The importance of habitat quality for marine reserve – fishery linkages

Lynda D. Rodwell, Edward B. Barbier, Callum M. Roberts, and Tim R. McClanahan

Abstract: We model marine reserve – fishery linkages to evaluate the potential contribution of habitat-quality improvements inside a marine reserve to fish productivity and fishery catches. Data from Mombasa Marine National Park, Kenya, and the adjacent fishery are used. Marine reserves increase total fish biomass directly by providing refuge from exploitation and indirectly by improving fish habitat in the reserve. As natural mortality of the fish stock decreases in response to habitat enhancement in the reserve, catches increase by up to 2.6 tonnes (t)·km^{-2}·year^{-1} and total fish biomass by up to 36 t·km^{-2}. However, if habitat-quality improvement reduces the propensity of fish to move out of the reserve, catches may fall by up to 0.9 t·km^{-2}·year^{-1}. Our results indicate that habitat protection in reserves can underpin fish productivity and, depending on its effects on fish movements, augment catches.

Résumé : La modélisation des liens entre une réserve marine et une pêche commerciale nous a permis d'évaluer la contribution potentielle de l'amélioration de la qualité de l'habitat dans la réserve à la productivité des poissons et à la récolte. Des données provenant du parc national marin de Mombasa, au Kenya, et des pêches commerciales de la région ont servi a démontrer que les réserves marines accroissent la biomasse totale des poissons directement, en procurant des refuges contre l'exploitation, et indirectement, en améliorant la qualité de l'habitat dans la réserve. À mesure que la mortalité naturelle du stock de poissons diminue à la suite de l'amélioration de l'habitat dans la réserve, l'augmentation des prises peut atteindre 2,6 tonnes (t)·km^{-2}·an^{-1} et celle de la biomasse totale des poissons 36 t·km^{-2}·an^{-1}. Cependant, si l'amélioration de la qualité de l'habitat réduit la tendance des poissons à quitter la réserve, la réduction des prises peut atteindre 0,9 t·km^{-2}·an^{-1}. Nos résultats indiquent que la protection de l'habitat dans les réserves peut soutenir la productivité des poissons et, selon son effet sur les déplacements, augmenter les prises.

[Traduit par la Rédaction]

Introduction

The deterioration of marine habitats and the depletion of fish stocks worldwide are of major concern to fisheries managers and conservationists (Agardy 2000). It is believed that habitat loss is the single greatest cause of the worldwide decline in biodiversity (Wilcove et al. 1998) and has serious implications for ecosystem functioning and integrity (Walters and Wethey 1996). Some of the most threatened habitats include coastal estuarine habitat (such as mangroves) and coral reefs.

Fishing with destructive fishing gears is a major cause of habitat deterioration in many temperate and tropical regions. Seabed habitat has been greatly degraded and even destroyed by the direct effects of dredging, trawling, long-lining, and dynamite fishing (Dayton et al. 1995; Roberts 1995). Despite this, it is only recently that research has focused on the effects of fishing on habitat structure and the potential implications for associated faunal communities (Jennings and Kaiser 1998; Turner et al. 1999). Though some ecologists have worked on the relationship between benthic community ecology and fish habitat function (e.g., Dayton et al. 1995), less research has focused on the implications of damage to habitat for demersal fishes. Habitat is known to profoundly affect the productivity of a fish stock and is therefore believed to be fundamentally important to fishery production (Dayton et al. 1995). For example, studies on the impact of loss of mangroves, often the result of deforestation and aquaculture expansion (Spalding et al. 1997), indicate that the losses to the fishery may be considerable because mangrove forests act as nursery grounds for the fishery (Barbier 2000). However, the direct impact of the degradation of coral reef habitat on fisheries is as yet uncertain.

Fisheries management tools such as taxes, quotas, and licenses fail to protect essential habitats such as coral reefs because habitat loss or degradation can occur at even low levels of fishing effort (National Research Council 2000). Many researchers have pointed out the necessity of habitat protection for sustainable marine resource exploitation (e.g., Roberts 1997*b*; Benaka 1999). In response, marine-protected areas have increasingly been established to tackle the prob-

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lems of biodiversity loss and habitat deterioration and more recently have gained support as a fisheries management tool that can help to enhance fish stocks (Lauck et al. 1998; Conover et al. 2000; Roberts et al. 2001). Reserves appear to be the best management tool for the restoration and preservation of the structure and functioning of entire ecosystems on which fisheries depend (Conover et al. 2000). They can also ease problems of by-catch, which can perturb ecosystems at local and regional levels (Collins et al. 2000). Areas protected from fishing invariably support higher levels of fish biomass and diversity (for review, see Halpern (2003)). However, although new results indicate that the reserve concept is sound (Roberts et al. 2001), the fishery benefits of reserve establishment are still being debated and the contribution of habitat protection to catches has yet to be fully determined.

Despite wide recognition that marine reserves allow the recovery of degraded marine habitat (e.g., Koenig et al. 2000; Roberts 2000*a*), models of marine reserves fail to consider explicitly the contribution of habitat quality to the fishery (e.g., Holland and Brazee 1996; Hannesson 1998; Sanchirico and Wilen 2001). In this paper we add to these studies by investigating the ecosystem value of marine reserves, evaluating the specific contribution of habitat-quality improvements inside a marine reserve to fish productivity and fishery catch in adjacent fishing grounds. We focus on a tropical marine reserve that protects a coral reef habitat. We extend the model in Rodwell et al. (2002), which focused on the processes of fish and larval movement patterns between reserve and fishing ground, optimal reserve size, and exploitation rates, by including an explicit habitat-quality term — a live coral cover proxy. Rugosity (a measure of the roughness of the substrate) could also be used as a habitat-quality proxy. In a model investigating the effects of seafloor habitat on juvenile cod survivorship, Lindholm et al. (2001) use vertical relief as a measure of habitat complexity. Rodwell et al. (2002) found that under almost all movement conditions (not a closed system), a reserve could enhance catches in a moderately to heavily exploited fishery (≥40% exploitation rate). They assume spatial homogeneity in the marine management area, acknowledging that this as an oversimplification. In this study, we consider two processes that may be affected by habitat-quality improvements in the marine reserve. The first is the decrease in natural mortality of the fish stock in response to habitat enhancement in the reserve. This positive relationship between habitat complexity and survivorship of coral reef fishes has been supported by many field studies (e.g., Roberts and Ormond 1987; McClanahan 1994). The second process considered is the restriction of movement of fish from the reserve to the fishing grounds as habitat quality improves inside the reserve. We consider habitat selection (discussed by MacColl (1990)) in two ways: (*i*) initially we assume the simplified case of fish moving in a density-dependent fashion irrespective of habitat quality, and (*ii*) then we consider a behavioural response of fish to the habitat-quality gradient between reserve and fishing grounds by restricting movement. This is similar to the movement patterns described by MacCall (1990) in which immigration and emigration are affected by gradients in quality of local habitat.

We use Mombasa Marine National Park (MNP) and adjacent fishing grounds as the case study site. Both live coral cover and fish biomass have increased significantly inside Mombasa MNP since its establishment (McClanahan and Kaunda-Arara 1996; Rodwell 2001). Though the exact relationship between fish biomass and habitat quality is uncertain, improved habitat quality could provide more food and refuge for fish, thereby reducing natural mortality levels (Dayton et al. 1995; Walters and Wethey 1996). This effect of habitat quality on natural mortality alone we term the "single habitat-quality effect". We test three relationships between natural mortality and habitat quality: logarithmic, linear, and polynomial.

The habitat-quality effect on the movement of fish is difficult to determine in the field and is likely to vary among species. We consider a "double habitat-quality effect" in which both the natural mortality of the fish stock declines in response to habitat-quality improvements and the habitat-quality gradient between the reserve and fishing grounds slows the rate of fish movement out of the reserve. This could have negative implications for fishery catches if the spillover from reserves to fishing grounds is significantly reduced.

In the following section we describe the model of marine reserve – fishery linkages. We then apply the model to a case study, Mombasa MNP and its adjacent fishery. We carry out sensitivity analysis to determine the implications of various habitat quality effects on the fishery in terms of catch, total fish biomass, and the exploitation rate at which it becomes profitable to establish a reserve. Results indicate that habitat-quality improvements are likely to make a significant contribution to the fishery.

The model

This deterministic and discrete-time model describes the dynamics of a fish stock subdivided between a fully protected marine reserve and adjacent fishing grounds. The term fully protected refers to protection from fishing only. Tourist activities such as diving and snorkelling can still take place inside the reserve. The total stock comprises two distinct substocks, X_1 and X_2 that occupy the reserve and the fishing grounds, respectively. The reserve habitat quality (q_1) is dependent on time since reserve establishment (t), i.e., $q_1 = q(t)$. The habitat quality of the fishing grounds is represented by q_2. In reality, q_2 is likely to decline over time if exploitation continues. In this model we take a constant base level of habitat quality in the fishing grounds to give a conservative estimate of the habitat-quality gradient between reserve and fishing grounds. As the reserve is fully protected from fishing, there is only catch (H) from the fishing grounds. The dynamics between the reserve and the fishing grounds are described by the transfer of recruits resulting from larval dispersal (T) and the movement of fish (M). Both fish and larval movement are explicitly modelled by employing a spawner–recruit relationship. The difference equation system describing the dynamics of the reserve and fishing ground stocks is given by eqs. 1 and 2:

$$(1)\quad X_{1,t+1} = (1 - \mu_1(q_{1,t}))X_{1,t} + R(X_{1,t}) - M(\overline{X}_{1,t}, \overline{X}_{2,t}, \alpha, \sigma, q_{1,t}, q_2) - T(R_{1,t}, R_{2,t}, \alpha, \theta)$$

$$(2)\quad X_{2,t+1} = (1 - \mu_2)X_{2,t} - H(X_{2,t}) + R(X_{2,t}) + M(\bar{X}_{1,t}, \bar{X}_{2,t}, \alpha, \sigma, q_{1,t}, q_2) + T(R_{1,t}, R_{2,t}, \alpha, \theta)$$

$X_{1,t}$ denotes the biomass of the fish stock in the reserve at time t, and $X_{2,t}$ represents the biomass of the fish stock in the fishing grounds at time t. In this study we do not consider a particular species but an aggregated fish stock because of the lack of complete species-specific catch data. $\mu_1(q_{1,t})$ and μ_2 are the average natural mortality estimates measured as a proportion of fish biomass levels X_1 and X_2, respectively. The natural mortality of the fish stock in the reserve varies with the level of habitat quality, i.e., $\mu_{1,t} = \mu(q_{1,t})$. $q_i = C_i/A_i$ for $i = 1, 2$, where C_i is the area of live coral cover of i (in km^2) and A_i is the area of i (in km^2). $M(\bar{X}_{1,t}, \bar{X}_{2,t}, \alpha, \sigma, q_{1,t}, q_2)$ is the net movement of fish between the reserve (area 1) and the fishing grounds (area 2) in time period t, where the density of stock i is given by $\bar{X}_{i,t} = X_{i,t}/A_i$, $i = 1, 2$. α is the proportion of management area protected, i.e., $\alpha = A_1/A$, where A represents the total management area. σ is the mobility coefficient of fish. The net fish movement can be positive or negative depending on the comparative stock densities. If the stock density within the reserve is greater than the stock density in the fishing grounds, the net fish movement is positive (i.e., outward from the reserve to the fishing grounds) and vice versa. Similarly, the transfer of recruits resulting from larval dispersal, $T(R_{1,t}, R_{2,t}, \alpha, \theta)$ can be positive or negative. $R(X_{1,t})$ and $R(X_{2,t})$ represent recruit production for stocks X_1 and X_2, respectively at time t. θ is the proportion of larvae retained. The remaining larvae disperse. Catch is treated simply as a function of fish biomass in the fishing grounds i.e., $H_t = H(X_{2,t})$.

Functional forms

Habitat quality over time

Habitat quality can be influenced by many factors such as time since protection, pollution, tourist visitation, fishing effort, and effects such as coral bleaching. However, in Mombasa MNP and the adjacent fishing grounds, pollution is not a significant problem (Mwangi et al. 2001). If pollution affects the area at all, we assume that it does so evenly and so does not contribute to a habitat-quality gradient between the reserve and the fishing grounds. Furthermore, damage resulting from tourist activities such as diving and snorkelling is limited (Muthiga and McClanahan 1997). By far the most significant factor in determining habitat quality is the substrate's complexity, which is closely correlated to live coral cover (Rodwell 2001; T.R. McClanahan, unpublished data). Highly complex substrate provides refuge for fish, thereby reducing mortality rates and increasing fish abundance. In Kenya, high catch intensity in fishing grounds has reduced the number of sea urchin predators, allowing the population of sea urchins to burgeon. In turn sea urchins scrape the corals, reducing diversity and complexity (McClanahan 1994). In this paper we focus our analysis on the case in which protection allows habitat quality to gradually improve (i.e., live coral cover to increase) inside the marine reserve.

Reserve habitat quality is treated as a variable dependent on time since protection. The data from Mombasa MNP indicate a positive relationship between live coral cover and time since protection up until the coral bleaching event of March 1998 when live coral cover fell dramatically (McClanahan and Kaunda-Arara 1996; Rodwell 2001; T.R. McClanahan, unpublished data). Episodic impacts such as coral bleaching are beyond the scope of this study; therefore, only data from 1987 to 1997 are used to estimate the "habitat quality over time since protection" function for the model (Fig. 1).

In the fishing grounds adjacent to Mombasa MNP, habitat quality has remained fairly constant since reserve establishment. However, inside the reserve, habitat quality has increased significantly over time. The habitat-quality differential ($\bar{q}_t$) between Mombasa MNP and the unprotected fishing grounds increased between 1987 ($t = 1$) and 1997. The best "realistic" fit for $\bar{q}_t$ is the logarithmic function given by eq. 3. Although power, cubic, and quadratic functions fit the data better over the 10 years of data, when extrapolated over the 30 years, they gave unrealistic ranges.

$$(3)\quad \bar{q}_t = q_{1,t} - q_{2,t} = a_1 \ln t + a_2$$

where $a_1 = 14.8$ and $a_2 = 0.67$. This gave an R^2 estimate of 0.79 and $p = 0.003$. Despite this high R^2, this function may not accurately portray the trend in $\bar{q}_t$ over time. It is likely that $\bar{q}_t$ will level off rather than continue to increase. By using this function in the model simulations, the habitat-quality effect on natural mortality may be overstated. However, the relationship was extrapolated over 30 years for the simulations and the range of $\bar{q}_t$ was $0\% \leq \bar{q}_t \leq 51\%$ from time $t = 1$ to $t = 30$, respectively. This seems highly plausible because the differential observed in the field reached approximately 40% after less than 10 years (Rodwell 2001).

The habitat-quality gradient between the reserve and fishing grounds tends to a factor of 5 ($q_1/q_2 \simeq 0.55/0.11$) and so the inverse gradient, which influences the rate of fish movement, tends to 0.2 ($q_2/q_1 \simeq 0.11/0.55$). The greater the difference in habitat quality of the two areas, the greater the effect on fish movement.

Natural mortality vs. habitat quality

Natural mortality of fish inside the reserve is a variable dependent on reserve habitat quality, i.e., $\mu_1(q_{1,t})$. The empirical data from Mombasa could not confirm the exact relationship between habitat quality and fish biomass or natural mortality rates, though fish biomass was positively associated with live coral cover (Rodwell 2001). Three functions are explored in the model simulations to simply illustrate possible contrasting changes in natural mortality resulting from habitat-quality improvements (Fig. 2). In each case, natural mortality is assumed to be negatively related to habitat quality, i.e., $\mu'(q_1) < 0$. In the polynomial function, mortality falls at an increasing rate, $\mu''(q_1) > 0$. In the linear function, it falls at a constant rate, $\mu''(q_1) = 0$. In the logarithmic function, it falls at a decreasing rate, $\mu''(q_1) < 0$. The natural mortality rate in each case is assumed to stabilise after 30 years. This time acts as a threshold beyond which natural mortality does not fall any further. Rodwell (2001) found an exponential relationship between fish biomass and the "reserve effect" (i.e., the presence of the reserve). This implies that the logarithmic function may be the most appropriate fit for the fish biomass and natural mortality relationship (assuming an inverse relationship exists between fish

Fig. 1. Habitat-quality (live coral cover) differential between Mombasa Marine National Park and the adjacent fishing grounds ($q_1 - q_2$) versus time since reserve establishment.

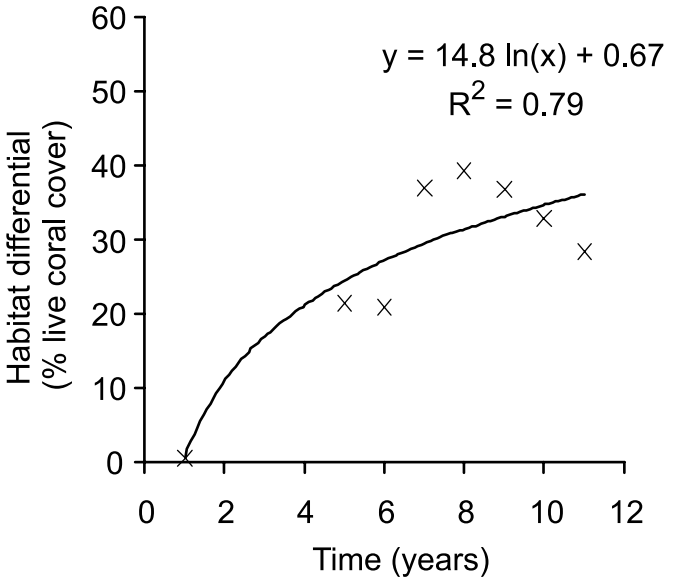
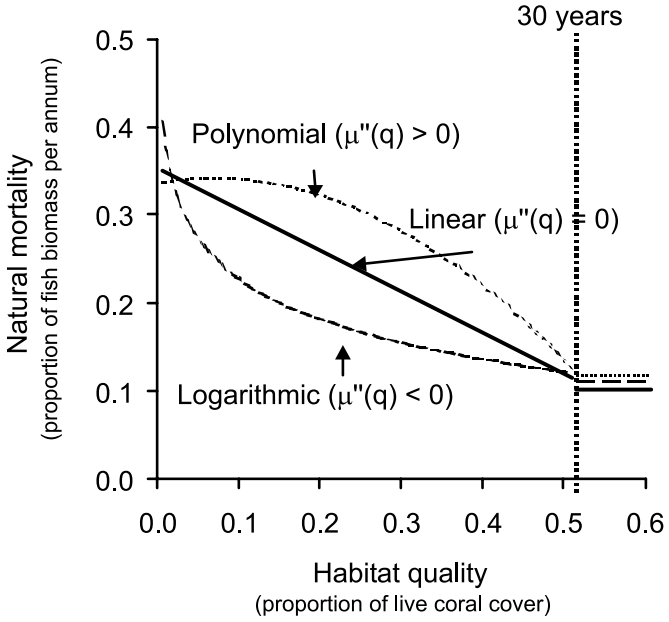


Fig. 2. Three relationships modelled between natural mortality of fish and habitat quality in the reserve: logarithmic, linear, and polynomial (over 30 years of protection).



biomass and natural mortality and the reserve effect includes habitat-quality improvement). We use realistic ranges of natural mortality based on the literature (Pauly and Ingles 1981; between 10 and 40% per annum) and fit the functions within these ranges. A proportion of the fivefold increase in fish biomass density resulting from reserve creation could be accounted for by the increase in the natural survival rate from 60 to 90%. The details of the functions are given below.

Polynomial function: $\mu(q_1) = -d_1(q_1)^2 + d_2q_1 + d_3$, where $d_1 = 1.12$, $d_2 = 0.16$, and $d_3 = 0.34$. For this relationship, the range of μ_1 was $0.13 \leq \mu(q_1) \leq 0.34$ for 30 years and μ_2 remained constant at 0.34. Beyond 30 years, $\mu_1 = 0.13$.

Linear function: $\mu(q_1) = -c_1q_1 + c_2$, where $c_1 = 0.47$ and $c_2 = 0.35$. In this case, the range of μ_1 was $0.11 \leq \mu(q_1) \leq 0.35$ for 30 years and μ_2 remained constant at 0.35. Beyond 30 years, $\mu_1 = 0.11$.

Logarithmic function: $\mu(q_1) = -b_1\ln q_1 + b_2$, where $b_1 = 0.066$ and $b_2 = 0.076$ and the range of μ_1 was $0.12 \leq \mu(q_1) \leq 0.4$ for 30 years and μ_2 remained constant at 0.4. Beyond 30 years, $\mu_1 = 0.12$.

With these levels of natural mortality (0.4, 0.35, 0.34) in the fishing grounds, the exploitation range tested was $0.1 \leq \omega \leq 0.6$.

The simulations were run for 30 years. Beyond the 30-year time period, the natural mortality of the reserve is assumed to stabilise. The functional forms used are to simply illustrate different response rates over the 30-year time period only.

Fish movement

The movement of fish is a function of the habitat-quality gradient between the reserve and the fishing grounds. We include the (inverse) habitat-quality gradient in the movement function, i.e., $M_t = f(q_2/q_{1,t}, \rho)$, where ρ represents the degree to which the habitat-quality gradient slows down the movement process. A potential impact of habitat-quality improvements is that the protected region will provide more food and refuge. This can result in a lower proportion of fish biomass leaving the reserve, which may counter the density-dependent movement effect. In their study, Lindholm et al. (2001) assume that the movement rate of juvenile cod from an area is the inverse of the habitat complexity score for that area. The fish movement function used in this model is given by

$$M_t = \sigma A\alpha(1-\alpha)\left[\left(\frac{q_2}{q_{1,t}}\right)^{\rho}\overline{X}_{1,t} - \overline{X}_{2,t}\right] \quad (4)$$

where $0 \leq \sigma \leq 1$, $0 \leq \rho \leq 1$, $dM_t/d\rho < 0$ (i.e., as ρ increases, fish movement out of the reserve declines) and $dM_t/d(q_{1,t}/q_2) < 0$ (i.e., as the habitat quality inside the reserve improves, relative to fishing ground habitat quality, fish movement out of the reserve declines). Therefore, $dM_t/d(q_2/q_{1,t}) > 0$. By substituting $\overline{X}_1 = X_1/\alpha A$ and $\overline{X}_2 = X_2/(1-\alpha)A$ and cancelling through, eq. 4 can also be written as

$$M_t = \sigma[(q_2/q_{1,t})^{\rho}(1-\alpha)X_{1,t} - \alpha X_{2,t}]$$

If $\rho = 0$, there is no habitat effect on fish movement. We refer to this as the single habitat-quality effect, i.e., habitat quality only affects natural mortality. If $0 < \rho \leq 1$, then the habitat-quality gradient slows down the movement of fish from the reserve to the fishing grounds, which we term the double habitat-quality effect because both natural mortality and fish movement are affected by habitat-quality changes. If $\rho = 1$, the restriction to movement could be strong depending on the magnitude of the habitat-quality gradient between the reserve and fishing grounds. σ represents the natural mobility coefficient of the fish stock, which is influenced by life history characteristics rather than by environmental factors.

Other functional forms

Other functional forms are the same as those used in Rodwell et al. (2002), which are summarised below.

*Catch (*H*)*

In this model, we take catch levels to be privately determined in the fishery reflecting the property rights in place. The catch function used is a simple linear relation between catch and biomass in the fishing grounds:

$$(5) \qquad H_t = \omega X_{2,t}$$

where ω is a constant representing the exogenous exploitation rate as proportion of the exploitable fish biomass $X_{2,t}$; ω may reflect the rate at which marginal benefits equate with marginal costs (optimal fishing policy in remaining fishing grounds) or total revenues equate with total costs (open access in remaining fishing grounds). This type of catch function may also represent a linear total allowable catch quota system (such as that used by Conrad 1999).

Recruit production (R_1 *and* R_2*)*

A proportion of biomass X is taken as a proxy for spawning stock biomass and so the Beverton–Holt recruit production function for the reserve is

$$(6) \qquad R_{1,t} = \varepsilon_1 X_{1,t}/(\gamma_1 \varepsilon_1 X_{1,t} + \beta_1)$$

where $R_{1,t}$ is the recruit production of the reserve fish stock in time period t; $X_{1,t}$ is the reserve fish biomass in time period t; γ_1 and β_1 are recruitment parameter estimates for the reserve stock for a given initial growth rate; and ε_1 is the proportion of the reserve fish biomass that is reproductively mature.

For the fishing ground stock, the Beverton–Holt recruit production function is

$$(7) \qquad R_{2,t} = \varepsilon_2 (X_{2,t} - H_t)/[\gamma_2 \varepsilon_2 (X_{2,t} - H_t) + \beta_2]$$

where ε_2 is the proportion of the fishing ground stock that is reproductively mature. We make two assumptions about recruit production in the fishing grounds. (*i*) ε_1 and ε_2 are constant over the time period. We take the mean values of ε_1 and ε_2 over the time period from the Mombasa data. Alternatively, ε_1 and ε_2 would vary over time. (*ii*) The only spawners are those remaining after catch, i.e., $\varepsilon_2(X_2 - H)$ in each time period (for discussion, see Rodwell et al. (2002)).

*Recruit transfer (*T*)*

Larval movement patterns are described by the larval retention factor θ. The recruit transfer function is

$$(8) \qquad T_t = (1 - \theta)[(1 - \alpha)R_{1,t} - \alpha R_{2,t}] \quad \text{for } 0 \le \theta \le 1$$

where θ is the proportion of larvae retained. This will depend on the relationship between dispersal distance, the reserve size (and shape) (Carr and Reed 1993), currents (Roberts 1997*a*), tides, and the swimming capabilities of the larvae (Warner et al. 2000). If $\theta = 0$, then there is no larval retention and the larvae disperse uniformly. If $\theta = 1$, then full retention of larvae occurs. This results in no transfer of recruits between the reserve and the fishing ground.

Steady-state equations

The steady-state equations for the reserve and fishing ground stocks are given by eqs. 9 and 10, respectively:

$$(9) \qquad -\mu_1(q_1^*)X_1^* - \sigma A\alpha(1-\alpha)\left[\left(\frac{q_2}{q_1^*}\right)^{\rho}\bar{X}_1^* - \bar{X}_2^*\right] + \alpha(1-\theta)\left[\frac{\varepsilon_1 X_1^*}{\gamma_1\varepsilon_1 X_1^* + \beta_1} + \frac{\varepsilon_2(1-\omega)X_2^*}{\gamma_2\varepsilon_2(1-\omega)X_2^* + \beta_2}\right] + \theta\left[\frac{\varepsilon_1 X_1^*}{\gamma_1\varepsilon_1 X_1^* + \beta_1}\right] = 0$$

$$(10) \qquad -(\mu_2 + \omega)X_2^* + \sigma A\alpha(1-\alpha)\left[\left(\frac{q_2}{q_1^*}\right)^{\rho}\bar{X}_1^* - \bar{X}_2^*\right] + (1-\alpha(1-\theta))\left[\frac{\varepsilon_1 X_1^*}{\gamma_1\varepsilon_1 X_1^* + \beta_1} + \frac{\varepsilon_2(1-\omega)X_2^*}{\gamma_2\varepsilon_2(1-\omega)X_2^* + \beta_2}\right] - \theta\left[\frac{\varepsilon_1 X_1^*}{\gamma_1\varepsilon_1 X_1^* + \beta_1}\right] = 0$$

From these equations we derive X_1^* and X_2^* from which we can determine total biomass ($X_1^* + X_2^*$) and catch ($H^* = \omega X_2^*$). The values of total biomass and catch with habitat-quality effects can then be compared with the values with no habitat-quality effect.

Model application

Before using the model to determine the conditions in which reserve habitat-quality improvements augment fish biomass and catch levels, we first apply the model using data from Mombasa MNP and its adjacent fishery. Mombasa MNP is a marine reserve on the Kenyan coast fully protected from fishing. It was officially established in 1987–1988 but did not achieve full enforcement until 1992 (McClanahan and Kaunda-Arara 1996). The adjacent fishery is one of semisubsistence. Fish biomass and substrate data have been collected using replicate visual transects and line transects at sites inside and outside the reserve since 1987 by T.R. McClanahan and colleagues at the Coral Reef Conservation Project in Mombasa. Catch data have also been collected at fish-landing sites adjacent to the marine reserve since 1991. These catch data are not complete because of various data collection problems such as night fishing and fishers taking home catches, which are therefore not recorded. However, they do provide an indication of catch trends. A full description of data and the study site is given in Rodwell (2001).

The model simulations were run using STELLA®, which is a simultaneous difference equation solver developed by High Performance Systems (www.hps-inc.com).

Parameter estimates

We assume moderate levels of fish movement ($\sigma = 0.2$) equivalent to between 5 and 12% of the reserve stock spilling over into the fishing grounds per annum (Rodwell et al.

Fig. 3. A comparison of recorded (open circles) and predicted (solid diamonds) catch per unit area for the Mombasa fishery (60% exploitation) for the 12 years after reserve establishment. The official time of reserve establishment is 1988; 1992 is the time of full enforcement.

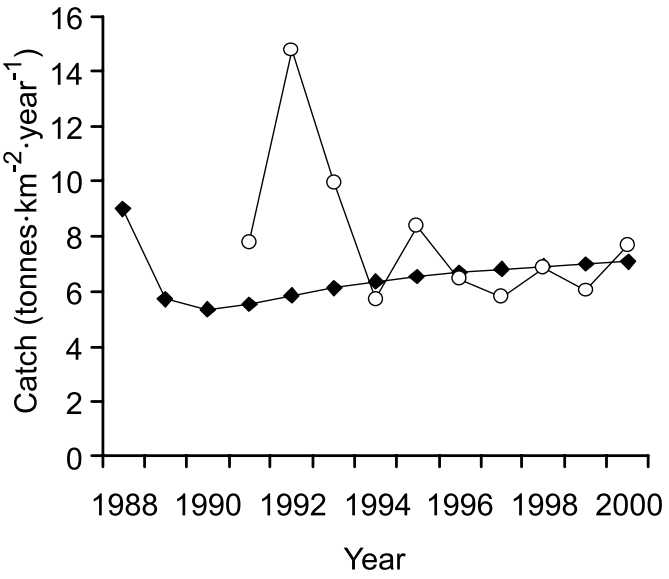
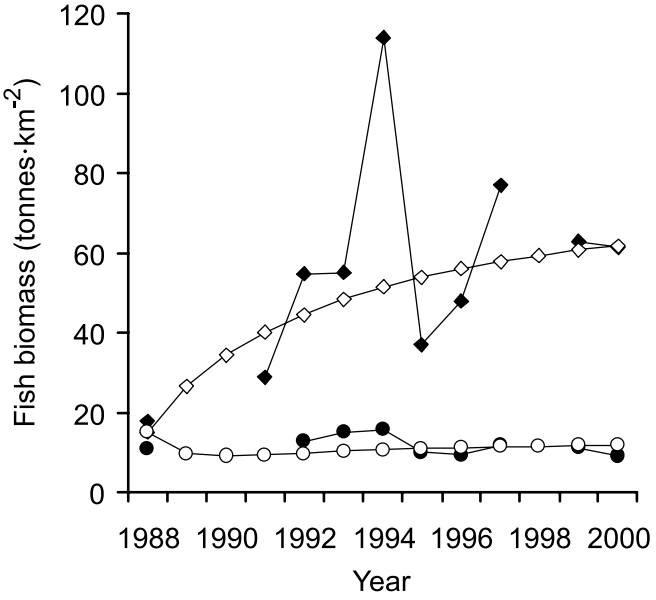


Fig. 4. A comparison of recorded (solid symbols) and predicted (open symbols) fish biomass levels in the reserve (diamonds) and fishing grounds (circles) in the Mombasa fishery (60% exploitation) for the first 12 years after reserve establishment.



2002) and 50% larval retention ($\theta = 0.5$). The initial growth rate of 85% was estimated from data on fish biomass growth in Mombasa MNP (Rodwell 2001). γ_1 and γ_2 were estimated given the values of μ_1 and μ_2. The remaining parameter estimates used in the simulations were as follows: $\mu_1 = 0.1$ to 0.4; $\mu_2 = 0.4$ (logarithmic), 0.35 (linear), and 0.34 (polynomial); $\gamma_1 = 0.00548$ (logarithmic), 0.00575 (linear), and 0.00581 (polynomial); $\gamma_2 = 0.00234$ (logarithmic), 0.00246 (linear), and 0.00248 (polynomial); β_1, $\beta_2 = 0.1$; $\varepsilon_1 = 0.7$; $\varepsilon_2 = 0.2$; $q_{1,t} = 0.11$ to 0.51; $q_2 = 0.11$; $\alpha = 0.3$; $\rho = 0$ to 1; and $\omega = 0$ to 0.6.

Results

The Mombasa case was best represented by the results for 60% exploitation (the highest exploitation rate run with this model). Of the three habitat quality – natural mortality functional forms, the logarithmic form represented the data best, with catches and fish biomass levels stabilising as they appear to be doing in Mombasa MNP and the fishing grounds. For each functional form, the closest catch and biomass levels to the recorded data were achieved for the case when $\rho = 0$, i.e., when there was only a single habitat-quality effect and no effect on fish movement out of the reserve.

Fishery catch

The year of reserve establishment was taken as 1988. However, catch data were only available from 1991 onwards. The catch per unit area in 1992 was very high, 14.8 tonnes (t)·km^{-2}·year^{-1} (Fig. 3), but this may be attributable to poaching in the reserve during that year. The end of 1992 may represent the time of true full enforcement of the park (McClanahan and Kaunda-Arara 1996). This would explain the difference in model results and recorded catch per unit area over the 1988–1994 period (Fig. 3). However, the model predictions towards the end of the 13-year period are very close to the recorded data.

Fish biomass

Fish biomass data were available from 1988 (McClanahan 1994; McClanahan and Kaunda-Arara 1996; T.R. McClanahan, unpublished data). For the years between 1988 and 1991, Mombasa MNP was only partially protected. The model predictions are very close for the fishing grounds case but the reserve case was more variable, fluctuating about the predicted values (Fig. 4). In the sensitivity analysis, we compare the steady-state results (after 30 years).

Sensitivity analysis

In this section, we explore the potential consequences of habitat-quality changes on catches and total fish biomass levels for different scenarios of habitat-quality effects, exploitation rates, and relationships between natural mortality and habitat quality.

Methods

Firstly, we simulated the scenario of a reserve without a habitat-quality effect. We then considered the single habitat-quality effect ($\rho = 0$). The results were compared with the without habitat-quality effect scenario to determine the percent increase or decrease in catch and total biomass levels resulting from habitat-quality effects. We did this for each of the functional forms of natural mortality versus habitat quality (logarithmic, linear, and polynomial).

We tested the double habitat-quality effect in which fish movement is also dependent on habitat quality. The absolute values of q_1 and q_2 are used in this case. This allowed for a meaningful habitat-quality ratio, $q = q_1/q_2$, to be used for the movement function. $q_1 = q_2 = 0.11$ at time $t = 0$. $q_1(t)$ varied

as a logarithmic function with time, whereas q_2 remained constant at 0.11 (the approximate proportion of live coral cover when the reserve was established in 1987–1988). The sensitivity of results to the value of ρ was tested. We then compared these results with those of the without habitat-quality effect.

To illustrate the potential impact of habitat-quality effects on the optimal combination of reserve size and exploitation rates, we compared the results of catch levels under different scenarios: with no reserve; with a reserve without habitat-quality effect; with a single habitat-quality effect; and with moderate ($\rho = 0.5$) and strong ($\rho = 1$) double habitat-quality effects. We used the scenario of logarithmic habitat-quality effect, 85% initial growth rate and 30% reserve size, i.e., $\alpha = 0.3$ (based on the Mombasa case).

Results

Without habitat-quality effect

The results (given in Table 1) are steady-state levels of catch and total fish biomass (30 years after reserve protection). Highest total fish biomass levels were achieved when exploitation was lowest and vice versa, ranging from 416 t (16 t·km^{-2}) at an exploitation rate of 60% ($\omega = 0.6$) to 1050 t (39 t·km^{-2}) at an exploitation rate of 10% ($\omega = 0.1$) (for the logarithmic function). The total management area is 26.75 km^2. The highest catch levels (when the reserve covers 8 km^2 of the management area, 30%, i.e., $\alpha = 0.3$) were achieved when the exploitation rate was 40% ($\omega = 0.4$) and the lowest when exploitation was 10% ($\omega = 0.1$), ranging from 68 t·km^{-2} (3.6 t·km^{-2}·year^{-1}) to 126 t·km^{-2} (6.7 t·km^{-2}·year^{-1})(for the logarithmic function). The single and double habitat-quality effects results are compared with these results in the following sections. Note that at the time of reserve establishment ($t = 0$), the natural mortality levels in the whole management area are equal, i.e., $\mu(t = 0) = \mu_1(t = 0) = \mu_2(t = 0)$.

Single habitat-quality effect

What if natural mortality declines in response to habitat-quality improvements?

The greatest habitat-quality effect for both catch and total biomass was found when exploitation is the highest level ($\omega = 0.6$) and the least effect was noted when exploitation is the lowest level ($\omega = 0.1$) (Table 2). This is consistent with the findings of other studies (e.g., Holland and Brazee 1996; Sladek-Nowlis and Roberts 1997). Catches were found to increase by between 13 and 39% (0.5–2.6 t·km^{-2}·year^{-1}). This range is due to both different exploitation rates and functional relationships between habitat quality and natural mortality. Total fish biomass increased by between 40 and 92% (7–36 t·km^{-2}).

Under our assumptions, improvements in habitat quality always result in increased total fish biomass. The greatest habitat-quality effect in terms of both catch and total fish biomass was with the logarithmic functional relationship between habitat quality and natural mortality. This can be explained by the immediate rapid decline in natural mortality as a result of small improvements in habitat (see Fig. 2). This may vary from species to species according to the degree of dependence on live coral cover and associated benthic complexity.

Double habitat-quality effect

What if natural mortality declines and fish movement is hindered in response to improving habitat quality in the reserve?

The results of the double habitat-quality effects (shown in Table 2) are again with respect to the without habitat-quality effect values. As for the single habitat-quality effect, the greatest effect is when exploitation is most intense ($\omega = 0.6$) and least effect when exploitation is low ($\omega = 0.1$). The results of the moderate double habitat-quality effect (i.e., when $\rho = 0.5$) indicate small increases in catch between 1 and 15% (0.04–1 t·km^{-2}·year^{-1}) for all functional forms and large increases in biomass between 51 and 130% (9–51 t·km^{-2}) resulting from the habitat-quality effects.

In the case of a strong habitat-quality effect on movement ($\rho = 1$), habitat quality limits fish movement so much that catches can decline by between 3 and 12% (0.1–0.9 t·km^{-2}·year^{-1}) depending on the functional form and the exploitation rate. However, the total fish biomass level is even higher than the moderate effect between 55 and 156% (9–61 t·km^{-2}) because more fish remain protected inside the reserve. The increase in fish biomass will be seen inside the reserve only because fish will stay inside the reserve, increase in individual size, and produce more eggs. In fact, fish biomass in the fishing grounds will decline because of the low "spillover" rate. This accounts for the fall in catch (by up to 12%).

The catch levels with single and double and without habitat-quality effects are similar whether the fishery is facing low or high exploitation, only the magnitudes differ (see Fig. 5). Catches are highest with the single habitat-quality effect because there is no effect on fish movement. Spillover into the fishing grounds can therefore result in an increase in catches. The lowest catches are seen when the movement effect is strongest ($\rho = 1$). In this case, the habitat quality gradient effect outweighs the density-dependent effect and the fish stay inside the reserve. Even if this were the case, the fall in catches would be small, between 3 and 12%. We can see that even if $\rho = 0.8$ (still a high restriction on fish movement), catches can be higher than without a habitat-quality effect (Fig. 5).

Of the possible habitat-quality effects on catch (shown in Fig. 6), the scenario which best illustrated the Mombasa case is that of a single habitat-quality effect. In this case, catches will be greater with the 30% reserve than without when the exploitation rate exceeds 20% of exploitable biomass. This compares to approximately the 30% exploitation rate when there is no habitat-quality effect (Rodwell et al. 2002). The strong double habitat-quality effect would result in a higher level of exploitation at which it becomes preferable to create a reserve (approximately 34%).

The highest total fish biomass levels are reached when there is the highest movement effect, $\rho = 1$ (see Fig. 7). The lowest total fish biomass levels occur when habitat neither reduces natural habitat nor restricts movement out of the reserve, i.e., the case without a habitat-quality effect.

Discussion

Most economic studies have failed to consider habitat-quality improvement as an economic benefit of marine reserves (but see Mangel (2000)). In this study, we have high-

Table 1. Range of equilibrium catch and biomass levels without habitat-quality effects.

Functional forms	Catch (tonnes·year^{-1})	Total biomass (tonnes)	Catch/area (tonnes·km^{-2}·year^{-1})	Total biomass/area (tonnes·km^{-2})
Logarithmic ($\mu(0) = 0.4$)	68 → 126	416 → 1050	3.6 → 6.7	16 → 39
Linear ($\mu(0) = 0.35$)	74 → 135	450 → 1150	3.9 → 7.2	17 → 43
Polynomial ($\mu(0) = 0.34$)	76 → 137	455 → 1170	4.1 → 7.3	17 → 44

Table 2. Single and double habitat-quality effects on fishery catch and total fish biomass.

Habitat-quality effect	Functional forms	Catch (% Δ)	Total biomass (% Δ)	Δ catch/area (tonnes·km^{-2}·year^{-1})	Δ total biomass/area (tonnes·km^{-2})
Single	Logarithmic	+20 → +39	+55 → +92	+0.7 → +2.6	+9 → +36
	Linear	+16 → +31	+47 → +77	+0.6 → +2.2	+8 → +33
	Polynomial	+13 → +25	+40 → +65	+0.5 → +1.8	+7 → +29
Double ($\rho = 0.5$)	Logarithmic	+7 → +15	+74 → +130	+0.25 → +1.0	+12 → +51
	Linear	+4 → +9	+63 → +110	+0.16 → +0.65	+12 → +47
	Polynomial	+1 → +4	+51 → +91	+0.04 → +0.29	+9 → +40
Double ($\rho = 1$)	Logarithmic	–3 → –4	+86 → +156	–0.11 → –0.27	+14 → +61
	Linear	–4 → –8	+70 → +131	–0.16 → –0.58	+12 → +56
	Polynomial	–4 → –12	+55 → +107	–0.16 → –0.88	+9 → +47

lighted the specific contribution of habitat improvements to the fishery by including an explicit habitat-quality function in the marine reserve – fishery model. We have shown that habitat-quality improvements can augment fish biomass and catch levels. The degree to which catch or biomass can increase depends on the nature of the relationship between natural mortality and habitat quality as well as whether the habitat-quality differential influences the rate of fish movement from the reserve to the fishing grounds. However, the sensitivity analysis indicates that habitat-quality improvements from reserve protection are likely to benefit the fishery wherever reserves are established. Only in the case where there is strong restriction to fish movement ($\rho \geq 0.9$) do catches fall, and even then the loss in catch is small. Habitat-quality improvements inside marine reserves can also reduce the exploitation rate at which it becomes profitable for the fishery to establish a reserve.

The greatest benefits to fishery catch from habitat-quality improvements in a marine reserve will be derived from locating the reserve where habitat can recover quickly once protected (an area that is not subject to other stresses such as pollution or sedimentation) and where the fish species respond quickly to these improvements (those with a logarithmic response rather than polynomial). The rate and extent of fish biomass buildup or biodiversity in reserves can be hindered by poor quality habitat (Roberts 2000*a*). High quality habitats are likely to sustain the highest rates of recovery and eventually attain higher biomass or biodiversity than lower quality habitats. However, this has not yet been tested empirically. Though reserves placed in areas of higher habitat quality may perform better (Benaka 1999; Roberts 2000*a*), some of these places may also be prime fishing grounds. Conservation and fishing objectives may conflict in the short term.

The fishery will also benefit if adult and juvenile fish movement is not restricted severely by a habitat-quality gradient. This may be consistent with the idea of protecting an area of lower habitat quality, e.g., one that has been more severely damaged than its surrounding area. If the initial habitat-quality gradient is less than 1 (i.e., $q_1/q_2 < 1$), the improvements in habitat quality in the reserve may lead to q_1 (reserve habitat quality) tending towards q_2 (fishing ground habitat quality) or surpassing it. There is also a conservation argument for protecting lower quality habitats. Protecting these areas may assist their recovery from harmful fishing or other activities. However, tourists are less likely to pay to visit these areas.

Clearly some locations would benefit more from protection than others. For example, we found that heavily exploited fisheries will benefit more from habitat-quality improvements than low exploitation fisheries. However, the absence of perfect knowledge of which locations these are should not prevent the establishment of reserves to protect threatened habitats and fish stocks. Marine reserves have shown significant ecological benefits regardless of the characteristics of the habitat they protect (Conover et al. 2000; Roberts 2000*b*).

Mombasa MNP and the adjacent fishery appear to have all of the right ingredients to benefit from habitat-quality improvements. The results of the simulations are, however, limited by assumptions made, including 50% larval retention and moderate natural mobility of fish ($\sigma = 0.2$). Larval export is thought to be the process by which tropical fisheries can benefit most from marine reserves (Plan Development Team 1990). Other studies of marine reserves assume wide uniform larval dispersal (e.g., Holland and Brazee 1996; Pezzey et al. 2000). If this is the case, in reality, our findings may underestimate the true fishery catch benefits of reserves. However, if fish mobility is zero (not moderate as assumed), the habitat-quality effect on fish movement would also be zero and only the single habitat-quality effect should be considered. Though Lindholm et al. (2001) do not directly investigate the effects of habitat-quality improvement on catch levels, their finding that total juvenile survivorship increases with a reserve is consistent with the finding that catches may be enhanced. However, if fish move into a protected area because of the improvement in habitat quality, as they suggest,

Fig. 5. Catch levels with single (ρ = 0; open circles), double (ρ = 0.5, crosses), 0.8 (horizontal lines), and 1 (shaded triangles) and without (solid diamonds) habitat-quality effects: (*a*) least effect at low exploitation (10%); (*b*) greatest effect at high exploitation (60%). (Note different scales on *y* axes for *a* and *b*.)

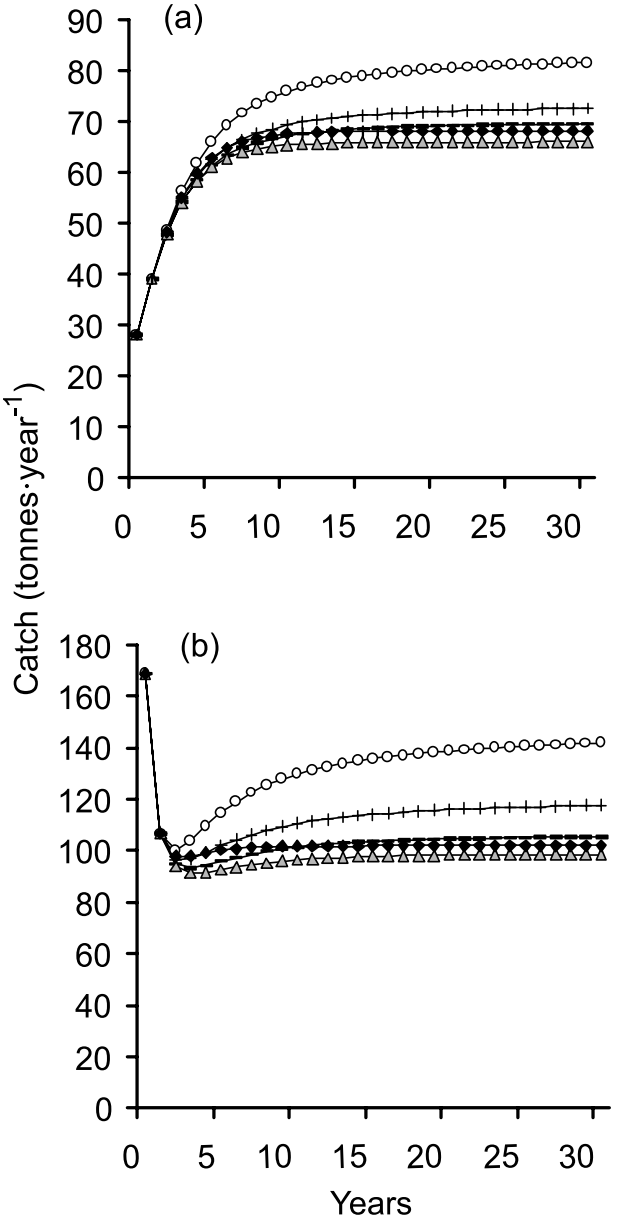
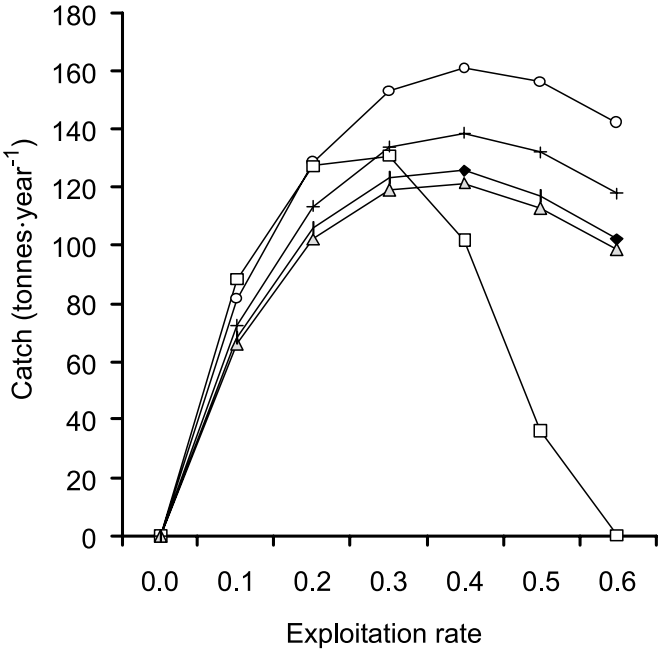


Fig. 6. Steady-state catch levels (30 years) with no reserve (open squares), with single (ρ = 0; open circles), double (ρ = 0.5; crosses), 1 (shaded triangles), and without (solid diamonds) habitat-quality effects. The scenario is one of logarithmic habitat-quality effect, 85% initial growth rate, 40% initial natural mortality (μ = 0.4), and with reserve proportion of 0.3.



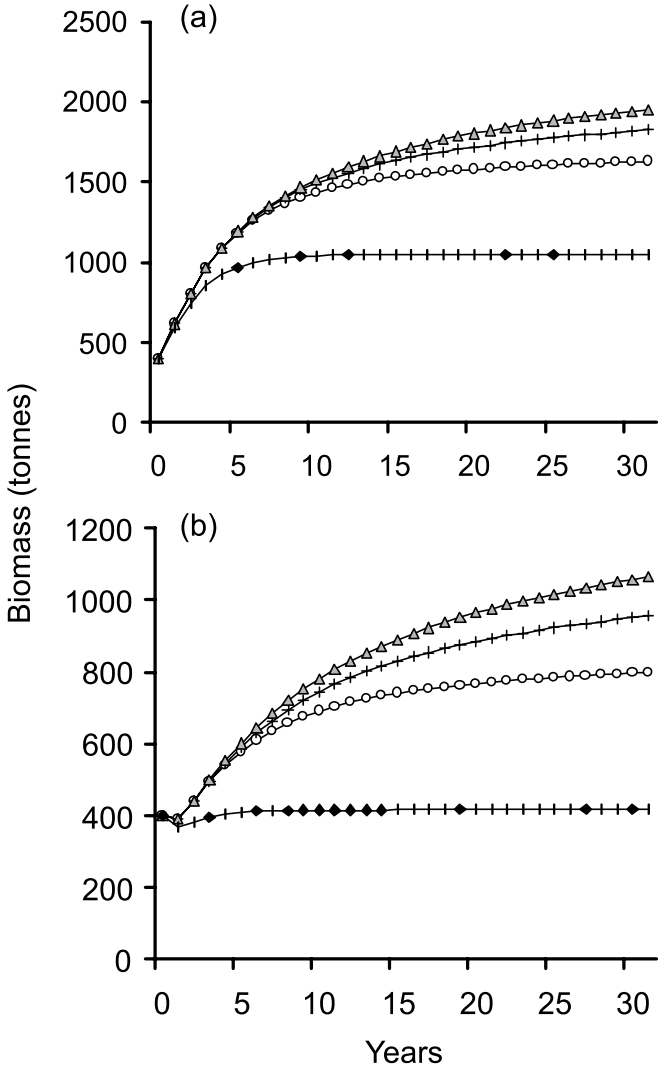
there is likely to be a negative impact on catches. This result is wholly dependent on the assumption that movement rates are the inverse of the habitat complexity score. This may well be a plausible assumption for vagile temperate species, but it is less likely to reflect the reality for more sedentary tropical species.

One simplification of this model is the use of aggregated biomass. If complete age- or size-class catch and biomass data were available, the model could have included more detail on the effects of protection (fish and habitat) at various fish life stages. The use of aggregated biomass was appropriate for the data available. It was also used consistently and so should not have produced any biases for or against marine reserve establishment.

As with any study of this nature, there are still many unknowns. However, by modelling a case study site for which some data are available and by simulating various plausible scenarios, we have attempted to ground our model in reality.

The findings support the potential of marine reserves as a valuable ecosystem-based tool that allows both the buildup of fish biomass (as a result of refuge from predation and the increase in reproductive capacity) and habitats to recover from destructive fishing practices or the consequences of ecosystem shifts resulting from fishing. Habitat-quality improvement has been widely ignored in economic studies on marine reserves despite there being much ecological data suggesting that this is an important benefit of reserve establishment. Though precise relationships between fish natural mortality and habitat quality are unknown, our model results indicate that habitat-quality effects should be added to the list of economic, as well as ecological, benefits of marine protection. Depending on the extent to which fish movement is hindered by the habitat-quality gradient between the reserve and fishing grounds, these benefits may manifest themselves in increases in both fishery catches and total fish biomass levels or simply higher fish biomass levels in the reserve. In either case, marine reserves appear to be useful tools in assuring the sustainability of the fishery through both the direct protection of fish species, allowing them to increase in individual size (e.g., McClanahan and Kaunda-Arara 1996; Russ and Alcala 1996) and become more fecund (Sadovy 1996), and the indirect improvement of their essential habitat.

Fig. 7. Total fish biomass levels with single (ρ = 0; open circles), double (ρ = 0.5; crosses), 1 (shaded triangles), and without (solid diamonds) habitat-quality effects: (*a*) least effect at low exploitation (10%); (*b*) greatest effect at high exploitation (60%). (Note different scales on *y* axes for *a* and *b*.)



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