A MODEL OF TROPICAL MARINE RESERVE-FISHERY LINKAGES

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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. In this paper we examine the contribution of fully protected tropical marine reserves to fishery enhancement by modeling marine reserve-fishery linkages. The consequences of reserve establishment on the long-run equilibrium fish biomass and fishery catch levels are evaluated. In contrast to earlier models this study highlights the roles of both adult (and juvenile) fish 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 fish migration scenarios are analyzed 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. Simulation results suggest that the establishment of a fully protected marine reserve will always lead 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 fish and larval movement. If the fishery faces low levels of exploitation, catches can be optimized without a reserve

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but with controlled fishing effort. With high fish migration from the reserve, catches are optimized with the reserve. The optimal area of the marine reserve depends on the exploitation rate in the neighboring fishing grounds. For example, if exploitation is maintained at 40%, the ‘optimal’ reserve size would be 10%. If the rate increases to 50%, then the reserve needs to be 30% of the management area in order to maximize catches. However, even in lower exploitation fisheries (below 40%), a small reserve (up to 20%) provides significantly higher gains in fish biomass than losses in catch. Marine reserves are a valuable fisheries management tool. To achieve maximum fishery benefits they should be complemented by fishing effort controls.

KEY WORDS: Fully protected marine reserves, fisheries management, adult and juvenile fish migration, larval dispersal, larval retention, spawner-recruit, coral reefs, optimal reserve area.

1. Introduction. There is growing concern over the excessive and unsustainable exploitation of our marine resources and fishery 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], [1996b], PDT [1990]).

This paper highlights the potential contribution of fully protected tropical marine reserves to fishery enhancement through the development of a 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 fish ‘spillover’ and ‘larval transport’. Following protection, as stocks inside reserves build up, the reserve becomes more densely populated leading to a net emigration of adult and juvenile fish to fishing grounds, or otherwise the ‘spillover effect’ (Rowley [1994]). This ‘spillover effect’ has been predicted by theory and modeling
(Polacheck [1990], DeMartini [1993], Man et al. [1995]) and suggested by some empirical studies (e.g. Attwood and Bennett [1994], Russ and Alcala [1996b], McClanahan and Kaunda-Arara [1996], McClanahan and Mangi [2000]). However, measuring spillover in the field can be troublesome due to the complex nature of reef communities, the lack of fish catch time series data and problems with 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 fish ‘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 described here follows those of Holland and Brazee [1996], Holland [2000], Sumaila [1998], Sanchirico and Wilen [1999], [2001], Hannesson [1998], Conrad [1999], Pezzey et al. [2000], Sladek-Nowlis and Roberts [1997, 1999]. These models have focused on either adult and juvenile fish movement in temperate sites (e.g. Conrad [1999]) or larval transport in tropical sites (e.g. Pezzey et al. [2000]). For some fish 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 behavior 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 areas. Although a large number of coral reef species are site-attached and have limited adult movement (Apeldoorn et al. [1997]), many of the important commercial species such as parrotfish, rabbitfish and emperors have moderate levels of movement. For example, McClanahan and Mangi [2000] found an average emigration rate from the Mombasa Marine Park of 0.5, suggesting good movement across the park boundaries. Adult fish ‘spillover’ could be an important factor in the tropics, though it may be limited to a region of a few kilometers beyond the reserve boundary.

The objective of this paper is to examine the effects of marine reserves on the equilibrium levels of fish biomass and catch in a tropical fishery under different conditions of fish and larval movement. In contrast to
earlier models, we model these movement processes explicitly through a spawner-recruit model. This allows for distinctly different behavioral and movement patterns of fish and larvae to be explored. We first outline the basic theoretical model describing the biological dynamics of two homogeneous stocks—in the reserve and fishing grounds—and then add exploitation to the system. We determine the conditions under which the biological steady state can be attained. A spawner-recruit model is then used to describe the stock dynamics with explicit adult and juvenile fish migration and larval dispersal effects. The cases of uniform larval dispersal, 50% uniform larval retention and complete larval retention combined with zero, moderate and high levels of fish migration are analyzed in turn. Modeling 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 exploitation rate in the fishery. The numerical simulations are based on data from Mombasa Marine National Park, Kenya, which is referred to as the ‘reserve’ in this paper.

2. The general model. In this section we describe a deterministic, discrete time model of 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. Figure 1 illustrates the basic dynamics of the marine reserve and fishery linked by the processes of adult and juvenile fish migration and recruit transfer (resulting from larval dispersal).

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 dynamics between a marine reserve and an adjacent fishing ground, it is necessary to divide the stock into two sub-stocks 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 from fishing, 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 $T$, recruit transfer, and $M$, the migration of adult and juvenile fish.

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

\begin{align}
X_{1,t+1} &= X_{1,t} + G(X_{1,t}) - M(X_{1,t}, X_{2,t}, \alpha, \sigma) - T(R_{1,t}, R_{2,t}, \alpha, \theta) \\
X_{2,t+1} &= X_{2,t} + G(X_{2,t}) + M(X_{1,t}, X_{2,t}, \alpha, \sigma) + T(R_{1,t}, R_{2,t}, \alpha, \theta)
\end{align}

where $G(X_{i,t})$ are the net biological growth functions of each stock. $M(X_{1,t}, X_{2,t}, \alpha, \sigma)$ is the net migration between the reserve (Area 1) and the fishing ground (Area 2) of adult and juvenile fish. If $M(X_{1,t}, X_{2,t}, \alpha, \sigma)$ is positive, there is a net migration out of the reserve. If $M(X_{1,t}, X_{2,t}, \alpha, \sigma)$ is negative, there is a net migration into the reserve. Similarly the transfer of recruits due to increased larval dispersal, $T(R_{1,t}, R_{2,t}, \alpha, \theta)$, can be positive or negative. $R_{1,t}$ and $R_{2,t}$ represent the recruit production of stocks $X_1$ and $X_2$, respectively, at time $t$. $\theta$ is the proportion of larvae retained.

With the fishery. Including extraction from fishing grounds we obtain a two-dimensional dynamical system (3) and (4) which describes the
link between a marine reserve and an adjacent fishery

\begin{align}
X_{1,t+1} &= X_{1,t} + G(X_{1,t}) - M(X_{1,t}, X_{2,t}, \alpha, \sigma) - T(R_{1,t}, R_{2,t}, \alpha, \theta) \\
X_{2,t+1} &= X_{2,t} + G(X_{2,t}) - H(X_{2,t}) + M(X_{1,t}, X_{2,t}, \alpha, \sigma) \\
&\quad + T(R_{1,t}, R_{2,t}, \alpha, \theta)
\end{align}

where \( H(X_{2,t}) \) is the catch from fishing ground (Area 2) at time \( t \), i.e. catch in time period \( t \) is simply a function of the exploitable fish biomass. Given the values for \( X_{1,0} \) and \( X_{2,0} \) the system can be iterated forward in time to equilibrium \( (X^*_1, X^*_2) \) when \( \Delta X_1 = 0 \) and \( \Delta X_2 = 0 \) where

\begin{align}
\Delta X_1 &= G(X_{1,t}) - M(X_{1,t}, X_{2,t}, \alpha, \sigma) - T(R_{1,t}, R_{2,t}, \alpha, \theta) \\
\Delta X_2 &= G(X_{2,t}) - H(X_{2,t}) + M(X_{1,t}, X_{2,t}, \alpha, \sigma) + T(R_{1,t}, R_{2,t}, \alpha, \theta)
\end{align}

Given appropriate functional forms, a corresponding value \( H(X^*_2) \) can be determined at this equilibrium. Depending on the functional forms of \( G(\cdot), M(\cdot) \) and \( T(\cdot) \), the system described by equations (3) and (4) may display a variety of dynamical behaviors. It is possible that the system may converge to one or more steady states, have periodic cycles or even deterministic chaos.

3. The spawner-recruit model. 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 fish and larval movement. The spawner-recruit relationship allows us to make a distinction between stock growth originating from recruit production, \( R \), and the stock that ‘escapes’ catch \( (X - H) \). Since benefits may accrue from both the ‘spillover’ of adult and juvenile fish 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]). Adjusting the difference equation system (3) and (4) by using a spawner-recruit relationship,
we obtain

\begin{align}
X_{1,t+1} &= (1 - \mu_1)X_{1,t} + R(X_{1,t}) - M(\overline{X}_{1,t}, \overline{X}_{2,t}, \sigma) - T(R_{1,t}, R_{2,t}, \alpha, \theta) \\
X_{2,t+1} &= (1 - \mu_2)X_{2,t} - H(X_{2,t}) + R(X_{2,t}) \\
&\quad + M(\overline{X}_{1,t}, \overline{X}_{2,t}, \sigma) + T(R_{1,t}, R_{2,t}, \alpha, \theta)
\end{align}

where $\mu_1$ and $\mu_2$ are the natural mortality estimates of stocks $X_1$ and $X_2$, respectively, and $R(X_{1,t})$ and $R(X_{2,t})$ are the recruit production for stocks $X_1$ and $X_2$. Pairs of data $(X_{1}^*, X_{2}^*)$ which satisfy $\Delta X_1 = 0$ and $\Delta X_2 = 0$ are found for the steady state where

\begin{align}
\Delta X_1 &= R(X_{1,t}) - \mu_1 X_{1,t} - M(\overline{X}_{1,t}, \overline{X}_{2,t}, \alpha, \sigma) - T(R_{1,t}, R_{2,t}, \alpha, \theta) \\
\Delta X_2 &= R(X_{2,t}) - \mu_2 X_{2,t} - H(X_{2,t}) + M(\overline{X}_{1,t}, \overline{X}_{2,t}, \alpha, \sigma) \\
&\quad + T(R_{1,t}, R_{2,t}, \alpha, \theta)
\end{align}

**Functional forms.** In order to simulate the model results for given parameter estimates we must specify appropriate functional forms of catch, effort, migration and recruitment functions:

*Catch, $H_t$.* The catch function is that of a simple linear relation between catch and biomass

\begin{equation}
H_t = \omega X_{2,t}
\end{equation}

where $\omega$ represents the exogenous exploitation rate as proportion of the exploitable fish biomass $X_{2,t}$ and $0 \leq (\mu_2 + \omega) \leq 1$ (since the total mortality cannot exceed $X_2$). Though a very simplistic form, this fits well with the data on observed fish biomass and recorded catch from the study site, see Appendix 1.

*Adult and juvenile fish migration, $M$.* The migration function solely describes the movement of adult and juvenile fish since the biomass estimates employed are based on the observation of only adult and juvenile fish (McClanahan and Kaunda-Arara [1996]).
The migration of adult and juvenile fish will depend on the size of the reserve, the mobility coefficient and the comparative densities of the reserve and fishing ground stocks. The reserve stock size is given by $A\alpha X_1$ and the fishing ground stock size is $A(1-\alpha)X_2$. The probability of the reserve stock moving out into the fishing ground is $(1-\alpha)$ and the probability of the fishing ground stock moving into the reserve is $\alpha$. With a mobility coefficient $\sigma$, the migration rate out of the reserve is $\sigma A\alpha (1-\alpha)X_1$ and the migration rate into the reserve is $\sigma A\alpha (1-\alpha)X_2$. Therefore, the net migration of adult and juvenile fish from the reserve to the fishing ground is given by

$$(12) \quad M(X_{1,t},X_{2,t}) = \sigma A\alpha (1-\alpha)(X_1 - X_2), \quad \text{where} \quad 0 \leq \sigma \leq 1$$

This function is based on that used by Hannesson [1998]. The inclusion of $\alpha(1-\alpha)$ eliminates the possibility of the migration out of the reserve exceeding the reserve stock, i.e. $X_1 > M$ always. We assume the area is proportional to carrying capacity and is spatially homogeneous. The model is kept simple by excluding the possibility that some areas have a higher carrying capacity than others due to 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 adult and juvenile fish 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 reserve 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. $\sigma$ indicates the propensity of animals in a stock to migrate. It is possible that migration of adult and juvenile fish will only begin when the density gradient has reached some ‘threshold level’. However, for simplicity, so long as $\sigma > 0$ and the stock densities are not equal there is assumed to be some movement between the areas. The propensity of individuals to move is likely to be affected by the shape and design of the reserve. High-edge-to-area ratios will encourage even mainly sedentary species to ‘spillover’ (Buechner [1987]). However we do not deal with this directly in this model.
Recruit production, $R_1$ and $R_2$. 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 estimates which indicate a decline in recruitment at high biomass levels (Guénette and Pitcher [1999], Ricker [1954]). Taking a proportion of biomass $X$ to be a proxy for spawning stock biomass, the Beverton-Holt recruitment function for an unexploited stock 'i' is given by

\[ R_{i,t} = \frac{\varepsilon_1 X_{i,t}}{\gamma_i \varepsilon_1 X_{i,t} + \beta_i} \]

where $R_{i,t}$ is recruit production of the stock $i$ in time period $t$, $X_{i,t}$ is biomass of the stock $i$ in time period $t$, $\gamma_i$ and $\beta_i$ are recruitment parameter estimates for the stock $i$ for a given initial growth rate, $\varepsilon_1$ is the proportion of the reserve stock which is reproductively mature. This was calculated from size class data.\(^1\)

For an exploited stock $i$ the Beverton-Holt recruit production function is

\[ R_{i,t} = \frac{\varepsilon_2 (X_{i,t} - H_{i,t})}{\gamma_i \varepsilon_2 (X_{i,t} - H_{i,t}) + \beta_i} \]

where $\varepsilon_2$ is the proportion of the exploited stock which is reproductively mature.

We make three assumptions about recruit production in an exploited stock:

1. $\varepsilon_2$ is less than $\varepsilon_1$ for all time periods, i.e. a smaller proportion of an exploited stock will be reproductively mature than in an unexploited stock because the largest fish will be caught first. Individual fish length is exponentially related to fecundity, usually $F = aL^3$, (Sadovy [1996]). Field data suggest that even after only one year of full protection reproductive capacity is enhanced (see Appendix 2).

2. $\varepsilon_2$ 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.

3. Spawners in the exploitable stock are a proportion, $\varepsilon_2$, of the fish biomass remaining after catch, $(X_2 - H)$. Unlike natural mortality
and exploitation, spawning in tropical reef species may be seasonal (Sadovy [1996]). Some exploitation will take place before spawning. Since the largest fish, the spawners, are caught first, this will reduce recruit production (see discussion).

Recruit transfer, $T$. There is some debate as to whether reserves retain much of their larval output (Roberts [1997], Roberts [1998], Bellwood [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 is

$$T = (1 - \theta)(1 - \alpha)R_1 - \alpha R_2$$  \hspace{1cm} \text{where} \hspace{0.5cm} 0 \leq \theta \leq 1$$

$\theta$ is the proportion of larvae retained. $\theta = 0$ represents zero retention, i.e. uniform larval dispersal. $\theta = 1$ represents a closed system, with respect to larvae, where each stock simply replenishes itself with new recruits. The proportion of larvae retained will depend on the relationship between the dispersal distance and the reserve size (and shape). We take $\theta = 0.5$, i.e. 50% larval retention to be our third scenario.

Steady state equations. Employing the above functional form specifications the steady state solutions can be found by solving the following equations for $(X_1^*, X_2^*)$:

$$-\mu_1 X_1^* - \sigma A \alpha (1 - \alpha) \left[ X_1^* - X_2^* \right]$$

$$+ \alpha (1 - \theta) \left[ \frac{\varepsilon_1 X_1^*}{\gamma_1 \varepsilon_1 X_1^* + \beta_1} + \frac{\varepsilon_2 (1 - \omega) X_2^*}{\gamma_2 \varepsilon_2 (1 - \omega) X_2^* + \beta_2} \right]$$

$$+ \theta \left[ \frac{\varepsilon_1 X_1^*}{\gamma_1 \varepsilon_1 X_1^* + \beta_1} \right] = 0$$

$$- (\mu_2 + \omega) X_2^* + \sigma A \alpha (1 - \alpha) \left[ X_1^* - X_2^* \right]$$

$$+ (1 - \alpha (1 - \theta)) \left[ \frac{\varepsilon_1 X_1^*}{\gamma_1 \varepsilon_1 X_1^* + \beta_1} + \frac{\varepsilon_2 (1 - \omega) X_2^*}{\gamma_2 \varepsilon_2 (1 - \omega) X_2^* + \beta_2} \right]$$

$$- \theta \left[ \frac{\varepsilon_1 X_1^*}{\gamma_1 \varepsilon_1 X_1^* + \beta_1} \right] = 0$$

4.1 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, and its adjacent fishery, the North Mombasa fishery. The park stretches the length of the coast and is physically bounded by the reef, only extending a few hundred meters beyond. Since fishers are not able to fish in the rougher waters beyond the reef, they only fish on two sides of the rectangular park. This will have consequences for the benefits to them from ‘spillover’. This model does not directly take account of the shape and design of the park, which may be responsible for some ‘loss’ of larvae and fish spillover to inaccessible fishing areas beyond the reef. We assume that all areas beyond the park are exploitable.

The model describes the dynamics of two stocks, $X_1$ 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 attempting to tackle the question of multispecies dynamics at work in coral reef environments.

In the first simulation we test the significance of fish and larval movement on catch and biomass levels in the fishery for three different initial stock growth rates of 10%, 35% and 60% per annum. Based on calculations of reserve biomass growth since protection, 35% best represents the Mombasa case (McClanahan and Kaunda-Arara [1996], McClanahan [unpublished data]). Growth rates of 10% and 60% 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 exploitation rate outside the reserve.

We used the computer program STELLA® for simulating the model and testing its sensitivity.

4.2 Parameter estimates. Estimating growth parameters was problematic since little is known about the overall growth of fish stocks on coral reefs (Polunin et al. [1996]). We therefore used three scenarios of initial growth 10%, 35% and 60% per annum and determined 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 $\gamma$ and $\beta$ and $\mu$ were based on the overall growth of a stock 100% of which is reproductively mature. However, we acknowledge in the model the important effect protection has on the reproductive capacity of the protected stock relative to the exploited stock. In Mombasa, it was found that by 2000 (8 years after protection was fully enforced) the reproductive gradient between the stocks was significant, approximately 70% to 20% of fish biomass (see Appendix 2). These values are likely to underestimate the true reproductive gradient because egg production per unit biomass is greater for large fish than small. For example, one 10 kg grouper may produce as many eggs as 93 0.5 kg groupers (Sadovy [1996]). The levels of reproductive capacity are represented by $\varepsilon_1$ and $\varepsilon_2$ 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 1.²

4.3 Results. The simulations were run for 30 years, which was always long enough to reach equilibrium. The stocks usually reached equilibrium after about 10 to 15 years. This represents the time it may take before the benefits of protection are fully realized. All equilibria were found to be stable for the parameters chosen. $t = 0$ represents the time period in which the reserve was established. The initial biomass was based on the value of 150 kg/ha inside and outside the park derived from underwater visual census estimates (McClanahan and Kaunda-Arara [1996]). The initial total biomass was estimated to be approximately 400 tonnes in the whole management area.

4.3.1 Simulation 1—effects of fish 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 $\alpha$ in this simulation. Figure 2 shows the variation in equilibrium catch for various exploitation rates outside the reserve and
<table>
<thead>
<tr>
<th>Parameters</th>
<th>Estimates</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\mu_1, \mu_2$</td>
<td>0.2</td>
<td>Natural mortality of adult and juvenile fish in stocks 1 and 2. Taken to be the same for both stocks and based on ‘moderate’ estimates of Pauly [1980] and Pauly and Ingles [1981].</td>
</tr>
<tr>
<td>$\omega$</td>
<td>0 to 0.8</td>
<td>Exploitation rate—a proportion of exploitable biomass.</td>
</tr>
<tr>
<td>$\gamma_1$</td>
<td>0.0000269 (10%), 0.0000143 (35%), 0.0000096 (60%)</td>
<td>Recruit production parameter estimates based on the initial values of $X_1$. Low, medium and high initial growth rates indicated.</td>
</tr>
<tr>
<td>$\gamma_2$</td>
<td>0.0000115 (10%), 0.0000061 (35%), 0.0000041 (60%)</td>
<td>Recruit production parameters for fishing ground stock $X_2$. Low, medium and high initial growth rates indicated.</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>0.0000081 (10%), 0.0000043 (35%), 0.0000029 (60%)</td>
<td>Recruit production parameters for ‘without reserve’ scenario, i.e. initial growth rate of the total stock.</td>
</tr>
<tr>
<td>$\beta_1, \beta_2, \beta$</td>
<td>0.1</td>
<td>Recruit production parameter estimates. Fixed for all growth rates.</td>
</tr>
<tr>
<td>$\epsilon_1$</td>
<td>0.7</td>
<td>Proportion of reserve biomass reproductively mature. Calculated from existing size classes data and length at first maturity estimates (Appendix 2).</td>
</tr>
<tr>
<td>$\epsilon_2$</td>
<td>0.2</td>
<td>Proportion of fishing ground biomass reproductively mature. Calculated from existing size classes data and length at first maturity estimates (Appendix 2).</td>
</tr>
<tr>
<td>$\epsilon$</td>
<td>0.2</td>
<td>Proportion of total biomass reproductively mature for ‘without reserve’ scenario.</td>
</tr>
<tr>
<td>$\sigma$</td>
<td>0, 0.2, 0.9</td>
<td>Propensity of adult and juvenile fish 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 exploitation rate and larval retention level.</td>
</tr>
<tr>
<td>$\theta$</td>
<td>0, 0.5, 1</td>
<td>Proportion of larvae retained—representing uniform dispersal, uniform 50% larval retention, complete larval retention, respectively.</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>800/2675</td>
<td>Proportion of management area protected.</td>
</tr>
</tbody>
</table>
2a. Zero fish migration

2b. Moderate fish migration
FIGURE 2. Equilibrium catch levels for nine combinations of fish and larval movement. The exploitation rate is the percentage of fish biomass in the fishing ground extracted each year.

2c. High fish migration

The estimates of marine catches in this area have ranged from 10–19 tonnes/km²/year (McClanahan et al. [1999], Linden and Sporrong [1999]). The main results for catch levels are summarized in Table 2.

For the closed system (with no fish or larval movement between areas), catch with the reserve clearly remains below catch without reserve. With 50% larval retention, the exploitation rate would have to exceed 45% of exploitable biomass before catch with the reserve exceeds catch without. For zero fish migration and an exploitation rate above 40% of exploitable biomass, catch with the reserve can exceed...
TABLE 2. Conditions under which catch with reserve (comprising 31% of the management area) can exceed catch without the reserve.

<table>
<thead>
<tr>
<th>Movement</th>
<th>Larval Movement</th>
<th>Complete retention</th>
<th>50% retention</th>
<th>Uniform dispersal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zero</td>
<td>catch without &gt;</td>
<td>catch with &gt; catch</td>
<td>catch with &gt; catch</td>
<td>catch with &gt; catch</td>
</tr>
<tr>
<td></td>
<td>catch with</td>
<td>without at 45%</td>
<td>without at 40%</td>
<td>without at 40%</td>
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<tr>
<td></td>
<td>collapses at 70%</td>
<td>exploitation and</td>
<td>exploitation and</td>
<td>above.</td>
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<td>exploitation.</td>
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<tr>
<td>Adult</td>
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<td>catch with &gt; catch</td>
<td>catch with &gt; catch</td>
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<tr>
<td>Moderate</td>
<td>without at 40%</td>
<td>without at 35%</td>
<td>without at 35%</td>
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<td>juvenile</td>
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<td>above.</td>
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<tr>
<td>fish</td>
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<tr>
<td>High</td>
<td>without at 30%</td>
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catch without reserve for the case of uniform larval dispersal. For moderate fish migration and an exploitation rate above 35%–40% of exploitable biomass (depending on larval movement scenarios), catch with the reserve exceeds catch without reserve. For high fish migration and a exploitation rate 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 fish migration the optimal solution can be found without a reserve when the exploitation rate is 30% of total biomass. It is interesting to observe that there is a very thin line between achieving the optimal exploitation rate without a reserve and it is becoming preferable to reserve 31% of the grounds.

For high levels of fish migration, however, the ‘optimal’ solution is found with the 31% reserve and an exploitation rate in the neighboring fishing ground of 40% of the exploitable biomass. Our results indicate that, the greater the level of fish migration, the lower the exploitation rate at which it becomes preferable to have the reserve.

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

Predictably, total fish biomass was greater with a reserve under all conditions of larval and fish 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 (225, 415, 600 kg/ha) for the 10%, 35% and 60% scenarios. Figure 3 shows the patterns of fish biomass equilibrium for various scenarios of fish and larval movement under the initial stock growth rate of 35% per annum.

Both fish and larval movement patterns strongly influence the equilibrium levels of fish biomass. The higher the proportion of larvae retained in the reserve, the higher the biomass. The higher the degree of fish migration from the reserve, the lower total biomass in the fishery since a greater biomass becomes exploitable. Sustainable exploitation rates are inversely related to biomass levels.

4.3.2 Simulation 2—optimal reserve area and exploitation rate. If a reserve is to be established it is desirable to know what size it should be and what conditions of exploitation should exist outside in order to maximize fishery benefits.

This simulation was run for the combination of moderate fish migration and 50% larval retention. This case may best represent the dynamics in a coral reef environment where some fish species experience limited migrations such as snapper and grunts (Appeldoorn et al. [1997]) and others are sedentary, or site-attached, e.g. damselfishes and butterflyfishes (Pohlin and Roberts [1996]) and where larvae generally disperse widely but some retention may occur (Roberts [1997], [1998], Bellwood [1998], Sale and Cowen [1998]). Figure 4 shows the relationship between equilibrium catch levels, reserve area and exploitation rate for a stock with a 35% initial growth rate.
3a. Zero fish migration

3b. Moderate fish migration
FIGURE 3. Equilibrium biomass levels for nine combinations of fish and larval movement. The exploitation rate is the percentage of fish biomass in the fishing ground extracted each year.

From Figure 4a we can see that an optimal catch of 117 tonnes/year (4.42 tonnes/km²/year) can be obtained with no reserve and with an exploitation rate of 30%. This was the same for a stock with initial growth rate of 10% and 60% per annum but the optimal catch was 55 tonnes/year (2.1 tonnes/km²/year) and 205 tonnes/year (7.8 tonnes/km²/year), respectively. If the exploitation rate in the fishery is 40% or above, establishing a marine reserve can give catch benefits.

The optimal size of the reserve will depend on the exploitation rate in the fishery. For example, if the exploitation rate in the fishery is 50% the reserve should be 30% of the management area. However, the establishment of the reserve itself may influence the exploitation rate if fishing effort becomes more concentrated. We can therefore look at the problem in a different way, if a reserve (of a given size) is established (in response to overexploitation or for conservation benefits) what should the exploitation rate in the neighboring fishery be to maximize catches? This is illustrated best in Figure 4b which shows the ranges of reserve areas and appropriate accompanying exploitation rates. These are summarized in Table 3.
FIGURE 4a. Exploitation rates at which reserves provide catch benefits.

FIGURE 4b. Reserve areas and accompanying exploitation rates to maximize catch.
TABLE 3. Ranges of reserve size with maximizing exploitation rate.

<table>
<thead>
<tr>
<th>Reserve size (%)</th>
<th>Exploitation rate (%)</th>
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<tbody>
<tr>
<td>$0 \leq \alpha \leq 30$</td>
<td>30</td>
</tr>
<tr>
<td>$30 &lt; \alpha &lt; 60$</td>
<td>40</td>
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<tr>
<td>$60 \leq \alpha &lt; 80$</td>
<td>50</td>
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<tr>
<td>$80 \leq \alpha &lt; 90$</td>
<td>60</td>
</tr>
<tr>
<td>$90 \leq \alpha &lt; 100$</td>
<td>70</td>
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</table>

The establishment of the reserve, therefore, would be best accompanied by a restriction on exploitation in the fishing ground. The size of the reserve established would dictate the level of exploitation outside which would maximize the catch. Reserves will benefit overexploited fisheries but, to achieve the maximum benefit, must be accompanied by controls on fishing effort outside.

An interesting point to note is that even if the ‘optimal’ 30% exploitation rate exists in the fishery (same for 10% and 60% growth rates) Figure 4b clearly illustrates the loss of catch resulting from establishing a reserve of up to 20% is minimal. With a 10%, 15% or 20% reserve, 96%, 94% and 91% of maximum catch could still be obtained with accompanying gains in total fish biomass of 14%, 22% and 30% (shown in Figure 5).

Figure 5 simply illustrates the equilibrium fish biomass levels for various combinations of reserve area and exploitation rate. The results are intuitive. High levels of extraction lead to lower fish biomass. Larger reserves lead to higher biomass. For the ‘optimal’ combination of 0% reserve and 30% exploitation rate the equilibrium total biomass would be approximately 400 tonnes (150 kg/ha). However, the maximum biomass is 1400 tonnes (525 kg/ha) when there is no exploitation.

5. 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 cannot benefit from the marine reserve, though protection will still lead to higher total biomass levels. Movement patterns
FIGURE 5. Total fish biomass for various exploitation rates and reserve sizes. The exploitation rate is the percentage of fish biomass in the fishing ground extracted each year. The reserve area is the percentage of the management area which is fully protected.
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 and pattern of reserves in the network (Ballantine [1995], Shackell and Willison [1995]). Without directly describing these attributes, we have chosen a variety of parameter values to reflect nine possible combinations of fish and larval movement patterns. For cases where there is some degree of either fish or larval movement to the fishing ground, our study supports those who promote marine reserves as a fishery enhancement tool in moderately to heavily exploited fisheries (e.g. Holland and Brazee [1996], Sladek-Nowlis and Roberts [1997]). We also advocate the use of marine reserves in circumstances where major uncertainties exist over the state of fishery biomass and catch levels.

Catches can be maximized without a reserve if exploitation outside the reserve can be restricted to 30% of the exploitable biomass. However, even in a low exploitation fishery a small decline in catch due to small reserve would be rewarded with significant increases in total biomass. With a 10%–20% reserve, only 4%–9% catch would be lost compared to 14% to 30% gain in total biomass and the accompanying ecological benefits reserves offer such as habitat protection. 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.

**Time patterns.** The recruit production function implies that exploitation occurs before spawning, Equation (14). This can be justified to some extent by the seasonal spawning patterns of some reef species and the targeting of the largest fish. Since spawning occurs at discrete points in time and exploitation is continuous, spawners must survive some level of exploitation. In addition the spawners are likely to be the largest fish—those most vulnerable to fishing. Therefore, many are likely to be caught before or as they reach maturity. Many fish caught at spring tides in Mombasa are full of eggs (personal observation) confirming that spawning is affected.
To test a more generous recruitment assumption, we also ran the simulation with all spawning occurring before exploitation. The results showed that the exploitation rate in the fishing grounds would have to be above 40% (high fish mig), 60% (moderate fish mig) or 80% (zero fish mig) before a reserve could offer catch benefits. Predictably, fish biomass was again significantly higher with the reserve than without.

Reproductive capacity. Reserve creation will increase the reproductive capacity of the protected stock. 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 modeled as a variable.

Growth rate. We based our estimate of initial growth rate of the stock (35% per annum) on data of biomass levels in Mombasa Marine National Park in 2000 (8 years after protection) compared to pre-park levels (McClanahan and Kaunda-Arara [1996], McClanahan [unpublished data]). Ideally, for this spawner-recruit type model, we would have access to separate estimates for recruit production and natural mortality of each stock.

Movement patterns of fish and larvae. We limited our choice of parameter values for $\sigma$ to 0, 0.2 and 0.9. For each of these the equilibrium was stable. The value of 0.2 gave a moderate rate of fish movement of between 5% and 12% of the park fish stock. This was thought to best represent the Mombasa MNP case. However, we could extend the sensitivity analysis to cover a wider range of values.

The density-dependent form of the fish migration function does not allow for source-sink dynamics which may come into play. With high
‘permanent’ fish 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 and juvenile fish 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 exploitation rate at which it became preferable to establish a reserve when fish migration is zero. In fact, for each initial growth rate, if larval retention is 90%, the exploitation rate 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 generalized life characteristics of recruit production and natural mortality. In doing this, we treat the stock as a 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 the exploitation rate as the proportion 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. We use biomass estimates derived from underwater visual census from Mombasa. These may give a good idea of the comparative levels of biomass spatially and temporally but biases may exist in this type of estimation (Jennings and Pohjola [1995], St. John et al. [1990], Willis et al. [2000], Watson and Quinn [1997], Kulbicki [1998], Blomqvist [1991], Thompson and Mapstone [1997], Benedetti-Cecchi [1996]). In addition biomass estimates are not always available and so the 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 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.

The establishment of a reserve is likely to have an impact on the existing exploitation rate ($\omega$). As more fishers may be concentrated into a smaller area, $\omega$ is likely to increase as $\alpha$ (the reserve area) increases. It would be valuable to incorporate this type of relationship into the model and simulate for possible implications.

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 reef topographic complexity (e.g. McClanahan [1994]). Though these are inherently linked, little study has been done on the indirect benefits of habitat protection on fishery catch.

Both the Mombasa MNP and the adjacent fishing grounds are situated in a region comprising a lagoon and a fringing coral reef. In this respect, there is some similarity in the habitat structure of the two areas. However, live coral cover in Mombasa MNP has increased dramatically over the years of protection (McClanahan [1994]). This has implications for the productivity and survival rates of the protected fish stocks. This is the subject of a further paper (Rodwell et al. [2001]).

6. Concluding comments. Many of the world’s tropical reef fisheries are overexploited and in danger of collapse. Best estimates indicate that the North Mombasa fishery is currently being exploited at a level of approximately 80% of the exploitable biomass (see Appendix 1). This study indicates that, had this exploitation rate 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 would require their cooperation and participation. Possible measures to compensate, retrain or offer alternative employment to
Fishers should be considered in the initial plans and costs of implementing these management decisions.

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. However, in reality, in coral reef environments, exploitation is extremely difficult to control. Marine reserves may suffer from some poaching activities, but appear on the whole to be easier to enforce than many traditional management tools, particularly in these tropical, developing countries (Roberts and Polunin [1993]). Biological and economic uncertainties add weight to the case for marine protected areas as a buffer against stochastic events and fishery decline. Further ecological data are required to make accurate predictions of the effect of protection on the growth of a fish stock, habitat quality and movement patterns of adult fish, juvenile fish and larvae. In addition, more research is required into the most effective design, shape and location of these reserves and fishing effort controls outside them.

Marine reserves are an important component of sustainable tropical fisheries management. However, many existing reserves suffer from a lack of adequate management (McClanahan [1999]). The benefits of reserves will only be fully realized when they are properly enforced. When enforced, they augment fish biomass, protect essential habitats and can improve catches in previously moderately or heavily exploited fisheries. Reserves will be most effective when coupled with fishing effort controls in adjacent fisheries.

**Appendix**

1. **Catch/Biomass function for the North Mombasa fishery.**

**Biomass.** We used observed fish biomass data collected through visual census carried out at the Coral Reef Conservation Project, Mombasa. The study site for fish counts is on a coral reef and the fishing ground substrate comprises mainly sand and seagrasses. Different
species are present and visible in each region. Cryptic species and seagrass species are not observed in the transects. Biomass estimates are likely to be underestimates for this reason. In addition underwater visual census biases do exist (Jennings and Polunin [1995], St. John et al. [1990], Willis et al. [2000], Watson and Quinn [1997], Kulbicki [1998], Blomqvist [1991], Thompson and Mapstone [1997], Benedetti-Cecchi [1996]).

Recorded catch data³ underestimate actual catch for the following reasons:

- fishers operating at night do not declare their catches,
- take-home catch is removed before catches are weighed,
- fisheries staff are often absent from work and do not submit data for missing work days,
- unofficial landing sites exist where fishers using illegal gears often land catches so as not to be detected (Glaesel [1997]).

We used matching data pairs of catch and biomass in time and space. Using the 16 pairs of data points, we obtain a relationship between recorded catch and observed biomass in the fishing grounds adjacent

FIGURE 6. The linear relationship between recorded catch and observed fish biomass (with zero intercept).
to the marine park.

In order to get an idea of the exploitation rate adjacent to Mombasa MNP we used the estimate of Glaesel [1997] that recorded catch may be underestimated by as much as a factor of 5. If biomass too is underestimated perhaps by a factor of 2, the exploitation rate would be 80% of the exploitable biomass. This is, of course, a very rough calculation, but indications are that the North Mombasa fishery is very heavily exploited so this does not seem outrageous.

2. Reproductive capacity $\varepsilon_1$ and $\varepsilon_2$. The reproductive capacity of the fish stock was taken as the percentage of the fish biomass that was reproductively mature. Estimates of maximum length of all species were taken from Smith and Heemstra [1991]. The median, maximum length for each family group was calculated from these estimates. The estimate for the ‘others’ category was based on the mean maximum length for each family group—an estimation based on Sadovy [1996]. Fish biomass data were categorized in size classes: 3–10, 10–20, 20–30, 30–40 and 40cm plus. For the reproductive capacity analysis these classes taken to represent: 3–10 cm, 11–20 cm, 21–30 cm, 31–40 cm, 41 cm upwards. To calculate the level of mature biomass, biomass in each size class was assumed to be evenly distributed. Therefore, if the length at maturity was estimated to be 22 cm (e.g. Lutjanidae), then all biomass in classes ‘31–40’ and ‘41 upwards’ plus 90% of the ‘21–30’ size class were considered mature. Some accuracy was lost by not having fish biomass estimates in smaller size classes or even exact lengths.

Figure 7 shows the estimates of average reproductive capacity of the fish biomass at Mombasa (fully protected), Ras Iwatine (gear-restricted) and Vipingo (unprotected). Mombasa had the highest reproductive capacity at all times post-park establishment, ranging from approximately 53% in 1988 to nearly 70% in 2000. The average reproductive capacity in Mombasa between 1988 and 2000 was 65%. Raw Iwatine, the gear-restricted site, was found to have a reproductive capacity averaging approximately 46% in the period 1992 to 2000. The reproductive capacity of the unprotected stock at Vipingo was very low, averaging 19% between 1988 and 2000.

The area in which the restriction on beach seines is effective is 375 ha ($3.75 \text{ km}^2$) of the fishing ground. The remaining fishing grounds, approximately 1500 ha ($15 \text{ km}^2$), are unprotected. These areas were
FIGURE 7. A comparison of reproductive capacity estimates for Mombasa, Ras Iwatine and Vipingo between 1988 and 2000—measured as the percentage of fish biomass which is reproductively mature.

used as weights when calculating the average reproductive capacity of all fishing grounds between 1988 and 2000. This was found to be approximately 24%. Since there are no data for Ras Iwatine before 1992, the reproductive capacity estimates based on data from 1992 to 2000 are 69% in the park and 24% in the fishing grounds.

ENDNOTES

1. 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.

2. For simulation 2 the value of α varied. With the initial values of X1 and X2 the recruitment parameters γ1 and γ2 also changed. The program made these changes automatically. All other parameters were kept the same.

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

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REFERENCES


PDT (Plan Development Team) [1990], The Potential of Marine Fisheries Reserves for Reef Management in the U.S. Southern Atlantic, NOAA-NMFS Tech. Memo. 261, Miami, FL, U.S.A.
TROPICAL MARINE RESERVE-FISHERY LINKAGES 485


J.A. Stamps, M. Buechner and V.V. Krishnan [1987], *The Effects of Edge Permeability and Habitat Geometry on Emigration from Patches of Habitat*, The Amer. Naturalist **129**, 533–552.


