Incorporating ontogenetic dispersal, ecological processes and conservation zoning into reserve design

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\textbf{Abstract}

Computational methods for marine reserve design are frequently used as decision-support tools for the identification of conservation areas. Most reserve-selection algorithms minimise the cost of the reserve system whilst aiming to meet specified biodiversity objectives. Here, we extend a widely-used selection algorithm, Marxan, to incorporate several important considerations related to biodiversity processes and management. First we relax the scorched earth assumption to allow conservation features in non-reserve zones to contribute explicitly to conservation objectives. To achieve this, we generate conservation targets at landscape scales rather than focusing purely on the representation of features within reserves. Second, we develop the notion of spatial dependencies further to incorporate spatial heterogeneity in the value of individual conservation features such as habitat types. We use the example of ontogenetic migrations of fish from mangroves to coral reefs because it nicely demonstrates how spatial ecological processes generate predictable heterogeneity in habitat value that should be considered in the reserve design process. Lastly, we show how habitat value can be disaggregated into ecosystem processes and services. Using a case study for the Belize Barrier Reef we compare reserve networks generated using our new approach with the results of traditional analyses. Consideration of the contribution of different protection zones, connectivity among habitats and more complex management goals resulted in up to a 52% increase in the mean biomass of commercially and ecologically-important fish species represented in the landscape. Our approach strengthens the ecological basis of reserve-design algorithms and might facilitate the uptake of ecosystem-based management into reserve design.

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1. Introduction

Conservation planning often aims to ensure the persistence of natural features, typically by protecting a representative selection of each (Halpern and Warner, 2003; Margules and Pressey, 2000a). One of the most important tools available to achieve these goals is the establishment of networks of reserves (Leslie et al., 2003). The identification of reserve networks, or even the location of individual reserves, is a spatially-complex process requiring consideration of many biophysical and socioeconomic factors such as geographic patterns in ‘biodiversity’ and the costs of setting areas aside. Ideally, the placement of reserves would be informed by spatially-realistic models of multiple species, capable of incorporating spatially-dependent processes and the response of populations to reserves, but this is rarely practical. To simplify this task, a number of reserve (or site) selection algorithms have been developed that use computational methods to build potential networks from individual planning units (Cook and Auster, 2005; Early and Thomas, 2007; McDonnell et al., 2002; Noss et al., 2002; Possingham et al., 2000; Stewart et al., 2003). These algorithms provide an explicit framework for integrating conservation targets and goals and have the desirable attribute of searching for conservation scenarios that are near-optimal in terms of minimising the cost of conservation management while meeting pre-specified biodiversity objectives.

Reserve-selection algorithms target surrogates of biodiversity such as habitats, but in the absence of information stating otherwise usually assume that these do not vary in space. Yet, in an increasing number of ecosystems, ecological data on spatially-dependent processes and intra-habitat patterns of community structure are becoming available (Condit et al., 2002; Harborne et al., 2006b; Price, 2002; Ries et al., 2004). Incorporating such spatially-dependent information into the reserve-selection algorithms is therefore an important step in improving the ability of such algorithms to represent ecologically-meaningful patterns of diversity.
community structure, and the distribution of particularly-important flora and fauna. This paper describes the incorporation of two spatially-dependent processes into the algorithm Marxan (Ball and Possingham, 2000), which is routinely used for marine reserve design. We derive these approaches from recent ecological studies of Caribbean coral reef ecosystems and while the resulting algorithms will be directly transferable throughout most of the region, the approach taken here can be used in any ecosystem for which comparable data are available. First, we describe in detail the need to adopt a landscape-scale measure of management goals that combines the contributions of both reserve and non-reserve sites. This approach provides the flexibility to consider the impacts of multi-use zoning and implicitly recognises that populations in reserves are not independent from those outside reserves. Second, we develop the notion of spatial dependencies within the landscape to incorporate spatial heterogeneity in the value of individual conservation features such as habitats. We use the example of ontogenetic migrations of fish from mangroves to coral reefs because it nicely demonstrates how spatial ecological processes generate predictable heterogeneity in habitat value that should be considered in the reserve design process. Lastly, we extend our case study to show how habitat value can be disaggregated into ecosystem processes and services. This approach allows levels of key ecosystem processes to be maximised whilst also minimising losses to certain ecosystem services. As such, we believe the approach is a step towards building ecosystem resilience into reserve-selection algorithms.

1.1. Reserve zoning: integrating reserve and non-reserve contributions to management goals

Many approaches to reserve design make the implicit assumption that the ‘earth is scorched’ beyond reserve boundaries (i.e., that non-reserve areas do not contribute to biodiversity goals). This might be an appropriate strategy when non-reserve areas are likely to become grossly disturbed or if considering heavily-exploited species. However, this assumption has questionable relevance to situations where habitat might deteriorate in quality, but where species are unlikely to become functionally extinct (Mumby, 1999). Indeed, not only do non-reserve areas contribute to the biodiversity of a landscape – albeit at perhaps lower levels than potential reserves – but the processes of larval dispersal and adult migration ensure that the maintenance of diversity within reserves is at least partly influenced by the status of populations beyond reserve borders (Sale et al., 2005). Moreover, responses to reserve establishment are not necessarily restricted to the reserves themselves. Marine reserves can yield a wide range of benefits outside reserves, including spillover effects (Roberts et al., 2001), increase of aesthetic and recreational values (Bhat, 2003; Bohnsack, 1993) and reduction of the probability of extinction (Grafton et al., 2005). Therefore, reserve design should consider the reserve and non-reserve contributions to management goals explicitly.

Reserve-design algorithms will need a new structure and parameterisation to integrate the contributions of both reserve and non-reserve areas to landscape-scale conservation. Each conservation zone needs to be identified and its associated contribution to management goals estimated. The simplest scenario segregates reserves from non-reserve areas but more complex zonations could be considered, such as a hierarchy of levels of resource exploitation. Estimating the contribution of reserves and non-reserves to conservation also requires a temporal scale. For example, non-reserve levels of a species might decline rapidly after harvesting begins whereas populations in reserves could take many years to recover (McClanahan and Graham, 2005). Importantly, the response of management goals to each level of protection (hereafter referred to as different protection zones) is likely to vary among biodiversity surrogates such as habitat types. Lastly, the spatial heterogeneity generated by differential effects of protection zones and habitat responses requires a convenient framework for integration. Altering the calculation of reserve and non-reserve costs provides such a framework.

Reserve cost is typically measured as a function of area during the reserve-selection process (see McDonnell et al., 2002), under the assumption that larger reserve areas will result in greater economic losses (Balmford et al., 2004). However, measuring the cost of a reserve network by its area alone fails to account for differences in per unit area costs among planning units (e.g., Naidoo et al., 2006). Local differences in productivity, species composition and environmental conditions, all of which will have a direct effect upon the socioeconomic cost or value of a planning unit are thus ignored in this situation. As an alternative, the cost of a reserve network can be expressed as the required financial outlay (Balmford et al., 2004), or as the opportunity cost to alternative uses, such as the foregone benefits from fishing (Richardson et al., 2006; Stewart et al., 2003; Stewart and Possingham, 2005). Here, our first modification of reserve-selection algorithms is to extend the calculation of cost to consider the relative cost of reserve and non-reserve planning units and in so doing assess the ecological and economic potential of management goals in the entire landscape. The approach presented here uses fish biomass as a proxy for economic and ecological value. Whilst this is sensitive to habitat type it should be considered only a step towards the uptake of ecosystem-based management into reserve design. We believe that a combination of optimisation tools and dynamical models of populations (e.g., Kaplan et al., 2006; Walters et al., 2007) and fishing effort will be required to accurately predict the response of populations to different configurations of reserves and the resulting changes in economical costs and ecological benefits. These models would need to be dynamic, structured (by age, size or life stage) and spatially realistic. The development of such models, their parameterisation and incorporation within the reserve selection framework is both theoretically and computationally complex. Despite these complexities, however, we believe this approach will be the way forward in ecosystem-based management.

1.2. Spatial context of planning units in landscape (ontogenetic migration)

One advantage of relaxing the scorched earth perspective and incorporating the contribution of non-reserve areas to conservation targets is that the framework is flexible enough to incorporate the outcomes of spatial processes like spillover of organisms beyond reserve boundaries. This idea can be extended to consider the outcomes of other spatial ecological processes such as the migration of organisms among habitat patches or, in essence, any spatial demographic process of predictable impact on conservation features. We illustrate this principle using the outcome of ontogenetic migrations of fishes among mangroves, seagrass beds and coral reefs.

Many Caribbean coral reef fish utilise mangrove forests as nurseries during their juvenile phase, before migrating to their adult reef habitat (Nagelkerken et al., 2000). The presence of mangroves has been shown to enhance the biomass of both commercially and ecologically-important fish, including parrotfish, on neighbouring coral reefs (Mumby et al., 2004). Insights from a study in Belize were used to generate an algorithm for the identification of connected mangroves and coral reefs (Mumby, 2006). Here, we extend this approach so that the consequences of a habitat patch’s connectivity to mangroves are incorporated explicitly into the quantification of reserve costs. Although home range estimates and spillover calculations (Botsford et al., 2009; Kramer and Chapman, 1999) suggest that spillover of fish biomass from reserve to non-reserve
areas is likely to occur and may even be induced by the spatial density gradient caused by variable levels of protection (Kellner et al., 2008), here we assume zero spillover since there is no evidence for it being substantial in our study area. Similarly, although larval export from reserves is likely to occur, there is no empirical evidence that this mechanism is likely to produce a significant enhancement to populations outside reserves. Due to a lack of information on these effects and the challenges of incorporating them into reserve-selection algorithms we have therefore chosen to ignore larval export in this analysis. While computationally difficult, spatially explicit and dynamic models with dispersal have been constructed for fully optimising reserve site selection (Costello and Polasky, 2008) and we believe that future reserve-selection algorithms should be informed by such models if sufficient data are available to support them.

1.3. Optimising ecosystem processes and services

Combining the steps taken above, we can quantify the value of specific conservation features (e.g., habitat patches on a map) and incorporate the anticipated effects of different protection zones and the consequences of ontogenetic migrations among ecosystems. However, we can take one further step and disaggregate the type of value assigned to individual conservation features or biodiversity surrogates.

Habitats provide many important ecosystem services such as coastal defence and fisheries. In addition, they may also possess a “functional value”, indicating their importance to physical and ecological processes (Harborne et al., 2006a). These ecosystem processes such as herbivory, planktivory and bioerosion underpin the dynamics of individual species, productivity of ecosystems, and their vulnerability to and recovery from disturbance. The case study developed here enables us to quantify spatial heterogeneity in two distinct groups of reef fishes: herbivores and commercially-important species.

Many exercises in systematic conservation planning select levels of representation on the basis of the observed or predicted occurrence of biodiversity surrogates. Target levels of representation are typically equal, or adjusted according to factors such as natural rarity and vulnerability to threats (Margules and Pressey, 2000a). Here we explicitly incorporate ecosystem-based management objectives through the development of target levels of representation for habitats that reflect the relative importance of different habitats for particular ecosystem processes and services (rather than targeting individual ecosystem services directly as in Chan et al. (2006)). For example, planners may wish to maximise particular ecosystem processes in reserves, particularly if they contribute positively to conservation goals. In contrast, it may be desirable to minimise the representation of habitats that are important for ecosystem services, such as fisheries, in order to minimise economic impacts.

In the present study we focus on reserve design for Caribbean coral reefs, largely because much is known about spatially-explicit aspects of their ecology and the processes driving the ecosystem. The health of coral reefs is dependent upon the outcomes of complex relationships between corals, macroalgae and grazing fish. Grazers such as parrotfish influence the cover of macroalgae on reefs (Kramer, 2003; Williams and Polunin, 2001). Since macroalgae compete for space with corals (McCoy et al., 2001), grazers can reduce the amount of competition that corals experience with algae. It has been shown that if the level of grazing is low then coral reefs can switch from a coral-dominated to an algal-dominated state, from which it may be difficult or impossible to recover (Mumby et al., 2007). We therefore develop algorithms that allow the level of fish grazing to be maximised across the seascapes.

In summary, we extend existing reserve-selection theory to consider ecosystem processes and services at a landscape-scale to integrate the contribution of different protection zones and the existence of ontogenetic migrations among habitat patches. Whilst we apply this methodology to a case study for the Belize Barrier Reef our aim is to highlight the importance of spatial processes in general reserve design and to provide a basis from which a greater range of research questions can be addressed.

2. Materials and methods

2.1. Reserve-selection algorithm

Following the philosophy of Marxan (e.g., Leslie et al., 2003; Noss et al., 2002; Possingham et al., 2000), the reserve-selection problem can be defined as one of minimising the cost of reserves whilst aiming to meet specified targets for conservation feature (e.g., habitat) representation (Bedward et al., 1991; Leslie et al., 2003; Pressley et al., 1993). Here we extend the methodology of Marxan to distinguish the contribution of conservation features to ecosystem processes and services and to integrate information on non-reserve areas and the outcomes of ontogenetic connectivity among habitats. For terminology relating to reserve selection see Table 1.

Let the total number of conservation features (in this case habitat classes) be \( N \), and the total number of planning units be \( M \). We formulate the problem as follows:

Minimise the objective function

\[
\min \sum_{i=1}^{M} c_i + BLM \left( \sum_{i=1}^{M} x_i b_i - \sum_{i=1}^{M} x_i d_{ik} \right),
\]

subject to the constraints

\[
\sum_{i=1}^{M} a_{ij} x_i \geq f_j \sum_{i=1}^{M} a_{ij} \quad \text{for all} \quad j = 1, \ldots, N,
\]

\[
x_i \in \{0, 1\} \quad \text{for all} \quad i = 1, \ldots, M,
\]

where \( x_i \) is 1 if planning unit \( i \) is selected to be in a reserve network and \( x_i = 0 \) if \( i \) is not in the reserve network, \( c_i \) is the cost of planning unit \( i \), \( b_i \) is its boundary length and \( d_{ik} \) is the common boundary length of planning units \( i \) and \( k \). BLM is the boundary length modifier, an adjustable parameter that controls the importance of minimising the reserve system boundary length relative to its cost. Eq. (1) is the objective function, used to describe the cost of the reserve network. Eq. (2) represents the set of constraints that have

<table>
<thead>
<tr>
<th>Table 1</th>
<th>Terminology for reserve-selection algorithm.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conservation feature</td>
<td>Biodiversity surrogate (habitat) that we aim to conserve</td>
</tr>
<tr>
<td>Landscape representation target</td>
<td>Total proportion of the landscape that we aim to protect, where we define the landscape as the combined area of all conservation features</td>
</tr>
<tr>
<td>Habitat representation target</td>
<td>Proportion of the existing area of a habitat (conservation feature) that we aim to protect (e.g., 20%)</td>
</tr>
<tr>
<td>Planning units</td>
<td>Square selection units (containing conservation features) that could be inside or outside the reserve system (Ball and Possingham, 2000)</td>
</tr>
<tr>
<td>Boundary length modifier (BLM)</td>
<td>Parameter specifying the relative importance placed on minimising the boundary length relative to minimising cost (see the following section for more information)</td>
</tr>
</tbody>
</table>
to be met by the algorithm. In this case these describe the representation target levels \( t_j \) for each habitat \( j \), numbers between zero and one, where \( a_j \) is the area of habitat \( j \) in planning unit \( i \) (note that \( i \) and \( k \) always index planning units, whilst \( j \) indexes habitat types).

Optimisation of the objective function was carried out using simulated annealing (Kirkpatrick et al., 1983; Metropolis et al., 1953; Possingham et al., 2000) thereby selecting combinations of planning units that complement one another with respect to their spatial location and the conservation features that they contain. At each iteration the algorithm considers making a simple change to the reserve network and evaluates the effect that this will have upon the effectiveness of the network, corresponding to the value of the objective function. A component of effectiveness is often expressed in terms of the level of fragmentation exhibited by the reserve network. There are ecological and economic reasons why planning units should be clustered together to form reserves with a low boundary length to area ratio (see Possingham et al., 2000).

To control this, the objective function contains an expression corresponding to the total perimeter or boundary length of reserves (Andelman et al., 1999; Fischer and Church, 2003; Possingham et al., 2000). The boundary length modifier variable controls the relative importance of minimising boundary length to other components of the objective function (McDonnell et al., 2002; Possingham et al., 2000). Low values of the BLM result in fragmented networks composed of many small reserves. The larger the BLM, the greater the emphasis that is placed upon minimising the boundary length, and thus the more spatially compact and manageable the resulting reserve systems are (Ball and Possingham, 2000). A feasible solution generated by the algorithm is one that contains a set of planning units such that all the targets are met. Better solutions will have lower values of the objective function.

Two aspects of the objective function were modified in order to incorporate ecosystem processes vs. services, reserve and non-reserve contributions to conservation targets, and the effects of mangrove-reef connectivity. This resulted in the creation of four scenarios to investigate the effects of extending the Marxan approach.

### 2.2. Changing targets to incorporate ecosystem processes and services

Target levels of habitat representation were selected using two methods, denoted hereafter with the symbols TARG\( G \), and TARG\( GM \). Under the first scenario (TARG\( G \)), representation targets for all habitats were equal to the total landscape representation target, specifying the proportion of the landscape that we are aiming to designate in reserves; under TARG\( GM \), the representation target for each habitat reflects the predicted biomass of fish species within that habitat. Rather than explicitly targeting individual fish species in the objective function, this method enables such species to be incorporated without the need for maps of their spatial distribution, which are often difficult to obtain. Habitat targets also have the potential to incorporate information on other ecosystem processes and services.

For scenario TARG\( GM \) we develop a method for generating target levels of representation \( t_j \) for each habitat \( j \) (i.e. proportions of the total existing area of each habitat \( j \)). Target levels are derived so that the sum of the target areas is equal to a predefined landscape level of representation (in the example below, 0.2, or 20% of the landscape). Rather than setting individual target levels of representation manually we determine them through an iterative process. Target levels derived are not independent of each other, but depend upon the relative importance of the different habitats for ecosystem services and processes. Individual targets are constrained by the value of habitats for commercial fishing.

Target levels of representation under TARG\( GM \) reflect ecological processes by being equal to the total predicted biomass of ecologically-important species \( (B_{ij}) \), per unit area multiplied by a factor \( y \) used to rescale biomass units into target levels of representation. However, regardless of how valuable a biodiversity surrogate is for conservation, the needs of stakeholders require that a limit be set upon the amount to be set aside in reserves. Target levels \( t_j \) are unable to exceed a prescribed limit \( L_j \).

\[
t_j = \begin{cases} 0 & \text{if } yB_{ij} < L_j, \\ \frac{yB_{ij}}{L_j} & \text{otherwise.} \end{cases}
\]

The multiplier \( y \), used to convert biomass data into habitat targets, has no units and is determined using a goal seeking algorithm. The value of \( y \) is calculated to ensure that the target areas, as a proportion of the total area of the landscape, sum to the total landscape level of representation (e.g., 0.2, or 20% of the entire landscape in the example below)

\[
0.2 = \sum_j t_j H_j
\]

where \( H_j \) is the total area of habitat \( j \) in the landscape. Thus, the planner can specify the maximum proportion of the existing area of habitat \( j \) that may be allocated to reserves, so that surrogates with high conservation value are not able to be reserved entirely.

We assume that the main opposition to reserves will be from fishermen. The limits upon the proportion of the existing area of each habitat able to be reserved \( L_j \), are derived using the total predicted biomass of commercially-important species \( B_{ij} \), under the assumption that protecting those habitats with the greatest predicted value of \( B_{ij} \) will result in the greatest reductions in fisheries yields. The \( L_j \) are derived using the following equation:

\[
L_j = K_{\text{min}} + \frac{B_{ij}}{\max(B_{ij})} (K_{\text{max}} - K_{\text{min}})
\]

where \( B_{ij} \) is linearly transformed to be between 0 and 1 with the habitat containing the highest biomass of commercially-important species having a value of 0, and \( K_{\text{max}} \) and \( K_{\text{min}} \) are the maximum and minimum limits upon the target level of representation, respectively. \( K_{\text{max}} \) and \( K_{\text{min}} \) can be prescribed by the planner and in this study have been set to values of 0.5 and 0.3 respectively. This choice of values is arbitrary and used for illustrative purposes only. In reality, limits upon representation would be informed by local socio-economic and ecological conditions. In this case, the limits upon the level of representation are scaled so that the habitat with the highest biomass of commercially-important fishes (in our case study, dense patch reefs) is limited to a maximum of 30% of its existing area. Habitats with a lower biomass of fished species are able to be reserved in greater proportions. The maximum limit upon the level of representation, given to the habitat with the fewest commercially-important species (algal-dominated habitats), is 50% of its existing area. It should be noted that these limits are upon the level of representation, and that whether or not these limits are reached will depend upon the predicted biomass of ecologically-important species in a given habitat.

### 2.3. Changing the cost function to incorporate conservation zoning and mangrove-reef connectivity

#### 2.3.1. Incorporating conservation zoning: reserves vs. non-reserves

The cost term in Eq. (1) differs subtly from that used in Marxan in that it depends on all planning units rather than only upon those within the reserve network (in Marxan the first term of the equation sums over \( c_M \), and not \( c_i \)). Incorporating non-reserve sites in the cost function enables negative costs, or gains, resulting from the conservation of ecologically-important species to be included. We define the ecological value of the landscape as the sum of the biomass of ecologically-important species within and outside
reserves. Similarly, maximising the biomass of commercially-important species across the landscape would be a valid conservation goal. However, this latter goal could reduce the biomass of fish available to commercial fisheries. Therefore, we consider the biomass of commercially-important species within reserves to represent the foregone benefits from fishing, under the assumption that there is no spillover of fish biomass to non-reserve areas in our study area. To minimise economic losses we aim to maximise the biomass of commercially-important species outside reserves and therefore to minimise the total biomass within reserves (subject to meeting the conservation targets). If there were economic gains due to spillover of fish into non-reserve areas, these could be incorporated into the reserve-selection algorithm at this stage. Since spillover is a complex process that depends on factors such as size-structure, fish mobility and the size of reserves, and that could have a wide range of impacts this would require the development of a dynamic population model for the commercially-important species.

In our case study for Belize, as in many other parts of the Caribbean, those herbivorous species that are harvested (e.g., parrotfish) are fished only on an artisanal basis and are not targeted by commercial fisheries. However, such ecologically-important species may still benefit from the protection of a reserve because they are often caught as by-catch. For example, large-bodied parrotfish are highly susceptible to fish traps (Rakitin and Kramer, 1996). In addition to resulting in lower incidences of mortality (Hawkins and Roberts, 2004), reserves may also alter the community structure, size-distribution and grazing intensity of parrotfish (Mumby et al., 2006).

Since the biomass of ecologically-important fish is dependent upon whether a planning unit is in or outside the reserve system, each planning unit $i$ has two possible total biomass values (summed over all habitats within that planning unit), here labelled $R_{ci}$ if the planning unit is in a reserve and $F_{ci}$ if the planning unit is fished and therefore not in a reserve. Similarly, we label the biomass of commercially-important species if the planning unit is within or outside a reserve as $R_{ci}$ and $F_{ci}$ respectively. We develop a new landscape metric $E$, defined as the sum of the values of all planning units:

$$E = \sum_{i=1}^{M} (x_i (R_{ci} - R_{ci}) + (1 - x_i)(F_{ci} + F_{ci})).$$

This function gives equal weighting to the ecological and economic costs; alternative weightings could be incorporated to reflect local socioeconomic priorities. In this case study no fish species were both ecologically and commercially important. If, however, such species were to be incorporated into the objective function they would contribute to both the benefit and cost of reserves. If commercially-important species are assumed to also possess some value from a biodiversity or tourism perspective, this may be incorporated by discounting the value of $R_{ci}$ to reflect the joint fishery cost and conservation benefit of having fished species in a reserve. Since the aim is to maximise the economic and ecological potential we do so by minimising $-E$ (equivalent to maximising $E$). Planning units with the highest ratio of ecological species biomass to commercial species biomass will be considered by the algorithm to be of the most value (or correspondingly of the least cost).

We consider minimising the area of reserves, as in Marxan (Possingham et al., 2000), under the assumption that larger reserve areas will result in greater management costs, although costs will also depend on their compactness. In addition, we consider maximising the landscape metric $E$. We incorporate these goals into the first term of the objective function as follows:

$$\sum_{i=1}^{M} C_i = (1 - x) \sum_{i=1}^{M} x_i A_i - zE,$$

where $A_i$ is the area of planning unit $i$. The weighting $z (0 \leq z \leq 1)$ represents the relative importance assigned to minimising $-E$ compared with that of minimising the total area of reserves (as in Stewart and Possingham, 2005). For example, an $z$ value of 0.5 would correspond to giving an equal weighting to the two cost components.

Here we focus on comparing $z = 0$ with $z = 1$ to demonstrate the effects of substituting the familiar areal constraint with a more complex landscape goal that incorporates different protection zones, spatial context (mangrove-reef connectivity) and specific ecosystem processes and services among planning units (minimising $-E$). We refer to these cost functions as $COST_A$ and $COST_C$ from hereon. By incorporating spatial heterogeneity in the value of sites the second cost scenario would be expected to generate different results to the first. However, the degree to which reserve networks generated under the two scenarios will differ will depend on the individual case study and the spatial arrangement of habitat patches.

2.3.3. Combining costs and targets to generate planning scenarios

Combinations of costs and targets generated four scenarios, labelled from hereon as $COST_A$-$TARG_\text{a}$, $COST_A$-$TARG_\text{c}$, $COST_A$-$TARG_\text{BM}$ and $COST_\text{BM}$-$TARG_\text{BM}$, where $COST_A$-$TARG_\text{a}$, for example, represents the scenario where the aim is to minimise the area of reserves and target levels of representation are equal for all habitats.

The landscape representation targets and boundary length modifier were also varied to explore different conservation priorities. Since the aim is to compare methods for defining targets and cost we did not ‘lock’ the existing marine protected areas in Belize into our reserve networks. Each combination of scenarios and total landscape level of representation was repeated for 1000 runs.

2.4. Case study: Belize Barrier Reef

Belize has one of the most extensive and diverse reef ecosystems in the world, comprising fringing reefs, inshore lagoonal reefs, three atolls and the second largest barrier reef in the world (Gibson et al., 1998). Currently the main uses of the barrier reef ecosystem are tourism and commercial fisheries. Marine reserves have been established in Belize with a variety of objectives, including tourism management, biodiversity protection, and fisheries management (Sobel and Dahlgren, 2004). There are currently thirteen marine protected areas (totalling over 23,000 hectares), seven of which comprise the Belize Barrier Reef Reserve System, which was inscribed on the World Heritage Site List in 1996. Here we divide the study area into 8266 planning units, each $1 \times 1$ km in size (Fig. 1).

Thirteen habitats were mapped using Landsat Thematic Mapper satellite imagery and included coral reefs, seagrass beds, mangroves and algal-dominated systems (Mumby et al., 1995). Each habitat in the map was considered a conservation feature. Recommendations for the conservation of diversity and maximisation of

\[ \sum_{i=1}^{M} C_i = (1 - x) \sum_{i=1}^{M} x_i A_i - zE. \]
fisheries yield typically suggest that a minimum of 20% and an optimum of 30–50% of the total management area be set aside in reserves (Airame et al., 2003; Roberts et al., 2002; Turpie et al., 2000). Therefore, we used a range of conservation goals such that either 10%, 20%, or 30% of the total landscape area was set aside in reserves. Coral reef habitats were considered connected to mangroves if the perimeter of mangroves within a 200 km² region exceeded 50 km and the distance from reefs to the nearest mangrove did not exceed 10 km (Mumby, 2006).

Field data were needed to quantify the contribution of each habitat to one ecosystem process (grazing) and one ecosystem service (fisheries). Grazing was represented as the total biomass of eight important species of herbivore in the families Scaridae (parrotfishes), Acanthuridae (surgeonfishes) and Pomacentridae (damsel-fishes). Fisheries were represented by pooling the biomass of eleven commercially-important fish species in the families Serranidae (including groupers), Lutjanidae (snappers) and Haemulidae (grunts). In this case study no species were both ecologically and economically important. All biomass values were obtained by surveying between five and 10 transects per site and converting the length-frequency distribution of fishes into biomass using the allometric scaling relationships of Bohnsack and Harper (1988). Full details of survey methods are given elsewhere (Mumby et al., 2004, 2006). The data were obtained in the Bahamas as part of a large-scale systematic assessment of reef habitat diversity. Each habitat was sampled between 2002 and 2004 at two hierarchical scales: among islands \( (n = 5) \) and among reefs within an island \( (n = 3) \). All data were pooled for the purposes of this study. Applying habitat characteristics from the Bahamas to a map of Belize is a reasonable approximation because the habitats are virtually identical and at least 90% of the species are found at both locations.

2.5. Evaluating reserve networks

Several complementary methods were used to evaluate the differences among reserve networks generated by the reserve-selection algorithm. For each scenario, output from the algorithm...
included (1) the reserve systems generated in each run, (2) the best solution from all runs that met the conservation targets with minimal cost, and (3) irreplaceability (Leslie et al., 2003; Pressey et al., 1994). Irreplaceability gives the number of times each planning unit was selected to be in a reserve network as a proportion of the total number of reserve networks generated (1000 runs) and can be considered a measure of a planning unit's importance for inclusion in reserves. Sets of individual irreplaceable planning units can be considered as ‘priority areas’ for conservation. Truly irreplaceable planning units would be selected in every run of the algorithm, but since all our conservation target habitats were represented in more than one planning unit and there are no planning units ‘locked’ into the system, our algorithm did not generate any such planning units for Belize.

Irreplaceability thresholds of 60%, 70%, 80% and 90% of runs were compared with a threshold in which a planning unit was defined as irreplaceable if it had a greater irreplaceability than would be expected by chance (Fig. 2). To do this we repeated the method of Stewart and Possingham (2005) by generating a random distribution of selection frequencies for 1000 runs using the average number of planning units selected by the algorithm to be in the reserve system (C). Assuming that every planning unit has an equal probability \( p \) of success of being selected then \( p = C/M \), where \( M \) is the total number of planning units (in this case study 8266). The number of times a planning unit with probability \( p \) of being selected appears in 1000 runs will have a binomial distribution if selection is purely random. The threshold for irreplaceability was set at the upper 95% confidence limit of this distribution (labelled >95% UCL in Fig. 2) as planning units with selection frequency counts greater than this threshold were unlikely to be selected in the reserve network due to random sampling alone.

Similarity of reserve networks was compared using a kappa statistic (Cohen, 1960) as in Wilson et al. (2005). This statistic assesses the extent to which reserve networks overlap after removing overlap due to chance:

\[
kappa = \frac{P_o - P_c}{1 - P_c},
\]

where \( P_o \) is the proportion of planning units that overlap and \( P_c \) the proportion of planning units that overlap due to chance. A kappa value of 1 corresponds to identical reserve networks; 0 corresponds to no more overlap than expected by chance and a value of \(-1\)
indicates no overlap of networks. Outputs were grouped by BLM, cost objective and by the total landscape representation target.

### 2.5.1. Effects of protection zones

Here we quantify differences in species biomass between reserve and non-reserve areas, thereby allowing conservation features in different protection zones to contribute explicitly to conservation objectives. Two levels of management were considered: marine reserves and non-reserve areas. The implicit time scale was 20 years because reserve effects were quantified in the Exuma Cays Land and Sea Park (Bahamas) which has been fully protected from fishing since 1986 (Mumby et al., 2006). For each of the 19 species of ecologically or economically important fishes, we quantified the average difference in biomass in Montastraea and gorgonian habitats between reserves and neighbouring non-reserve areas of the Bahamas. To apply these data from the Bahamas to a case study for Belize fishing techniques and effort were assumed to be similar in the two locations. Whilst these both vary continually over time, the dominant fishery species: grouper, lobster and conch are the same in both regions. At the time at which the data were collected fishing was at a low intensity, trapping not being an important source of fishing in either region (Mumby, personal observation). Whilst both the Bahamas and Belize have large reef ecosystems with similar species and levels of fishing, the application of these methods to other regions would require the collection of local biomass data to establish the effects of marine reserves.

#### 2.5.2. Effects of spatial patch context (ontogenetic migration)

The contribution of mangrove-reef connectivity on the biomass of adult reef fish in Belize and Mexico was determined using data and models developed by Mumby et al. (2004). This study took advantage of a natural experiment to isolate the effects of vastly reduced mangrove coverage on the biomass of both ecologically and economically important reef fish. Whilst reserves can produce greater overall changes in biomass, the presence of nearby nursery habitats can more than double the biomass of species within habitats such as gorgonian and patch reefs. For development of an algorithm, the biomass enrichment of mangroves was assumed to apply equally to fished and protected systems. The study of mangrove impacts focused on Montastraea reefs and patch reefs and we assume that similar effects apply to seagrass beds (albeit with less obvious results because of lower fish densities in this habitat). This assumption is reasonable because many of the species influenced by mangroves on reefs migrate to seagrass beds at night to forage (Burke, 1995). We assume that the effects of marine reserves observed on Montastraea reefs in the Bahamas also apply to patch reefs, which have similar vertical structure and are often intensively fished (Table 2). Other habitats were assumed to undergo no changes in biomass as a result of reserves or proximity to nursery habitats.

To standardise data, for each habitat we scaled the biomass per unit area of each ecologically-important species (e.g., ~46 g 200 m⁻² for queen triggerfish Balistes vetula in Acropora palmata reef habitat) to a percentage of the maximum biomass of this species observed across all habitats (405 g 200 m⁻² in dense gorgonians for queen triggerfish); usually these were in unfished areas with adjacent nursery habitats. This gave each habitat a relative value between 0 and 1 for each ecologically-important species (46/405 ~ 0.11 for queen triggerfish in Acropora reefs). These values were summed over all ecologically-important species within the habitat to give an index corresponding to the relative importance of each habitat for ecologically-important fishes under conditions with and without reserves and adjacent mangroves (shown rescaled between 0 and 100 in Table 2). This was repeated for the commercially-important species.

### 3. Results

A large number of solutions satisfied each set of conservation targets: 100% of runs for a target of reserving 30% of the landscape, and >95% of runs for lower target levels of landscape representation.

#### 3.1. Target levels of representation

We selected a single arbitrary value for the boundary length modifier to enable a comparison of the two targets scenarios. We experimented with the value of the BLM (see Supplementary Information) and found a value of approximately 10 to be appropriate for generating manageable reserve networks composed of around 20–25 reserves. Under scenario COSTₐ–TARGₐ, with target habitat representation levels dependent upon the predicted species biomass, a greater total area C was selected to be in reserves than when habitat representation targets were equal (Table 3). Consequently, the reserve networks generated under equal targets were more efficient at minimising reserve area. The average number of reserves in networks was also greater when the targets depended upon the relative value of the habitats for ecologically-important species (Table 3).

#### Table 2

<table>
<thead>
<tr>
<th>Habitat type</th>
<th>Ecologically important</th>
<th>Commercially important</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No mangroves</td>
<td>Mangroves</td>
</tr>
<tr>
<td></td>
<td>Fished</td>
<td>Reserve</td>
</tr>
<tr>
<td>Montastraea reef</td>
<td>14 22</td>
<td>15 23</td>
</tr>
<tr>
<td>Acropora palmata reef</td>
<td>40 40</td>
<td>40 40</td>
</tr>
<tr>
<td>Sparse gorgonians</td>
<td>6 10</td>
<td>6 11</td>
</tr>
<tr>
<td>Dense gorgonians</td>
<td>21 99</td>
<td>22 100</td>
</tr>
<tr>
<td>Patch reef</td>
<td>18 27</td>
<td>18 29</td>
</tr>
<tr>
<td>Dense patch reef</td>
<td>47 64</td>
<td>47 65</td>
</tr>
<tr>
<td>Sparse seagrass</td>
<td>0 0</td>
<td>0 0</td>
</tr>
<tr>
<td>Medium-density seagrass</td>
<td>0 0</td>
<td>0 0</td>
</tr>
<tr>
<td>Dense seagrass</td>
<td>0 0</td>
<td>0 0</td>
</tr>
<tr>
<td>Lobophora</td>
<td>18 18</td>
<td>18 18</td>
</tr>
<tr>
<td>Shallow forereef</td>
<td>40 40</td>
<td>40 40</td>
</tr>
<tr>
<td>Algal-dominated habitat</td>
<td>2 2</td>
<td>2 2</td>
</tr>
<tr>
<td>Sand</td>
<td>0 0</td>
<td>0 0</td>
</tr>
</tbody>
</table>
The larger total area selected to be in reserves under scenario TARGBM resulted in fewer potential combinations of planning units that could form those reserves. In this case, since the probability $C/M$ of a planning unit being selected to be in reserves was greater, the irreplaceability threshold based on a random distribution of these selection frequencies was also greater than when habitat representation targets were equal. These differences in irreplaceability thresholds explain the number of irreplaceable planning units being smaller under scenario TARGBM than TARGc (Table 3).

For nine of the 12 habitats target levels of representation $t_j$ under scenario TARGBM were $>0.3$ and unaffected by the landscape target level of representation. This is since targets for the high value habitats (e.g., patch reefs) reached their limits $L_j$ even at low levels of landscape representation (e.g., 10% landscape target). For example, the target for Montastraea reefs was 0.46 for 10%, 20% or 30% landscape representation targets. As such, similarity between target levels under scenarios TARGBM and TARGc for those habitats increased with the landscape representation level. The kappa statistic comparing reserve networks generated under the two target scenarios showed an increasing trend with the target level of representation (Table 3), which we assume to be a result of increasing similarities among targets levels.

The total predicted biomass of ecologically-important species was greater for a given total landscape target when the individual habitat representation targets were not equal (Fig. 3a). Further, a larger proportion of the total biomass of these species was found in reserves when COSTL-TARGBM was used rather than COSTL-TARGc. The total biomass of ecologically-important species was similar for the three landscape levels of representation (10%, 20% and 30%) under scenario COSTL-TARGBM (Fig. 3a). Scenario COSTL-TARGBM aims to maximise the ecological potential of the landscape for a given landscape representation target by placing a greater value upon reserving those habitats with a high biomass of ecological species. In this study those habitats with a relatively high biomass of ecologically-important fish species, such as Montastraea reef and patch reefs were rarer in the landscape than those with a lower biomass. The most commonly-occurring habitat, seagrass, has a low biomass of all eight herbivorous fish species. In this case, the ecological value of the seascape was already maximised, subject to the $L_j$ constraint with 10% of the landscape represented, and increasing the landscape representation target to 30% only increased the areal target for seagrass habitats. In contrast, if the target habitat levels of representation were equal then increasing the total landscape target had an increasingly beneficial effect upon both the total biomass of these species, and the proportion of the total that was represented in reserves.

As for ecologically-important fishes, the total biomass of commercially-important fish species was larger if the target levels of representation for habitats reflected the predicted fish species biomass (scenario COSTL-TARGBM, Fig. 3b). The proportion of the total biomass that was within reserves was also higher under the scenario where the habitat target levels of representation were not equal (Fig. 3b). This is because many of the habitats with a high biomass of ecologically-important species have a correspondingly high biomass of commercially-important species.

### 3.2. Comparing cost objectives

The results presented here include the effects of habitat context: the degree of mangrove connectivity. Similar results were obtained when mangrove connectivity was ignored, although the total predicted biomass of both ecologically important and commercially-important fish species within and outside reserves was approximately 2% lower (see Fig. 4).

Whilst a BLM of zero, where the perimeter of reserves is not considered to be a cost in the objective function, is comparable for different cost functions, higher BLMs might not be considered equivalent. That is, a BLM of 10 under scenario COSTL-TARGBM could generate a

### Table 3

<table>
<thead>
<tr>
<th>Target function</th>
<th>BLM</th>
<th>Landscape representation (%)</th>
<th>Mean number of reserves</th>
<th>Mean area of planning units</th>
<th>Number of irreplaceable sites</th>
<th>Kappa</th>
</tr>
</thead>
<tbody>
<tr>
<td>TARGc10</td>
<td>10</td>
<td>10</td>
<td>19.1</td>
<td>65.45</td>
<td>2801</td>
<td>0.31</td>
</tr>
<tr>
<td>TARGBM10</td>
<td>10</td>
<td>20</td>
<td>20.1</td>
<td>841.2</td>
<td>1403</td>
<td>0.45</td>
</tr>
<tr>
<td>TARGc20</td>
<td>10</td>
<td>20</td>
<td>22.8</td>
<td>1305.7</td>
<td>3079</td>
<td></td>
</tr>
<tr>
<td>TARGBM20</td>
<td>10</td>
<td>20</td>
<td>26.9</td>
<td>1423.7</td>
<td>2254</td>
<td></td>
</tr>
<tr>
<td>TARGc30</td>
<td>10</td>
<td>30</td>
<td>23.3</td>
<td>1971.2</td>
<td>3379</td>
<td></td>
</tr>
<tr>
<td>TARGBM30</td>
<td>10</td>
<td>30</td>
<td>23.9</td>
<td>1989.4</td>
<td>2842</td>
<td></td>
</tr>
</tbody>
</table>

Fig. 3. The influence of different representation targets upon the predicted biomass of (a) ecologically and (b) commercially-important fish species within and outside reserves. Pairs of bars provide a comparison between scenarios in which representation targets are equal to the total landscape representation target and those in which the representation target for each habitat reflects the predicted biomass of fish species within that habitat, labelled as % and BM respectively. Each bar corresponds to the total predicted biomass and is divided into two sections. The grey and white bars correspond to the biomass within and outside reserves respectively. The x axis shows the total landscape target and hatching is used to denote those scenarios in which the representation targets were not equal for each habitat. The cost function (minimising $E$) incorporates protection level zoning, mangrove-reef connectivity and specific ecosystem processes and services among planning units and the BLM is 0.
different degree of spatial clustering to a BLM of 10 under scenario COSTL-TARGBM. We selected BLMs that achieved a given level of clustering to compare the different cost scenarios. For example, to achieve approximately 20 reserves in the network we used a BLM of 11.4 under COSTA-TARGBM, and a BLM of 11.1 under scenario COSTL-TARGBM for the same landscape target level of representation (30%). Four different values of the BLM were chosen so that no priority was given to minimising boundary length (BLM = 0) or so that reserves generated by the algorithm would comprise, on average, approximately 20, 50 or 100 individual reserves.

Comparing the scenarios in which habitat target levels of representation reflect the biomass of ecologically-important species, the total area of reserves was 11% greater when the goal was to minimise \( -E \) (COSTL-TARGBM) rather than to minimise area, COSTA-TARGBM (results averaged for the four BLMs, Table 4). This is because scenario COSTL-TARGBM does not prioritise minimising reserve area, but rather focuses on maximising the potential of the landscape. As such, the mean total biomass (summed over all commercially and ecologically-important fish species within and outside reserves) was higher when biomass was considered explicitly by the algorithm (Table 4 and Fig. 4). As might be expected, the new conservation targets had a greater effect on the total biomass than the introduction of the new cost function (Fig. 4). Averaging the results over the three landscape target levels of representation (10%, 20% and 30%) cost accounted for a 3% increase in total biomass whereas the new targets resulted in a 29% increase. The combined impacts of the three innovations ranged from a 15% to 52% increase in mean total biomass (summed over all commercially and ecologically-important fish species within and outside reserves) for the different planning scenarios (marker shape denotes targets and marker colour, cost) and three important fish species within and outside reserves for the different planning scenarios (marker shape denotes targets and marker colour, cost) and three important fish species within and outside reserves for the different planning scenarios (marker shape denotes targets and marker colour, cost) and three different landscape representation targets with a BLM of ~11. COSTL represents the scenario in which cost reflects the biomass of species within the landscape, but mangrove-reef connectivity is not included.

![Fig. 4. Mean total biomass (summed over all commercially and ecologically-important fish species within and outside reserves) for the different planning scenarios (marker shape denotes targets and marker colour, cost) and three different landscape representation targets with a BLM of ~11. COSTL represents the scenario in which cost reflects the biomass of species within the landscape, but mangrove-reef connectivity is not included.](image)

Table 4

<table>
<thead>
<tr>
<th>Cost function</th>
<th>BLM</th>
<th>Mean number of reserves</th>
<th>Mean area of planning units</th>
<th>Mean number of irreplaceable sites</th>
<th>Mean total biomass</th>
<th>Mean foregone benefits</th>
<th>Kappa</th>
</tr>
</thead>
<tbody>
<tr>
<td>COSTA</td>
<td>0</td>
<td>225.6</td>
<td>3689.1</td>
<td>1751</td>
<td>9537.2</td>
<td>5871.0</td>
<td>0.23</td>
</tr>
<tr>
<td>COSTL</td>
<td>0</td>
<td>163.7</td>
<td>4046.6</td>
<td>1206</td>
<td>9674.0</td>
<td>6063.7</td>
<td>0.64</td>
</tr>
<tr>
<td>COSTA</td>
<td>5.7</td>
<td>102.5</td>
<td>2012.5</td>
<td>2626</td>
<td>9204.2</td>
<td>5363.1</td>
<td>0.75</td>
</tr>
<tr>
<td>COSTL</td>
<td>5.8</td>
<td>101.7</td>
<td>2342.7</td>
<td>3012</td>
<td>9259.5</td>
<td>5480.7</td>
<td>0.83</td>
</tr>
<tr>
<td>COSTA</td>
<td>7.35</td>
<td>49.8</td>
<td>2082.0</td>
<td>3014</td>
<td>9222.0</td>
<td>5391.7</td>
<td></td>
</tr>
<tr>
<td>COSTL</td>
<td>7.32</td>
<td>50.5</td>
<td>2266.2</td>
<td>2889</td>
<td>9279.6</td>
<td>5480.7</td>
<td></td>
</tr>
<tr>
<td>COSTA</td>
<td>11.4</td>
<td>20.4</td>
<td>2062.5</td>
<td>3112</td>
<td>9230.5</td>
<td>5395.2</td>
<td></td>
</tr>
<tr>
<td>COSTL</td>
<td>11.05</td>
<td>20.6</td>
<td>2229.4</td>
<td>3112</td>
<td>9310.2</td>
<td>5497.3</td>
<td></td>
</tr>
</tbody>
</table>

In general, minimising area resulted in fewer irreplaceable planning units for a given threshold of irreplaceability. This is because planning unit costs are more similar if cost is proportional to area than when cost depends upon the predicted fish biomass within a planning unit. Smaller priority areas correspond to greater flexibility in reserve design. Similarity among priority areas generated using different cost functions was dependent upon the definition of irreplaceability. If, for example, priority areas were defined as those planning units selected in at least 20% of the runs, then both sets of irreplaceable planning units (generated with the two cost functions) met all the conservation targets. At intermediate thresholds for defining irreplaceability, we observed greater differences in the number of targets met under the two cost scenarios. For example, if we defined irreplaceable planning units as those selected in half or more of the runs then although the difference in the number of irreplaceable planning units for the two scenarios was small, scenario COSTL-TARGBM met three (25%) more of the conservation targets. Minimising area is therefore less efficient when there are fewer priority areas.

Defining the threshold for irreplacability as the 95% upper confidence limit of the random distribution of selection frequencies (Stewart and Possingham, 2005), the arrows in Fig. 5 demonstrate that these thresholds were similar for scenarios COSTA-TARGBM and COSTL-TARGBM. Both scenarios included ~3000 irreplaceable planning units, or 37% of the total landscape area. Since these sets of irreplaceable planning units met all of the conservation targets (Fig. 5), they can be considered potential reserve networks, although the total number of planning units was greater than the desired total landscape level of representation. It is possible that such reserve networks, being formed from sites that are chosen repeatedly by the algorithm, may have a greater chance of meeting conservation and economic goals, although flexibility in reserve design would have to be sacrificed to achieve this since there is only one set of irreplaceable sites for a given irreplaceability threshold and scenario.

The kappa statistic comparing the two cost objectives shows that their outcomes converge as the value of the BLM increases particular trade off regarding the relative value of biomass of fishes within and outside reserves. Alternative weightings could be incorporated to reflect local socioeconomic priorities. The value of such weightings would determine whether or not foregone benefits from fishing are deemed to outweigh gains in biomass throughout the landscape.
have been underestimated, and it might be possible to reduce ecological potential of the landscape and minimising opportunity costs. If, alternatively, there is significant spillover of fish biomass from reserves into non-reserve areas (not modelled here) then the costs. If, alternatively, there is significant spillover of fish biomass beyond reserve boundaries then the costs. Although fishing of parrotfish is banned in Belize this is not the case for other species such as reef fish. Future work will consider the spillover effects of fishing on other species.

In this case study, there is thus a trade-off between maximising the number of targets met by these irreplaceable sites (right axis and circles) for different thresholds of irreplaceability generated under scenarios COSTA-TARGBM (open circles and diamonds) and COSTI-TARGBM (filled circles and diamonds). Arrows denote thresholds of irreplaceability (based upon a comparison with a randomly distributed set of selection frequencies).

(Table 4). This is because there are fewer options for generating highly clustered reserve networks that meet the conservation objectives as the BLM increases. The irreplaceable planning units selected by scenarios COSTA-TARGBM and COSTI-TARGBM for a total landscape level of representation of 30%, for example, overlapped substantially (Fig. 6), with a kappa value of 0.83. At high BLMs there is still a benefit (higher total biomass of commercially and ecologically-important fish within the landscape) from minimising −E rather than minimising area, but this benefit is relatively small compared with the benefit gained with more fragmented reserve networks (Table 4).

4. Discussion

Computational methods for marine reserve design are frequently used as decision-support tools for the identification of conservation areas. Here we modified the standard Marxan toolbox (Ball and Possingham, 2000) to investigate the impacts of incorporating heterogeneity in ecosystem state. This was achieved by allowing conservation features in non-reserve zones to contribute explicitly to conservation objectives, disaggregating habitat value into ecosystem processes and services and considering spatial dependencies within the landscape resulting from ontogenetic dispersal. Our modifications demonstrate how information on the entire landscape can be integrated to produce reserve networks that attempt to maximise the landscape-scale value of ecosystem processes whilst minimising the loss of important ecosystem services.

The new approach for generating target levels of representation for habitats (reflecting their relative importance for particular ecosystem processes and services) resulted in a greater total biomass of both ecologically and commercially-important fish in the landscape. The proportion of the total biomass of these species that was within reserves was also greater than when habitat target levels of representation were equal. This is because many of the habitats with a high biomass of ecologically-important species have a correspondingly high biomass of commercially-important species. In this case study, there is thus a trade-off between maximising the ecological potential of the landscape and minimising opportunity costs. If, alternatively, there is significant spillover of fish biomass from reserves into non-reserve areas (not modelled here) then the biomass of commercially-important species outside reserves could have been underestimated, and it might be possible to reduce economic losses whilst simultaneously increasing the benefits for ecologically-important species.

By modifying the cost component of the objective function we have provided a method for integrating the contributions of both reserve and non-reserve areas to landscape-scale conservation. Further, the use of biomass data enables, not only the economic value of habitats (as in Stewart and Possingham, 2005), but also their ecological value to be included in the calculation of costs. When compared with the scenario in which cost is measured only as a function of the area of reserves, the incorporation of different protection zones resulted in an increase in both the ecological and economic potential of the landscape.

Ontogenetic migration occurs in many ecosystems (see Law and Dickman, 1998, for example) and the framework developed here could be applied to other species and habitats to take into account spatial heterogeneity in the value of habitats. The extent to which mangrove-reef connectivity makes a difference to the reserve networks generated by the algorithm will depend on the magnitude of the effect and the degree to which that effect plays out in the complex spatial arrangement of habitat patches. In this case study, mangrove connectivity only exerted a weak influence on reserve design because its major impacts were confined to reef habitats whose cover was a relatively minor component of the landscape. The method would be expected to generate more striking results in other ecosystems or in fringing reef systems which tend to have a greater proportion of hard-bottom habitat.

Our methods for the inclusion of fish biomass data have a number of limitations. In reality, reserve effects on species abundance will not be constant across the landscape. Rather the impacts of reserves and the response of fishermen to their implementation will depend upon population connectivity, the size and spatial distribution of reserves and how well connected they are (Botsford et al., 2001; Kaplan et al., 2006; Walters et al., 2007). Incorporating intra-habitat variation in species biomass would be likely to influence the spatial distribution of priority areas for conservation.

The value of fished areas for commercially-important species is calculated using biomass data that reflect only the unfished part of the population, no information being available on the extracted biomass. Since the proportion of the total biomass outside reserves that is extracted is not linearly related to the unextracted biomass we are unable to infer the extracted biomass from which the real economic value of the fishery is derived. Ideally, to assess the economic value of habitats outside reserves an approach that explicitly incorporates and weights the importance of the extracted biomass and the unextracted biomass is required. Also, if substantial spillover of fish beyond reserve boundaries were to occur then fisheries yields and therefore economic losses would depend, not only upon the area of each habitat within reserves, but also upon population connectivity and oceanography. The inclusion of such spatial processes is beyond the scope of this paper, since it would involve the creation of models of fish population dynamics and of fishing effort and the nesting of these models within the optimisation algorithm.

In this study, species were considered to be of economic importance only if they were targeted by commercial fisheries. Artisanal fisheries, however, will also determine the economic value of species, and if incorporated here would result in some species being of both ecological and economic value. Spatial variation in target species will also result in local conditions in which some species contribute to both ecosystem processes and services. For example, although fishing of parrotfish is banned in Belize this is not the case in other regions of the Caribbean. The impacts of the inclusion of such species on the outcomes of the reserve-selection process will depend largely upon their estimated economic value relative to their value for conservation.
The framework provided in this study can incorporate a number of other important ecosystem processes and services. It must, however, be acknowledged that fine-scale data on ecosystem processes and services are challenging to obtain. In addition to herbivory, additional data would enable the inclusion of other processes such as planktivory and primary productivity (estimated using depth and current flow patterns). Historical maps of sea surface temperatures and light could also be used to estimate the susceptibility of different reefs to coral bleaching. The inclusion of such data would enable the selection of reserves that are more likely to be resilient to future climate change. Similarly, alternative ecosystem services that could be incorporated include the provision of building resources & pharmaceutical products, both of which would be prevented within marine reserves.

In this study we have outlined three steps towards incorporating spatial heterogeneity in the landscape. We do, however, consider this approach to be only a first step towards ecosystem-based management. The method developed here can be adapted to incorporate more sophisticated reserve models that anticipate direct interactions between reserve and non-reserve areas, such as spillover. The use of this planning tool in conjunction with dynamic models of populations and fishing effort could provide a good check on many of the difficult assumptions that the reserve-selection approach requires, revealing whether solutions are capable of supporting persistent populations.

Reserve plans frequently use habitat maps as a spatially continuous surrogate of diversity (Margules and Pressey, 2000b; McNeill, 1994; Noss, 1987). Only recently, however, have the underlying assumptions of this approach been tested. For example, a widely-used assumption is that the composition of each habitat remains constant irrespective of its geographic location, yet this has been demonstrated to be inappropriate in some terrestrial systems where community structure becomes increasingly different with greater separation of patches of the same habitat (Oliver et al., 2004). In reality, the composition of habitat patches varies because of differences in patch size, shape, disturbance and connectivity (Acosta and Robertson, 2002; Calabrese and Fagan, 2004; Farina, 1998). Whilst single species population models can be applied to spatially-structured landscapes (e.g., Van Teeffelen et al., 2006), it remains challenging to predict the impact of patch metrics (shape, connectivity, etc.) on conservation features (i.e. to predict how the value of conservation features would change across the seascape in accordance with patch metrics). We provided an exception here in which new insight into the effects of ontogenetic connectivity of
reef fish from mangroves to coral reefs enabled the consequences of an important ecosystem process to be assimilated into the reserve design process. The methodology developed to do this can be applied to any spatial ecological process.

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Appendix A. Supplementary material


References


