 years under each of the fishing regimes, without a reserve and with each reserve design separately. Spawning stock biomass in year 100 was calculated using size-specific weight data based on figures in Guenette and Pitcher (1999)(Table 1). Catch weight for each year was calculated in the same way and averaged over 100 years of data from each model run. Each run was completed twice, first with the effort from the reserve area being eliminated and second with the effort being reallocated equally between the open areas. In the

by-catch model, redirection of fishing effort also increased by-catch by a similar proportion. The simulations in which effort was not redirected were run to capture the behaviour of localized or highly seasonal fisheries, where effort has to be transferred to a different fish species, or a different industry altogether. The redirected effort simulations represent situations in which fishing effort can be relocated in time and space to exploit the same species.

Realistic size-specific fresh fish prices (Table 1) were used to calculate the value of the catch at the end of each year of each model run. Once catches had been valued they were discounted with a rate of 10% and summed over the hundred years (Equation 2).

$$B_0 = \frac{B_t}{(1+r)^t} \quad [2]$$

B_0 = discounted benefit; B_t = benefit at time t ; r = discount rate (0.10); t = time in years.

Results

Figure 2 shows the effects of different reserve placements on the equilibrium spawning stock biomass. Increasing intensities of fishing depress spawning stock biomass. In virtually all circumstances, reserves increase spawning stock biomass over the open access case. The fractional gains in spawning stock biomass with reserves are greater at higher fishing intensities. Reserves on the spawning grounds, or networked across spawning grounds and the migration route to them from the fishing grounds, are most effective. This is because they protect adult fish at their most vulnerable. In only one case, that of a feeding ground reserve with no by-catch and fishing effort redirected (Figure 2d), a reserve decreased spawning stock biomass over the open access case. This is because fishing effort was displaced from an area with low stock vulnerability to fishing, to an area where it was much higher (spawning grounds). Redirection of fishing effort and juvenile vulnerability to by-catch both tended to reduce spawning stock biomass.

Figure 3 shows the effects of different reserve placements on catch, compared to the open access case. Reserves tend to become more beneficial as fishing intensities increase. At the lowest fishing intensity, reserves tend to decrease catches, while at the highest they mostly increase them. Redirection of fishing effort tends to increase catches over cases where the displaced effort was lost. Reserves on the feeding grounds are especially beneficial to catches in cases where

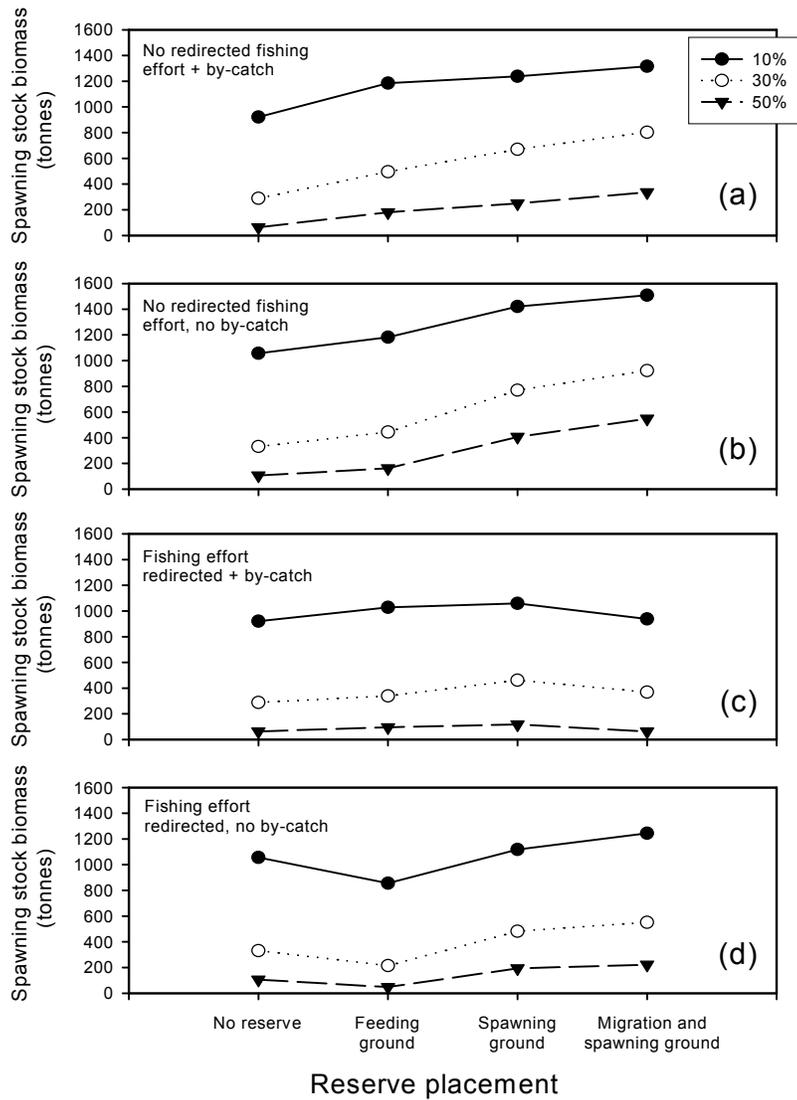


Figure 2: Effects of reserves on levels of spawning stock biomass. Results show the biomass present at the end of 100 year simulations for three different levels of fishing: light (10% of stock caught per year), moderate (30% of stock caught per year) and intense (50% of stock caught per year).

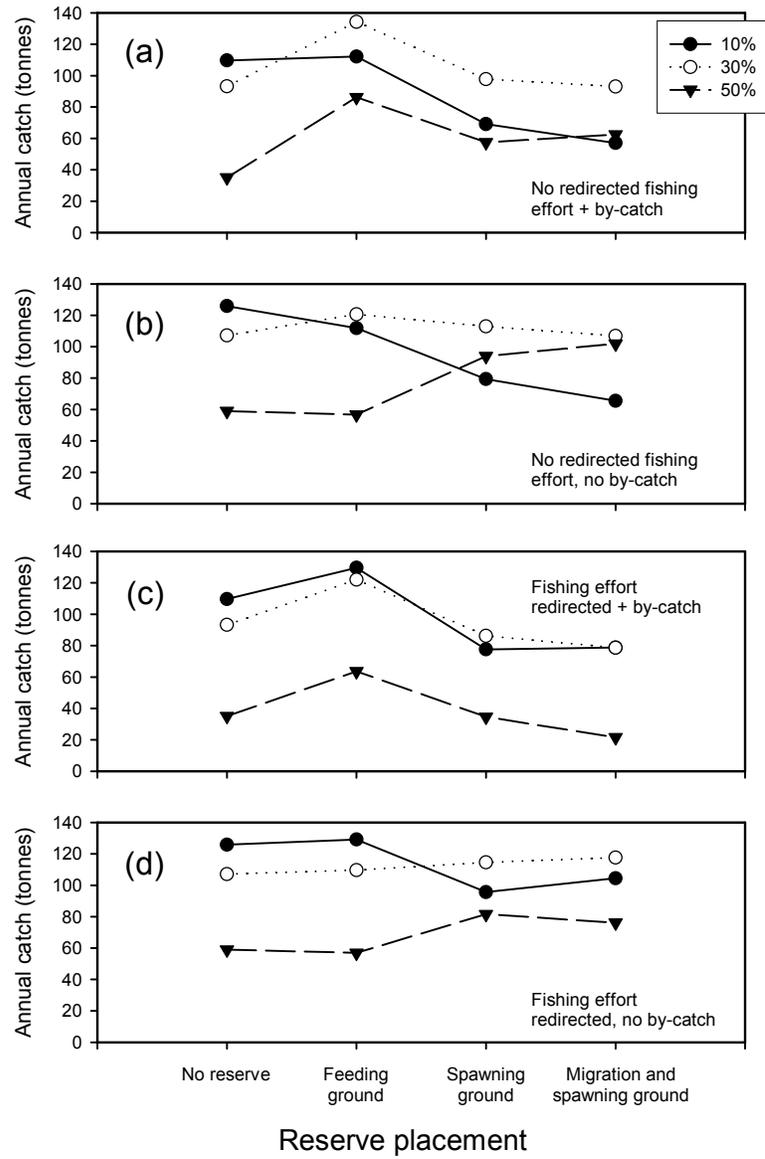


Figure 3: Effects of reserves on fish catches. Results show the average annual catch over the full 100 year simulations for three different levels of fishing: light (10% of stock caught per year), moderate (30% of stock caught per year) and intense (50% of stock caught per year).

juveniles are vulnerable to by-catch mortality. This is because they eliminate by-catch mortality on the nursery grounds (= feeding grounds). Reserves that protect juveniles prevent growth overfishing, significantly increasing yield-per-recruit. In cases without by-catch, protecting the stock where it was most vulnerable (spawning grounds) produces larger catches.

Figure 4 shows the present value of catches discounted at 10% over the 100 year sample periods. Discounting tends to devalue reserves, more so at lower fishing intensities than high. This is because discounting favours short-term profit at the cost of longer-term sustainability. However, reductions of present value by reserves over open access were relatively small at the highest fishing intensity. Certainly, such costs should be traded off against the clear benefit of increased spawning stock biomass that reserves offer. Reserves that eliminate by-catch (on the feeding grounds) were useful in increasing the present value of catches (Figures 4a & c).

Discussion and Conclusions

Several conclusions can be drawn from this model. Fixed location marine reserves can be beneficial to migratory species, especially in places where fishing effort is high. Almost all reserve scenarios produced substantial gains in spawning stock biomass. The lower the level of spawning stock, the greater the risk of recruitment overfishing or stock collapse (Lauck et al. 1998, Mangel 2000). In terms of catch, reserve benefits were closely linked to fishing intensity. Reserves tended to increase catches at high intensities and decrease them when fishing was light.

Although redirection of fishing effort reduces benefits from increased spawning stock biomass, in general redirection did not negate benefits, except in the case where a reserve redirected effort from a place where the stock was less vulnerable to one where it was more vulnerable. This concern has been raised by others who caution that establishing reserves could do more harm than good, for example by redirecting effort into fish nursery grounds (Horwood et al. 1998). However, this problem can easily be overcome by establishing reserves in networks that protect vulnerable sites and concentrate fishing effort into places where the stock is less prone to capture. Reserves that protected juveniles from by-catch mortality were highly effective at increasing catch.

This paper demonstrates an expanded approach to modeling that is computationally simple, but more effectively captures the dynamics of migratory species. The findings run

counter to those from simpler models that ignore spatial heterogeneity in the behaviour of fish and fishers. Fishers have long taken advantage of migratory behaviour and habitat use patterns to target areas with the greatest CPUE. Protected area strategies can also take advantage of such behaviour to offer protection to places where it will be most effective.

Such an expanded modeling approach is essential for properly evaluating effects of marine reserves. Nevertheless, our model did not account for any effects of reserve protection on habitat and the consequences this could have for stock protection. It could easily be extended to achieve this. Fish could be programmed to survive better in reserves, or grow faster in them as habitat complexity increases over time. Furthermore, the effects of behavioural modification could be accounted for by allowing fish to spend longer in reserves on their migrations as they respond to higher quality habitat within them. Such modifications would likely increase the magnitude of reserve effects detected. However, the model should also be extended to more realistically account for changes in fishing patterns that reserve establishment might create (see Holland in press for an example).

The potential benefits of reserves for migratory species are just beginning to be recognized (Hutchings 1995, Guenette and Pitcher 1999, Guenette et al. 1999, Norse et al. in press, Roberts in press). In fact, fishery managers have long been experimenting with a form of reserve for migratory species - the single species closure. It is common practice to close areas to fishing to protect juvenile fish from capture to increase yield-per-recruit (Rogers 1997), or to protect spawning aggregations (Hutchings 1995, Johannes 1998). Fully-protected reserves are qualitatively different from such closures because they offer habitat benefits that single species measures don't. These could critically augment reserve efficacy through increases in habitat complexity and carrying capacity, and improved feeding conditions. Fully-protected reserves offer a more holistic, ecosystem level approach to management.

Migratory species, especially large pelagics like billfish, tunas and sharks, are among the most economically valuable of fish but present approaches to management are failing them badly (Safina 1998, Norse et al. in press). We desperately need to offer greater protection to this spectacular but vulnerable fauna or some species might disappear altogether (Safina 1998, Roberts & Hawkins 1999). Establishing fully-protected reserves in areas where those species are most under pressure from fisheries could help maintain their long-term survival.

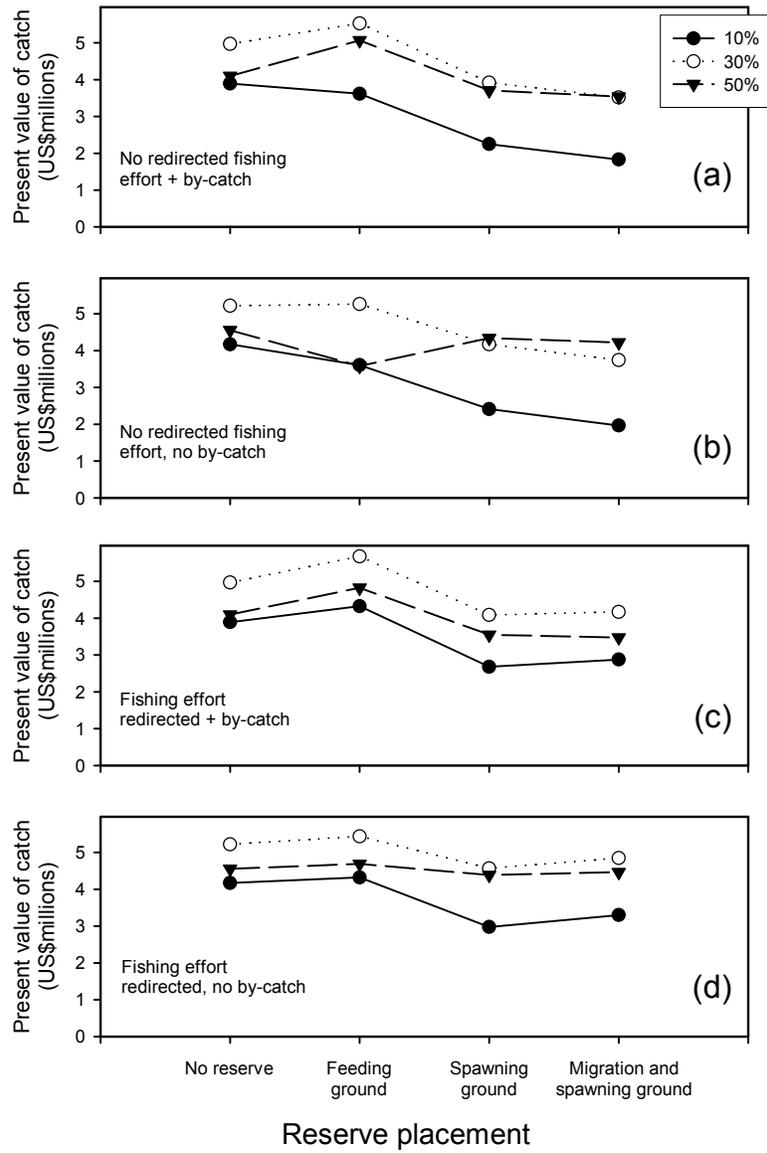


Figure 4: Effects of reserves on the present value of fish catches, discounted at 10% over 100 years of catch data for each simulation run at three different levels of fishing: light (10% of stock caught per year), moderate (30% of stock caught per year) and intense (50% of stock caught per year).

Acknowledgements

We would like to thank The Pew Charitable Trusts for supporting this work. We are indebted to Dan Lloyd of HPS Inc. who answered our queries about the use of STELLA. Thanks are also due to Rachel Graham, Julie Hawkins, Will Heyman and Elliott Norse for helpful discussions on how to make reserves effective for migratory species.

References

- Auster, P. J. & R. J. Malatesta. (1995). Assessing the role of non-extractive reserves for enhancing harvested populations in temperate and boreal marine systems. Pages 82-89 in N.L. Shackell and J.H.M. Willison, eds. Marine protected areas and sustainable fisheries. Science and Management of Protected Areas Association, Wolfville, Nova Scotia.
- Auster, P. J., R. J. Malatesta & C. L. S. Donaldson. (1997). Distributional responses to small-scale habitat variability by early juvenile silver hake, *Merluccius bilinearis*. Environmental Biology of Fishes 50: 195-200.
- Auster, P. J. & R. W. Langton. (1999). The effects of fishing on fish habitat. American Fisheries Society Symposium 22: 150-187.
- Allison, G. W., J. Lubchenco & M. H. Carr. (1998). Marine reserves are necessary but not sufficient for marine conservation. Ecological Applications 8: S79-S92.
- Appeldoorn, R. S., C.W. Recksiek, R.L. Hill, F.E. Pagan & G.D. Dennis. (1997). Marine protected areas and reef fish movements: the role of habitat in controlling ontogenetic migration. Proceedings of the 8th International Coral Reef Symposium, Panama 2: 1917-1922.
- Bohnsack, J. A. (1998). Application of marine reserves to reef fisheries management. Australian Journal of Ecology 23: 298-304.
- Conrad, J. M. (1999). The bioeconomics of marine sanctuaries. Journal of Bioeconomics 1: 205-217.
- Cushing, D.H. (1988). The Provident Sea. Cambridge University Press, Cambridge.
- Daan, N. (1993). Simulation study of effects of closed areas to all fishing, with particular reference to the North Sea ecosystem. Pages 252-258 in K. Sherman, L. M. Alexander & B. D. Gold, eds. Large Marine Ecosystems: Stress, Mitigation and Sustainability. A.A.A.S. Press, Washington, DC, USA.
- Dodson, J. J. (1997). Fish migration: an evolutionary perspective. Pages 10-36 in J.-G. J. Godin, ed., Behavioural Ecology of Teleost Fishes, Oxford University Press, Oxford.
- Gotceitas, V., S. Fraser & J. A. Brown. (1995). Habitat use by juvenile Atlantic cod (*Gadus morhua*) in the presence of an actively foraging and non-foraging predator. Marine Biology 123: 421-430.
- Gotceitas, V., S. Fraser & J. A. Brown. (1997). Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 54: 1306-1319.
- Gotceitas, V., D. A. Methven, S. Fraser & J. A. Brown. (1999). Effects of body size and food ration on over-winter survival and growth of age-0 Atlantic cod, *Gadus morhua*. Environmental Biology of Fishes 54: 413-420.
- Gerber, L. R., S. J. Andelman, L. W. Botsford, S. Gaines, A. Hastings, S. Palumbi, and H. P. Possingham. *In press*. Population models for marine reserve design: a synthesis. Ecological Applications.
- Guénette, S., T. Lauck & C. Clark. (1998). Marine reserves: from Beverton and Holt to the present. Reviews in Fish Biology and Fisheries 8: 251-272.
- Guénette, S. & T. J. Pitcher. (1999). An age-structures model showing the benefits of marine reserves in controlling overexploitation. Fisheries Research. 39: 295-303.
- Hannesson, R. (1998). Marine reserves: what would they accomplish? Marine Resource Economics 13: 159-170.
- Harden Jones, F. R. (1968). Fish Migration. Edward Arnold, London.
- Hastings, A. & L. Botsford. (1999). Equivalence in yield from marine reserves and traditional fisheries management. Science 284: 1-2.
- Heyman, W. D., R. T. Graham, B. Kjerfve & R. E. Johannes. *In press*. Whale sharks, *Rhincodon typus*, aggregate to feed on fish spawn in Belize. Marine Ecology Progress Series.
- Holland, D. S. & R. J. Brazee. (1996). Marine reserves for fisheries management. Marine Resource Economics 11: 157-171.
- Holland, D. S. *In press*. A bioeconomic model of marine sanctuaries on Georges Bank.
- Holland, K.M., P. Kleiber and S.M. Kajiura. (1999). Different residence times of yellowfin tuna, *Thunnus albacares*, and bigeye tuna, *T. obesus*, found in mixed aggregations over a seamount. Fishery Bulletin 97: 39-395.
- Horwood, J. W., J. H. Nichols & S. Milligan. (1998). Evaluation of closed areas for fish stock conservation. Journal of Applied Ecology 35: 893-903.
- Hutchings, J. A. (1995). Seasonal marine protected areas within the context of spatio-temporal variation in the northern cod fishery. Pages 39-47 in N.L. Shackell and J.H.M. Willison, eds. Marine protected areas and sustainable fisheries. Science and Management of Protected Areas Association, Wolfville, Nova Scotia.
- Jennings, S. & M. J. Kaiser. (1998). The effects of fishing on marine ecosystems. Advances in Marine Biology 34: 201-352.
- Johannes, R. E. (1998). The case for data-less marine resource management: examples from tropical nearshore finfisheries. Trends in Ecology and Evolution 13: 243-246.
- Kira, G. (2000). The Unforgettable Sea of Cortez. Baja California's Golden Age 1947-1977. The Life and Writings of ray Cannon. Cortez Publications, La Paz.
- Kramer, D. L., R. W. Rangeley & L. J. Chapman. (1997). Habitat selection: patterns of spatial distribution from behavioural decisions. Pages 37-80 in J.-G. J. Godin, ed., Behavioural Ecology of Teleost Fishes, Oxford University Press, Oxford.
- Lauck, T., C. W. Clark, M. Mangel & G. R. Munro. (1998). Implementing the precautionary principle in fisheries management through marine reserves. Ecological Applications 8: S72-S78.
- Lindholm, J. B., P. J. Auster & L. S. Kaufman. (1999). Habitat-mediated survivorship of juvenile (0-year) Atlantic cod *Gadus morhua*. Marine Ecology Progress Series 180: 247-255.
- Man, A., R. Law & N. V. C. Polunin. (1995). Role of marine reserves in recruitment to reef fisheries: a metapopulation model. Biological Conservation 71: 197-204.
- Mangel, M. (2000). On the fraction of habitat allocated to marine reserves. Ecology Letters 3: 15-22.
- Mangel, M. *In press*. Trade-offs between fish habitat and fishing mortality and the role of reserves. Bulletin of Marine Science.
- McClanahan, T. R. & B. Kaunda-Arara. (1996). Fishery recovery in a coral-reef marine park and its effects

- on the adjacent fishery. *Conservation Biology* 10: 1187-1199.
- Murawski, S. A., R. Brown, H.-L. Lai & P. J. Rago. *In press*. Large-scale closed areas as a fishery management tool: the Georges Bank experience. *Bulletin of Marine Science*.
- Murray, S. N. et al. (1999). No-take reserve networks: sustaining fishery populations and marine ecosystems. *Fisheries* 24(11): 11-25.
- Norse, E. A. et al. *In press*. Marine reserves for large pelagic fishes. Chapter 20 in E. Norse & L. Crowder, eds. *Marine Conservation Biology: The Science of Maintaining the Sea's Biodiversity*. Island Press, Washington DC, USA.
- Pezzey, J. C. V., C. M. Roberts & B. T. Urdal. (2000). A simple bioeconomic model of a marine reserve. *Ecological Economics* 33: 77-91.
- Polacheck, T. (1990). Year around closed areas as a management tool. *Natural Resource Modeling* 4: 327-354.
- Quinn, J., S. R. Wing & L. W. Botsford. (1993). Harvest refugia in marine invertebrate fisheries: models and applications to the red sea urchin, *Strongylocentrotus franciscanus*. *American Zoologist* 33: 537-550.
- Roberts, C. M. (1997). Ecological advice for the global fisheries crisis. *Trends in Ecology and Evolution* 12: 35-38.
- Roberts, C. M. *In press*. Benefits of fully-protected marine reserves for migratory species. *Reviews in Fish Biology and Fisheries*.
- Roberts, C.M. & R.F.G. Ormond. (1987). Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Mar. Ecol. Prog. Ser.* 41: 1-8.
- Roberts, C. M. & J. P. Hawkins. (1999). Extinction risk in the sea. *Trends in Ecology and Evolution* 14: 241-246.
- Rogers, S. I. (1997). A Review of Closed Areas in the United Kingdom Exclusive Economic Zone. Science Series Technical Report No. 106. Centre for Environment Fisheries and Aquaculture Science, Lowestoft, UK.
- Russ, G. R. & A. C. Alcala. (1996). Do marine reserves export adult fish biomass? Evidence from Apo Island, Central Philippines. *Marine Ecology Progress Series* 132: 1-9.
- Safina, C. (1998). *Song for the Blue Ocean*. Henry Holt and Company, New York.
- Sanchirico, J. & J. Wilen. (1996). Bioeconomics of marine reserves. Paper prepared for the 7th Annual Conference of Environmental and Resource Economists, Lisbon, Portugal, June 27th -29th 1996.
- Sanchirico, J. & J. Wilen. (1998). Marine reserves: is there a free lunch? *Forthcoming*.
- Sladek Nowlis, J. S. & C. M. Roberts. (1997). You can have your fish and eat it too: theoretical approaches to marine reserve design. *Proceedings of the 8th International Coral Reef Symposium, Panama* 2: 1907-1910.
- Sladek Nowlis, J. S. & C. M. Roberts. (1999). Fisheries benefits and optimal design of marine reserves. *Fishery Bulletin* 97: 604-616.
- Sladek Nowlis, J. S. & M. M. Yoklavich. (1998). Design criteria for rockfish harvest refugia from models of fish transport. Pages 32-40 in M. M. Yoklavich, editor. *Marine harvest refugia for west coast rockfish: a workshop*. NOAA Technical Memorandum NMFS-SWFSC-255, Silver Springs, Maryland, USA.
- Szedlmayer, S. T. & J. C. Howe. (1997). Substrate preference in age-0 red snapper, *Lutjanus campechanus*. *Environmental Biology of Fishes* 50: 203-207.
- Szedlmayer, S. T. & K. W. Able. (1996). Patterns of seasonal availability and habitat use by fishes and decapod crustaceans in a southern New Jersey estuary. *Estuaries* 19: 697-709.
- Tupper, M. & R. G. Boutillier. (1995). Effects of habitat on settlement, growth, and post-settlement survival of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 52: 1834-1841.
- Williamson, M. (1974). *The Analysis of Biological Populations*. Edward Arnold, London.

Questions:

Anthony Charles: The Scotian Shelf Haddock Box is a closed area for haddock species. It was proposed and maintained by fishermen. Scientists and economists went along with it, but they often say, "A dead fish is a dead fish"; it does not matter if you kill them on spawning grounds or if you kill them elsewhere. Have you faced that argument on the natural science side?

Callum Roberts: People do remark that protecting spawning grounds is bad, because you are just pushing fishing effort to other places. The answer to that is to put reserves in a network to capture those vulnerable points. A dead fish is a dead fish, but if you see dead fish with their gonads full, then obviously they have not completed their reproductive cycle, and they are unable to reproduce. Fishing on spawning grounds is particularly damaging because it disrupts spawning activity. If trawlers go in and disperse spawning fish, what is the effect on fertilization rates and reproductive success? As a precaution, closure on spawning grounds will give significant benefits.

Dirk Zeller: Groupers are more vulnerable to fishing when they are migrating to spawning grounds than at spawning grounds themselves. Sometimes it is an individual issue whether spawning grounds are important.

Jim Seger: In modeling, I thought it was not an issue of "a dead is a dead fish". It might be helpful to close down high CPUE areas.

Callum Roberts: We need to move to a new position where that kind of vulnerability is protected or the industry will be gone when the stock collapses from recruitment failure.

Table 1: Parameters used in the model for each of the twelve size classes of fish.

Fish size class	Natural mortality (% per year)	Fishing mortality (% per year)			Fecundity (eggs per fish)	Initial stock size (million fish) ³	Weight per fish (kg)	Price of fish (US\$ per kg)
		Light	Moderate	Intense				
1	Stock dependent ¹	2	2	2	0	620924	0.03	0
2	30	5	20	40	80	84	0.12	2.25
3	20	5	20	40	270	58	0.48	2.25
4	20	5	20	40	640	42	1.44	2.25
5	20	5	20	40	1250	33	2.88	3
6	20	10	30	50	2160	25	5.18	3
7	20	10	30	50	3430	18	8.29	3
8	20	10	30	50	5120	13	11.6	3.75
9	20	15	40	60	7200	10	15.08	3.75
10	20	15	40	60	10000	7	18.1	3.75
11	20	15	40	60	13310	5	19.91	3
12	20	15	40	60	17280	3	21.9	3

¹Mortality of size class 1 fish was density-dependent, with a Beverton-Holt recruitment function assumed (see text).

²In models with by-catch, size class 1 fish were subjected to by-catch mortality from a different fishery with 13% mortality under the light fishing regime, 23% mortality under the moderate, and 53% under the heavy regime.

³The initial stock size was set at the equilibrium population size at the end of a 100 year run under the light fishing regime with no by-catch and open access.

A BIOECONOMIC ANALYSIS OF TROPICAL MARINE RESERVE-FISHERY LINKAGES: MOMBASA MARINE NATIONAL PARK

Lynda D. Rodwell¹, Edward B. Barbier¹, Callum M. Roberts¹ and Tim R. McClanahan²

¹Environment Department, University of York, York, YO10 5DD, U.K.

²Coral Reef Conservation Project, P.O. Box 99470, Mombasa, Kenya.

All correspondence to: Lynda Rodwell

Email: ldr102@york.ac.uk

Abstract

The excessive and unsustainable exploitation of our marine resources has led to the promotion of marine reserves as a fisheries management tool. Marine reserves – areas in which fishing is restricted or prohibited - can offer opportunities for the recovery of exploited stock and fishery enhancement. This paper focuses on the contribution of fully-protected tropical marine reserves to fishery enhancement through the development of a bioeconomic model of marine reserve-fishery linkages. The consequences of reserve establishment on equilibrium biomass and fishery catch levels are evaluated. In contrast to earlier models, this study highlights the roles of both adult (and juvenile) migration and larval dispersal between the reserve and fishing grounds by employing a spawner-recruit model. Uniform larval dispersal, uniform larval retention and complete larval retention combined with zero, moderate and high adult migration scenarios are analysed in turn. The numerical simulations are based on Mombasa Marine National Park, Kenya – a fully-protected coral reef marine reserve comprising approximately 30% of former fishing grounds. The establishment of this fully-protected marine reserve leads to an increase in total fish biomass. If the fishery is moderately to heavily exploited, total fishery catch will be greater with the reserve in all scenarios of adult and larval movement. If the fishery faces low levels of exploitation, catches can be optimised without a reserve but with controlled fishing effort. With high adult migration from the reserve, catches are optimised with the reserve. The optimal area of the marine reserve is found to be between 15% and 25% (depending on population growth rate) if fishing intensity in the adjacent fishery does not exceed 40% of exploitable biomass. If fishing effort can not be controlled, larger reserves are required to maximise catch. Since fishing effort in tropical fisheries is inherently difficult to regulate, marine reserves prove to be an essential component of their management.

Keywords: *bioeconomics, fully-protected marine reserves, fisheries management, adult and juvenile migration, larval dispersal, larval retention, spawner-recruit, coral reefs, optimal reserve area.*

Introduction

There is growing concern over the excessive and unsustainable exploitation of our marine resources and fisheries scientists, marine biologists and now economists are searching for possible solutions to the problem. Conventional fisheries management tools such as quotas, gear restrictions and season lengths have failed to produce sustainable fisheries catches (Roberts and Polunin 1991, Munro 1996). This is particularly the case in developing tropical countries where much exploitation is for subsistence and few resources are available for management. Marine reserves have been proposed as an alternative or complementary fisheries management tool, offering opportunities for the recovery of exploited stock, fishery enhancement, biodiversity conservation, habitat protection and research (Bohnsack 1990, Roberts and Polunin 1991,1993, Rowley 1994, Russ and Alcala 1996a,b, PDT 1990).

This paper highlights the potential contribution of fully-protected tropical marine reserves to fishery enhancement through the development of a bioeconomic marine reserve-fishery model. We define a fully-protected marine reserve as an area in which all fishing and extraction are prohibited. Such marine reserves could enhance adjacent fisheries through adult and juvenile ‘spillover’ and ‘larval transport’. Following protection, as stocks inside reserves build up, the reserve becomes more densely populated leading to a net emigration of adults and juveniles to fishing grounds, or otherwise the ‘spillover effect’ (Bohnsack 1996). This ‘spillover effect’ has been predicted by theory and modelling (Polacheck 1990, DeMartini 1993, Man et al. 1995) but has seldom been tested in the field primarily due to the complexity of reef communities, the lack of fish-catch times series data and the problem of study design (Roberts and Polunin 1993). Due to the larger stocks of bigger fish, reserves could also contribute to fisheries by increasing egg production in the reserve by orders of magnitude (Davis and Dodrill 1989, PDT 1990). Eggs and larvae may disperse, reducing the chances of recruitment failures in the fishing grounds. The two processes of adult and juvenile ‘spillover’ and ‘larval transport’ are critical to the success of marine reserves as fishery enhancement tools and are the focus of this paper.

The model developed here follows those of Holland and Brazeel (1996), Sanchirico and Wilen (1996, 1998), Conrad (1999) and Pezzey et al. (2000). These models have focused on either adult and juvenile movement in temperate sites (e.g. Conrad 1999) or larval transport in tropical sites (e.g. Pezzey et al. 2000). For some species adults are highly vagile and larvae disperse widely. For others adults can be mainly sedentary (Roberts 1996). Marine reserves can potentially have contrary effects depending on the characteristics of the species involved. Many authors have contrasted the behaviour of species in tropical and temperate systems, suggesting that coral reefs are dominated by species that are sedentary as adults and temperate regions by those that are mobile. However, in reality there are sedentary and mobile species in both and some tropical species experience limited migration (Appeldoorn et al. 1997). McClanahan and Mangi (2000) found moderate¹ dispersal of parrotfishes, emperors and rabbitfishes in their study of spillover effects from Mombasa Marine National Park in Kenya. Adult 'spillover' could be an important factor in the tropics, though it may be limited to a region of a few hundred metres beyond the reserve boundary.

The objective of this paper is to examine the effects of marine reserves on the equilibrium levels of biomass and catch in a tropical fishery under different conditions of adult and larval movement. In contrast to earlier models, we model these movement processes explicitly through a spawner-recruit model. This allows for distinctly different behavioural and movement patterns of adults and larvae to be explored. We first develop the basic theoretical model describing the biological dynamics of two homogeneous populations – in the reserve and fishing grounds – and then add exploitation to the system. We examine the conditions under which the biological steady state can be attained and test the local stability about this state. A spawner-recruit model is then used to describe the population dynamics with explicit adult and juvenile migration and larval dispersal effects on recruit production. The cases of uniform larval dispersal, 50% uniform larval retention and complete larval retention combined with zero, moderate and high levels of adult migration are analysed in turn. Modelling these various scenarios proves a valuable exercise in light of the difficulty in

estimating 'spillover' effects and larval transport in the field. In a second simulation we consider the optimal area of the reserve and catch intensity in the fishery. The numerical simulations are based on data from Mombasa Marine National Park, Kenya.

The general model of marine reserve-fishery linkages

The purpose of this section is to develop a deterministic bioeconomic model in discrete time which describes the interaction between the fish stock in a fishing ground and that of an adjacent marine reserve. The model is used to assess the impact of marine protection on the steady state fish biomass and catch by contrasting the with and without reserve biomass and catch levels.

A typical fisheries model employs a single stock equation which describes the changes of stock X from one time period to the next. To model the possible population dynamics between a marine reserve and an adjacent fishing ground, it is necessary to sub-divide the stock into two distinct populations of X_1 and X_2 which occupy Area 1 – the reserve – and Area 2 – the fishing ground – respectively (figure 1). We assume that there is no loss of fish or larvae to areas inaccessible to fishers. This implies that if the fish are not in the protected region they are exploitable. The marine reserve is fully-protected, therefore the only form of exploitation is catch, H , from the fishing ground. The two bi-directional movement processes between the reserve and the fishing ground are described by T_R , recruit transfer and M_a , the migration of adults and juveniles.

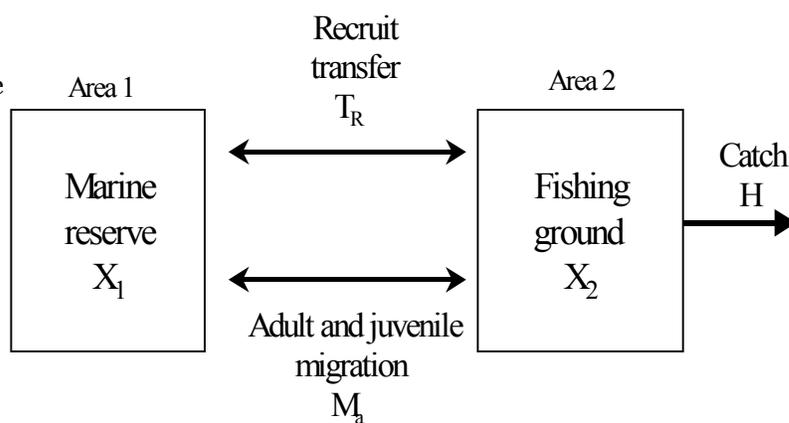


Figure 1: Marine reserve - fishery linkages - illustrating recruit transfer, T_R , and adult and juvenile migration, M_a , between a fully-protected marine reserve and a fishing ground.

¹ Based on Polacheck (1990) and DeMartini (1993) measures of transfer rates.

Biological dimension

If $X_{1,t}$ denotes the biomass of the population in the reserve at time t and $X_{2,t}$ represents the biomass of the population in the fishing ground at time t , the equations describing the adjustment of the resource stock in the absence of exploitation are:

$$X_{1,t+1} = X_{1,t} + G(X_{1,t}) - M_a(\bar{X}_{1,t}, \bar{X}_{2,t}) - T_R(R_{1,t}, R_{2,t}, \alpha_1, \theta) \quad (1)$$

$$X_{2,t+1} = X_{2,t} + G(X_{2,t}) + M_a(\bar{X}_{1,t}, \bar{X}_{2,t}) + T_R(R_{1,t}, R_{2,t}, \alpha_1, \theta) \quad (2)$$

where $G(X_{1,t})$ and $G(X_{2,t})$, are the net biological growth functions of each population.

$M_a(\bar{X}_{1,t}, \bar{X}_{2,t})$ is the net migration between the reserve (Area 1) and the fishing ground (Area 2) of adults and juveniles, where the density of population i is given by $\bar{X}_{i,t} = X_{i,t}/A_i$, $i = 1, 2$. A_i is the area of 'i' in hectares. This assumes that area is proportional to carrying capacity and so space is homogenous. If $M_a(\bar{X}_{1,t}, \bar{X}_{2,t})$ is positive, there is a net migration out of the reserve. If $M_a(\bar{X}_{1,t}, \bar{X}_{2,t})$ is negative, there is a net migration into the reserve. Similarly, the transfer of recruits due to larval dispersal, $T_R(R_1, R_2, \alpha_1, \theta)$ can be positive or negative. α_1 is the proportion of management area protected i.e. $\alpha_1 = A_1/A$, where A_i is the area of the reserve and A represents the total management area. $R_{1,t}$ and $R_{2,t}$ represent the recruit production of populations X_1 and X_2 respectively at time t . θ is the degree of larval retention.

Economic dimension

When renewable resources such as fish are exploited commercially, it is common to assume that the rate of catch per unit time is a function of both the size of the exploitable stock and the economic inputs devoted to exploitation, i.e. $H_t = H(X_t, E_t)$ where H_t is the catch, X_t is the exploitable biomass and E_t is the fishing effort (measured in numbers of boats, fishers or number of fishing hours) in time period t . Fishing effort is determined by the level of profits. However, for this model, we assume that in tropical fisheries the level of fishing effort is determined by the level of exploitable fish biomass i.e. $E_t = E(X_{2,t})$. Many tropical fisheries are dominated by subsistence and semi-

subsistence fishers. We assume that if fish are plentiful, fishing effort will increase and if fish are scarce, fishing effort will decline. Therefore, we can say $H_t = H(X_{2,t}, E(X_{2,t}))$. We simplify this by writing catch as a function of exploitable fish biomass $H_t = h(X_{2,t})$. In fact, we have evidence to support this assumption (appendix 1)

Dynamical system

These assumptions allow us to solve the two dimensional dynamical system (3) and (4) which describes the link between a fully-protected marine reserve and the adjacent fishery.

$$X_{1,t+1} = X_{1,t} + G(X_{1,t}) - M_a(\bar{X}_{1,t}, \bar{X}_{2,t}) - T_R(R_{1,t}, R_{2,t}, \alpha_1, \theta) \quad (3)$$

$$X_{2,t+1} = X_{2,t} + G(X_{2,t}) - h(X_{2,t}) + M_a(\bar{X}_{1,t}, \bar{X}_{2,t}) + T_R(R_{1,t}, R_{2,t}, \alpha_1, \theta) \quad (4)$$

where $h(X_{2,t})$ is the catch from fishing ground (Area 2) at time t . Given the values for $X_{1,0}$ and $X_{2,0}$ the system can be iterated forward in time to equilibrium (X_1^*, X_2^*) . Given appropriate functional forms, a corresponding value h^* can be determined at this equilibrium.

Steady state equilibrium

Depending on the functional forms of $G(\cdot)$, $M_a(\cdot)$ and $T_R(\cdot)$ the system described by (3) and (4) may display a variety of dynamic behaviours. It is possible that the system may converge to one or more steady states, have periodic cycles or even deterministic chaos. In the long run steady state, each population X_1 and X_2 is constant. i.e. $X_{1,t+1} = X_{1,t} = X_1$ and $X_{2,t+1} = X_{2,t} = X_2$. The steady state equilibria of the system are found by searching for pairs of (X_1^*, X_2^*) which satisfy $U(X_1^*, X_2^*) = X_{1,t+1} - X_{1,t} = 0$ and $V(X_1^*, X_2^*) = X_{2,t+1} - X_{2,t} = 0$:

$$U(X_1^*, X_2^*) = G(X_1^*) - M_a(\bar{X}_1^*, \bar{X}_2^*) - T_R(R_1^*, R_2^*, \alpha_1, \theta) = 0 \quad (5)$$

$$V(X_1^*, X_2^*) = G(X_2^*) - h(X_2^*) + M_a(\bar{X}_1^*, \bar{X}_2^*) + T_R(R_1^*, R_2^*, \alpha_1, \theta) = 0 \quad (6)$$

We tested for local stability about this equilibrium (appendix 2).

A spawner-recruit model of marine reserve-fishery linkages

In this section we move from the general model to a more specific model using a spawner-recruit relationship and particular functional forms to explicitly model both adult, juvenile and larval movement. The spawner-recruit relationship allows us to make a distinction between population growth originating from recruit production, R , and the population that 'escapes' catch ($X-H$). Since benefits may accrue from both the 'spillover' of adults and juveniles and larval dispersal from the reserve to the fishing grounds, it is necessary to include both factors in the model (Russ and Alcala 1996a, 1996b, Rakitin and Kramer 1996). By adjusting the difference equation system (3) and (4) by using a spawner-recruit relationship we obtain:

$$X_{1,t+1} = (1 - \mu_1)[X_{1,t} - M_a(\bar{X}_{1,t}, \bar{X}_{2,t})] + R(X_{1,t}) - T_R(R_{1,t}, R_{2,t}, \alpha_1, \theta) \quad (7)$$

$$X_{2,t+1} = (1 - \mu_2)[X_{2,t} - h(X_{2,t}) + M_a(\bar{X}_{1,t}, \bar{X}_{2,t})] + R(X_{2,t}) + T_R(R_{1,t}, R_{2,t}, \alpha_1, \theta) \quad (8)$$

where: μ_1 and μ_2 are the natural mortality estimates of populations X_1 and X_2 respectively and $R(X_{1,t})$ and $R(X_{2,t})$ are the recruit production for populations X_1 and X_2 . $U(\cdot)$ and $V(\cdot)$ can now be written:

$$U(X_1^*, X_2^*) = -\mu_1 X_1^* - (1 - \mu_1)[M_a(\bar{X}_1^*, \bar{X}_2^*)] + R(X_1^*) - T_R(R_1^*, R_2^*, \alpha_1, \theta) \quad (9)$$

$$V(X_1^*, X_2^*) = -\mu_2 X_2^* - (1 - \mu_2)[h(X_2^*) - M_a(\bar{X}_1^*, \bar{X}_2^*)] + R(X_2^*) + T_R(R_1^*, R_2^*, \alpha_1, \theta) \quad (10)$$

Functional forms

We specify the following functional forms for catch, adult and juvenile migration, recruit production and recruit transfer:

Catch, H - The catch function which best fits the Kenyan artisanal fishery is that of a simple linear relation between catch and biomass:

$$H_t = \omega X_t \quad (11)$$

where ω represents fishing intensity as a proportion of exploitable fish biomass. The data used to establish the relation between biomass and catch were those available on observed biomass and recorded catch data for sites within the fishing ground². A full explanation of the derivation of the catch function is given in appendix 1.

Adult and juvenile migration, M_a - The migration function solely describes the movement of adults and juveniles since the biomass estimates employed are based on the observation of only adults and juveniles (McClanahan and Kaunda-Arara 1996). The most intuitively appealing form of the adult and juvenile migration function is a density-dependent function such as:

$$M_a(\bar{X}_1, \bar{X}_2) = \sigma \left[\frac{X_1}{A_1} - \frac{X_2}{A_2} \right] \quad (12)$$

This is the same as that used by Conrad (1999). By taking this relationship we assume the area is proportional to carrying capacity and is spatially homogeneous. We keep the model simple by excluding the possibility that some areas of habitat have a higher carrying capacity than others due to greater habitat quality and food availability.

A density-dependent migration function is possibly more relevant to coral reef environments than temperate since the majority of migration of adults and juveniles from the reserve is likely to be a response to growing fish densities in the reserve (Rakitin and Kramer 1996). In temperate regions the movement in and out of reserves may be due more to the migratory nature of many exploited species (Horwood et al. 1998).

This density-dependent function indicates that when density per unit area in the reserve exceeds density per unit area in the fishing ground there is a positive gradient of migration towards the fishing ground. σ indicates the propensity of animals in a population to migrate. It is possible that the migration of adults and juveniles may only begin when the density gradient has reached some "threshold level". However, for simplicity, so long as $\sigma > 0$ and the population densities are

² Sources of data: Coral Reef Conservation Project, Mombasa and Fisheries Department, Mombasa.

not equal, there is assumed to be some movement between the areas.³ The propensity of individuals to move is likely to be affected by the shape and design of the protected region. High edge-to-area ratios will encourage even mainly sedentary species to ‘spillover’ (Buechner 1987).

Recruit production, R_i and R_e - We adopt the Beverton-Holt recruitment function in which recruitment tends to an upper limit as spawning stock increases (Beverton and Holt 1957). Coral reef data seem to best fit this rather than the Ricker function, which indicates a decline in recruitment at high biomass levels (Ricker 1954, Guénette and Pitcher 1999). Taking a proportion of biomass X to be a proxy for spawning stock biomass, the Beverton-Holt recruit production function for a protected population ‘ i ’ is:

$$R_{i,t} = \frac{\varepsilon_1 X_{i,t}}{\gamma_i \varepsilon_1 X_{i,t} + \beta_i} \quad (13)$$

where:

$R_{i,t}$ is recruit production for population ‘ i ’ in time period t

$X_{i,t}$ is biomass of population ‘ i ’ in time period t

γ_i and β_i are recruitment parameter estimates for population ‘ i ’ for given initial natural growth rates.

ε_i is the proportion of the reserve population which is reproductively active. This was calculated from size class data⁴.

For an exploited population ‘ i ’ the Beverton-Holt recruit production function is:

$$R_{i,t} = \frac{\varepsilon_2 (X_{i,t} - H_{i,t})}{\gamma_i \varepsilon_2 (X_{i,t} - H_{i,t}) + \beta_i} \quad (14)$$

where ε_2 is the proportion of the exploited population which is reproductively active.

We make three assumptions about recruit production in the exploited population:

³ The propensity to migrate could alternatively be directly

$$\text{proportional to the density gradient i.e. } \sigma \propto \left[\frac{X_1}{A_1} - \frac{X_2}{A_2} \right]$$

⁴ These data were obtained by visual census of transects inside Mombasa Marine National Park. We take the average value over the period since the park’s establishment.

ε_2 is less than ε_1 for all time periods. i.e. a smaller proportion of an exploited population will be reproductively active than in an unexploited population because the largest fish will be caught first. Individual fish length is exponentially related to fecundity (usually $F=aL^3$) (Sadovy 1996). This is supported by the data even in the first time period.

ε_2 may vary over time but, since this represents the area which is constantly exploited, we treat it as a constant giving it the average value over the period since the park’s establishment.

The only spawners are those remaining after catch i.e. $\varepsilon_2(X-H)$ in each time period. Again a reasonable assumption, since it would be unrealistic to assume that every adult fish was able to spawn before being caught.

‘Recruit transfer’ T_R - There is some debate as to the extent to which reserves retain their larval output (Roberts 1997, 1998, Bellwood et al. 1998, Sale and Cowen 1998). We therefore simulate possible scenarios: uniform larval dispersal, 50% uniform larval retention and the extreme case of complete larval retention.

The recruit transfer function:

$$T_R = (1 - \theta)[(1 - \alpha_1)R_1 - \alpha_1 R_2] \quad (15)$$

for $0 < \theta < 1$

where θ is the degree of retention.

$\theta = 0$ represents zero retention i.e. uniform larval dispersal.

$\theta = 1$ represents a closed system (with respect to larvae) where each population simply replenishes itself with new recruits.

The degree of retention will depend on the relationship between dispersal distance and the reserve size (and shape). We take $\theta = 0.5$ i.e. 50% larval retention to be our third scenario.

Resource adjustment equations

Employing the above functional form specifications, the resource adjustment equations for the model are:

$$\begin{aligned}
 U(X_1^*, X_2^*) = & -\mu_1 X_1^* - (1 - \mu_1) \left[\sigma \left(\frac{X_1^*}{A_1} - \frac{X_2^*}{A_2} \right) \right] + \alpha_1 \left[\frac{\varepsilon_1 X_1^*}{\gamma_1 \varepsilon_1 X_1^* + \beta_1} + \frac{\varepsilon_2 (1 - \omega) X_2^*}{\gamma_2 \varepsilon_2 (1 - \omega) X_2^* + \beta_2} \right] \\
 & + (1 - \alpha_1) \theta \left[\frac{\varepsilon_1 X_1^*}{\gamma_1 \varepsilon_1 X_1^* + \beta_1} \right] - \alpha_1 \theta \left[\frac{\varepsilon_2 (1 - \omega) X_2^*}{\gamma_2 \varepsilon_2 (1 - \omega) X_2^* + \beta_2} \right] \quad (16)
 \end{aligned}$$

$$\begin{aligned}
 V(X_1^*, X_2^*) = & -\mu_2 X_2^* - (1 - \mu_2) \left[\omega X_2^* - \sigma \left(\frac{X_1^*}{A_1} - \frac{X_2^*}{A_2} \right) \right] + (1 - \alpha_1) \left[\frac{\varepsilon_1 X_1^*}{\gamma_1 \varepsilon_1 X_1^* + \beta_1} + \frac{\varepsilon_2 (1 - \omega) X_2^*}{\gamma_2 \varepsilon_2 (1 - \omega) X_2^* + \beta_2} \right] \\
 & - (1 - \alpha_1) \theta \left[\frac{\varepsilon_1 X_1^*}{\gamma_1 \varepsilon_1 X_1^* + \beta_1} \right] + \alpha_1 \theta \left[\frac{\varepsilon_2 (1 - \omega) X_2^*}{\gamma_2 \varepsilon_2 (1 - \omega) X_2^* + \beta_2} \right] \quad (17)
 \end{aligned}$$

Numerical Simulations

Introduction

These simulations are based on data from the case study site Mombasa Marine National Park, a fully-protected marine reserve in a coral reef environment. The park stretches the length of the coast and is physically bounded by the reef, only extending a few hundred metres beyond (see map in appendix 3). Since fishers are not able to fish in the rougher waters beyond the reef, they actually only fish on two sides of the rectangular park. This will have consequences for the benefits to them from 'spillover'. The model developed here does not directly take account of the shape and design of the park, which may be responsible for some 'loss' of larvae and adult spillover to inaccessible fishing areas beyond the reef. The model assumes that all areas beyond the park are exploitable.

The model describes the dynamics of two populations X_1 and X_2 . We treat these as two communities with representative life characteristics such as natural mortality rates, recruit production and movement patterns, rather than attempt to tackle the question of multispecies dynamics at work in coral reef environments.

In the first simulation, we test the significance of adult and larval movement on catch and biomass levels in the fishery for three different initial population growth rates of 10%, 35% and 60%

per annum. It is thought that 35% best represents the Mombasa case, but the other rates are used to test the sensitivity of results. In the second simulation, we test for the optimal size of the reserve for each of the three growth rates and the corresponding sustainable fishing intensity outside the reserve.

We used the computer program Stella for establishing the model and testing its sensitivity and stability.

Parameter estimates

One of the most difficult tasks was estimating growth parameters. Little is known about the overall growth of fish populations on coral reefs (Polunin et al. 1996). We, therefore, used three scenarios of initial growth 10%, 35% and 60% per annum and found matching natural mortality and recruit production parameters which result in this initial growth level. Using the spawner-recruit model with biomass estimates, we assume that growth of biomass involves recruitment. In reality, biomass may grow over the short term purely by increased size of individual fish in reserves and not by new recruits. However, there will come a time when this increase in fish size will lead to increased egg production and potentially, new recruits.

Parameters γ and β and μ were based on the overall growth of a population 100% of which is reproductively active. However, we acknowledge in the model the important effect protection has

on the reproductive activity of the protected population relative to the exploited population. In Mombasa, it was found that by 2000 (8 years after protection was fully enforced) the reproductive gradient between the populations was significant – approximately 70% to 20% of fish biomass (appendix 4). These levels of

reproductive activity are represented by ε_1 and ε_2 in the model. Ideally these would be variables in the model (rather than parameters) dependent on ‘time since protection’ and habitat quality. The parameter estimates used to solve the model are given in table 1.

Table 1: Parameter estimates and ranges for simulations

Note: For simulation 2 the value of α_1 was varied. With the changes in the initial values of X_1 and X_2 the recruitment parameters γ_1 and γ_2 also changed. The program was designed to make these changes automatically. All other parameters were kept the same.

Parameters	Estimates	Description
μ_1	0.2	Natural mortality of adult/juveniles in populations 1 and 2. Taken to be the same for both populations and based on ‘moderate’ estimates of Pauly (1980) and Pauly and Ingles (1981)
μ_2	0.2	
γ_1	0.0000269(10%)	Recruit production parameter estimates based on the initial values of X_1 . Low, medium and high initial growth rates indicated.
	0.0000143(35%)	
	0.0000096(60%)	
γ_2	0.0000115(10%)	Recruitment parameters for fishing ground population. Low, medium and high initial growth rates indicated.
	0.0000061(35%)	
	0.0000041(60%)	
γ	0.0000081(10%)	Recruitment parameters for without reserve scenario i.e. total population initial growth rate. Low, medium and high growth rates indicated.
	0.0000043(35%)	
	0.0000029(60%)	
β_1	0.1	Recruit production parameter estimate.
β_2	0.1	Fixed for all growth rates.
β	0.1	
ε_1	0.7	Proportion of unexploited population biomass reproductively active. Calculated from existing size classes data and length at first maturity estimates (appendix 4).
ε_2	0.2	Proportion of exploited population biomass reproductively active. Calculated from existing size classes data and length at first maturity estimates (appendix 4).
σ	0,100,500	Propensity of adults and juveniles to move between reserve and fishing ground: zero, moderate, high reflecting varying vagility of species. These values resulted in 0%, 5-12% and 15-50% of reserve biomass migrating to the fishing ground, respectively, depending on fishing intensity and larval retention levels.
θ	0,0.5,1	Retention of larvae - representing uniform dispersal, uniform 50% larval retention, complete larval retention respectively.
ω	0 to 1	Estimate of fishing intensity - a proportion of exploitable biomass:
α_1	800/2675	Proportion of management area protected = $A_1/(A_1+A_2)$

Results

The simulations were run for 30 years, which was always long enough to reach equilibrium. The populations usually reached equilibrium after about 10 to 15 years. This represents the time period it may take before the benefits of protection are realised. $t=0$ represents the time of reserve establishment. The initial biomass values were based on 150 kg/ha density inside and outside the park based on visual census estimates (McClanahan and Kaunda-Arara 1996) giving a total biomass of approximately 400 tonnes of fish in the management area.

Simulation 1 – effects of adult and larval movement

Mombasa Marine National Park comprises approximately 800 ha of the total 2675 ha of accessible management area – approximately 31%. This was the value of α_1 in this simulation. Figure 2 shows the variation in equilibrium catch for various levels of fishing intensity outside the reserve and the comparative catch without a reserve for a population with initial growth rate of 35% per annum.

2a. Zero adult migration with varying larval retention

2b. Moderate adult migration with varying larval retention

2c. High adult migration with varying larval retention

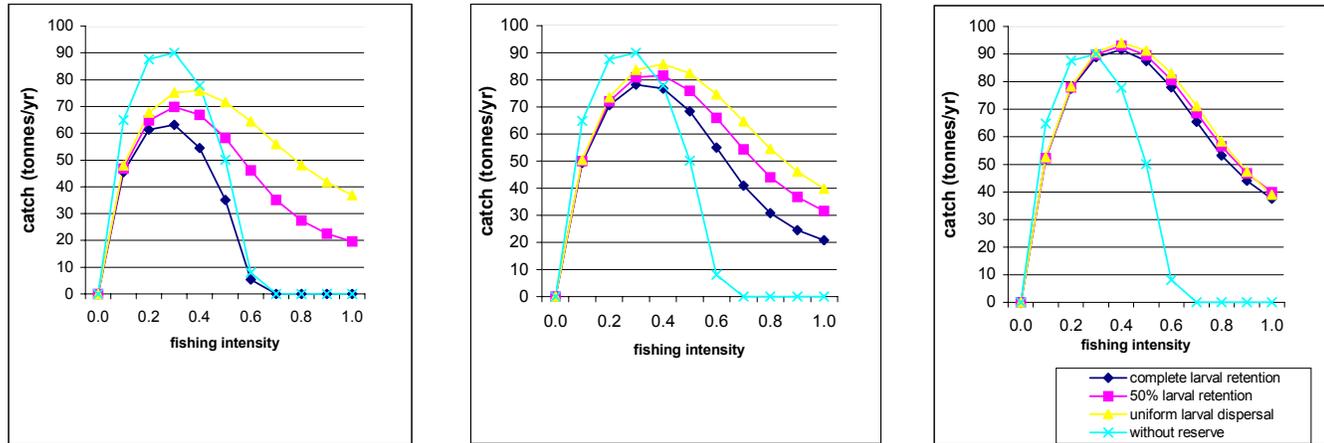


Figure 2: Fishery catch levels with various scenarios of adult and larval movement for a population with an initial growth rate of 35%.

The model was run for the three growth rates (10%, 35% and 60%). The shapes of the curves for all growth rates are much the same for each combination of adult and larval movement. The difference lies in the magnitude of catch obtainable under each initial growth rate. With 10%, 35% and 60% initial growth rates the maximum obtainable catches are approximately

50, 90 and 140 tonnes/year respectively (with a fishing intensity of between 30% and 40%). This is equivalent to 2.7, 4.8 and 7.5 tonnes/km²/year. The estimates of marine catches in this area have ranged from 3-13 tonnes/km²/year and maximum sustainable yields of 5-10 tonnes/km²/year (Obura 1999). The main results for catch levels are summarized in table 2.

Table 2: Results of Simulation 1: Conditions under which catch with the reserve (comprising 31% of the management area) can exceed catch without the reserve

Movement patterns		<i>Larval</i>		
		Complete retention	50% retention	Uniform dispersal
Adult and Juvenile	Zero	catch without > catch with fishery collapses at 70% fishing intensity	catch with > catch without at 45% fishing intensity	catch with > catch without at 40% fishing intensity
	Moderate	catch with > catch without at 40% fishing intensity	catch with > catch without at 35% fishing intensity	catch with > catch without at 30% fishing intensity
	High	catch with > catch without at 30% fishing intensity	catch with > catch without at 30% fishing intensity	catch with > catch without at 30% fishing intensity

For zero adult migration and fishing intensity above 40% of exploitable biomass, catch with the reserve exceeds catch without reserve for the case of uniform larval dispersal. With 50% larval retention, fishing intensity would have to exceed 45% of exploitable biomass before catch with the reserve exceeds catch without. For the closed system (with no adult or larval movement between areas), catch with the reserve clearly remains below catch without reserve.

For moderate adult migration and fishing intensity above 35-40% of exploitable biomass (depending on larval movement scenarios), catch with the reserve exceeds catch without reserve.

For high adult migration and fishing intensity above 30%, catch with the reserve exceeds catch without reserve for all larval movement scenarios.

If the management objective is to maximize catch levels, we should note that for zero and moderate adult migration the optimal solution can be found without a reserve when the fishing intensity is 30% of total biomass. It is interesting to observe that there is a very thin line between achieving the optimal fishing intensity without a reserve and it becoming preferable to reserve 31% of the grounds.

For high levels of adult migration, however, the optimal solution is found with the 31% reserve and fishing intensity in the neighbouring fishing ground is 40% of the exploitable biomass. Our results indicate that, the greater the level of adult migration the lower the fishing intensity at which it becomes preferable to have the reserve. However, we should comment that if adult migration from the reserve is too high $\sigma > 675$ approximately, the equilibrium becomes unstable. The fish fluctuate between the protected and unprotected regions due to the changing population density gradient. If adult migration out of the reserve were permanent, the benefits of stock build up would be nullified.

These optimal solutions depend on the assumptions that the fishing effort can be controlled and biomass levels are known. If this is the case, decision makers with the sole objective of maximising catch should be advised to restrict catch to 30% of total biomass and forget about the reserve if there is only low to moderate degree of adult 'spillover'. However, if effort can not be controlled, we need to look for the best obtainable solution under prevailing conditions of exploitation. If fishing intensity exceeds 45%, then it becomes preferable, from the point of view of maximising catch, to establish a reserve so long as there is at least some adult or larval movement out of it. The results also show that, if fishing

intensity exceeds 70% of the exploitable biomass, without the reserve, the fishery would collapse.

Predictably, total biomass was greater with a reserve under all conditions of larval and adult movement. Again, the shapes of the curves are the same for all initial growth rates and combination of movement patterns, but the equilibrium biomass magnitudes vary greatly. The maximum biomass levels (obviously under conditions of zero exploitation) were 600, 1100 and 1600 tonnes for the 10%, 35% and 60% scenarios. Figure 3 shows the patterns of biomass equilibrium for various scenarios of adult and larval movement under the initial population growth rate of 35% per annum.

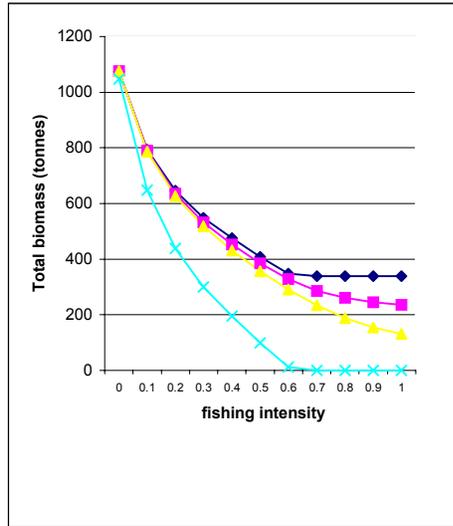
Both adult and larval movement patterns strongly influence the equilibrium levels of biomass. The higher the degree of larval retention in the reserve, the higher the biomass. The higher the degree of adult migration from the reserve, the lower total biomass in the fishery since a greater biomass becomes exploitable. Fishing intensities that are sustainable are inversely related to biomass levels. The results show that fishing intensities exceeding 70% will lead to a stock collapse in the absence of the marine reserve.

Simulation 2 – optimal area and fishing intensity to maximise catch

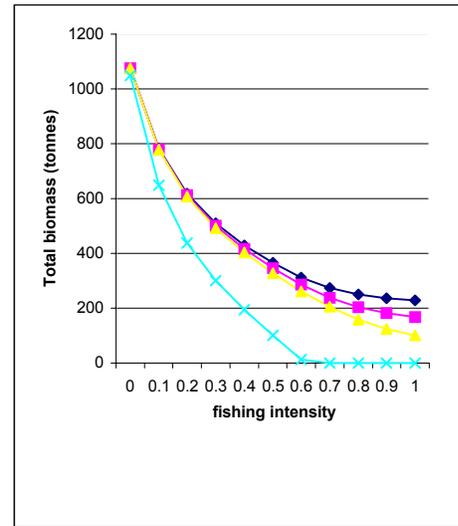
This simulation was run for the combination of moderate adult migration and 50% larval retention case. Figure 4 shows the relationship between equilibrium catch levels, area and fishing intensity for a population with a 35% initial growth rate. We can see the optimal size of the reserve is 25% when accompanied by a fishing intensity of 40% in the neighbouring fishing ground. The optimal catch was approximately 135 tonnes/year (6.7 tonnes/km²/year).

This combination of optimal area and fishing intensity was the same for a population with initial growth rate of 10% per annum but the optimal catch was 65 tonnes/year (3.2 tonnes/km²/year). For a population with an initial growth rate of 60% the optimal size of the reserve was found to be 15%, accompanied by a fishing intensity of 30% outside the reserve. This would yield a catch of 220 tonnes/year (9.7 tonnes/km²/year). The higher the initial growth rate, the higher the equilibrium biomass and catch levels obtained at 30 years. It is not surprising that with a higher equilibrium biomass, derived from the 60% initial growth rate, the optimal size of the reserve is less than with the lower initial growth rates. What may be surprising

3a. Zero adult migration with varying larval retention



3b. Moderate adult migration with varying larval retention



3c. High adult migration with varying larval retention

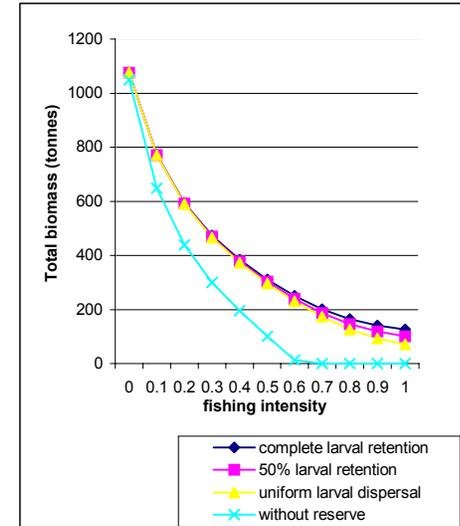
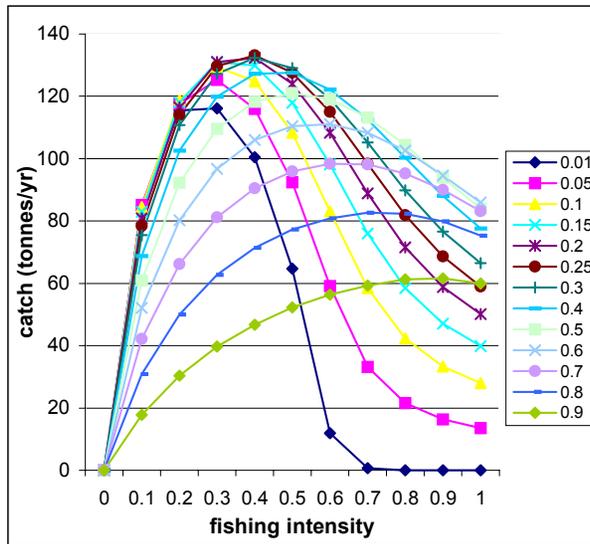


Figure 3: Total biomass with various scenarios of adult and larval movement for a population with an initial growth rate of 35%.

4a. Fishing intensity (x axis) - Lines represent area protected



4b. Area (x axis) - Lines represent fishing intensity

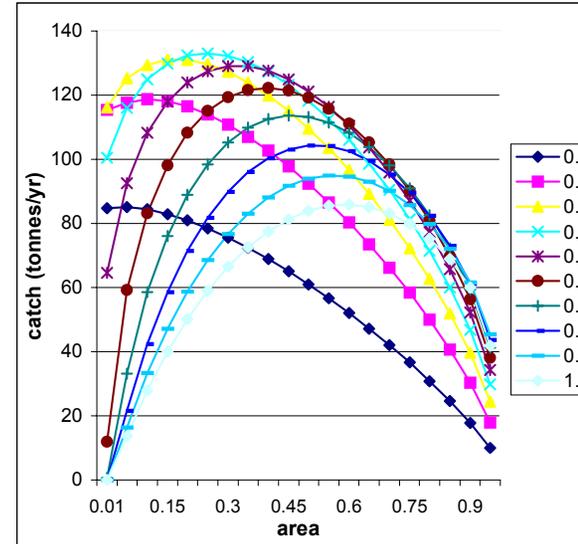


Figure 4: Optimal reserve size and fishing intensity for maximising fishery catch

is that the optimal fishing intensity outside the reserve is lower. However, we can see that this combination still yields a higher catch per unit area as we would expect.

The size of the reserve influences the optimal fishing intensity outside the reserve. For example for an initial growth rate of 35% for a reserve of: 0 to 20%, the optimal fishing intensity is 30%; 20 to 60%, the optimal fishing intensity can increase to 40%; 60 to 80%, a fishing intensity of 60% outside the reserve can be sustained. For a reserve of above 80% of the management area, it is possible to sustain fishing intensity of 80% in the remaining fishing ground due to the moderate levels of adult spillover and larval dispersal which replenish the stock.

Figure 5 simply illustrates the equilibrium biomass levels for various combinations of reserve area and fishing intensity. The results are intuitive. High levels of fishing intensity lead to lower biomass. Larger reserves lead to higher biomass. For the 'optimal' combination of 25% reserve and 40% fishing intensity the equilibrium total biomass would be approximately 640 tonnes.

Discussion

The movement patterns of adult and juvenile fish and larvae between a marine reserve and fishing ground are critical to the question of whether tropical marine reserves can enhance fishery production. If there is no movement, i.e. the system is closed, clearly the fishery can not benefit from the marine reserve, though protection will still lead to higher total biomass levels. Movement patterns will, to some extent, be determined by the location, shape, size and design of the reserve (Carr and Reed 1993, Stamps et al. 1987) and, additionally, the number of reserves in a network (Ballantine 1995). Without directly describing shape, location and design of the reserve and restricting our model to one reserve, we have chosen a variety of parameter values to reflect nine possible combinations of adult and larval movement patterns. For cases where there is some degree of either adult or larval movement to the fishing ground, our study supports those which promote marine reserves as a fishery enhancement tool in moderately to heavily exploited fisheries. We also advocate the use of marine reserves in circumstances where major uncertainties exist over the state of fishery biomass and catch levels.

In order to maximise catch, we recommend an optimal marine reserve size of 25% of the management area accompanied by controlled

fishing intensity of 40% of the exploitable biomass per annum. Where fishing effort is unmonitored and uncontrolled, we recommend larger reserves to protect fisheries against collapse. Our results are clearly limited to the assumptions made. Here we discuss each of these assumptions in turn and recommend further investigation where appropriate.

Recruit production

We have limited our recruit production function for the exploited population to one in which spawning in the fishing ground occurs after exploitation. However, exploitation occurs throughout the year, so it is plausible that some fish spawn before being caught, especially as many species spawn regularly over extended periods (Sadovy 1996).

Reserve creation will increase the reproductive capacity of the protected population. We incorporated parameters of reproductive capacity into the model based on data from Mombasa. Large (and most fecund) fish are most vulnerable to fishing and therefore their exploitation will create a gradient of reproductive capacity between protected and unprotected regions soon after the creation of a protected region. As time passes and large fish become less abundant, smaller fish will be exploited, particularly where gears are unselective. This suggests that the gradient of reproductive capacity, between the fishing ground and reserve, is likely to change over time. We have, however, restricted our analysis to a fixed set of parameters based on data from Mombasa. Further study could examine the consequences of the reproductive gradient being modelled as a variable.

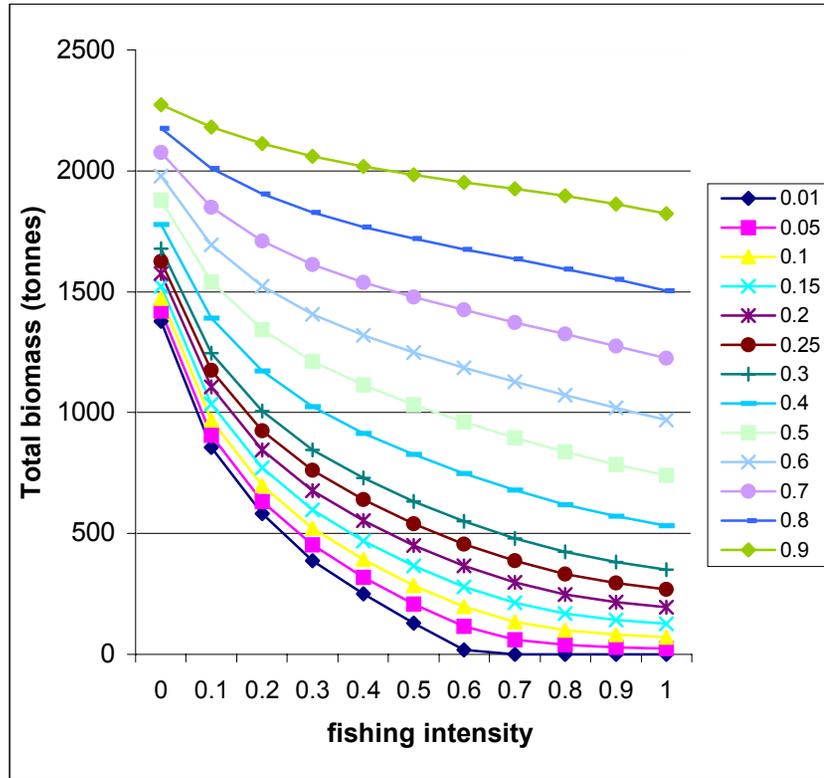
Growth rate

Accurate data on the growth rate of a population at various times since protection was unavailable. We based our estimate of initial growth rate of the population (35% per annum) on data of biomass levels in Mombasa Marine National Park in 2000 (8 years after protection) compared to pre-park levels. Ideally, for this spawner-recruit type model, we would have access to separate estimates for recruit production and natural mortality of each population.

Movement patterns of adults and larvae

We limited our choice of parameter values for σ to 0, 100 and 500. For each of these the equilibrium was stable. We could extend the sensitivity analysis to cover a wider range of values. We tested to find the point at which the equilibrium biomass and catch levels would become unstable. We found this to be at $\sigma = 675$ approximately. Another restriction to our model is the density-dependent form of the

5a. Fishing intensity (x axis) - Lines represent area protected



5b. Area (x axis) - Lines represent fishing intensity

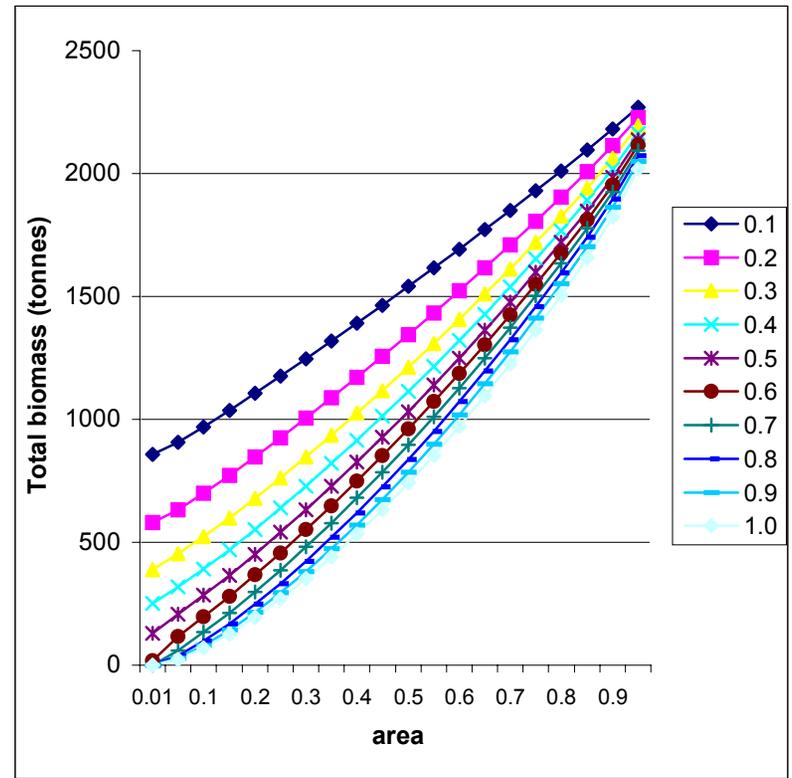


Figure 5: Total biomass with various reserve areas and fishing intensities

adult migration function. This form explains the oscillation of fish stocks between fishing ground and reserve for high levels of adult migration. In reality, perhaps some source-sink dynamics may come into play. With high 'permanent' adult migration out of the reserve fish stocks would not have the opportunity to build up. It would be beneficial to extend this study to consider other possible adult movement patterns.

The results for only three different levels of larval movement were shown in the simulations. However, we also tested the level of larval retention and fishing intensity at which it became preferable to establish a reserve when adult migration is zero. In fact, for each initial growth rate, if larval retention is 90%, the fishing intensity at which it becomes preferable to establish a reserve is between 60 and 70%.

Single species/Multispecies

We do not assess the effect of reserve creation on each species individually because of lack of matching species biomass and catch data. We simply address the question of the general state of total fishery biomass and catch by considering the community as a whole with generalised life characteristics of recruit production and natural mortality. In doing this, we treat the stock as single species. If complete data were available on each of the main commercial species we could extend the study to compare and contrast the effects of the reserve on each and, additionally, on species composition in the fishery.

Catch function

We measure fishing intensity as the percentage of exploitable biomass extracted each year. The linear catch function is an oversimplification but serves to show a range of comprehensive results. It also assumes that we know the level of the exploitable biomass in the fishery. Though we have visual census results for Mombasa and these give a good idea of the level of biomass, these data are not always available and so extrapolation to other locations may be difficult.

It would be useful to determine a relationship between effort and catch but to do so one needs to have an appropriate measure of effort in tropical fisheries. This may be the number and type of gears used. Different gears have varying effects on the fish community and the habitat. The number of fishers is not clearly related to the catch levels. For example, whether 30 or 15 fishers operate on the same pullseine the catch may be the same. Number of boats is an inappropriate measure of effort since many fishers do not use boats.

Habitat Quality/Spatial heterogeneity

With this model we do not tackle the question of habitat quality and spatial heterogeneity in the role of marine reserves. There is empirical evidence to support marine reserves as tools to enhance both fishery biomass (e.g. Russ 1985) and increase live coral cover (e.g. McClanahan 1994). Though they are inherently linked, little study has been done on the indirect benefits of habitat protection on fish biomass and, in turn, fishery catch.

Concluding Comments

Many of the world's tropical reef fisheries are overexploited and in danger of collapse. Best estimates indicate that the Mombasan fishery is currently being exploited at a level of at least 70% of the exploitable biomass (appendix 1). This study indicates that, had this fishing intensity persisted in the absence of this reserve, by 2010 the fishery would have crashed. To obtain optimal catch levels in Mombasa, measures should be taken to control fishing effort beyond the park boundaries. In the absence of controls, Mombasa may have to see an increase in the size of the reserve to secure future catches. Both of these measures have serious implications for local fishing communities. Implementing either policy successfully requires their co-operation and participation. Measures to compensate, retrain or offer alternative employment to displaced fishers and traders should be fundamental to the management process.

Fisheries managers keen to obtain the optimal catch from tropical fisheries need to tackle the ever growing problem of overexploitation and lack of enforcement of fisheries regulations. Quotas, gear restrictions and seasonal closures are often popular 'solutions'. If catches were monitored and controlled and we had perfect knowledge of the state of fish resources, marine reserves would not be needed as a tool to enhance fishery catches. Reserve benefits would be limited to biodiversity conservation, research and tourism. However, in reality in coral reef environments, fishing intensity is extremely difficult to control. Biological and economic uncertainties add weight to the case for marine protected areas as a buffer against stochastic events and fishery decline. Fully-protected marine reserves prove to be an essential component of tropical fisheries management.

References

- Appeldoorn, R.S., Recksiek, C.W., Hill, R.L., Pagan, F.E. and Dennis, G.D. (1997). Marine protected areas and reef fish movements: the role of habitat in controlling ontogenetic migration. *Proc. 8th Int. Coral Reef Symp., Panama 2*: 1917-1922.
- Ballantine, W.J. (1995). Networks of "no-take" marine reserves are practical and necessary. Chapter in *Marine protected areas and sustainable fisheries*, Shackell, N.L. and Willison, J.H.M., eds. Science and Management of Protected Areas Association, Wolfville, Nova Scotia.
- Bellwood, D.R., Leis, J.M. and Stobutzki, I.C. (1998). Fishery and reef management. *Science* 279: 2021-22
- Beverton, R.J.H. and Holt, S.J. (1957). On the dynamics of exploited fish populations. London: Chapman and Hall, 533pp.
- Bohnsack, J.A. (1990). The potential of marine fishery reserves for reef fish management in the U.S. Southern Atlantic. NOAA Technical Memorandum NMFS-SEFC-261.
- Bohnsack, J.A. (1993). Marine reserves: They enhance fisheries, reduce conflicts, and protect resources. *Oceanus* 36: 63-71.
- Bohnsack, J.A. (1996). Maintenance and recovery of reef productivity. Chapter in *Reef Fisheries*, Polunin, N.V.C. and Roberts, C.M. eds. Chapman and Hall Series in Fish Biology and Fisheries No. 20. Chapman and Hall, London. 477pp.
- Buechner, M. (1987). Conservation in insular parks: simulation models for factors affecting the movement of animals across park boundaries. *Biol. Conserv.* 41: 57-76.
- Carr, M.H. and Reed, D.C. (1993). Conceptual issues relevant to marine harvest refuges: examples from temperate reef fishes. *Can. J. Fish Aquat. Sci.* 50: 2019-28.
- Conrad, J.M. (1999). The bioeconomics of marine sanctuaries. *Journal of Bioeconomics* 1: 205-217.
- Davis, G.E. and Dodrill, J.W. (1989). Recreational fishery and population dynamics of spiny lobsters, *Panulirus argus*, in Florida Bay, Everglades National Park, 1998-1990. *Bulletin of Marine Science* 44(1): 78-88.
- DeMartini, E.E. (1993). Modeling the potential of fishery reserves for managing Pacific coral reef fishes. *Fishery Bulletin* 91: 414-427.
- Glaesel, H. (1997). Fishers, Parks and Power: the Socio-environmental dimensions of marine resource decline and protection on the Kenyan coast. PhD (Geography), University of Wisconsin- Madison, Madison.
- Guénette, S. and Pitcher, T.J. (1999). An age-structured model showing the benefits of marine reserves in controlling over-exploitation. *Fisheries Research* 39: 295-303.
- Holland, D.S. and Brazee, R.J. (1996). Marine reserves for fisheries management. *Marine Resource Economics* 11: 157-171.
- Horwood, J.W., Nichols, J.H. and Milligan, S. (1998). Evaluation of closed areas for fish stock conservation. *Journal of Applied Ecology* 35(6): 893-903.
- Kaunda-Arara, B. and Ntiba, M.J. (1997). The reproductive biology of *Lutjanus fulvivflamma* (Pisces: Lutjanidae) in Kenyan inshore marine waters. *Hydrobiologia* 353: 153-160.
- Man, A., Law, R. and Polunin, N.V.C. (1995). Role of marine reserves in recruitment to reef fisheries: a metapopulation model. *Biological Conservation* 71: 197-204.
- McClanahan, T.R. (1994). Kenyan coral reef lagoon fish: effects of fishing, substrate complexity and sea urchins. *Coral Reefs* 13: 231-241.
- McClanahan, T.R. and 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, T.R. and Mangi, S. (2000). Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecological Applications* (in press).
- Munro, J.L. (1996). The scope of tropical reef fisheries and their management. Chapter in *Reef Fisheries*, Polunin, N.V.C. and Roberts, C.M. eds. Chapman and Hall Series in Fish Biology and Fisheries No. 20. Chapman and Hall, London. 477pp.
- Nzoika, R.M. (1984). The evaluation of marine fishery resources in Kenya. In Iversen, S.A. and Myklerou S. (eds). *Proceedings of the NORAD-Kenya seminar to review marine fish stocks and fisheries in Kenya*. Mombasa, Kenya. 13-15 March 1984. Institute of Marine Institute, Bergen, Norway: 27-32.
- Obura, D.O. (1999). Status Report Kenya. In Coral reef degradation in the Indian Ocean: Status reports and project presentations, Linden, O. and Sporrang, N. eds. CORDIO: 33-36.
- Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *J. Cons. Int. Explor. Mer* 39: 175-192.
- Pauly, D. and Ingles, J. (1981). Aspects of the growth and natural mortality of exploited coral reef fishes. *Proc. Fifth Int. Coral Reefs Symp.*, Manila 1: 89-98.
- Pezzey, J.C.V., Roberts, C.M. and Urdal, B. (2000). A simple bioeconomic model of a marine reserve. *Ecological Economics* 33(1): 77-91.
- Plan Development Team (PDT) (1990). The potential of marine fisheries reserves for reef management in the U.S. Southern Atlantic (ed. Bohnsack, J. A.) NOAA NMFS Tech. Memo. NMFS-SEFC-261: 44pp
- Polacheck, T. (1990). Year around closed areas as a management tool. *Natural Resource Modeling* 4(3): 327-354.
- Polunin, N.V.C. and Roberts, C.M. (1996). Reef fisheries. Chapman and Hall Series in Fish Biology and Fisheries No. 20. Chapman and Hall, London. 477pp.
- Polunin, N.V.C., Roberts, C.M. and Pauly, D. (1996). Developments in tropical reef fisheries science and management. Chapter in *Reef Fisheries*, Polunin, N.V.C. and Roberts, C.M. eds. Chapman and Hall Series in Fish Biology and Fisheries No. 20. Chapman and Hall, London. 477pp.
- Rakitin, A. and Kramer, D.L. (1996). Effect of a marine reserve on the distribution of coral reef fishes in Barbados. *Marine Ecology Progress Series* 131: 97-113.
- Ricker, W.E. (1954). Stock and recruitment. *Journal of Fish. Res. Board Canada* 11(5): 559-623.
- Roberts, C.M. (1996). Settlement and beyond: population regulation and community structure of reef fishes. Chapter in *Reef Fisheries* Polunin, N.V.C. and Roberts, C.M. eds. Chapman and Hall Series in Fish Biology and Fisheries No. 20. Chapman and Hall, London. 477pp.
- Roberts, C.M. (1997). Connectivity and management of Caribbean coral reefs. *Science* 278: 1454-1457.
- Roberts, C.M. (1998). Fishery and reef management. *Science* 279: 2022-23.
- Roberts, C.M. and Polunin, N.V.C. (1991). Are marine reserves effective in management of reef fisheries? *Review in Fish Biology and Fisheries* 1: 65-91.
- Roberts, C.M. and Polunin, N.V.C. (1993). Marine reserves: simple solutions to managing complex fisheries? *Ambio* 22: 363-368.
- Rowley, R.J. (1994). Case studies and reviews: Marine reserves in fisheries management. *Aquatic Conservation: Marine and Freshwater Ecosystems* 4: 233-254.
- Russ, G.R. (1985). Effects of protective management on coral reef fishes in the Central Philippines. *Proc. 5th Int. Coral Reef Cong.* Tahiti, 4: 219-24.
- Russ, G.R. and Alcala, A.C. (1996a). Marine reserves: rates and patterns of recovery and decline of large predatory fish. *Ecological Applications* 6: 947-961.

- Russ, G. R. and Alcala, A.C. (1996b). Do marine reserves export adult fish biomass? Evidence from Apo island, Central Philippines. *Marine Ecology Progress Series* 132: 1-9.
- Sadovy, Y.J. (1996). Reproduction of reef fishery species. Chapter in *Reef Fisheries*, Polunin, N.V.C. and Roberts, C.M. eds. Chapman and Hall Series in Fish Biology and Fisheries No. 20. Chapman and Hall, London. 477pp.
- Sale, P.F. and Cowen, R.K. (1998). Fishery and reef management. *Science* 279: 2022
- Sanchirico, J. and Wilen, J. (1996). Bioeconomics of marine reserves. Paper prepared for the 7th annual Conference of Environmental and Resource Economists. Lisbon, Portugal. June 27-9, 1996.
- Sanchirico, J. and Wilen, J. (1998). Marine reserves: is there a free lunch? *Resources for the Future Discussion paper* 99-09, March 1998.
- Stamps, J.A. Buechner, M. and Krishnan, V.V. (1987). The effects of edge permeability and habitat geometry on emigration from patches of habitat. *The American Naturalist* 129: 533-552.

Questions

Michael Murphy: Did your model distinguish between the significant impacts of adult movement and larval dispersal on total harvest?

Lynda Rodwell: Adult movement has a greater significance on catch than larval dispersal. This is because when adults move they also influence the larval production (or recruit production) in each area. We can see that in the cases where there is high adult migration, whether larvae are completely retained or dispersed uniformly makes little difference to the equilibrium catch level. The adults have spread throughout the management area thereby redistributing larval production. We must acknowledge though that if adult migration is too high, the benefits of protection may be negated because stocks do not have the chance to build up in the marine reserve. We chose parameters which restricted adult migration to below this level.

Of course, larval dispersal also plays an important role. When adult migration is assumed to be zero, larval dispersal makes the difference between fishery collapse at high levels of exploitation and sustainable (albeit below optimal) catches in the fishing grounds.