

USING SITING ALGORITHMS IN THE DESIGN OF MARINE RESERVE NETWORKS

HEATHER LESLIE,^{1,5} MARY RUCKELSHAUS,² IAN R. BALL,³ SANDY ANDELMAN,⁴ AND
HUGH P. POSSINGHAM^{3,4}

¹*Department of Zoology, 3029 Cordley Hall, Oregon State University, Corvallis, Oregon 97331 USA*

²*Northwest Fisheries Science Center, National Marine Fisheries Service, 2725 Montlake Boulevard E,
Seattle, Washington 98112 USA*

³*Departments of Mathematics and Zoology, University of Queensland, St. Lucia, Queensland 4072, Australia*

⁴*National Center for Ecological Analysis and Synthesis (NCEAS), 735 State Street, Suite 300, Santa Barbara,
California 93101 USA*

Abstract. Using benthic habitat data from the Florida Keys (USA), we demonstrate how siting algorithms can help identify potential networks of marine reserves that comprehensively represent target habitat types. We applied a flexible optimization tool—simulated annealing—to represent a fixed proportion of different marine habitat types within a geographic area. We investigated the relative influence of spatial information, planning-unit size, detail of habitat classification, and magnitude of the overall conservation goal on the resulting network scenarios. With this method, we were able to identify many adequate reserve systems that met the conservation goals, e.g., representing at least 20% of each conservation target (i.e., habitat type) while fulfilling the overall aim of minimizing the system area and perimeter. One of the most useful types of information provided by this siting algorithm comes from an “irreplaceability analysis,” which is a count of the number of times unique planning units were included in reserve system scenarios. This analysis indicated that many different combinations of sites produced networks that met the conservation goals. While individual 1-km² areas were fairly interchangeable, the irreplaceability analysis highlighted larger areas within the planning region that were chosen consistently to meet the goals incorporated into the algorithm. Additionally, we found that reserve systems designed with a high degree of spatial clustering tended to have considerably less perimeter and larger overall areas in reserve—a configuration that may be preferable particularly for sociopolitical reasons. This exercise illustrates the value of using the simulated annealing algorithm to help site marine reserves: the approach makes efficient use of available resources, can be used interactively by conservation decision makers, and offers biologically suitable alternative networks from which an effective system of marine reserves can be crafted.

Key words: conservation planning; Florida Keys; habitat diversity; marine reserves; optimization; representative; reserve selection; simulated annealing; siting algorithms; spatial clustering.

INTRODUCTION

There is a great deal of international interest in marine reserves and their potential for biodiversity conservation. Many countries throughout the world have initiated strategies that include the development of representative marine reserve networks as part of integrated coastal-zone management programs (e.g., Kelleher et al. 1995, ANZECC Task Force on Marine Protected Areas 1998, Department of Fisheries and Oceans–Canada [DFO] 2000, Federal Register 2000). Such efforts have arisen as recognition has grown of the pressures on marine resources, which include coastal land development, aquaculture and fisheries. At present, we have a unique opportunity to create the kind

of marine reserve systems we would have established in terrestrial ecosystems before some habitats were almost entirely modified for alternative uses. Once we acknowledge the urgency of developing a system of marine reserves, the question is how best to design and implement marine reserves to efficiently conserve biodiversity and achieve other possible reserve objectives most effectively.

The purpose of this paper is to describe how reserve-siting algorithms can be used to help identify marine reserve systems that comprehensively represent all habitat types in a sensible spatial arrangement. Reserve-siting algorithms have rarely been used in marine contexts (see Ward et al. [1999] for a notable exception), although several applications (e.g., Channel Islands National Marine Sanctuary, Great Barrier Reef Marine Park) have been initiated since we began this work. As in terrestrial systems, the designation of marine reserves has primarily been ad hoc in the past, and driven by opportunity rather than strategic objectives

Manuscript received 12 October 1999; revised 10 December 2000; accepted 8 February 2001; final version received 19 March 2001; feature accepted 21 February 2002. For reprints of this Special Issue, see footnote 1, p. S3.

⁵ E-mail: leslieh@science.oregonstate.edu

and systematic approaches. We believe that systematic, strategic reserve selection is always preferable to an ad hoc approach, as it maximizes the chances of creating a representative system of reserves, ensures a transparent and defensible process, and makes the most efficient use of available resources (Pressey et al. 1993, Margules and Pressey 2000). Furthermore, once alternative scenarios for comprehensive and efficient marine reserve networks have been identified, they can be used as benchmarks against which to evaluate the advisability of pursuing site-specific conservation opportunities that may arise.

Here we focus on the problem of representing a group of conservation targets, specifically benthic marine habitats, within a geographic area. This basic approach has been applied in terrestrial systems in the past (Margules et al. 1988, Groves et al. 2002) and more recently in marine systems (Ward et al. 1999, Beck and Odaya 2001). In marine environments, community- and ecosystem-level characteristics may be better captured by schemes based on habitat types, as opposed to species richness or endemism (Schwartz 1999, Ward et al. 1999). We illustrate this approach to reserve design by applying simulated annealing, a relatively new and flexible optimization tool (Kirkpatrick et al. 1983, Ball 2000), to a data set from the Florida Keys. Using this method, we were able to identify potential systems that met the conservation goals (i.e., specified level of habitat representation). In other words, we generated multiple network scenarios that included ≥ 10 , ≥ 20 , or $\geq 30\%$ of all habitat types within the study region while minimizing a combination of reserve system area and reserve system perimeter.

Algorithms: one reserve-selection tool

In order to explain our choice of the simulated annealing algorithm, we review the underlying rationale of using computer-based siting algorithms to help solve reserve selection problems. Consider, for example, a group of conservation decision makers whose efforts are focused on three species, or conservation targets, which they want to represent in at least two sites. If there are ten sites from which to create a network, it is feasible that the reserves could be selected "by inspection," i.e., by searching through the options and arriving at one or more combinations that meet the conservation goals. Alternatively, if the decision makers have tens or even hundreds of conservation targets and thousands of potential sites, as is often the case in regional conservation planning situations (e.g., Davis et al. 1999), the selection problem quickly becomes intractable. If there are 1500 possible sites (or planning units, as they are often called), then there would be 2^n or 2^{1500} possible reserve systems! Computer-based siting algorithms can be used to reduce this enormous set of possibilities to a reasonable suite of network scenarios that meet the conservation goals.

At the core of reserve selection problems, whether marine or terrestrial, is the overall objective of minimizing the area encompassed with the network of reserves (Pressey et al. 1993). This objective is derived from the idea that, while from a biodiversity-conservation perspective one might want to maximize the area within reserves, social and economic constraints demand an efficient and limited area within reserves (Possingham et al. 2000). Given this aim, the representation of defined conservation targets, such as species or habitat types, enters into the model as a constraint. Such constraints are often referred to in the conservation planning literature as "conservation goals," whereas "conservation targets" refer to the specific species, habitats, or biological communities of conservation interest (e.g., Groves et al. 2002). We follow that convention here.

The various algorithms available to solve the "minimum representation problem," as it was first defined by Kirkpatrick et al. (1983), may be broadly divided into several types: iterative, optimizing, and simulated annealing. Iterative algorithms order each planning unit according to set of criteria, and then choose the highest ranking site. Some of the most popular iterative or heuristic algorithms are focused on maximizing species richness (the "greedy" algorithm) or representing rare species within the network (the "rarity" algorithm). While iterative algorithms run quickly and operate in a fairly intuitive manner (e.g., Margules et al. 1988, Rebelo and Siegfried 1992, Nicholls and Margules 1993, Pressey et al. 1997), they generate only one solution and it is very unlikely to be the optimal one (Possingham et al. 1993, Underhill 1994, Pressey et al. 1997).

Alternatively, the reserve-selection problem can be formulated as an Integer Linear Program (ILP) and standard mathematical programming methods then can be used to find the optimal solution (Cocks and Baird 1989, Church et al. 1996). Pressey et al. (1997) compared heuristic algorithms with the solution found using an ILP, and found that heuristics generated solutions within 5–20% of the optimal one. Unfortunately, the optimization method fails when the number of potential planning units is large (more than a few hundred), because of the tremendous computing time needed to solve such a large problem in a reasonable time (Possingham et al. 2000). Additionally, ILPs produce only one optimal solution; whereas multiple solutions are often desirable in a conservation planning situation. Finally, if we are interested in reserve systems that are spatially clustered, then the Integer Linear Programming problem becomes a Non-linear Integer Linear Programming problem. In these cases it is even harder to guarantee optimal solutions.

Because of the findings reviewed above, we chose to use the third type of algorithm, simulated annealing, in this illustrative exercise. Simulated annealing min-

imizes objective functions based on the process of annealing metals or glass (Kirkpatrick et al. 1983). The algorithm starts with a completely random reserve system, and trial solutions are iteratively explored through sequential random changes to the set of planning units in the system. At each step, the new set of units is compared with the previous set, and the best one is accepted (Possingham et al. 2000). The strength of this approach is its avoidance of local optima. Yet by allowing the selected set of planning units, or sites, to move through suboptimal space, the algorithm creates more opportunities to reach the global minimum. As the process continues, the algorithm becomes choosier about what changes lead to the "best" system of sites. The simulated annealing algorithm consistently has outperformed simpler iterative or heuristic algorithms, such as the greedy and rarity-based selection algorithms, in that it delivered solutions composed of the same or a smaller number of sites (Ball 2000, Possingham et al. 2000).

Also, the use of simulated annealing enables us to explicitly and efficiently incorporate spatial information into the reserve selection process. In the past, most reserve-siting algorithms have ignored space, and selected a system of sites from those available without explicitly considering the spatial relationship among sites (Possingham et al. 2000). Where space has been incorporated in iterative site-selection methods, it has typically been accomplished by merely selecting sites that are in close physical proximity to one another (e.g., Nicholls and Margules 1993). This approach, termed an adjacency constraint, is unlikely to deliver efficient systems because there will be a tendency to build on initially selected sites without exploring completely new alternatives. Here we explore scenarios for reserve networks that represent conservation targets—in this case, marine habitats—efficiently with respect to both the total area and perimeter of the system. By designing systems with low perimeter values, or boundary lengths, we generate options that are well connected, a quality that may be preferable for both biological and sociopolitical reasons (see Roberts et al. 2003). For example, currents and other oceanographic phenomena can greatly influence the transport and dispersal of many marine organisms, especially the early planktonic larval stages (Roberts 1997). Connectivity among reserve sites can provide for transfer of larvae and material among biological populations and ecosystems, and a spatially condensed network may reduce enforcement and management costs (see Roberts et al. 2003).

METHODS

Our goal in this exercise was to investigate how siting algorithms can be used to help evaluate the merits of possible marine reserve networks using objective criteria. The data we used and the conservation goals of representing 10, 20, and 30% of all habitat types

within the region were chosen for illustrative purposes only. The choice of a particular habitat classification scheme can significantly influence the scenarios identified by this and other decision support tools. To move beyond this heuristic exercise and actually apply this approach to a specific planning situation would require (1) articulation by stakeholders of clear conservation objectives (e.g., preserve the habitat diversity within the Florida Keys National Marine Sanctuary [FKNMS]), (2) identification of conservation targets including habitats, species, or surrogates (e.g., focus conservation on the 26 habitat types defined and mapped for the FKNMS), (3) delineation of appropriately scaled sites or planning units based on the targets chosen (e.g., use a 1-km² planning unit for accounting of habitat representation in the reserve systems), and (4) specification of conservation goals, or desired levels of representation of the targets (e.g., include 20% of the total area of each habitat type in the final reserve system), as well as a clear statement about the underlying rationale for those choices. Our intent is to show how siting algorithms can contribute to the network design effort once those requirements have been met.

The reserve selection problem

The implicit objective of this reserve design exercise was to minimize the total "cost" of the system, in terms of area and boundary length, while ensuring that the conservation goal for each habitat type was achieved. These goals were expressed as a proportion of the overall distribution of each habitat type within the region covered by the data set (Table 1). The magnitude of the conservation goals may be based on biological (e.g., the results of a population viability analysis of a target species), or policy information (e.g., a national mandate to protect 20% of the coral reefs in U.S. waters), or even on social considerations (e.g., the inclusion of reserve areas for recreation or educational values). The reserve system cost may be the actual cost of the area, or more likely in a marine context, the opportunity cost or management cost incurred when marine reserves are implemented. Additional reserve network objectives beyond the selection of the most efficient, least costly set of sites can be incorporated as mathematical equations in the algorithm.

For example, given the cost-minimization objective and the constraints imposed by the user (in this case, protect 20% of every habitat type), the situation can be formulated as a standard mathematical programming problem (Possingham et al. 2000) as follows.

Minimize the objective function

$$\sum_{i=1}^M c_i x_i + \text{BLM} \left(\sum_{i=1}^M x_i l_i - \sum_{i=1}^M \sum_{k=1}^M x_i x_k b_{ik} \right)$$

subject to the following constraints:

TABLE 1. Twenty-percent conservation goals for each of the 23 habitat types.

Habitat type	Conservation goal (ha)
Bare substrate	
Carbonate mud	29.8
Carbonate sand	11.5
Organic mud	3 330.8
Patch reef	
Aggregated	549.5
Coral or rock patches	1 275.9
Halo	19.8
Individual	168.0
Aggregated with halo	104.6
Platform margin reef	
Remnant	2 781.2
Drowned spur and groove	2 051.3
Shallow spur and groove	71.8
Reef rubble	231.4
Back reef	8.8
Hard bottom	
Soft corals, sponges, algae	244.0
<50% seagrass	20 111.5
Continuous seagrass	
Moderate to dense	38 200.0
Dense patches in matrix of small patches (<50%)	671.6
Continuous seagrass (sparse)	422.4
Patchy seagrass	
Moderate to dense with blowouts	22 287.0
Dense patches with hard bottom	3 323.4
Sand/mud with small seagrass patches	4 524.0
Scattered seagrass patches	135.8
Unknown bottom	17 832.8
Unclassified ocean water	0
Inland water	0
Land	0

Note: Goals are based on the total expanse (in hectares) within the study region.

$$\sum_{i=1}^M a_{ij}x_i > t_j \sum_{i=1}^M a_{ij} \quad \text{for all } j = 1, \dots, N$$

$$x_i \in \{0, 1\} \quad \text{for all } i = 1, \dots, M$$

where x_i are the control variables such that if $x_i = 1$ then site i is selected for the reserve system and if $x_i = 0$ then site i is not in the reserve system; c_i is the "cost" of site i , in this paper simply the area of site i ; l_i is the perimeter or boundary length of site i ; b_{ik} is the common boundary length of sites i and k ; and BLM is a Boundary Length Modifier that converts the reserve system area and its boundary length into a common currency. The constraints ensure an adequate fraction of each habitat type is conserved where a_{ij} is the area of habitat type j in site i , and t_j sets the target fraction for each habitat type (in this paper we assume $t_j = 10, 20$, or 30% for all j , depending on the scenario in question). There are N different habitats spread across M different sites.

Interpreting the mathematical programming problem we note that a feasible solution is one which selects a set of sites (using the control variables x_i) such that all the constraints are satisfied (which means the conservation goals, such as 20% of each habitat type are met by the network scenarios generated). These constraints, one for each habitat type, can be thought of collectively as a biodiversity-conservation constraint or overall conservation goal and can be modified to suit different cases. For example, we may wish to set the level of representation $>20\%$ for certain habitat types. Our objective was to find feasible solutions that minimized the objective function. In this case the objective function was a nonlinear combination of the total area of the reserve system and the boundary length of the reserve system. The boundary length modifier, BLM, determines the relative importance placed on minimizing the boundary length relative to minimizing area. When the BLM is very small then the solution algorithm will concentrate on minimizing area, whereas when the BLM is relatively large then the solution method will put highest priority on minimizing the boundary length of the feasible reserve system.

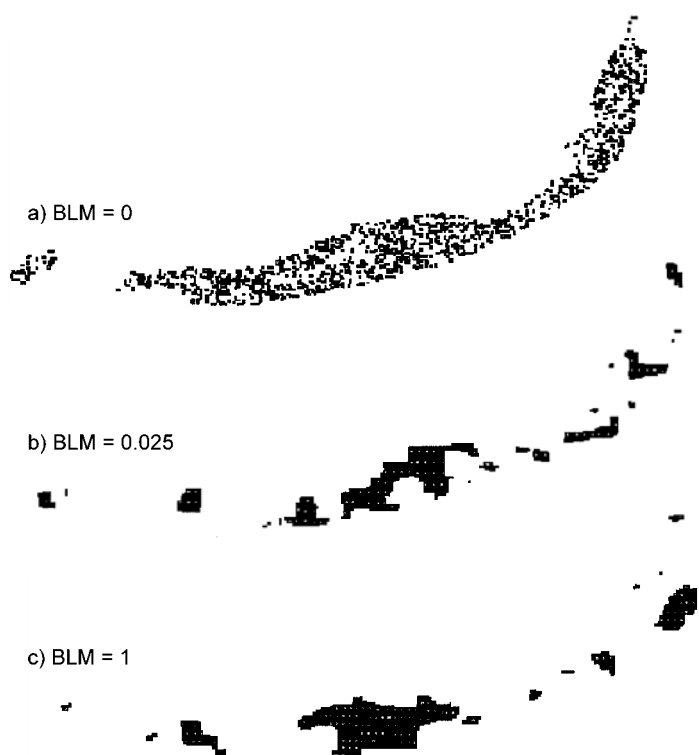
There are many methods for solving nonlinear integer programming problems such as the one above. However, for large data sets with hundreds or thousands of possible sites and tens of habitat types there are no methods that guarantee finding the optimal solution in a reasonable time. Consequently we chose to use simulated annealing to solve the problem because it can quickly find a variety of good solutions. Previous studies indicate that simulated annealing solutions are almost always superior to those found by heuristic algorithms (Ball 2000).

Reserve selection algorithm

We used the reserve design package SPEXAN (version 3.1; Ball and Possingham, Adelaide University, Adelaide, Australia) to identify potential adequate reserve systems for the Florida Keys problem (Ball and Possingham 1999). By adequate, we mean systems that meet the articulated conservation goals. SPEXAN is an acronym for SPatially EXplicit ANnealing, and the program applies a combination of algorithms for selecting reserves centered around simulated annealing (Kirkpatrick et al. 1983, Csuti et al. 1997), but also allowing heuristic and iterative improvement (Ball and Possingham 1999). The program has been interfaced with a geographical information system (ArcView 3.2, Environmental Systems Research Institute, Redlands, California, USA) project, enabling the user to map the network scenarios generated using different conservation targets.

The information needed to run the software includes a unique identification number for each site, a unique number (and name) for each of the habitat types, and the area of each habitat type j within each site i , a_{ij} .

FIG. 1. The best reserve network scenarios generated with SPEXAN 3.1 using the 20% conservation goal, 1-km² planning units, and 26 habitats. As the boundary length modifier (BLM) increases, placing more weight on minimizing the overall system perimeter rather than the system area, the selected units form more spatially clustered reserves. The scenario where BLM = 0.0001 is not shown, as it looks nearly identical to the BLM = 0 scenario.



The user then specifies conservation goals, or the total fraction of each habitat in the data set that must be represented in the final set of reserve sites chosen (the t_i in the reserve design problem). A cost function can be used to vary the relative value of sites included in a reserve system, depending on their attributes (e.g., habitat or species type). In this case the cost of each site was simply the area of each site and hence the same for each site ($c_i = 1$ or 100 km²).

In this exercise, our objective was to minimize the total cost of the system in terms of area and total perimeter, while ensuring that at least 10, 20, or 30% of every one of the 23 target habitat types was represented across the entire system. Inland water, land, and unspecified "water" habitat types were also delineated in this database, but these types had conservation goals of zero. Thus they were included in the reserve scenarios only due to their proximity to the other habitat types with nonzero goals. Although we sought to represent all conservation target equally in this case (i.e., we tried to include as much soft, muddy bottom as seagrass bed), tools like SPEXAN enable the user to incorporate other, differential, conservation goals very easily.

The simulated annealing algorithm generates multiple reserve systems, one during each run. By changing the boundary length modifier (BLM), we varied the relative importance of reserve system perimeter to reserve system area to explore how reserve systems

changed with varying degrees of aggregation among the individual planning units (Fig. 1). In SPEXAN 3.1, if BLM is set at one, reserve scenarios are heavily weighted towards a high degree of aggregation, as more emphasis is placed on the minimization of the total perimeter rather than the total area of the reserve system. More highly aggregated marine reserve networks are often preferable, particularly for effective management, enforcement, and monitoring of the reserve system (see Roberts et al. 2003).

The data set

The 9500 km² of the Florida Keys National Marine Sanctuary (FKNMS) includes the archipelago of the Florida Keys, as well as areas of Florida Bay, the Gulf of Mexico, and the Atlantic Ocean (Fig. 2). Based on aerial photographs taken between December 1991 and April 1992, the National Ocean Service (NOS) and the Florida Department of Environmental Protection's (DEP) Florida Marine Research Institute mapped the habitats within the sanctuary, classifying them in four major categories: reefs, seagrasses, hardbottom, and bare substrata (NOS/DEP 1999). Twenty-three more specific habitat types also were identified within these groups (e.g., halo patch reefs, dense continuous seagrass), in addition to inland water, land, and unspecified "water," so we included a total of $N = 26$ habitats in the reserve selection problem. The total area of each habitat type within the planning region was used to

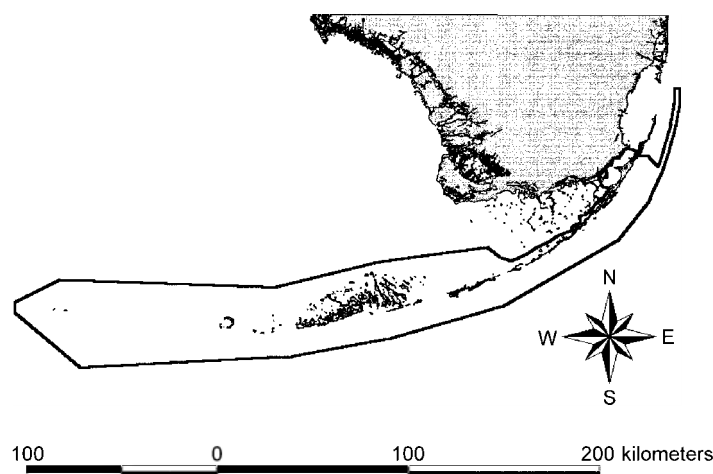


FIG. 2. The Florida Keys National Marine Sanctuary (FKNMS) encompasses 9500 km² of coastal and marine habitats in South Florida, USA.

calculate the conservation goals of 10, 20, and 30% for the first 23 habitats (Table 1). The minimum mapping unit was 0.5 ha (0.005 km²) for all habitat types (NOS/DEP 1999). The data are available on CD-ROM in digital format (ArcInfo and shapefile) with full documentation (NOS/DEP 1999).

We imposed a selection grid over the mapped habitat data to delineate the spatial location of potential sites to be included in the reserve system (the M sites in the reserve selection problem). The grid consisted of either (1) 10×10 km squares or (2) 1×1 km squares; we chose these two sizes in order to compare the influence of spatial resolution on the solutions. These 1- or 100-km² sites included one or more (up to 26) benthic habitat types. The amount of each habitat, j , in each site, i , was the basic data matrix, a_{ij} , input to the reserve selection problem.

Scenarios explored

Clustering of sites included in a system of reserves may be desirable for sociopolitical reasons, such as facilitating enforcement, as well as for biological reasons, depending on the scale of dispersal and disturbance in the system of interest. However there is a trade-off between clustering sites and the total area of the reserve system. We can change the emphasis placed on clustering by modifying the boundary length modifier (BLM) parameter in the objective function of the reserve design problem (and hence the algorithm SPEXAN). We ran 100 iterations of the simulated annealing algorithm using four different values of BLM = 0, 0.0001, 0.025, and 1, for the grids of 1- and 100-km² planning units. By increasing the BLM to 1, we gave preference to the inclusion of sites that minimized the overall perimeter, thereby clustering the sites in the reserve system. We compared the "best" of the 100 runs for each of the boundary length modifiers. The "best" scenario had the lowest value of the objective

function (a weighted sum of area and boundary length) in the reserve design problem.

We also explored how the fineness of the habitat classification data influenced the reserve scenarios generated. By collapsing the 26 habitat types into six coarser types (seagrass, reef, hard bottom, bare space, unknown habitat, and nontarget [i.e., inland water, land, and unspecified "water"]) we were able to investigate how the detail of habitat classification influenced the reserve systems generated.

We investigated how efficiently SPEXAN represented each habitat type to learn which habitats tended to be significantly overrepresented in the 1-km² unit, 26-habitat case. We could not evaluate which habitats may be more vulnerable to exclusion from a reserve network with this analysis because the overall aim of SPEXAN is to represent each habitat as efficiently as possible and to still minimize the cost of the overall network scenario. But we can comment on which habitats are likely to be overrepresented, given the conservation goals and overall objective of minimizing the network cost. In addition to reporting whether the conservation goal was fulfilled, SPEXAN reports the "target proportion met" (p), that is, how closely the reserve network scenario meets the conservation goal for each habitat type. These values theoretically can range between zero and infinity, though ours fell between 1.0 and 6.4. A target proportion value of 1.0 means the habitat type is represented in the reserve system at exactly the desired area, whereas a value of 6.4 means that the habitat type is overrepresented in the system by an area 640% larger than the stated goal. We define "overrepresentation" to be a value $\geq 30\%$ greater than the goal ($p \geq 1.3$). "Efficiency of representation" was defined as the number of those habitat types with proportion values close to 1.0 among each of the best runs, for the BLM = 0 or 1, for the three levels of the conservation goals.

TABLE 2. Reserve system solutions generated by the greedy and simulated annealing (SA) algorithms for 1-km² selection units.

Algo- rithm	Best area (km ²)	Minimum area (km ²)	Maximum area (km ²)	Best perimeter (km)	Minimum perimeter (km)	Maximum perimeter (km)
BLM†						
Simulated annealing						
0.0000	1228	1228	1249	3953	3899	4110
0.0001	1227	1223	1248	3489	3489	3718
0.0250	1473	1265	1690	720	720	1040
1.0000	1574	1288	2066	526	526	831
Greedy						
	1182	1182	1184	3428	3376	3506

Notes: The minimum area corresponds to the network scenario with the smallest area, and the maximum area corresponds to the scenario with the largest area, both out of 100 runs. Notation is similar for the perimeter values, also out of 100 runs. Evaluation of the best scenario (both area and perimeter) was based on the minimization of the reserve network cost, which is a combination of the total area and perimeter. SPEXAN 3.1 was used to generate the solutions. Assumptions were a 20% conservation goal, $n = 100$ runs, and 26 habitat types. The "greedy" algorithm did not take into account a "BLM" value, and therefore it is not listed.

† BLM, Boundary length modifier.

We used a subset of the data to compare the performance of the simulated annealing algorithm with the iterative "greedy" algorithm, both of which are available in the SPEXAN 3.1 software package (Ball and Possingham 1999).

For a subset of the 1-km² site problem we carried out an ad hoc irreplaceability analysis (Pressey et al. 1996) where we defined irreplaceability as the number of times a site was included in the reserve system out of 100 SPEXAN runs. This concept is inspired by, but different from, Pressey et al.'s (1994) notion of irreplaceability. We used this analysis to evaluate how different the network scenarios generated by the simulated annealing were from one another, and to investigate which habitats dominated the "irreplaceable" sites. This analysis was intended to identify those areas of the planning region that would be hardest to replace in a comprehensive reserve system and consequently those areas of highest priority for inclusion in a system of marine reserves. Planning units with a high irreplaceability value are the first sites that should be targeted for protection.

RESULTS

We varied several parameters of interest—the boundary length modifier (four levels), the planning unit size (1 km² or 100 km²), the number of conservation targets (26 or 6 habitats), and the overall conservation goal—to explore how they influenced the generated reserve network scenarios. Twenty-six habitat types were included and the conservation goal was fixed at 20%, unless otherwise stated.

Influence of spatial clustering and planning-unit size

We used two combinations of parameters to examine the influence of spatial clustering and planning-unit size: (1) 26 habitats and 1-km² planning units and (2) 26 habitats and 100-km² planning units (Table 2, Fig.

1). The boundary length modifier (BLM) was set at 0, 0.0001, 0.025, or 1 for each set of 100 SPEXAN runs.

For the grid of 1-km² planning units with no accounting for the spatial arrangement of the units (BLM = 0) the lowest scoring or best reserve system had an area of 1228 km². A change in the boundary length modifier from zero to 0.0001 resulted in a 12% drop in the total perimeter (i.e., boundary length) of the best reserve system scenario and a loss of one 1-km² planning unit from the area of the reserve system. Further increasing the boundary length modifier, to 0.025 and then to 1, resulted in further decreases of 79% and then 27% in the perimeter and additions of 246 km² and 101 km² of area to the network scenarios, respectively (Table 2, Fig. 3). The most highly connected (BLM = 1) best scenarios composed of 1-km² units had 87% less total perimeter than those scenarios generated without regard to spatial clustering (BLM = 0). As inspection of the best reserve scenarios indicates, the increase in the boundary length modifier resulted in a more clustered set of reserves (Fig. 1).

For the grid of 100-km² planning units and taking no account of reserve perimeter (BLM = 0) the lowest scoring or best reserve system had an area of 1600 km². Changing the boundary length modifier from zero to 0.0001 resulted in a 41% decrease in the total perimeter and two additional sites. Further increases in the boundary length modifier to 0.025 and then to 1, resulted in a further 14% decrease in the total perimeter of the best reserve systems. When the overall perimeter of the reserve scenario generated with a boundary length modifier of zero was compared to that generated with a boundary length modifier of 1, a 50% perimeter reduction was observed. As with the smaller planning units, an increase in the BLM resulted in a more highly connected network scenario (Table 3).

Influence of the habitat-classification scheme

We used four combinations of parameters to simultaneously examine the influence of the detail of the

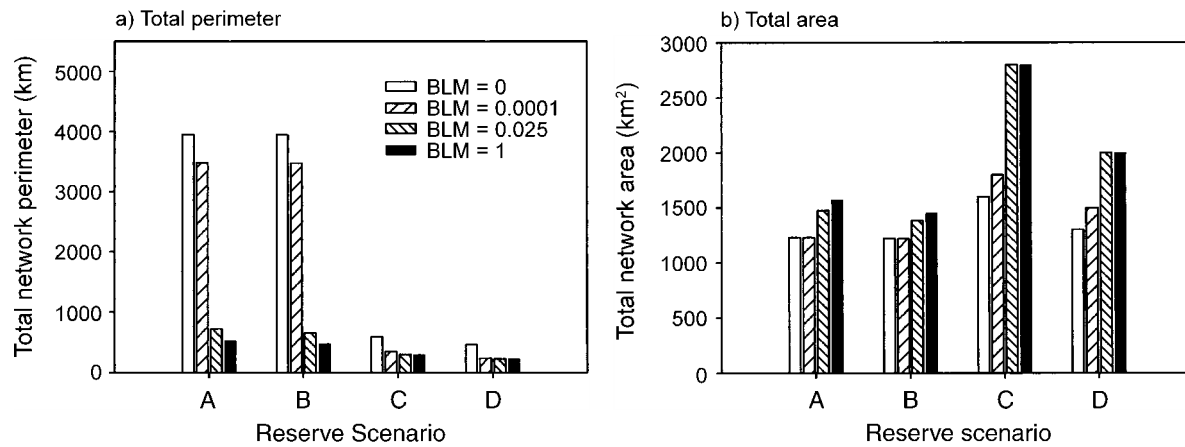


FIG. 3. Influence of the fineness of the planning-unit size (1- vs. 100-km² planning units) and the degree of habitat classification (26 vs. 6 habitat types) on the (a) total perimeter and (b) total area of the best reserve network scenarios (SPEXAN 3.1, $n = 100$). Key to reserve scenarios: A, 26 habitats and 1-km² units; B, 6 habitats and 1-km² units; C, 26 habitats and 100-km² units; D, 6 habitats and 100-km² units. "Best" is defined as the lowest cost network, which is a function of the area and perimeter of the system. The conservation goal was fixed at 20%. BLM stands for boundary length modifier.

habitat classification and planning unit size: (1) 26 habitats and 1-km² planning units; (2) six habitats and 1-km² planning units; (3) 26 habitats and 100-km² planning units; and (4) six habitats and 100-km² planning units (Fig. 3). The BLM was set at 0, 0.0001, 0.025, or 1.

With the 1-km² planning units, using six rather than 26 habitat types did not change the total area of the network scenarios generated considerably (Fig. 3). In contrast, with the 100-km² units, the two levels of habitat classification did not match up as well; the best scenario run with 26 habitats required 800 km² more area than the best scenario generated with six habitats (Fig. 3). This suggests that the scale of the habitat patches themselves were more closely aligned with the scale of the smaller planning unit. Likewise, we observed that the total area and perimeter of the best reserve scenarios differed depending on the use of 1- vs. 100-km² planning units. Networks with smaller planning units had larger perimeters, while scenarios

with larger units encompassed more area for a given boundary length modifier, BLM. Notably, the best aggregated network scenario (BLM = 1) generated using 100-km² planning units and 26 habitats required considerably more area than any other parameter combination to meet the 20% conservation goal.

Influence of conservation goal

Based on the results above, we chosen to focus on the scenarios generated using 26 habitat types and the 1-km² planning units. A change in the conservation goal from 20% to 10% or 30% of each habitat type within the reserve network affected the total area and perimeter of the network (Figs. 4, 5). With an increase in the BLM, and thus much greater aggregation of planning units, the total perimeter of the best scenarios was reduced dramatically in all three cases (Fig. 4a). Concurrently, the total network area grew with the increase in the BLM and the overall conservation goal (Figs. 4b, 5). Although this result is not surprising, the maps

TABLE 3. Reserve system solutions generated using a simulated annealing algorithm for 100-km² selection units.

BLM†	Best area (km ²)	Minimum area (km ²)	Maximum area (km ²)	Best perimeter (km)	Minimum perimeter (km)	Maximum perimeter (km)
0.0000	1600	1600	2000	592	504	696
0.0001	1800	1700	2300	349	309	481
0.0250	2800	2100	3500	298	298	395
1.0000	2800	2300	3400	298	298	376

Notes: SPEXAN 3.1 was used with $n = 100$ runs, 26 habitat types, and a 20% conservation goal. The minimum area corresponds to the network scenario with the smallest area, and the maximum area corresponds to the scenario with the largest area. These and the perimeter values are taken as results from 100 runs. Evaluation of the best scenario was based on the minimization of the reserve-network cost, which is a combination of the total area and perimeter.

† BLM, Boundary length modifier.

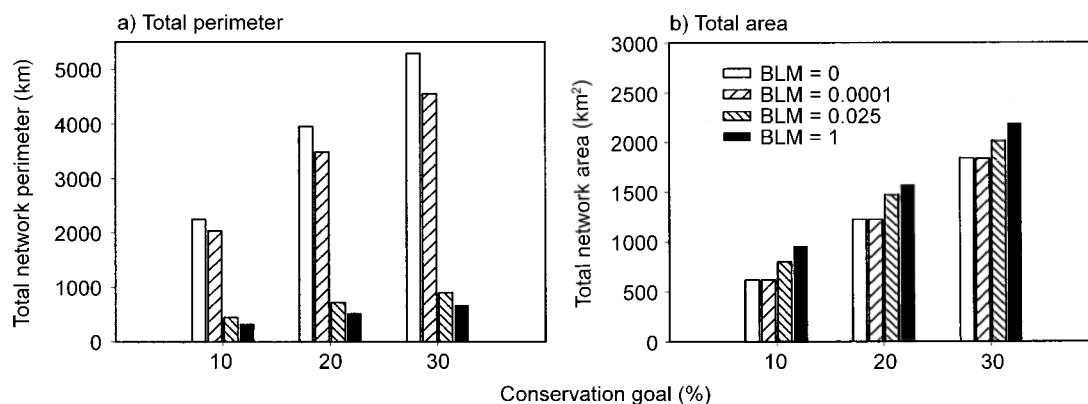


FIG. 4. Influence of the conservation goal (10%, 20%, or 30%) on (a) total perimeter and (b) total area of the best reserve network scenarios. "Best" is defined as the lowest-cost network, which is a function of the area and perimeter of the system (SPEXAN 3.1, $n = 100$, 26 habitat types, 1-km² planning units, boundary length modifier [BLM] = 1).

of lowest cost scenarios for the three conservation goals provide an instant visual guide as to how much area will be required to meet the different goals (Fig. 5). This feature of the tool has proven quite useful in interactive marine conservation planning settings (see Aíramé et al. 2003).

Efficiency of habitat representation

The conservation goals were met in all simulated annealing runs, for all parameter combinations. We investigated how efficiently SPEXAN represented each habitat type to learn which habitats tended to be significantly overrepresented in the 1-km² unit, 26-habitat case. "Efficiency of representation" was defined as the number of those habitat types with proportion values close to 1.0, among each of the best runs, for BLM = 0 or 1, for the three conservation goals.

The efficiency of representation did not change dramatically among the three conservation goals (Fig. 6). The number of overrepresented habitats (where $p \geq 1.3$) decreased as the conservation goal increased: this may have been an artifact of the data or a real trend worthy of further inquiry. There were fewer overrepresented habitats present in the best scenarios created using a BLM of zero, compared those generated with a BLM of one. In the most extreme case, for the 10% goal, the best reserve system scenario encompassed 15 overrepresented habitats, including various types of seagrass beds, coral reef, hard bottom and bare substrata, as well as the "unknown" type.

Performance of the greedy vs. simulated annealing algorithm

When the reserve scenarios generated by the simulated annealing algorithm (BLM = 1) were compared to those from an iterative "greedy" algorithm (also included in the SPEXAN program), interesting results emerged. Based on the data set with 26 habitat types

and 1-km² planning units, with the conservation goal of 20% in reserve, the iterative algorithm produced a lower cost solution than the simulated annealing, with 392 km² less area (Table 2). But the total perimeter of the reserve system generated by the greedy algorithm was 3428 km, while the simulated annealing's system perimeter was 85% shorter, at 526 km. This difference is reflected in the maps of the best "greedy" and simulated annealing solutions (Fig. 7), where one can see how the planning units generated through the iterative process are much more dispersed. Notably, not all conservation goals were met in all runs of the greedy algorithm. For four of the 100 runs, one conservation target (i.e., habitat type) was not adequately repre-

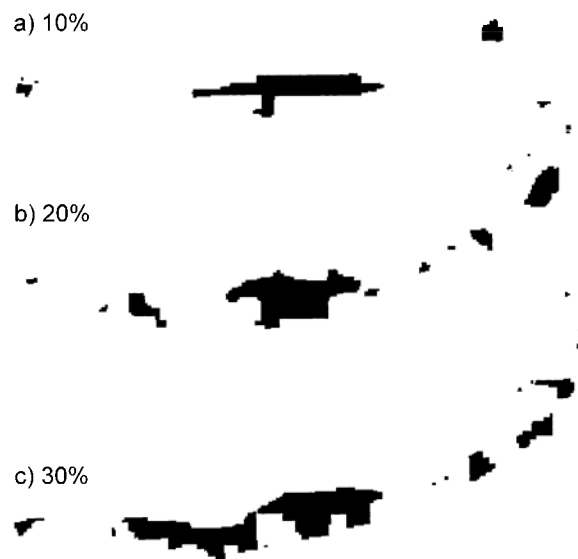


FIG. 5. The best reserve network scenarios generated to meet the 10%, 20%, and 30% conservation goals (SPEXAN 3.1, $n = 100$, 26 habitat types, 1-km² planning units, boundary length modifier = 1).

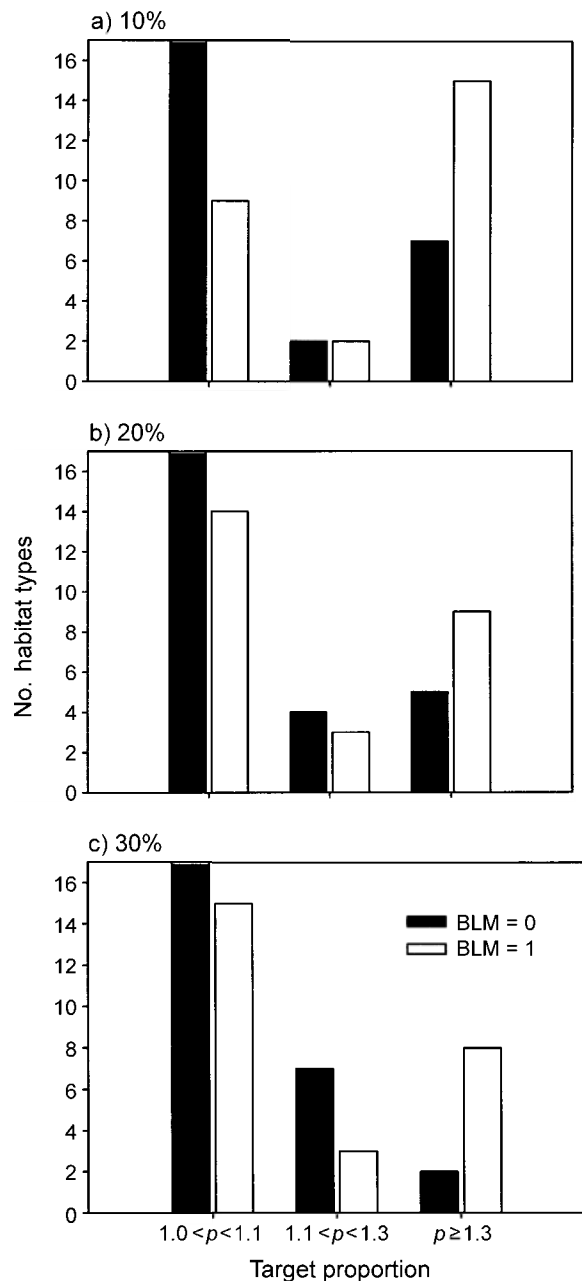


FIG. 6. The efficiency of representation of the conservation targets (i.e., habitats) for the conservation goals of (a) 10%, (b) 20%, and (c) 30% (SPEXAN 3.1, $n = 100$, 26 habitat types, 1-km² planning units, BLM = 0 or 1). Efficiency of representation was defined as the number of those habitat types with proportion values (p) close or equal to 1.0, indicating that the network scenario meets the conservation goal for the habitat. Overrepresentation was defined as a value $\geq 30\%$ greater than the goal ($p \geq 1.3$). BLM stands for boundary length modifier.

sented. The simulated annealing took approximately four hours to process the 11 000 line data set ($n = 100$ runs), while a single run of the greedy algorithm required two hours.

Irreplaceability analysis

We ran an ad hoc irreplaceability analysis on the network scenarios generated by simulated annealing using 26 habitat types and a BLM of one. We examined the results from both the 1- and 100-km² planning-unit grids, recording how many times each site was chosen during the 100 runs. For the 1-km² planning-unit case, which included 11 893 sites with habitat information, very few planning units were chosen $>50\%$ of the time to meet the 10, 20, or 30% conservation goals (Fig. 8). For the 20% goal specifically, 22 units were chosen $\geq 50\%$ of the time, although no one site was chosen $>59\%$ of the time. This result indicates that no planning unit is absolutely irreplaceable in this case. Nonetheless, a small number of sites were consistently represented in the reserve network scenarios, indicating sites for priority protection. More than 2000 planning units were never chosen during the 100 runs either because the target habitats were not represented or the data were not available. In the planning units chosen $\geq 50\%$ of the time, the following habitats represented $\geq 30\%$ of at least one planning unit: dense continuous seagrass beds, bare substrate (carbonate sand), patchy or sparse seagrass beds, and land.

For the 100-km² planning-unit case when the conservation goal was 20%, we had 164 sites with habitat data. Twenty-four planning units were chosen during the majority of the runs, and of these, five were chosen during every one of the 100 runs (Fig. 9). This result makes sense given that because there are so few planning units in the 100-km² case, there is less flexibility in selecting particular units. Even as the magnitude of the conservation goals and the scale of the planning

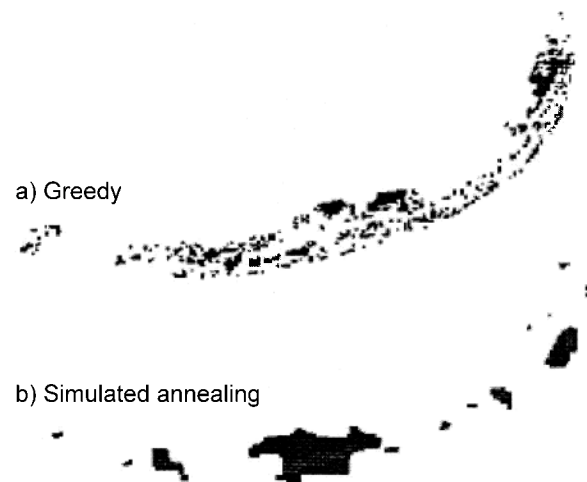


FIG. 7. (a) The greedy iterative algorithm creates a best (lowest cost) reserve scenario with less area but more total perimeter than that created by (b) the simulated annealing algorithm. Data mapped in ArcView 3.2 using output from SPEXAN 3.1 (20% conservation goal, $n = 100$, 26 habitat types, 1-km² planning units, boundary length modifier = 1).

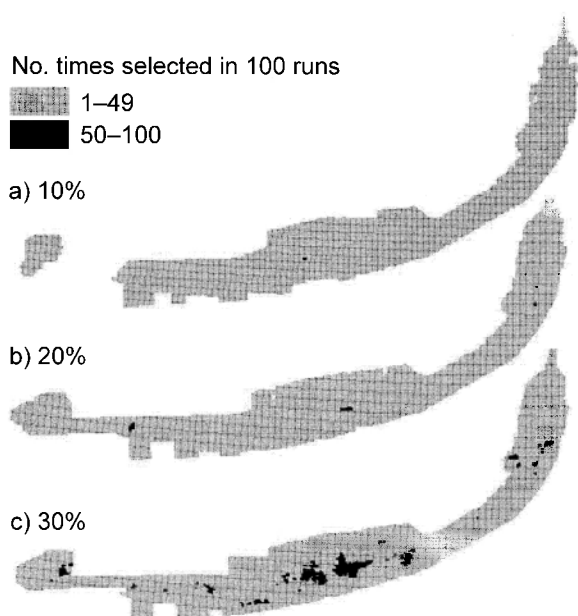


FIG. 8. Irreplaceability analyses of the (a) 10%, (b) 20%, and (c) 30% conservation goal. The number of 1-km² planning units displayed in the majority of runs increased with the level of the conservation goal. The figure was mapped in ArcView 3.2 using output from SPEXAN 3.1 ($n = 100$, 26 habitat types, 1-km² planning units, boundary length modifier = 1).

unit change (Figs. 8, 9), the same central area within the study region is consistently selected. This suggests a focal area for conservation and management activities.

We did a similar analysis on the results of the “greedy” algorithm for the scenarios generated using 26 habitat types, 1-km² planning units, and a conservation goal of 20%. Of the 11 893 possible sites within

the region, 1045 planning units were chosen $\geq 50\%$ of the time, including 651 that were chosen during every one of the runs. The vast majority, >9000 sites, were never chosen during the 100 runs. We found that the “greedy” algorithm produced many fewer different solutions in comparison to the simulated annealing scenarios, indicating that the iterative method did not effectively identify irreplaceable sites.

DISCUSSION

This paper reports on one of the first and few applications of reserve siting algorithms to marine systems to date (see Beck and Odaya 2001, Airamé et al. 2003). Using simulated annealing we were able to incorporate spatial information into the reserve network selection process, and explore how several key parameters—planning unit size, the detail of habitat classification, and the overall conservation goals—can influence the network scenarios generated. We found that simulated annealing produces many adequate reserve systems that meet the conservation goals and fulfill the overall objective of minimizing the system area and perimeter.

Comprehensive habitat representation can be achieved with systems that have varying degrees of spatial clustering. Network scenarios of scattered, largely disconnected reserves adequately represent the habitats (Fig. 1a), but they require considerably more perimeter than more connected networks. More compact reserve systems tend to have considerably less perimeter and larger overall areas in reserve. More compact reserve systems may be preferable for both ecological and sociopolitical reasons, as they can facilitate movement of organisms and biological materials, as well as enforcement and management of reserves (see Roberts et al. 2003).

Identifying “irreplaceable” sites within the study area is a very useful output of siting algorithms such

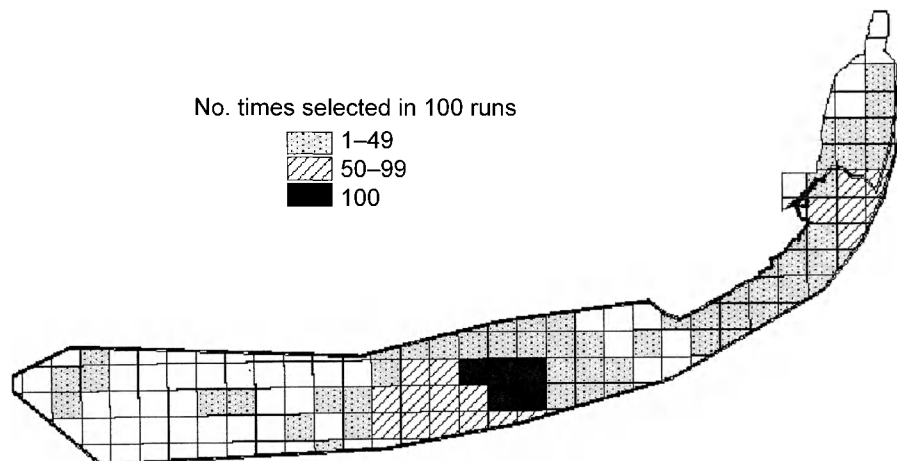


FIG. 9. Irreplaceability analysis of the reserve-network scenarios based on the 100-km² planning units with a 20% conservation goal. The figure was mapped in ArcView 3.2 using output from SPEXAN 3.1 ($n = 100$, 26 habitat types, boundary length modifier = 1).

as this, no matter what the objectives of the planning exercise. Such an analysis offers an effective way to glean valuable information about priority areas, while acknowledging the uncertainty inherent in the delineation of targets, model assumptions, and other parameters. In this case, very few 1-km² planning units were found to be absolutely irreplaceable (Fig. 8). That is, many different combinations of sites produced networks that met the conservation goals. The apparent lack of "irreplaceability" of any one site is encouraging in that it suggests there are many ways to create a reserve network that will meet the incorporated goals. Nonetheless, the analysis also highlighted those sites that were consistently included in the network scenarios: 22 sites of the 11 893 possible planning units in the region were included in the reserve scenarios during the majority of the runs. An analysis like this can be used to prioritize marine conservation planning and implementation activities across a broad region, indicating which areas within the region consistently contribute to meeting the conservation goals.

These results illustrate the value of considering multiple iterations of the conservation goals in the initial stages of planning a network of marine reserves, so that stakeholders gain a visual sense of how different goals affect potential network designs and implementation strategies. In this case, we examined the reserve networks that were generated using 10, 20, and 30% conservation goals. Both the total area and perimeter in reserve scaled linearly with the increases in the goal (i.e., the magnitude of habitat area to be protected). In contrast, efficiency of habitat representation did not. The 10% goal was the least efficient (Fig. 6). The networks that included 30% of each target habitat were more efficient than the 10% or 20% scenarios, as they encompassed the areas truly needed to fulfill the conservation goals. These findings make a strong case for designing aggregated networks of marine reserves since these networks meet conservation goals more efficiently and require less enforceable perimeter. The data also suggest that higher conservation goals may yield greater returns.

The results reported here suggest several general recommendations for interactive reserve design with siting algorithms like SPEXAN. First, build in time during the reserve design process for data compilation. Data compilation and management are among the most time-consuming and resource-intensive steps of designing a marine reserve network. If the decision is made to pursue a systematic approach to siting a network of marine reserves, reserve planners and stakeholders should expect to invest considerable time and money into gathering and analyzing the data needed to make informed decisions.

Second, make articulation and refinement of reserve network objectives an explicit part of the design process. While data are compiled, the design team can refine the

network objectives as well as consider alternative combinations of them, including protecting species of concern, preserving habitat linkages, maximizing public access, or enhancing fisheries. These network objectives can then be translated into appropriate conservation targets (species, habitats, etc.) and goals (or levels of protection or representation within the network)—which then can be incorporated into the algorithm. Mapping out the selection process and how scientific and socioeconomic data, expert opinions, and public input will be brought together is a step that can create a sense of common purpose among the stakeholders, regardless of their specific aims for the reserve network.

Third, use SPEXAN's multiple solutions as a starting point for network design. The strength of the simulated annealing algorithm is that it offers a variety of scenarios that meet the incorporated goals. With more options, stakeholders have a greater chance of creating an ecologically and socially sustainable system of marine reserves. Simulated annealing offers users a fast, interactive approach to summarizing information contained in large data sets. Its mapping capabilities enable stakeholders to gain a tangible sense of how the conservation goals translate into specific recommendations for marine reserve networks and how changing the goals can influence the possible network scenarios. Additionally, siting algorithms force clear articulation of the network objectives, which may further the siting process just as much as the generation of alternative network scenarios.

Finally, it is important to remember that simulated annealing is one of many tools that can be used in the design of marine reserve networks. In most cases, the reserve network design process will be an iterative one (e.g., Aïramé et al. 2003). A team will generate reserve scenarios that meet the initially articulated goals, the results will be presented to a larger group of stakeholders for comment, and then the team will use the algorithm and other siting tools, like expert opinion workshops, again to refine the goals and generate further network scenarios. In this case we focused on habitat representation in formulating our goals, but many other types of goals can be incorporated into the algorithm, such as representation of a certain number of occurrences of a species of concern, or inclusion of particular sites already in protected status. Data on species of special concern, recreational and fishing pressure, and land-based activities also could be incorporated into the algorithm. Some types of information are less easily incorporated into the algorithm, though they may be quite relevant. For example, anecdotal or non-quantitative data about fish spawning areas or the trajectory of development in abutting coastal counties may well inform placement of reserves, but may not be as easily incorporated into the algorithmic stage of the selection process. This information can be used after scenarios have been created to refine and create

a reserve network that meets the overall network objectives. Regardless of what types of constraints (or goals) are incorporated in the siting process, SPEXAN and other siting algorithms are most effective when used in tandem with other types of decision support tools, including expert workshops, geographic information systems and other mapping tools.

In terms of further avenues for research, these results suggest that the simulated annealing algorithm is a promising and powerful tool for marine reserve network design. Its ability to generate multiple biologically suitable scenarios is an exciting result that should be tested in other ecological systems and with other types of conservation targets. We are particularly interested in exploring how currents and other oceanographic features that connect marine populations and ecosystems can be incorporated into systematic siting tools, and in exploring how the spatial and temporal variability in these phenomena affect the network scenarios generated. Such information could be included by formulating an additional constraint within the algorithm, such as a score related to coastal upwelling intensity or the presence of retention zones. As the biological information on connectivity among marine populations and habitats evolves (e.g., Swearer et al. 1999, Cowen et al. 2000), our ability to design connected marine reserve networks will improve.

In addition, this tool offers a powerful means of integrating the natural (e.g., biological and oceanographic) and social (e.g., economic, sociological, and anthropological) science information needed to implement effective marine reserve networks, as well as to other types of marine conservation planning efforts. As this paper went to press, several efforts in the North America are moving in that direction (information on algorithm applications is available at the MARXAN website).⁶ One potential obstacle is the availability of data. Biological data are often difficult to obtain for marine ecosystems, particularly those far from shore. Gathering economic data presents other challenges: in many cases the relevant information are confidential or proprietary. Efforts to facilitate data exchange and compilation will be critical to systematic conservation planning, whether algorithms or other types of tools are employed.

Marine protected areas like the Florida Keys National Marine Sanctuary (FKNMS) offer a unique opportunity to test reserve design theory and implementation ideas. Fully protected marine reserves were a key part of South Florida's coastal zone management program long before the Sanctuary's establishment in 1990. In 1997, 23 fully protected marine reserves were established within the FKNMS with the primary objectives of biodiversity protection and sustainable ma-

rine resource management.⁷ In 2001, the 517 km² Tortugas Ecological Reserve was established in the westernmost part of the FKNMS, increasing the fully protected area Sanctuary-wide tenfold. The Tortugas 2000 process, as it was known, was led by a working group of stakeholders who analyzed the relevant economic, ecological and social information over a two-year period. To our knowledge, siting algorithms were not employed. Interestingly, however, the results of the analysis presented here resonated strongly with several Florida fisheries biologists and marine managers with whom we shared our work.

ACKNOWLEDGMENTS

We thank the members of the NCEAS Marine Reserves working group for their constructive comments, as well as the two anonymous reviewers. Additional support was provided by the Partnership for Interdisciplinary Studies of Coastal Oceans, the Lundeen Marine Biology Fund, the National Science Foundation Graduate Fellowship Program, and Environmental Defense. J. Bohnsack, D. Stoms, P. Halpin, and S. Wood provided key technical assistance. This is contribution number 37 of the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO), a Long-Term Ecological Consortium funded by the David and Lucile Packard Foundation, and contribution number 31 from the Working Group on the Science of Marine Reserves of the National Center for Ecological Analysis and Synthesis, a center funded by NSF (Grant No. DEB-94-21535), the University of California-Santa Barbara, the California Resources Agency, and the California Environmental Protection Agency.

LITERATURE CITED

- Airamé, S., J. E. Dugan, K. D. Lafferty, H. Leslie, D. A. McArdle, and R. R. Warner. 2003. Applying ecological criteria to marine reserve design: a case study from the California Channel Islands. *Ecological Applications* **13**: S170-S184.
- Australian and New Zealand Environmental and Conservation Council Task Force on Marine Protected Areas. 1998. Strategic plan of action for establishing the National Representative System of marine protected areas. Commonwealth of Australia, Canberra, Australia.
- Ball, I. R. 2000. Mathematical applications for conservation ecology: the dynamics of tree hollows and the design of nature reserves. Dissertation. University of Adelaide, South Australia, Australia.
- Ball, I. R., and H. P. Possingham. 1999. Spexan manual, version 3.1. Adelaide University, Adelaide, South Australia, Australia. [Available online: (<http://www.ecology.uq.edu.au/marxan.htm>).]
- Beck, M. W., and M. Odaya. 2001. Ecoregional planning in marine environments: identifying priority sites for conservation in the northern Gulf of Mexico. *Aquatic Conservation: Marine and Freshwater Ecosystems* **11**:235-242.
- Church, R. L., D. M. Stoms, and F. W. Davis. 1996. Reserve selection as a maximal covering location problem. *Biological Conservation* **76**:105-112.
- Cocks, K. D., and I. A. Baird. 1989. Using mathematical programming to address the multiple reserve selection problem: an example from the Eyre Peninsula, South Australia. *Biological Conservation* **49**:113-130.
- Cowen, R. K., K. M. M. Lwiza, M. M. Kamazimz, S. Sponaugle, C. B. Paris, and D. B. Olson. 2000. Connectivity of marine populations: open or closed? *Science* **287**:857-859.

⁶ URL: (<http://www.ecology.uq.edu.au/marxan.htm>)

⁷ URL: (<http://www.fknms.nos.noaa.gov/regs/welcome.html>)

- Csuti, B., S. Polasky, P. H. Williams, R. L. Pressey, J. D. Camm, M. Kershaw, A. R. Kiester, B. Downs, R. Hamilton, M. Huso, and K. Sahr. 1997. A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. *Biological Conservation* **80**:83–97.
- Davis, F. W., D. M. Stoms, and S. Andelman. 1999. Systematic reserve selection in the USA: an example from the Columbia Plateau ecoregion. *PARKS* **9**:31–41.
- Department of Fisheries and Oceans–Canada (DFO). 2000. Fisheries and oceans 2000–2001 estimates, part III: report on plans and priorities. Catalogue No. BT31-2/2001/III-56. Canadian Government Publishing (Public Works and Government Services Canada), Ottawa, Ontario, Canada.
- Federal Register (USA). 2000. Marine Protected Areas. Executive Order 13158 of May 26, 2000. Federal Register 65(105): May 31, 2000. Washington, D.C., USA. URL: (<http://ceq.eh.doe.gov/nepa/regs/eos/eo13158.html>)
- Groves, C. R., D. B. Jensen, L. L. Valutis, K. H. Redford, M. L. Shaffer, J. M. Scott, J. V. Baumgartner, J. V. Higgins, M. W. Beck, and M. G. Anderson. 2002. Planning for biodiversity conservation: putting conservation science into practice. *Bioscience* **52**(6):499–512.
- Kelleher, G., C. Bleakley, and S. Wells. 1995. A global representative system of marine protected areas. The World Bank, Washington, D.C., USA.
- Kirkpatrick, S., C. D. Gelatt, Jr., and M. P. Vecchi. 1983. Optimization by simulated annealing. *Science* **220**:671–680.
- Margules, C. R., A. O. Nicholls, and R. L. Pressey. 1988. Selecting networks to maximize biological diversity. *Biological Conservation* **43**:63–76.
- Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. *Nature* **405**:243–253.
- National Oceanic and Atmospheric Administration (NOAA). 1999. Turning to the sea: America's ocean future. U.S. Department of Commerce, Washington, D.C., USA.
- National Ocean Service and the Florida Department of Environmental Protection (NOS/DEP). 1999. Benthic habitats of the Florida Keys. [CD-ROM and metadata contained therein.] National Ocean Service, National Atmospheric Oceanic Administration, Silver Spring, Maryland, USA.
- Nicholls, A. O., and C. R. Margules. 1993. An upgraded reserve selection algorithm. *Biological Conservation* **64**:165–169.
- Possingham, H. P., I. Ball, and S. Andelman. 2000. Mathematical methods for identifying representative reserve networks. Pages 291–306 in S. Ferson and M. A. Burgman, editors. *Quantitative methods in conservation biology*. Springer-Verlag, New York, New York, USA.
- Possingham, H. P., J. R. Day, M. Goldfinch, and F. Salzborn. 1993. The mathematics of designing a network of protected areas for conservation. Pages 536–545 in D. J. Sutton, C. E. M. Pearce, and E. A. Cousins, editors. *Decision sciences: tools for today*. Proceedings of 12th National Australian Society for Operations Research (ASOR) Conference. ASOR, Adelaide, South Australia, Australia.
- Pressey, R. L., C. J. Humphries, C. R. Margules, R. I. Vane-Wright, and P. H. Williams. 1993. Beyond opportunism: key principles for systematic reserve selection. *Trends in Ecology and Evolution* **4**:124–128.
- Pressey, R. L., I. R. Johnson, and P. D. Wilson. 1994. Shades of irreplaceability: towards a measure of the contribution of sites to a reservation goal. *Biodiversity and Conservation* **3**:242–262.
- Pressey, R. L., H. P. Possingham, and J. R. Day. 1997. Effectiveness of alternative heuristic algorithms for identifying indicative minimum requirements for conservation reserves. *Biological Conservation* **80**:207–219.
- Pressey, R. L., H. P. Possingham, and C. R. Margules. 1996. Optimality in reserve selection algorithms: when does it matter and how much? *Biological Conservation* **76**:259–267.
- Rebelo, A. G., and W. R. Siegfried. 1992. Where should nature reserves be located in the Cape Floristic Region, South Africa? Models for the spatial configuration of a reserve network aimed at maximizing the protection of floral diversity. *Conservation Biology* **6**:243–252.
- Roberts, C. M. 1997. Connectivity and management of Caribbean coral reefs. *Science* **278**:1454–1457.
- Roberts, C. M., et al. 2003. Ecological criteria for evaluating candidate sites for marine reserves. *Ecological Applications* **13**:S199–S214.
- Schwartz, M. W. 1999. Choosing the appropriate scale of reserves for conservation. *Annual Review of Ecology and Systematics* **30**:83–108.
- Swearer, S. E., J. E. Caselle, D. W. Lea, and R. R. Warner. 1999. Larval retention and recruitment in an island population of a coral-reef fish. *Nature* **402**:799–802.
- Underhill, L. G. 1994. Optimal and suboptimal reserve selection algorithms. *Biological Conservation* **70**:85–87.
- Ward, T. J., M. A. Vanderklift, A. O. Nicholls, and R. A. Kenchington. 1999. Selecting marine reserves using habitats and species assemblages as surrogates for biological diversity. *Ecological Applications* **9**:691–698.