A General Model for Designing Networks of Marine Reserves

Enric Sala,[1]* Octavio Aburto-Oropeza,[2] Gustavo Paredes,[1] Ivan Parra,[3] Juan C. Barrera,[3] Paul K. Dayton[1]

There is debate concerning the most effective conservation of marine biodiversity, especially regarding the appropriate location, size, and connectivity of marine reserves. We describe a means of establishing marine reserve networks by using optimization algorithms and multiple levels of information on biodiversity, ecological processes (spawning, recruitment, and larval connectivity), and socioeconomic factors in the Gulf of California. A network covering 40% of rocky reef habitat can fulfill many conservation goals while reducing social conflict. This quantitative approach provides a powerful tool for decision-makers tasked with siting marine reserves.

Networks of marine reserves can be an important tool for the conservation of marine biodiversity (*1*). However, although there is an increasing body of theory about marine reserves (*1, 2*), there has been almost no practical application of theory on large spatial scales (from hundreds to thousands of km). Some theory suggests that marine reserves should protect more than 20% of the habitat to enhance fisheries (*3–6*), but there is no agreement on how much habitat should be protected to preserve biodiversity (*7*), nor on how to maintain ecological links (connectivity) between reserves (*8–10*).

To address these questions, we designed a network of marine reserves to protect biodiversity and complement fisheries management in the Gulf of California, a tropical marine biodiversity hot spot (*11*), by collecting basic biodiversity and ecological data from all important rocky coast habitats and applying them to a reserve-siting model based on optimization algorithms that maintain connectivity. The rocky shores of the Gulf of California harbor 10 distinct habitats along ~1000 km of latitude (*12*). As a starting point, we set a goal of protecting 20% of each representative habitat and 100% of rare habitats (*12*) and of the areas with the highest species richness. We also set a goal of maximizing the protection of ecosystem functioning by protecting larval sources (*13–16*) and nurseries for targeted fish species (*16*) and by ensuring the connectivity among populations through larval dispersal (*10*). Existing marine protected areas on the rocky coasts of the Gulf of California are negligible with regard to conservation at the regional scale; there is only one no-take area (Cabo Pulmo Marine National Park, 7111 ha) covering ~0.2% of the coastal area.

The biodiversity patterns of reef fishes in the Gulf of California showed clear gradients in species richness along latitude: The number of species decreased as the latitude increased (Fig. 1) (*17*). We used a canonical correspondence analysis to identify the main axes of variation in species abundance among habitats and sites. Latitude and depth explained 66% of the variation in the fish assemblages, indicating the existence of three main zoogeographic regions for reef fishes in the Gulf of California (*17*). Although the focus was on reef fish, we also addressed plant and invertebrate biodiversity, using habitat as a surrogate (*18*), and estimated the area of each habitat type around every island and along each section of coast (*17*).

To determine the existence and location of fish larval sources, we interviewed local fishers, conducted diving surveys from 1998 to 2000, and identified the location of spawning aggregations for seven commercial species (*15*). We focused on these large fishes because they are the only rocky-habitat species that spawn at specific locations and are targeted by fishers at spawning (*15*). Larval sources of noncommercial fishes, invertebrates, and algae exist throughout the habitat and are not restricted to a few specific locations. Hence, we assume that the protection afforded by a reserve network for commercial species will ensure sufficient larval production for nonthreatened species. We also identified the habitat requirements for recruitment of vulnerable fish species (*16, 19*).

We divided the rocky coasts of the Gulf of California into 69 planning units, for which we obtained information about biodiversity and ecological processes (*20*). Every planning unit had data on reef fish species richness, the presence of spawning aggregations and nurseries of commercial fishes, and the total area of each habitat. We used a model based on optimization algorithms to select a number of planning units that would fulfill the above conservation goals while minimizing the number of reserves (*17*) and would ensure connectivity among them. The distance between reserves in a network must be determined on the basis of larval dispersal patterns (*21*), although there is much

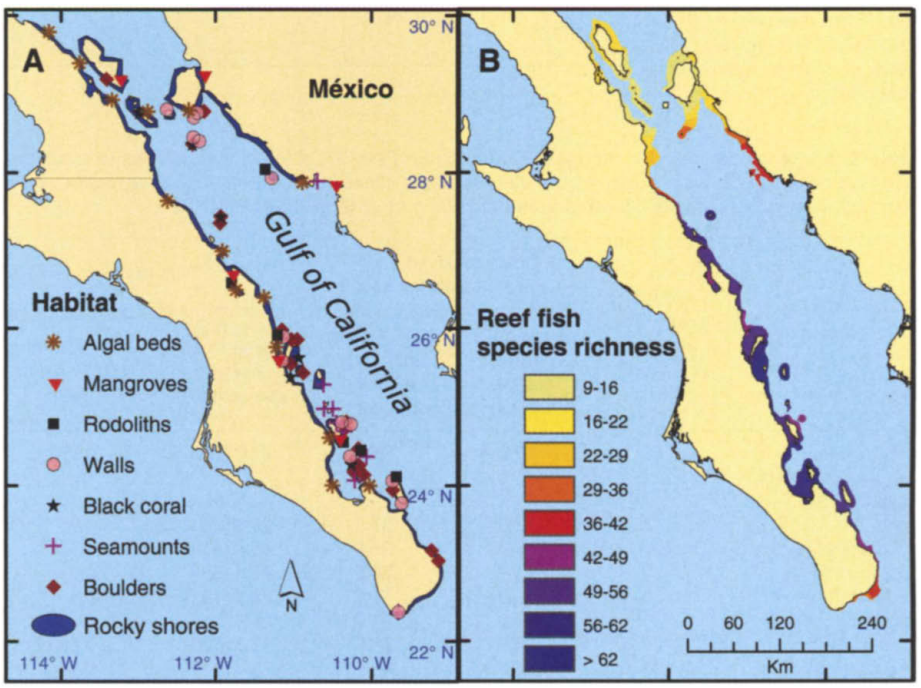

Fig. 1. (**A**) Map of the Gulf of California with location of the study area (rocky shores) and sampling sites. (**B**) Gradients of species richness of reef fishes on shallow rocky bottoms (boulders and walls, 5 to 20 m). Other habitats showed similar patterns, with decreasing species richness and increasing latitude.

[1]Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, La Jolla, CA 92093, USA. [2]Universidad Autónoma de Baja California Sur, La Paz, Baja California Sur, México. [3]Gulf of California Program—World Wildlife Fund, Hermosillo, Sonora, México.

*To whom correspondence should be addressed. E-mail: esala@ucsd.edu

uncertainty about dispersal patterns (*9, 22–24*). Assuming that a reserve network should consider mainly the connectivity between vulnerable species populations, we determined that the distance between adjacent reserves in the Gulf of California should not exceed 100 km (*25*). The selection model was replicated in each of the three zoogeographic regions.

The biologically optimal network involved 24 planning units in 15 aggregated reserves (Fig. 2). The network includes all rare habitats (corals and sea grasses), between 37 and 56% of abundant habitats (boulders, walls, sand, rodolith beds, and shallow algal beds), ~85% of less abundant habitats (black coral beds and seamounts), 89% of mangroves, and all spawning aggregations (Fig. 3 and Table 1). The network protects 44% of reef habitats in the planning region. The proportion of habitat types targeted for protection is evenly distributed in the three zoogeographic regions, except for rare habitats (*12*) (Fig. 3). The maximum distance between adjacent reserves is 89 km (median, 36 km; mean, 40 km) (Fig. 3).

We ran the reserve-siting model again, including fishing pressure, quantified as the density of small fishing boats (*17*). This solution reduces social conflicts by minimizing the overlap between reserves and heavily fished areas (*17*), although having reserves near fisheries can be beneficial to fishing (*26*). This network includes 17 planning units in 13 aggregated reserves covering 40% of reef habitats (Fig. 2). Taking fishing pressure into account does not significantly decrease the proportion of conservation goals achieved relative to the biologically optimal solution (Table 1), mainly because of the low human population density in the Gulf of California and the existence of large areas where coastal fishing pressure is still relatively low.

The most important benefit of this approach is the objectivity it provides to the process of siting marine reserves. Many reserves have thus far been selected more on the basis of social factors than on the basis of biodiversity needs (*2*). A null model of randomly placed reserves in the Gulf of California showed that although they can provide enough protection for the most abundant habitats, they fail to protect rare habitats (Table 1). The probability that a randomly designed network will achieve conservation goals for all habitats is only 7×10^{-4}. Randomly placed reserves would protect an average of only 30% of fish spawning aggregations, but the probability of protecting all aggregations is virtually zero. The probability of including more than 50% of fish nurseries is only 0.4% (Table 1). Ecological processes and critical habitats are not distributed homogeneously, hence reserve networks must be designed on the basis of spatially explicit quantitative data.

The reserve networks presented here allow for the preservation of biodiversity and complement fisheries management. The persistence of populations in a reserve network depends on the size and distance between individual reserves (*6, 21*). This network allows for the persistence of populations because individual reserves are sufficiently large (50 km) to ensure more than 90% local retention of algal propagules and more than 45% local retention of fish and invertebrate larvae (*25, 27*). It does not strictly address connectivity for macroalgae and some invertebrates because algae disperse at distances shorter than 5 km and many invertebrates disperse at distances shorter than 100 km (27). However, the average distance between the reserves is 40 km, ensuring connectivity for most fishes and many invertebrates. Fi-

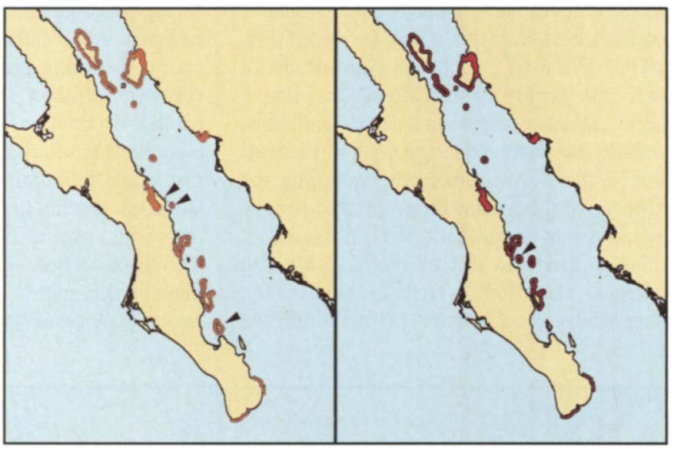

Fig. 2. Proposed networks of marine reserves for the Gulf of California. (**Left**) Biologically optimal network, and (**right**) network that reduces social conflict by excluding areas where fishing pressure and conservation collide. The arrowheads point to planning units removed (left) and added (right) to the network when considering fishing pressure. Some reserves in this figure are aggregates of smaller planning units.

Table 1. Conservation goals for the rocky coasts of the Gulf of California and achievements of the proposed networks of marine reserves. A null model was conducted, creating 10,000 networks of 24 planning units each, randomly allocated from the total pool of 69 planning units (*20*).

Element	Conservation goal (% of habitat protected)	Goals achieved (% of habitat protected)		Null model	
		Biologically optimal reserve network	Reserve network reducing social conflict	Mean (±SD) conservation goal achieved	*P* of achieving conservation goals
Habitat type Rocky (boulders and walls)	>20	41.0	37.8	27.0 (3.1)	0.99
Sand	>20	37.3	33.3	26.8 (2.8)	0.98
Coral communities	100	100	86.8	35.8 (41.9)	0.36
Seamounts	>20	85.9	80.2	23.4 (8.4)	0.64
Rodolith beds	>20	56.3	51.8	27.2 (13.6)	0.68
Sargassum beds	>20	44.4	41.7	26.5 (5.9)	0.92
Black coral beds	>20	84.9	82.6	15.3 (5.9)	0.22
Seagrass beds	100	100	100	36.4 (41.8)	0.14
Spawning aggregations	100	100	90	29.7 (11.3)	0
Nurseries (mangroves)	>50	88.9	64.3	20.8 (11.1)	0.004

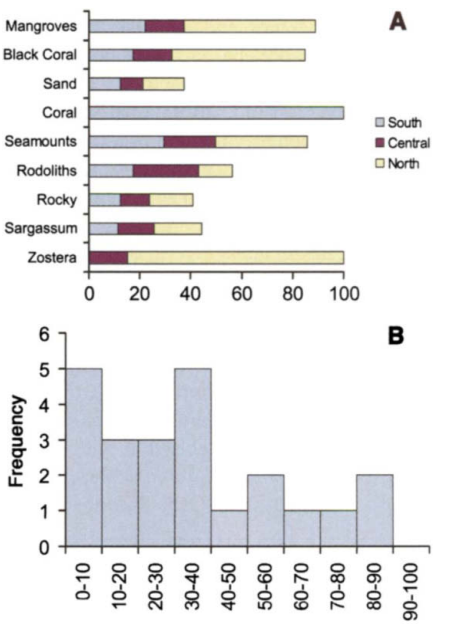

Fig. 3. Proportion (%) of total habitat included in the network for each habitat type and zoogeographic region (**A**) and frequency distribution of distances (in km) between reserves (**B**).

nally, the smallest network protects 40% of the habitat, which is in agreement with theoretical work on the minimum fraction of coastline posited for persistence of populations (*21*).

The use of explicit socioeconomic variables in addition to biodiversity data is particularly important because in marine systems, where fishing is a major threat, ecological criteria and socioeconomic measures are not independent (*28*). Moreover, portfolios of solutions can be presented to decision-makers (*29, 30*), who can then evaluate the costs and benefits of different management options within socioeconomic constraints. Prioritization of the reserves can be carried out with this model, using a stepwise selection that evaluates the contribution of each reserve to the preservation of total biodiversity. In the future, new conservation models that account for soft bottoms, pelagic habitats, marine mammals, sea turtles, coastal lagoons, and additional social factors, including future threats, should be developed to obtain networks of reserves to preserve all marine biodiversity. Meanwhile, this procedure can be applied to any coastal region and offers a constructive approach to integrating the economic, social, and biological concerns of marine biodiversity preservation.

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12. The major habitat types on the rocky coasts of the Gulf of California to a depth of 50 m are shallow algal (*Sargassum* spp.) beds, boulders, vertical walls, black coral beds, rodolith beds, sandy bottoms, seamounts, and mangroves. Rare habitats are coral communities and seagrass beds. Although corals are found throughout the Gulf of California, they only develop extensive communities in two sites in the southern gulf. Seagrass (*Zostera marina*) beds are found in only two places in the central and southern gulf.
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16. Our goal was to protect enough critical habitats to allow the long-term persistence of commercial species, although this is difficult to predict when heavy fishing occurs outside the reserves (*31*). A reserve network must include all known spawning aggregations of vulnerable reef fishes (*15*). Mangroves are the only vulnerable habitats that provide nurseries for vulnerable species (goliath grouper, broomtail grouper, and most snappers) (*17*). Juveniles of these species, however, are not threatened directly by fishing. We set a goal of protecting at least 50% of mangroves.
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25. Variability in ocean currents, spawning seasons, larval life histories, and dispersal distances (from meters to hundreds of kilometers) (*10, 27*) makes it virtually impossible to obtain a single value to measure connectivity between sites for all taxonomic groups. This suggests that marine reserves will not benefit all species evenly (*27*). However, not all species are equally threatened by anthropogenic activities. Although nontargeted, low-dispersal species may be preserved by creating small reserves (*32*), for heavily affected species we need to consider connectivity between reserves (*14*). Therefore, we focused on connectivity when considering vulnerable species. A study on the dispersal of grouper larvae in the Gulf of California indicates that average dispersal distances may be on the order of 150 km (*33*). Thus, to establish meaningful connectivity between reserves, we determined that they should be spread as evenly as possible throughout the Gulf of California, and we assumed that other commercial fishes, with similar larval life-spans to that of groupers, may have similar larval dispersal patterns. Moreover, marine fishes have a mean dispersal distance of ~100 km (*27*). To ensure sufficient dispersal of the larvae of vulnerable fishes between reserves, and between reserves and unprotected areas, we assumed that the largest gap between reserves should not exceed 100 km.
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35. This paper is dedicated to Bob Johannes, who died 4 September 2002. We thank S. Andelman, L. Botsford, J. Jackson, N. Knowlton, G. Sugihara, R. Warner, and three anonymous referees for comments on the manuscript; D. Wesson for her thoughtful discussions and critical editorial comments on the manuscript; E. Ballesteros, C. Sanchez, and all the Mexican students who helped in the field; and P. Beller, M. Carvajal, L. Findley, S. Acuña, T. Pfister, L. Fichman, J. Curtiss, and A. Tomba for providing advice and logistic support. Special thanks to M. Moreno and V. Noriega for assistance with the Geographic Information System and computer programming. This research is part of a larger effort led by the World Wildlife Fund, Conservation International, and other nongovernmental organizations and academic institutions to design a network of marine reserves in the Gulf of California and to work with the Mexican government for its implementation (*34*). We are grateful to the Instituto Nacional de Ecología of México for providing research permits and to the Moore Family Foundation, The Tinker Foundation, the Robins Family Foundation, the Gulf of California Program—World Wildlife Fund, N. Roberts, and B. Brummit for funding.

Supporting Online Material

www.sciencemag.org/cgi/content/full/298/5600/1991/DC1
Materials and Methods
Figs. S1 and S2

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Ectoderm to Mesoderm Lineage Switching During Axolotl Tail Regeneration

Karen Echeverri and Elly M. Tanaka*

Foreign environments may induce adult stem cells to switch lineages and populate multiple tissue types, but whether this mechanism is used for tissue repair remains uncertain. Urodele amphibians can regenerate fully functional, multitissue structures including the limb and tail. To determine whether lineage switching is an integral feature of this regeneration, we followed individual spinal cord cells live during tail regeneration in the axolotl. Spinal cord cells frequently migrate into surrounding tissue to form regenerating muscle and cartilage. Thus, in axolotls, cells switch lineage during a real example of regeneration.

Lineage restriction into ectodermal, mesodermal, and endodermal germ layers that occurs during development has been thought to be a process that is not reversed. However, recent data indicate that adult cells from various sources, including brain, skin, and bone marrow, can form cell types of other lineages when exposed to novel or foreign environments (*1–5*). Whether such examples represent true cases of cell-type switching and whether lineage switching represents a rare or frequent event are still being debated (*6, 7*).

Max Planck Institute of Molecular Cell Biology and Genetics, Pfotenhauerstrasse 108, D-01307 Dresden, Germany.

*To whom correspondence should be addressed. E-mail: tanaka@mpi-cbg.de