Exploring the effect of Marine Protected Areas on the dynamics of fish communities in the southern Benguela: an individual-based modelling approach

Dawit Yemane, Yunne-Jai Shin, and John G. Field


Marine Protected Areas (MPAs) have been suggested as a tool that can achieve some of the goals of an Ecosystem Approach to Fisheries (EAF), e.g. prevention of overexploitation, biodiversity conservation, recovery of overexploited population, but the consequences of their establishment on the dynamics of protected components are often unclear. Spatial and multispecies models can be used to investigate the effects of their introduction. An individual-based, spatially explicit, size-structured, multispecies model (known as OSMOSE) is used to investigate the likely consequences of the introduction of three MPAs off the coast of South Africa, individually or in combination. The simultaneous introduction of the MPAs affected varying proportions of the distribution of the modelled species (5–17%) and 12% of the distribution of the whole community. In general, the introduction of the MPAs in the different scenarios resulted in a relative increase in the biomass of large predatory fish and a decrease in the biomass of small pelagic fish. The simulation demonstrates that consideration of trophic interactions is necessary when introducing MPAs, with indirect effects that may be detrimental to some (mainly smaller prey) species.

Keywords: ecosystem models, individual-based models, Marine Protected Areas, southern Benguela.

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Introduction
Overharvesting is currently recognized as a major threat to the structural and functional organization of marine ecosystems (Gislason et al., 2000). A number of studies documents such effects on target and non-target components of ecosystems (Pauly et al., 1998; Jennings et al., 1999, 2002; Bianchi et al., 2000). They include direct biomass removal, changes in the size structure of both the target species and the community, changes in community diversity, and changes in the genetic structure of fish populations. Documentation of such impacts on various marine ecosystems, and uncertainties in fisheries management (Ludwig et al., 1993), led to what is currently termed the Ecosystem Approach to Fisheries (EAF; Garcia and Cochrane, 2005). EAF intends to achieve management of fisheries in a way that addresses the manifold needs of society without limiting the options for future generations to benefit from the wide-ranging goods and services provided by marine ecosystems (FAO, 2003). The move towards holistic approaches to ecosystems is associated with the development of indicators for gauging the effects of fisheries at different hierarchical levels in the ecosystem: population, community, and ecosystem levels (Rice, 2000, 2003; Rochet and Rice, 2005). The most difficult task is generally in incorporating the changes observed into management procedures. The move to an EAF necessitates refinement and/or introduction of new management measures to help achieve its objectives.

One of the measures that has been advocated for achieving the objectives of an EAF is the establishment of Marine Protected Areas (MPAs; Lauck et al., 1998; Apostolaki et al., 2002; Gell and Roberts, 2003; Babcock et al., 2005; Roberts et al. 2005). Despite renewed interest in MPAs, a number of studies (Allison et al., 1998; Apostolaki et al., 2002; Baskett et al., 2006) suggest that expected benefits from their establishment depends on a multitude of technical (size, location, and number of reserves) and biological factors (life-history traits, migration patterns, initial abundance of species, community structure, and species interactions). Further, the introduction and expected outcomes from MPAs are characterized by difficulties and uncertainties: uncertainties concerning the potential for improved yield that marine reserves are expected to offer, issues concerning their location and size, and societal (fishers) opposition to the exclusion of previously fished zones (Sant, 1996; Apostolaki et al., 2002). Before the physical introduction of MPAs, an understanding of possible consequences is crucial; one of the ways of gaining such understanding is through simulation modelling, another is learning lessons from the introduction of MPAs in other parts of the world. Attwood and Bennett (1995) used a discrete age-structured...
model with a spatial component to study the effects of the introduction of MPAs on the yield of three species of linefish targeted by recreational angling. They found variable responses of the three species to the sizes and locations of different MPAs and demonstrated that some combinations of MPA size and location are beneficial for the protected species.

The increasing interest in MPAs as a management tool is accompanied by the use of various types of model, as means of exploring the possible outcomes of their implementation. Examples are size-structured, spatially explicit, single-species models (Apostolaki et al., 2002), spatially explicit biomass production models (Stefansson and Rosenberg, 2005), and spatially structured multispecies models (Shin and Cury, 2001a; Baskett et al., 2006). Individual-based models (IBMs) are increasingly used for ecological research. The impetus behind their growing use, other than the increase in computing power and storage capacity, is that they allow various ecosystem processes to be addressed at different scales, especially at the level of individual fish (Huston et al., 1988). These include the consideration of variability among individuals, local interactions, the complete life cycle of an individual, an individual's history, and individual behaviour adapting to its changing internal and external conditions (Grimm, 1999; Grimm and Railsback, 2005).

OSMOSE (Object-oriented Simulator of Marine eOsYstem Exploitation) is a recently developed IBM that integrates the life cycle of a fish, with emphasis on trophic interactions (Shin and Cury, 2001b, 2004; Shin et al., 2004). It is also a multispecies model used to assess the indirect effects of fishing and allows one to calculate various types of ecosystem indicator. Here, we use OSMOSE to investigate the consequences of the introduction of three newly proposed MPAs off South Africa. The analysis contains a community of 12 interacting fish species that constitute the bulk of fish biomass and catch in the southern Benguela (Shannon et al., 2003).

Methods

The model: OSMOSE

OSMOSE is written in Java programming language and includes a hierarchical structure of model classes corresponding to those in an ecosystem. The model includes three biological classes: school, cohort, species; and two classes representing the two-dimensional spatial domain of the ecosystem: cell and grid. In this case, a cell is one box within a grid system (Figure 1). This hierarchical structure allows assessment of various features/attributes of the system at different levels in the hierarchy (e.g. size, abundance, or biomass can be tracked at population and community levels, and locally in subregions). The basic modelling unit is the school, which represents groups of individuals that share the same length, food requirement, and at any given time-step, the same spatial coordinate. In the simulation series presented here, the model time-step is 1 year divided into two semesters (6-month periods), reproduction takes place once at the end of each semester.
of a time-step, and fishing in the middle of the time-step. The other processes (foraging, predation, and growth) are assumed to be continuous, so occur in both semesters. The spatio-temporal dynamics of these processes also contribute to the stochasticity of the model. The time-step may be unrealistically long in terms of the mobility of most species, but this is compensated by the 200-year model run. As the structure and details of the model have been described already (Shin and Cury, 2001b, 2004; Shin et al., 2004; Travers et al., 2006), we here provide only a brief description of the processes. The main feature of OSMOSE lies in the predation process, which is assumed to be opportunistic and size-based. Figure 2 outlines the biological processes according to their order of execution in the model. Bracketed processes take place in both first and second semesters. This version of OSMOSE is not coupled to a hydrodynamic/biogeochemical model, as in the more recent version (Travers and Shin, in press).

The maximum biomass of non-piscivorous fish in the model corresponds to the carrying capacity constraint. The term

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**Figure 2.** Process flowchart for OSMOSE according to the order of execution in the model. Dot–dash–bracketed processes are those that occur in both semesters. Modified from Shin and Cury (2004).
"non-piscivorous fish" includes eggs, larvae, and juveniles of piscivorous fish and all stages of forage fish. At the beginning of each time-step and in each cell of the grid, the biomass of non-piscivorous fish is compared with the carrying capacity, and if the biomass exceeds that of the carrying capacity, then it will be reduced proportionally. Additional mortality is applied to the larval and juvenile stages of fish to account for the greater natural mortality these stages suffer; this parameter is used to calibrate the model (Shin et al., 2004).

For each species modelled, coordinates of the spatial distribution ranges are provided by age class and for each semester. At the beginning of each time-step, schools of each age class and species are distributed according to the distribution range of the species provided, as an input to the model. The model accounts for two types of movement. First, species are redistributed at the beginning of each semester to account for seasonal movements of age classes by species. Second, individuals move to forage within each time-step. Information on the spatial distribution of the species was obtained from the literature, research surveys, and in consultation with scientists from Marine and Coastal Management of South Africa’s Department of Environmental Affairs and Tourism. The distribution maps used here were published by Travers et al. (2004).

Both foraging and predation processes are applied to the piscivorous groups. Foraging is represented by the movement of fish towards neighbouring cells with greater biomass of potential prey. Potential prey items are defined according to their size relative to that of the predator. Predation in OSMOSE takes place once the following two criteria are satisfied: first, there must be a spatio-temporal co-occurrence of a predator and its prey within a cell, and second, the predator–prey length ratio must exceed the critical ratio of 3.5 estimated from FishBase (Shin and Cury, 2004). Once predators have exerted predation mortality on their prey, predation efficiency is calculated as the ratio of the quantity of food ingested by a predator to the amount required to fulfil its metabolic needs (Shin and Cury, 2001b). No explicit functional relationship was included to model predator–prey interactions, but ingestion rate was capped at 3.5 g per gramme body weight per annum.

The mean annual growth rate of fish at each age is calculated using the von Bertalanffy growth model. That rate is then adjusted to take into account the quantity of food ingested in relation to the critical ration for maintenance, so that the growth rate in length increases linearly with predation efficiency when the predation efficiency is greater than the maintenance threshold. As the food ration drops below the maintenance threshold, fish starve. When the quantity of ingested food is too little to fulfil maintenance requirements, then the rate of starvation mortality is calculated as a linear negative function of predation efficiency.

Fishing induces mortality in the middle of a time-step, at the end of the first semester. The theoretical number of fish removed from each school is computed using an exponential decay model of the type

\[ N_{t+1,a,s} = N_{a,s} \times (1 - \exp(-F_s)) \]  \[ a \in (a_{r,s}, a_{max,s}), \]  \[ \text{for } a \in (a_{r,s}, a_{max,s}). \]  \( (1) \)

where \( N_{t,a,s} \) is the number of fish of age \( a \) of species \( s \) removed by fishing, \( N_{a,s} \) the number of fish of age \( a \) of species \( s \), \( F_s \) the instantaneous fishing mortality rate of species \( s \), \( a_{r,s} \) the age of recruitment to the fishery for species \( s \), and \( a_{max,s} \) the longevity of species \( s \). Once \( N_{t,a,s} \) is calculated, then it is uniformly distributed among schools in each age class. Knife-edge selection (above the age of recruitment to the fishery \( a_{r,s} \)) is assumed in applying the fishing mortality.

When MPAs are introduced, the instantaneous fishing mortality \( (F_s) \) was redistributed to the area outside the MPAs by scaling \( F_s \) according to the ratio of the MPA to the total area:

\[ F_s' = F_s \left(1 - \frac{\text{MPA area}}{\text{Total area}}\right)^{-1}, \]  \( (2) \)

where \( F_s' \) is the scaled fishing mortality of species \( s \), \( F_s \) the instantaneous fishing mortality of species \( s \), and MPA area Total area the area of the MPA and the total area of the model spatial domain. This scaled fishing mortality is applied uniformly over the range of each species outside the MPA.

Each species in the model reproduces once at the end of each time-step. The number of eggs spawned is calculated using the relative fecundity of each species, the spawning biomass, and a 1:1 sex ratio.

Model parameterization

The modelled fish community includes 12 species in the southern Benguela (Table 1; which includes the scientific names of each species), selected because they represent ~76% of the biomass in the system and ~94% of the total catch, as reported from previous studies using Ecopath with Ecosim (Shannon et al., 2003). Those authors estimated that the 12 species account for 84% of the total consumption of biomass by fish and for 72% of consumption of the production of small pelagic fish. All species-specific biological parameters used as input to the model, and each species’ spatial distribution that accounts for life-history migration patterns on a semester basis, were obtained from Travers et al. (2006; Table 2).

Table 1. List of modelled species with the corresponding feeding guild.

<table>
<thead>
<tr>
<th>Species Name</th>
<th>Scientific name</th>
<th>Feeding guild</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anchovy</td>
<td>Engraulis encrasiciolus</td>
<td>Small pelagic (prey)</td>
</tr>
<tr>
<td>Chub mackerel</td>
<td>Scomber japonicus</td>
<td>Pelagic nomad (predator)</td>
</tr>
<tr>
<td>Shallow-water</td>
<td>Merluccius capensis</td>
<td>Demersal (large predator)</td>
</tr>
<tr>
<td>Deep-water hake</td>
<td>Merluccius paradoxus</td>
<td>Demersal (large predator)</td>
</tr>
<tr>
<td>Horse mackerel</td>
<td>Trachurus trachurus</td>
<td>Pelagic nomad (predator)</td>
</tr>
<tr>
<td>Kinglip</td>
<td>Genypterus capensis</td>
<td>Demersal (large predator)</td>
</tr>
<tr>
<td>Lanternfish</td>
<td>Lamparicytodes hectoris</td>
<td>Mesopelagic (prey)</td>
</tr>
<tr>
<td>Lightfish</td>
<td>Macrolicus muelleri</td>
<td>Mesopelagic (predator)</td>
</tr>
<tr>
<td>Round herring</td>
<td>Etrumeus whiteheadi</td>
<td>Small pelagic (prey)</td>
</tr>
<tr>
<td>Sardine</td>
<td>Sardinops sagax</td>
<td>Small pelagic (prey)</td>
</tr>
<tr>
<td>Silver kob</td>
<td>Argyrosmus inodorus</td>
<td>Demersal (large predator)</td>
</tr>
<tr>
<td>Snoek</td>
<td>Thyrsites atun</td>
<td>Pelagic nomad (large predator)</td>
</tr>
</tbody>
</table>

Feeding guild is meant to provide a general description of the species, because otherwise in OSMOSE, predator–prey interactions are not prespecified, and a species can be both prey and predator depending on its size and stage (see Methods).
### Table 2. Input parameters of the model for each species modelled.

<table>
<thead>
<tr>
<th>Species</th>
<th>Reproduction</th>
<th>Survival</th>
<th>Growth</th>
<th>Initialization biomass 1990s (tonnes)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\Phi$ ($a_{mat}$)</td>
<td>$a_{max}$</td>
<td>$a_{rec}$</td>
<td>$M_{add}$</td>
</tr>
<tr>
<td>Anchovy</td>
<td>8000</td>
<td>1</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Chub mackerel</td>
<td>300</td>
<td>3</td>
<td>8</td>
<td>2</td>
</tr>
<tr>
<td>Shallow-water hake</td>
<td>500</td>
<td>4</td>
<td>15</td>
<td>3</td>
</tr>
<tr>
<td>Deep-water hake</td>
<td>500</td>
<td>4</td>
<td>15</td>
<td>3</td>
</tr>
<tr>
<td>Horse mackerel</td>
<td>250</td>
<td>3</td>
<td>8</td>
<td>2</td>
</tr>
<tr>
<td>Kingklip</td>
<td>500</td>
<td>5</td>
<td>24</td>
<td>3</td>
</tr>
<tr>
<td>Lanternfish</td>
<td>646</td>
<td>0.5</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Lightfish</td>
<td>334</td>
<td>0.5</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Round herring</td>
<td>750</td>
<td>1</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>Sardine</td>
<td>2400</td>
<td>2</td>
<td>10</td>
<td>1</td>
</tr>
<tr>
<td>Silver kob</td>
<td>150</td>
<td>2</td>
<td>25</td>
<td>3</td>
</tr>
<tr>
<td>Snoek</td>
<td>130</td>
<td>3</td>
<td>10</td>
<td>2</td>
</tr>
</tbody>
</table>

- $\Phi$, relative fecundity; $a_{mat}$, age at maturity; $a_{max}$, longevity; $a_{rec}$, age at recruitment; $M_{add}$, additional mortality rate (to account for predation mortality rate from other components of the ecosystem not explicitly included in the model); $F$, instantaneous fishing mortality rate; $L_g$, von Bertalanffy growth parameters; $c$, Fulton’s body condition factor.

The spatial bounds of the modelled system cover the entire southern Benguela ecosystem from the Orange River (25°33’S 16°E) in the north to east of East London (37°33’S 28°E; Figure 1). Figure 1 also depicts the locations of three potential MPAs. The spatial grid consists of 542 cells each of 18 × 18 nautical miles.

Before running any of the simulations, the model was calibrated to a reference state, in this case the 1990s (1990–1999). It was calibrated by estimating additional larval mortality parameters, using the biomass of each species as a performance measure, i.e. by matching the estimated biomass with the observed biomass (Table 2). The calibration was done using a genetic algorithm developed specifically for the OSMOSE model by one of the authors (Y-JS).

**Simulations and analysis**

The ecological effects of the implementation of various MPAs were investigated at different locations off the coast (Figure 1). Three proposed MPAs were modelled, with the size and location specified after consultation with experts (C. G. Attwood, pers. comm.). The effects of such a spatial management strategy, based on the 1990s status of the ecosystem (fishing and natural mortality, initial abundance based on the 1990s biomass estimates), were simulated by introducing each of the proposed MPAs separately, then all three simultaneously (four scenarios in all). MPAs were introduced at the beginning of the simulation, and the areas were kept closed from fishing for the whole simulation run. The approach followed consisted of redistributing fishing mortality from the MPAs to the exploitable component of the species outside the MPAs. Fishing mortality was redistributed by scaling the global fishing mortality rate by the ratio of the MPA to the total area [Equation (2)]. Effectively, this procedure uniformly distributed the excess mortality that resulted from the protection of the component of the species inside an MPA onto the unprotected component of the same species. Changes in the biomass of each modelled species in the three MPAs were then quantified relative to the situation in which no MPAs were implemented. Each simulation experiment was an average of 30 simulations run for 200 years; the outputs from the last 100 years only were used to calculate the average biomass. The relative changes in the biomass in the different MPA scenarios are expressed here as the ratio of the biomass in a scenario ($B_{sc}$) over that in the reference state ($B_{ref}$), i.e. $B_{sc}/B_{ref}$. The reference state for the study was the state of the Benguela ecosystem during the 1990s, so model parameters (initialization biomass, growth, survival, and reproductive parameters) are those witnessed during the 1990s. The MPA scenarios refer to the three individual introductions of the MPAs (MPA in the south, the north, and the east) and the combined implementation of all three MPAs proposed.

Additionally, the multivariate technique second-stage non-metric multidimensional scaling MDS (Clarke and Gorley, 2006) was used to compare the community structure under the four MPA scenarios, and when no MPA is applied. Second-stage MDS is a recently developed approach for investigating changes in community structure, and it has been used mainly in marine benthic ecology for two general cases. The first is to investigate temporal changes in community structure when repeated sampling of sites is conducted over time. The second is to compare multiple resemblance matrices to assess changes in community structure. Here, the resemblance matrices are constructed based on the biomasses of the species in each cell (282 cells × 12 species) after root–root transformation ($Y = Y^{1/2}$) to reduce the influence of dominant species on the measure of resemblance. Five resemblance matrices, corresponding to the four scenarios of MPA introduction and one no-MPA scenario, were created for the second-stage MDS. A Bray–Curtis measure of similarity was used as a measure of resemblance for the first-stage MDS. A Spearman rank correlation ($\rho$) was used as a measure of match between each pair of resemblance matrices, then an MDS was constructed based on the resulting rank correlation matrix.
Results

The percentage area of distribution of the exploitable component of each species and the whole community varied among MPA configurations (Figure 3). When MPAs were introduced individually, the largest percentage of the distribution area of most species was protected by MPA_S off de Hoop (Figure 1). The simultaneous introduction of the MPAs as a network resulted in the protection of 5–17% of the distributions of the exploitable component of the species and ~12% of the distribution of the community.

The relative change in biomass of the modelled species within the MPAs differed when the MPAs were implemented alone or in combination (Figure 4). The introduction of the MPA off Tsitsikamma (MPA_E; Figure 1) resulted in a slight increase in the biomass of sardine and kingklip within the MPA, whereas the biomass of other species in the MPA remained close to the value before the introduction of the MPA (the reference state). Conversely, when the MPA was introduced off de Hoop (MPA_S), the biomasses of deep-water hake and silver kob increased, and those of all small pelagic species, chub mackerel, and horse mackerel decreased relative to the reference state. When simulating the introduction of MPA_N, an area off Namaqualand, most of the species in the region did not vary in biomass, but there was an increase in the biomass of three large predatory species (kingklip, silver kob, and shallow-water hake).

The simultaneous introduction of the three MPAs as a network resulted in an increase in the biomass of some large predatory fish within the MPAs (deep-water hake, silver kob), with the forage fish (small pelagics) kept at a relatively lower biomass. Remarkably, the biomass of deep-water hake inside the protected zones responded disproportionately to the creation of the MPAs, although the smallest proportion of its distribution area was protected. On the other hand, the introduction of MPAs separately or in combination did not affect the biomass of mesopelagic species (lanternfish, lightfish). Relieving the large predators from fishing mortality did not result in increased predation mortality on mesopelagic species within the MPAs. The response of the species within a particular MPA tended to vary (either amplified or dampened), depending on whether the MPA was introduced separately or jointly with other MPAs. For example, the responses of silver kob and deep-water hake were amplified within MPA_N when all three MPAs were introduced together, compared with the situation when MPA_N was applied alone. Conversely, the response of kingklip within MPA_N was dampened when all three MPAs were introduced together. In addition to the relative changes in the average biomass of each species, the relative changes in the coefficients of variation (CV) of annual biomass values for each species were also assessed (Figure 5). For most species, the CV remained close to that at the reference state, except anchovy, shallow-water hake, and lanternfish. Therefore, the relative change in the biomass of the species modelled in the different scenarios of MPA introduction is unlikely to be the result of an increase in variability.
The effects of establishing MPAs were also investigated for the whole model domain (Figure 6). Establishment of the reserves had cascading effects beyond the community in that specific reserve. The option that seemed to have less impact on the biomass of the modelled species relative to the reference state was the introduction of a reserve off Tsitsikamma (MPA_E). Under that option, the biomass of most species remained around the reference state, and the biomass was higher only for sardine and silver kob. With other options, the introduction of MPAs resulted in differential responses of the modelled species. There were few common responses to all scenarios, i.e. an increase in the biomass of some large predatory fish (silver kob, deep-water hake) and a reduction in the biomass of snoek (a migratory predatory species) and shallow-water hake. When the three MPAs were introduced simultaneously, the biomass of all small pelagic species (anchovy, sardine, and round herring), horse mackerel, and chub mackerel decreased.

The variable responses are also reflected in the subsequent multivariate analysis of the output using second-stage MDS (Figure 7), which compares the resemblance matrices from the four scenarios of MPA introduction with a resemblance matrix derived when no reserve was introduced. Three separate groups of community structure emerged, with the no-MPA option clearly separating out from the rest, in one corner (no_MPA), the community structure from the option when the MPA off de Hoop was established on the left (MPA_S), and the community structure obtained from the other three scenarios: MPA_E, MPA_N, and ALL (all three MPAs) to the right.

**Discussion**

Simulating the implementation of MPAs resulted in substantial changes to the relative biomasses of species within the MPAs and in the whole model domain. According to the simulations, the introduction of any of the three MPAs favoured the large predator component of the modelled community, mainly deep-water hake, kingklip, and silver kob, at least under the fishing strategy of the 1990s, but not snoek or shallow-water hake. In contrast, the creation of MPAs can be detrimental to forage species such as round herring, horse mackerel, and chub mackerel. Deep-water hake experienced the greatest fishing mortality of all the species modelled, so the results suggest that relieving part of hake fishing mortality in the MPA_S off de Hoop has a positive impact on deep-water hake biomass, but a negative impact on other species in the MPA and throughout the model domain. In the scenario with all three MPAs, deep-water hake had the smallest proportion of its area protected, but the subsequent increase in its biomass was the
second highest within the community. The fact that deep-water hake feeds heavily on mesopelagic fish (Shannon et al., 2003), whereas other forage populations decrease substantially in abundance may amplify the response of deep-water hake to the creation of MPA_S. In contrast, shallow-water hake remained below the reference level most of the time, which may be explained partly by competition with other large predators for small pelagic fish and increased predation on their juveniles by large deep-water hake. Hence, an increase in large predators and a decline in small forage species may be the result of direct predation by large predators on adults of prey species so that it indirectly reduces the competitive and predatory impact on early life stages of large predators. This process is known as the “cultivation effect” (Walters and Kitchell, 2001), and it has been shown to affect the dynamics and resilience of demersal species (Bundy and Fanning, 2005).

Figure 5. Relative change in the CV of the biomass of each species within the MPAs when they are applied individually (MPA_E Tsitsikamma, MPA_S de Hoop, MPA_N Namaqualand) and jointly (ALL). The CV of the biomass of each species in the MPAs is expressed as the ratio of the CV when the MPA was introduced ($CV_{sc}$) to the CV in the reference state ($CV_{ref}$).

Figure 6. Relative changes in the biomass of the species over the whole spatial domain (within and outside MPAs), when the reserves are implemented individually and jointly (MPA_E Tsitsikamma, MPA_S de Hoop, MPA_N Namaqualand, ALL three MPAs). $B_{ref}$ and $B_{sc}$ depict the biomass of each species before (reference state) and after the implementation of MPAs, respectively.

Figure 7. Second-stage MDS plot of the community structure under the four MPA options (MPA_E Tsitsikamma, MPA_S de Hoop, MPA_N Namaqualand, ALL three MPAs) and the reference state without MPA (no_MPA). The axes are relative and have no units.
MPAs, when introduced individually or simultaneously, can have effects that cascade throughout a modelled community. Using EcoSpace, Walters et al. (1999) derived a spatial trophic cascade in which predators tended to follow prey populations out of the MPA once they had reduced the biomass of their prey inside the MPA. This type of spatial trophic cascade was not common. However, the results of the present study show that the responses of some species within a particular MPA vary, depending on the way the MPAs are introduced: individually or simultaneously. The responses of some species are amplified within an MPA when an MPA is introduced simultaneously with others, and the converse holds true for other species.

The expected outcomes from MPAs can vary depending on whether fishing mortality is redistributed following the introduction of the MPA and, if so, how it is redistributed. The approach we adopted was to increase the instantaneous fishing mortality uniformly [Equation (2)] on the unprotected part of the species in proportion to the area protected. Scaling the fishing mortality of all modelled species by the same factor (ratio of MPA to total area) will probably result in overestimating the fishing mortality outside the MPA for those species that occupy just a small part of the MPA, and hence change the biomass. An earlier modelling study by Apostolaki et al. (2002), based on single species and without consideration of trophic interactions, showed the importance of effort redistribution on the potential outcomes of MPAs. They found that an MPA with effort distribution, as here, is beneficial in some cases (e.g. increases in yield, but a decline in spawning-stock biomass, SSB). Conversely, the situation without effort redistribution (i.e. having the same effort level for the unprotected area as before the introduction of the MPA) was always beneficial in terms of long-term yield and SSB. Redistributing fishing mortality may be unsustainable with an increase in the area designated as MPA, so highlighting the need for complementary management measures (e.g. reducing the overall effort in a fishery) when implementing MPAs.

This analysis supports the conclusion of various empirical studies on the role of marine reserves. Although MPAs provide benefits for a few species within an assemblage, maximum benefits are only achieved when used in conjunction with other fisheries management tools (Roberts et al., 2005), such as an overall reduction in fishing effort, catch quota, and introduction of size limits. When setting aside part of the coast (extending from inshore to offshore) as an MPA, consideration of the location, size, and biological interactions of the species within the MPA is essential (Allison et al., 1998). Although most species are mobile over the modelled spatial domain (a case in which reserves are believed to be less effective), this study shows that protecting a small proportion of a coastal area results in changes in individual species abundances within the reserves and can cascade to the whole system.

Some of the benefits of this type of ecosystem modelling, along with empirical data analyses, include the insights that can be gained with respect to the response of the modelled components of an ecosystem. Such insight includes unexpected species or community responses to an increase in any form of disturbance, resulting from complex species interactions (released or enhanced competition and predation, indirect effects on distant trophic levels, local interactions) and inherent population dynamics (compensation and depensation effects). With the current increasing concern about ecosystem approaches to fisheries management, MPAs are viewed as one of the key management measures for rebuilding overfished stocks, for protecting critical habitats, and for reducing the risk of stock collapse (Gell and Roberts, 2003). MPAs are often implemented as a bet-hedging strategy to reduce the risk of management failure. Exploring the population and community consequences of implementation through simulation experiments, before practical implementation, is critical to assessing the range of possible responses of the fish community to a planned MPA. To do this effectively, an understanding of community interactions is critical to the selection of the location and size of reserves, as evidenced by the results of various modelling studies (Walters, 2000; MacCall, 2002; Knowlton, 2004; Micheli et al., 2004).

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