available at www.sciencedirect.com

ScienceDirect

www.elsevier.com/locate/ecolecon

ELSEVIER

METHODS

Assessing the ecological and economic benefits of a no-take marine reserve

Jeffrey Wielgus[a],*, Enric Sala[b,c], Leah R. Gerber[a]

[a]*School of Life Sciences, Arizona State University, Tempe, Arizona 85287, USA*
[b]*Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, 9500 Gilman Drive, La Jolla, California, USA*
[c]*Centre d'Estudis Avançats de Blanes, Accés Cala Sant Francesc 14, 17300 Blanes, Spain*

ARTICLE INFO

ABSTRACT

The management of marine resources is often impeded by a lack of models to integrate ecological and economic information on exploited populations. We used available biological and economic data for an overexploited population of the leopard grouper (*Mycteroperca rosacea*) to study if closing parts of the population to fishing would allow sustainable use and maximum economic benefits. Our results suggest that fishing should be closed in all spawning areas and in at least 50% of the adjacent areas. High non-consumptive benefits would be achieved with large closures because the abundance of the leopard groupers, which is an important attribute for SCUBA divers, would increase. In a no-take reserve, the welfare gains of divers seemingly could compensate for losses incurred by fishers if parts of their fishing grounds are closed. An adaptive management scheme could provide a way to incorporate newly available information into management decisions for the no-take reserve.

1. Introduction

No-take marine reserves, which ban fishing activities within the reserve boundaries but allow non-consumptive uses, have become a widely advocated approach to facilitate the recovery of dwindling marine resources (Lauck et al., 1998; Guenette and Pitcher, 1999; Russ and Alcala, 2003; Gaylord et al., 2005) and to enhance fisheries in adjacent areas (Russ and Alcala, 1999; Roberts et al., 2001; Gell and Roberts, 2003; Willis and Millar, 2005). However, the economic costs of no-take reserves have seldom been considered in assessing their usefulness as tools for resource management (but see Sanchirico and Wilen, 2001 and Grafton et al., 2006 for theoretical assessments and Balmford et al., 2004 for an assessment of global costs), and the net economic benefits provided by marine reserves is uncertain (Grafton et al., 2006). In this paper we study if a no-take marine reserve can maximize the economic benefits from the use of a resource that is maintained at sustainable levels.

We studied the ecological and economic consequences of implementing a no-take marine reserve in the Gulf of California, Mexico. This region supports approximately 800 fish and 35 mammal species, and contains one of the highest numbers of endemic fish species worldwide (Roberts et al., 2002). In 2005, the islands of the Gulf of California and their

---

* *Corresponding author.* Current address: Fisheries Centre, University of British Columbia, 2202 Main Mall, Vancouver, Canada V6T 1Z4. Tel.: +604 240 0135; fax: +604 822 8934.
E-mail address: j.wielgus@fisheries.ubc.ca (J. Wielgus).
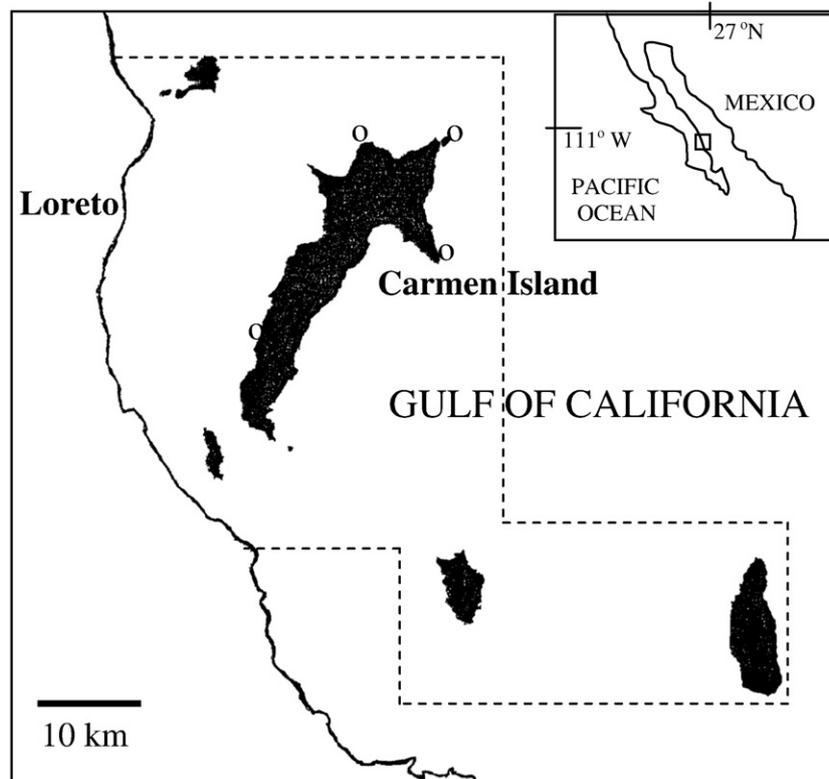
Fig. 1 – Location of Loreto Bay National Park and Carmen Island. The Park's limits are indicated with dashed lines, and the sites where leopard grouper abundance was measured are indicated by circles.

surrounding areas were included in UNESCO's World Heritage List. One of these areas was Loreto Bay National Park (LBNP, Fig. 1), established in 1996 to protect the biologically-rich area from industrial trawling and seining. Commercial fishing with hook and line and nets, as well as recreational fishing, are still permitted within the Park boundaries. The Park also supports other recreational activities such as SCUBA diving, whale watching, and kayaking (Wielgus et al., 2007). Approximately 70% of the population in the LBNP area is employed in the tourism sector (CONANP-SEMARNAT, 2002).

One of the most important resources for local commercial fisheries in the LBNP is the leopard grouper (*Mycteroperca rosacea*), which also plays a key ecological role as a top predator (Hobson, 1968). Leopard groupers inhabit rocky reefs surrounding the islands at the LBNP. Fish mature at approximately 35 cm total length (Heemstra and Randall, 1993), and they enter the commercial fishery when they reach this size. Every year, adult fish congregate to spawn in the same locations of the reefs, and they are easily targeted by fishers at this time (Sala et al., 2003). As many other species of groupers worldwide, populations of the leopard grouper in the Gulf of California are heavily exploited, and the species has been classified as vulnerable by the World Conservation Union (Morris et al., 2000).

The town of Loreto (pop. 12,000) is the largest hub for commercial fishing and tourism in the LBNP area (Gutiérrez-Barreras, 2001). Commercial fishing in the LBNP is conducted from 6 m-long boats with outboard engines, and the distance from Loreto (Fig. 1) is a major consideration in the selection of fishing sites. The islands adjacent to Loreto are preferred

fishing grounds for commercial fishers. These islands are also the site of most of the recreational SCUBA dives that take place in the LBNP. One of the main attractions for SCUBA divers is adult leopard groupers (Wielgus et al., 2007), which attain lengths of more than 1 m (Thomson et al., 2000) and exhibit striking coloration patterns. At Carmen Island, most dives take place in the shallow water just off the island.

A recent study on leopard groupers in the LBNP (Wielgus et al., 2007) indicated that the population at Carmen Island is declining. Conversations with fishers in Loreto revealed that fishers are aware of the decreasing catches of leopard grouper in the Park, and that fishers expect the LBNP Management Agency to develop and apply management plans to help the depleted fish populations to recover (Stamieszkin et al., in review). In this paper we examine if a no-take marine reserve at Carmen Island could maximize the flow of economic benefits from the sustainable use of the leopard grouper. In particular, we study the impact of a reserve of different locations and sizes on the growth rate of the leopard grouper and on the consumptive and non-consumptive economic benefits provided by the resource. We also discuss the potential benefits of adaptively managing a no-take marine reserve at Carmen Island.

2.   Methods

In this section we describe the economic and ecological data that were used in the simulations of reserve impact, define the

metrics for determining the performance of reserves of different location and size, and explain the procedure used to simulate the impact of reserve establishment.

2.1. Ecological data

Leopard grouper abundance was measured at 4 sampling sites off Carmen Island (Fig. 1) that were selected randomly from all sites known to contain rocky habitats large enough to permit replicate sampling. In September 2004, six 50×5 m transects were sampled at each site at depths of 5 and 20 m. To quantify the number of fish in each transect, a SCUBA diver randomly-selected a starting point and swam in a linear direction unreeling a 50-m measuring tape. The diver recorded the abundance and total length (to the nearest 5 cm) of juvenile (5–35 cm total length) and adult (>35 cm total length) leopard groupers within 2.5 m of each side of the measuring tape, following the methods of Harmelin-Vivien et al. (1985).

Distinct fish communities are found at depths of 5 and 20 m in the Gulf of California (Sala et al., 2002). However, it is not known if these depths represent distinct habitats for the leopard grouper, and if distinct processes of population dynamics occur at each depth. Hence, demographic matrices containing the annual vital rates for the leopard grouper have been previously estimated (Wielgus et al., 2007) under

assumptions of (1) distinct "shallow" (0–5 m depth) and "deep" (5–20 m) habitats, and (2) a single habitat comprising both depths (Fig. 2). Vital rates for the leopard grouper have also been estimated for El Niño and La Niña periods under these 2 assumptions (Wielgus et al., 2007; Fig. 2).

2.2. Economic data

Data on reported fish catches for the LBNP were obtained from the Loreto office of the Mexican Department of Agriculture and Fisheries (SAGARPA). From the latest complete dataset (2004), we estimated that the average weight of leopard groupers was 10 kg, the mean price charged by fishers was US $1.56/kg, and the average catch of leopard grouper was 90.14 kg per trip. Interviews with fishers in Loreto during April 2006 revealed that gasoline for a fishing trip from Loreto to Carmen Island cost an average of US $36.40. Gasoline is by far the largest direct expense of fishing in the LBNP, so we calculated the cost of fishing per kg of leopard grouper to be approximately US $0.40. Based on this cost estimate, the net revenue per kg was US $1.16. We estimated that average annual inflation is 4.52% based on Consumer Price Index data for Mexico from January 2001 to January 2006 (Bank of Mexico, 2006).

A recent stated-preference survey (Wielgus et al., in review) used a choice experiment to estimate the marginal price of
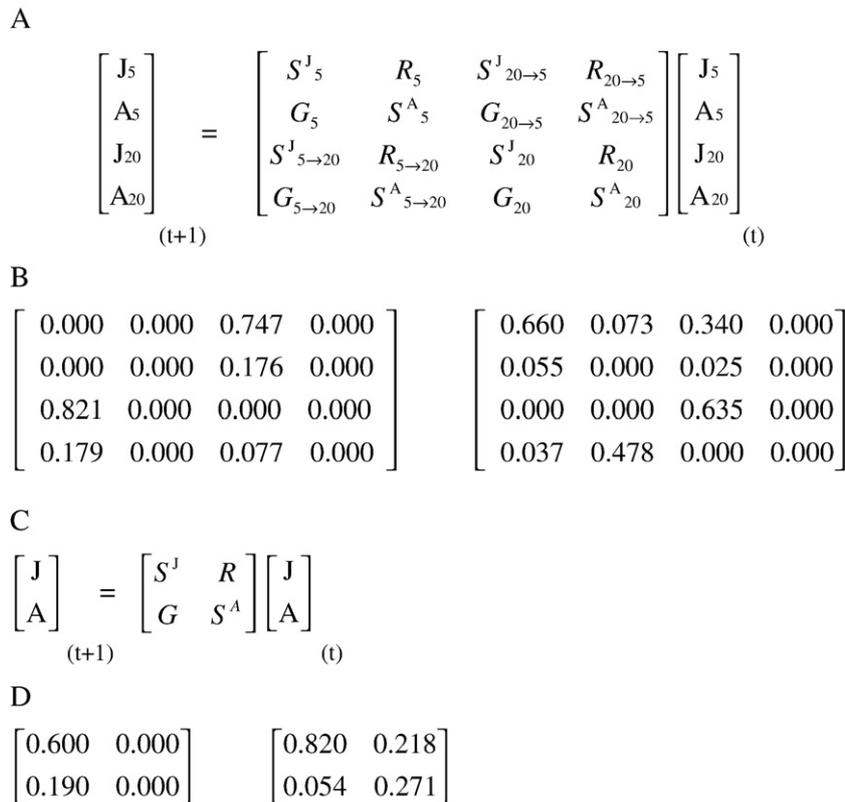
A

$$
\begin{bmatrix} J_5 \\ A_5 \\ J_{20} \\ A_{20} \end{bmatrix}_{(t+1)} = \begin{bmatrix} S^J_5 & R_5 & S^J_{20\to5} & R_{20\to5} \\ G_5 & S^A_5 & G_{20\to5} & S^A_{20\to5} \\ S^J_{5\to20} & R_{5\to20} & S^J_{20} & R_{20} \\ G_{5\to20} & S^A_{5\to20} & G_{20} & S^A_{20} \end{bmatrix} \begin{bmatrix} J_5 \\ A_5 \\ J_{20} \\ A_{20} \end{bmatrix}_{(t)}
$$

B

$$
\begin{bmatrix} 0.000 & 0.000 & 0.747 & 0.000 \\ 0.000 & 0.000 & 0.176 & 0.000 \\ 0.821 & 0.000 & 0.000 & 0.000 \\ 0.179 & 0.000 & 0.077 & 0.000 \end{bmatrix} \quad \begin{bmatrix} 0.660 & 0.073 & 0.340 & 0.000 \\ 0.055 & 0.000 & 0.025 & 0.000 \\ 0.000 & 0.000 & 0.635 & 0.000 \\ 0.037 & 0.478 & 0.000 & 0.000 \end{bmatrix}
$$

C

$$
\begin{bmatrix} J \\ A \end{bmatrix}_{(t+1)} = \begin{bmatrix} S^J & R \\ G & S^A \end{bmatrix} \begin{bmatrix} J \\ A \end{bmatrix}_{(t)}
$$

D

$$
\begin{bmatrix} 0.600 & 0.000 \\ 0.190 & 0.000 \end{bmatrix} \quad \begin{bmatrix} 0.820 & 0.218 \\ 0.054 & 0.271 \end{bmatrix}
$$

Fig. 2 – (A) Population dynamics for juvenile (J; 5–35 cm total length) and adult (A; >35 cm total length) leopard groupers (*Mycteroperca rosacea*) at Carmen Island (Gulf of California) for a two-habitat model, which considered the depths of 0–5 m and 5–20 m as different habitats (subscripts of 5 and 10 indicate these habitats, respectively). (B) Estimates of annual vital rates for the two-habitat model for El Niño periods (left) and La Niña periods (right) (from Wielgus et al., 2007). S is the probability of survival, R is juvenile recruitment, and G is juvenile growth. (C) Population dynamics for a single-habitat model, which considered the depths of 5 and 20 m as a single habitat. (D) Estimates of annual vital rates for the single-habitat model for El Niño years (left) and La Niña years (right) (from Wielgus et al., 2007).

fish that are important attributes for SCUBA divers in southern Baja California. Divers were interviewed at diving centers between July and December 2005. The study found that divers were willing to pay an average of US $0.60 per dive to observe an additional large fish such as a leopard grouper. From discussions with dive operators and preliminary data from the LBNP Management Agency obtained in April 2006, we estimated that approximately 1750 dives are made each year in the shallow areas at Carmen Island, and that divers make an average of two dives per day.

2.3. Measuring sustainability

As an index of the impact of a reserve on the sustainability of the leopard grouper population at Carmen Island we used the expected long-term population growth rate (or stochastic growth rate, λ^S), which is common practice in population viability analyses (Morris and Doak, 2002). Values of $\lambda^S \geq 1$ indicate a stable or increasing (sustainable) population. A maximum likelihood estimator of log λ^S can be calculated as

$$\log \lambda^S = \frac{\sum_{t=0}^{t-1} r_t}{T}, \tag{1}$$

where r_t is the log ratio of population abundance (number of fish) from consecutive years, and T is a large number (Cohen et al., 1983). We used a value of $T=100,000$ for the simulations (Caswell, 2001). An approximate 95% confidence interval for λ^S is given by $\log \lambda^S \pm 1.96(\text{var}(r)/T)^{1/2}$ (Heyde and Cohen, 1985). Analyses were conducted using MATLAB 7.0 (The Mathworks, Natick, Massachusetts).

Changes in population abundance over time can be described by $n_{t+1} = An_t$, where n_t is a row vector containing abundances of the population stage classes in year t, n_{t+1} is a row vector with stage abundances in year $t+1$, and $\mathbf{A}$ is a matrix containing vital rates for the individuals in the population (Fig. 2). To project population abundance over T for estimating λ^S, we multiplied the vector containing abundance values for 2004 by a single-habitat or two-habitat (shallow and deep) matrix containing the annual vital rates of the leopard grouper for El Niño or La Niña years. El Niño or La Niña matrices were selected randomly, conditional on the probability of occurrence of each (45.5% and 54.5%, respectively [Wielgus et al., 2007]). We multiplied the resulting values of abundance by $\mathbf{A}$ and repeated the procedure for all values of $t \leq T$, and estimated λ^S with Eq. (1).

2.4. Simulations of reserve establishment—general considerations

We simulated the impact of establishing a no-take reserve of varying sizes and locations at Carmen Island. Due to the absence of data for the leopard grouper, we used data on vital rates that are available for congeneric species.

The proportion of individuals of a population that survive over a period of one year is given by $S = e^{-Z}$, where Z is the instantaneous total mortality over the period (Gulland, 1969; Quinn and Deriso, 1999). The components of Z are instantaneous natural mortality (M) and instantaneous fishing mortality (F), which are additive (Gulland, 1969), so we estimated the annual probability of adult survival (S^A) as

$$S^A = e^{-(M^A + F^A)}. \tag{2}$$

Rates of instantaneous natural mortality for the leopard grouper have not been published, so we used an estimate (0.18) for the gag, *Mycteroperca microlepis* (Heppell et al., 2006). Applying Eq. (2) for the case of no fishing mortality (i.e., $F^A = 0$ and $M^A = 0.18$) yields $S^A = 0.84$. In the calculation of λ^S for areas that were simulated as a no-take reserve, we replaced the current probability of survival of adult fish (Fig. 2) with this survival rate.

2.5. Simulation of the establishment of a shallow no-take reserve

The low levels of juvenile recruitment at Carmen Island (Fig. 2) may be a consequence of the exploitation of its spawning aggregations. In the Caribbean, adult Nassau groupers (*Epinephelus striatus*) migrate up to hundreds of kilometers in shallow water on continues tracts of coral reefs (Carter et al., 1994; Bolden, 2000), but they appear not to migrate between reefs over deep waters (E. Sala, unpublished data). The islands of the LBNP are separated by deep water that may avert the movement of adult fish between islands. Assuming that larval dispersal occurs at scales in the order of tens of km, which is typical of many reef fish (Cowen et al., 2006), the persistence of the Carmen Island leopard grouper population may depend strongly on the island's own stock of adult fish (Fig. 1). At Carmen Island, spawning aggregations of adult fish occur at shallow areas (5 m depth and shallower, see Fig. 3) that are easily targeted by fishers. For this reason, we first simulated the effects of establishing a no-take reserve in the shallow area that contains the sites of spawning aggregations. In the Caribbean, the closure of a spawning aggregation of the red hind (*Epinephelus guttatus*) to fishing led to the recovery of the population (Nemeth, 2005).

We estimated the recruitment rates of the leopard grouper population at Carmen Island in the absence of fishing. Egg production is proportional to the size of female fish (e.g., Whiteman et al., 2005), so we used the potential annual egg
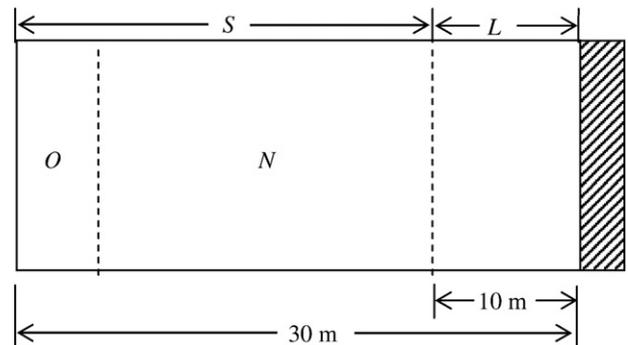

Fig. 3 – Schematic representation of the two depth zones off Carmen Island that were analyzed in the study: a shallow area, S (0–5 m depth) and a deep area, D (5–20 m depth). D is divided into a no-take reserve (N) and an area open to fishing (O). Average distances (in meters) from the Carmen Island coastline (depicted with hatched lines) are shown.

production (1,313,000 eggs per female per year) for a similar-sized fish, the scamp, *Mycteroperca phenax* (Harris et al., 2002). We multiplied this value by the larval survival for the gag (6×10^{-7}; Heppell et al., 2006), and obtained an estimate of 0.78 juveniles produced per female fish per year. Assuming a 1:1 sex ratio, we used 0.39 as the number of juveniles produced per adult fish per year (recruitment rate) when spawning aggregations are protected from fishing.

We estimated the adult survival rates resulting from the reserve. In the two-habitat model, we assumed an equal number of recruits produced by adult fish living at either depth. We also assumed that all adult fish that remain in the open area for the entire year are caught. The null or low probability of survival of adults at Carmen Island suggests that most of these fish are caught with the current fishing effort (Fig. 2). The number of commercial fishers in the LBNP may increase over the next decade (Gutiérrez-Barreras, 2001), so it is reasonable to assume that all adult fish that will be available to the fishery will continue to be caught. The two-habitat model included parameters for adult fish that move between the 2 depths (Fig. 3). We assumed that adult fish that remain in the shallow area have maximum survival ($S^A = 0.84$), while adult fish that move between both depths have $S^A = 0.42$ because they are protected from fishing while in the shallow area (i.e., adult fish prefer, and spend time at, each habitat equally).

The single-habitat model did not include parameters for fish movements (Fig. 2). The deep area is approximately 75% of the total area covered by the population (Fig. 3), and, assuming a homogeneous distribution of fish over the two depths, 25% of the population that survives natural mortality ($0.25 \cdot 0.84 = 0.21$) will be protected when the shallow area is closed to fishing, so we set $S^A = 0.21$.

2.6. Simulation of the establishment of a shallow and deep no-take reserve

2.6.1. Incorporating sustainability as a constraint
Because we found that closing only the shallow areas to fishing would not lead to a sustainable leopard grouper population at Carmen Island (see Results), we studied if closing a section of the deep area to fishing, in addition to closing the shallow area to protect spawning aggregations, would achieve a sustainable population and maximize economic benefits.

We first studied the relationship between reserve size and λ^S. We assumed a linear relationship between annual fishing mortality (H) and the fraction of the deep area that is closed to fishing (N):

$$H_N = H_O(1 - N), \tag{3}$$

where H_O is the annual fishing mortality when the entire deep area is open to fishing ($N=0$). As above, we assumed that all adult fish in areas open to fishing would be caught. We set $H_O = 0.84$ (the survival rate after subtracting natural mortality; see above) for adult fish that spend the entire year in the deep area, and $H_O = 0.42$ for adult fish that move between the deep area and the shallow area (which is now assumed to be a reserve). In the single-habitat model, 75% of the population that survives natural mortality ($0.75 \cdot 0.84 = 0.63$) will be caught

when the entire deep area is open to fishing, so we set $H_O = 0.63$. For reserves encompassing the shallow area and 0–100% of the deep area (in 10% intervals), we calculated the fishing catches in each year (H) using Eq. (3), and subtracted it from 0.84 to obtain S^A and λ^S.

Fish catches have increased in areas adjacent to a number of marine reserves (e.g., Russ and Alcala, 1999; Roberts et al., 2001; Gell and Roberts, 2003), and there is some evidence that an increased emigration of adult fish from inside reserves (spillover) may be a consequence of increased fish density in the reserves (Abesamis and Russ, 2005). We studied the effects of the possible spillover of adult fish from the reserve to the area open to fishing by simulating an increase of 10% and 20% in emigration rates, which is consistent with the colonization rates of new habitat by the gag (Lindberg et al., 2006x). We used the relationship $H = e^{F^A}$ (Gulland, 1969), where H is the proportion of adult fish caught during a year (annual fishing mortality). For both demographic models, we simulated increases in annual catches of 10% and 20% by increasing H correspondingly and computing S^A and λ^S.

2.7. Economic consequences of reserve establishment

We studied the economic implications of establishing a reserve that encompassed the shallow are and portions of the deep area over a 10-year planning horizon, which has been an adequate period for the recovery of grouper populations elsewhere (Chiappone et al., 2000; Russ and Alcala, 2003). For each fraction N of the deep area, we constructed 100 sets of 10 matrices for El Niño or La Niña that were randomly-selected according to the probability of occurrence of El Niño or La Niña years. For each set of matrices we calculated I, the net fishing revenue per m^2 over the planning horizon, as

$$I = \sum_{t=1}^{10} H_t \cdot D_t \cdot W \cdot p_t \tag{4}$$

where D_t is the number of adult fish per m^2, W is the mean weight of leopard grouper caught at the LBNP, and p_t is the price of 1 kg of fish in year t. We used average annual inflation to project the value of p in 2004 through the planning horizon. We calculated the expected net revenue over the planning horizon as the mean net revenue from the 100 sets of matrices, and compared the means corresponding to different reserve sizes using a Tukey test for multiple comparisons at the 5% significance level.

For SCUBA divers, the impact of reserve establishment on economic welfare was measured using Compensating Variation (CV),

$$CV_t = MP' \cdot (D_i - D_t), \tag{5}$$

where MP' is the marginal price of adult leopard groupers observed by divers per m^2, D_i is the number of adult fish per m^2 at the time of reserve establishment (assumed to be equal to the value for 2004), and D_t is the number of adult fish per m^2 expected at time t after reserve establishment. To compute MP', we divided the marginal price of leopard grouper per dive (US $0.60) by the approximate area observed by an average diver during a dive, 900 m^2 (Wielgus et al., 2003). For each set of 10

Deep reserve size	Two habitats			One habitat		
	E_c	$E_{0.10}$	$E_{0.20}$	E_c	$E_{0.10}$	$E_{0.20}$
0.0	0.953	0.947	0.942	0.830	0.817	0.805
0.1	0.962	0.954	0.947	0.841	0.824	0.811
0.2	0.971	0.962	0.954	0.853	0.834	0.819
0.3	0.982	0.971	0.963	0.867	0.845	0.828
0.4	0.994	0.982	0.972	0.884	0.858	0.838
0.5	1.007	0.994	0.982	0.903	0.874	0.850
0.6	1.022	1.006	0.993	0.926	0.892	0.865
0.7	1.039	1.021	1.006	0.952	0.912	0.881
0.8	1.057	1.036	1.020	0.981	0.936	0.899
0.9	1.077	1.053	1.035	1.014	0.963	0.921
1.0	1.099	–	–	1.051	–	–

Table 1 – Expected long-term population growth rate (λ^S) of leopard grouper for reserve sizes encompassing the shallow area and different fractions of the deep area at Carmen Island ("Deep reserve size")

Three levels of fish emigration rates from the reserve (spillover) were considered: E_c is the level expected if the reserve does not increase emigration rates; $E_{0.10}$ and $E_{0.20}$ are 10% and 20% increases in emigration rates, respectively. Estimates for a demographic model with two habitats are shown on the left side of the table, and estimates for a demographic model with a single habitat on the right side.

randomly-selected matrices of vital rates we calculated NC, the non-consumptive value per m² over the planning horizon, as

$$NC = \sum_{t=1}^{10} CV_t \cdot Y, \qquad (6)$$

where Y is the number of dives at Carmen Island during a year. The number of visitors in the LBNP has remained stable since the Park's establishment (R. López-Espinosa, LBNP Management Agency, personal communication), so we assumed that the annual number of dives at Carmen would remain constant over the 10-year planning horizon. We calculated the expected non-consumptive value over the planning horizon as the mean NC from the sets of matrices.

We estimated the total present value of leopard grouper per m² over the planning horizon as the sum of fishing net revenue (I) and the value of diving (NC), discounted with a 3% annual rate.

3. Results

Our simulations suggested that closing only the shallow area off Carmen Island to fishing would not lead to a sustainable leopard grouper population. For both demographic models, λ^S would be <1 even if the no-take reserve does not increase spillover (Table 1). For the two-habitat model, the minimum fraction of the deep area that would need to be closed to fishing to achieve a sustainable grouper population (in addition to closing the shallow area) is 50%, assuming no increases in spillover. With 10% and 20% increases in spillover, closing 60% and 70% of the deep area, respectively, would be required to achieve a sustainable population. For the single-habitat model, our results suggested that 90% of the deep area would need to be closed to fishing (in addition to the shallow area) assuming no increases in spillover, and that a no-take marine reserve protecting the entire leopard grouper population would be required to achieve sustainability if spillover increases by 10% or more (Table 1).

As expected, the economic benefits for fishers decrease with the size of a no-take reserve, while the benefits for divers increase (Figs. 4 and 5). For the two-habitat model, maximum

Fig. 4 – Mean discounted economic benefits per m² (with upper 95% confidence limits) of reserves encompassing the shallow area and different fractions of the deep area at Carmen Island for a 10-year planning horizon, for a model that considered two habitats for the leopard grouper. No increases in adult emigration rates from the reserve (spillover) are assumed. Means and confidence limits were obtained from 100 sets containing 10 randomly-selected matrices of vital rates for El Niño and La Niña years. Black bars are means of net revenue from commercial catches of leopard grouper; white bars are mean economic benefits to SCUBA divers (measured as Compensating Variation), and grey bars are means of the totals economic value (fishing and diving).
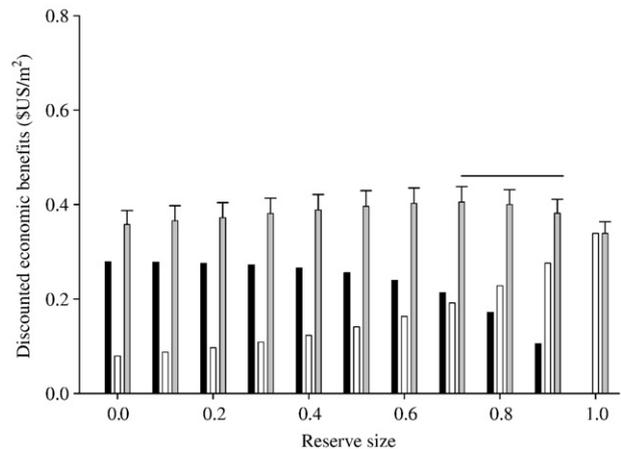
Fig. 5 – Mean discounted economic benefits per m² (with upper 95% confidence limits) of reserves encompassing different fractions of the deep area at Carmen Island for a 10-year planning horizon, for a model that considered a single habitat for the leopard grouper. No increases in adult emigration rates from the reserve (spillover) are assumed. The horizontal line joins reserve sizes with mean economic benefits that are not significantly different at the 5% significance level.

total benefits would occur at maximum reserve size (Fig. 4). For the single-habitat model, maximum total benefits occur at a reserve size encompassing the shallow area and 70%–90% of the deep area (Fig. 5).

4.   Discussion

We have illustrated an approach to study the ecological and economic effectiveness of a no-take marine reserve that takes into account existing ecological and economic information, and considers the use of the reserve by different stakeholder groups. Our results suggest that to ensure the persistence of leopard groupers at Carmen Island, and their use by commercial fishers and recreational divers, the shallow areas that contain spawning aggregations and between 50% and 100% of the adjacent deep areas should be closed to fishing. We found that maximum economic benefits would occur at closures of the shallow area and 70%–90% of the deep area. The high economic benefits from closing large portions of the area occur because of expected increases in the abundance of adult leopard grouper, which are an important attribute to SCUBA divers in the region.

A conservative management strategy would be to protect the entire leopard grouper population at Carmen Island from fishing. However, the local commercial fishers who traditionally catch this species at Carmen would lose part of their current income from fishing in the area. This issue of equity could in principle be tackled by capturing some of the willingness to pay for increased leopard grouper abundance by SCUBA divers (by means of increases in user fees, for example) to compensate fishers for their losses. In fact, the Kaldor–Hicks efficiency criterion would indicate that, with a reserve encompassing the entire leopard grouper population, the difference in the economic benefits of divers compared to the current situation (no protection) would be sufficient to potentially compensate fishers (Figs. 4 and 5). During informal conversations with one of this paper's authors (J. Wielgus), several fishers in Loreto indicated that, if provided with adequate training and technical advice, they would be willing to engage in economic activities that may provide more financial security than fishing. Capturing the increased consumer surplus of recreational divers may offer a means of financing the activities that are required to support the transfer of interested fishers to new productive endeavors, and this is an important topic that merits further research.

The enforcement of fishing regulations at the Loreto Bay National Park (LBNP) is problematic. The Park's Management Agency currently has only two boats for enforcement, hence enforcement is very poor and fishing on spawning aggregations using nets occurs commonly, despite being illegal. Enforcement would be facilitated if the shallow habitat is closed to all types of fishing, because observers on Carmen Island could easily detect boats that enter the shallow area, which extends only about 10 m offshore (Fig. 3). Similarly, a reserve that would encompass the shallow area and a fraction (or total) of the adjacent deep area would be easily enforced from Carmen Island.

Adaptive management (Holling, 1978; Walters and Hilborn, 1978; Walters, 1986) has been proposed as a management strategy for marine resources (Walters, 2000; Gerber et al., 2005; Grafton and Kompas, 2005). In adaptive management, the ecological and socioeconomic information that is available is used to generate policy options for resource management. Options that are predicted to yield the highest ecological and economic benefits are then applied throughout a trial period, and the observed responses of the ecological–economic system are used iteratively to improve management over time. Monitoring conducted after the trial period allows gaining insights on the response of the managed resource to the experimental management schemes. Adaptive management can be passive or active (Walters and Holling 1990). In passive adaptive management, a single management strategy is applied through a trial period, during which any additional information collected on the ecological–economic system is used to update the scientific models and to adapt the management strategy. In active adaptive management (reviewed in Grafton and Kompas 2005), an experiment is designed to test the results of a number of management strategies (e.g., reserves of different sizes and locations) over the trial period. Because of current budget and staff limitations that would preclude the monitoring of an experimental setup that included multiple reserves at the LBNP, we propose a passive adaptive management plan for the leopard grouper population at Carmen Island. This strategy would involve establishing a trial reserve at the Island and adjusting the size of the reserve as new ecological and economic information becomes available. A monitoring of grouper abundance would be conducted annually to evaluate the effects of the reserve. Additionally, any new ecological and economic information should be used to fine-tune the models that are used in the estimation of optimal reserve size. For the leopard grouper, this information may include rates of natural mortality and larval survival, which in our application had to be estimated using rates for other species.

A major impediment to employing adaptive management elsewhere has been the perception by managers that the implementation of trial policies is expensive and that it may put the managed resources at risk (Walters, 1997). Another problem with the implementation of adaptive management is the difficulty in convincing stakeholders that a trial approach to management will benefit their personal interests in the use of resources (Walters, 1997). However, nature reserves whose planning and management has included the needs and encouraged participation of local stakeholders have received support and compliance of regulations by the local communities (Russ and Alcala, 1999; Ludquist and Granek, 2005; Cash et al., 2007). The fishing communities in the LBNP have been involved actively in the management of the Park since its inception, and are likely to adhere to fishing closures at Carmen Island if the rationale for this proposed regulation is understood. Because fishing could be potentially allowed in the closed areas after the leopard grouper population recovers, fishers may perceive that the strategy of adaptive management takes their interests into consideration. From a manager's perspective, the lessons learned and information gathered with the adaptive management approach could be used to follow the recommendations in the Park's Management Plan to revise policy strategies so that they consider changes in the biological and socioeconomic conditions in the area (CONANP-SEMARNAT, 2002).

It is important to note that the economic value of reserves as potential "hedges" against uncertainty (reviewed in Grafton and Kompas, 2005) has not been contemplated in this paper. In a modeling study of the impact of marine reserves on net fisheries benefits, Grafton et al. (2006) have shown that in the presence of stochastic shocks to the population growth rate, marine reserves may generate economic benefits greater than those of other harvest-control mechanisms, even if they are applied to achieve bioeconomic optimality. In addition, research on the ecology of the leopard grouper at the LBNP would help to fill other significant knowledge gaps. For instance, the current abundance data for the LBNP is for depths of 5 and 20 m only. Although the leopard grouper is known to prefer relatively shallow areas (where most of the fishing is conducted), adult groupers have been observed at depths down to 50 m (Hobson, 1968). The management recommendations of the present study are limited to areas that encompass a maximum depth of 20 m, but future abundance surveys could help determine if fishing in deeper waters is significant and if it should be regulated.

Acknowledgements

REFERENCES

Abesamis, R.A., Russ, G.R., 2005. Density-dependent spillover from a marine reserve. Ecological Applications 15, 1798–1812.

Balmford, A., Gravestock, P., Hockley, N., McClean, C.J., Roberts, C.M., 2004. The worldwide costs of marine protected areas. Proceedings of the National Academy of Sciences of the United States of America 101, 9694–9697.

Bank of Mexico, 2006. National Consumer Price Index. Bank of Mexico, Mexico City. Available from http://www.banxico.org.mx/inpc/ (accessed April 2006).

Bolden, S., 2000. Long-distance movement of a Nassau grouper (Epinephelus striatus) to a spawning aggregation in the central Bahamas. Fishery Bulletin 98, 642–645.

Carter, J., Marrow, G.J., Pryor, V., 1994. Aspects of the ecology and reproduction of Nassau grouper Epinephelus striatus off the coast of Belize, Central America. Proceedings of the Gulf and Caribbean Fisheries Institute. Gulf and Caribbean Fisheries Institute, Charleston, South Carolina, pp. 65–111.

Cash, D.W., Clark, W.C., Alcock, F., Dickson, N.M., Eckley, N., Guston, D.H., Jäger, J., Mitchell, R.B., 2007. Knowledge systems for sustainable development. Proceedings of the National Academy of Sciences of the United States of America, 100, pp. 8086–8091.

Caswell, H., 2001. Matrix Population Models: Construction, Analysis, and Interpretation, 2nd edition. Sinauer Associates, Sunderland, Massachusetts, U.S.A.

Chiappone, M., Sluka, R., Sullivan Sealey, K., 2000. Groupers (Pisces: Serranidae) in fished and protected areas of the Florida Keys, Bahamas and northern Caribbean. Marine Ecology Progress Series 198, 261–272.

Cohen, J.E., Christensen, S.W., Goodyear, C.P., 1983. A stochastic age-structured population model of striped bass (Morone saxatilis) in the Potomac River. Canadian Journal of Fisheries and Aquatic Sciences 40, 2170–2183.

CONANP-SEMARNAT (Comisión Nacional de Areas Naturales Protegidas), 2002. Management Program-Loreto Bay National Park, 2nd edition. CONANP, Mexico City. (in Spanish).

Cowen, R.K., Paris, C.B., Srinivasan, A., 2006. Scaling of connectivity in marine populations. Science 311, 522–527.

Gaylord, B., Gaines, S.D., Siegel, D.A., Carr, M.H., 2005. Marine reserves exploit population structure and life history in potentially improving fishing yields. Ecological Applications 15, 2180–2191.

Gell, F.R., Roberts, C.M., 2003. Benefits beyond boundaries: the fishery effects of marine reserves and fishery closures. Trends in Ecology and Evolution 18, 448–455.

Gerber, L.R., Beger, M., McCarthy, M.A., Possingham, P.P., 2005. A theory for optimal monitoring of marine reserves. Ecology Letters 8, 829–837.

Grafton, R.Q., Kompas, T., 2005. Uncertainty and the active adaptive management of marine reserves. Marine Policy 29, 471–479.

Grafton, R.Q., Kompas, T., Von Ha, P., 2006. The economic payoffs from marine reserves: resource rents in a stochastic environment. Economic Record 82, 469–480.

Guenette, S., Pitcher, T.J., 1999. An age-structured model showing the benefits of marine reserves in controlling overexploitation. Fisheries Research 39, 295–303.

Gulland, J.A., 1969. Manual of Methods for Fish Stock Assessment. FAO Manuals in Fisheries Science No. 4. FAO, Rome.

Gutiérrez-Barreras, J.A., 2001. Marine and Coastal Report for the Municipality of Loreto, Baja California Sur, Mexico. Grupo Ecológico Antares, Loreto, Baja California Sur, Mexico. (in Spanish).

Harmelin-Vivien, M.L., Harmelin, J.G., Chauvet, C., Duval, C., Galzin, R., Lejeune, P., Barnabé, G., Blanc, F., Chevalier, R., Duclerc, J., Lasserre, G., 1985. Visual assessment of fish populations: methods and problems. Revue d'Ecologie (Terre Vie) 40, 467–539 (in French).

Harris, P.J., Wyanski, D.M., White, D.B., Moore, J.L., 2002. Age, growth, and reproduction of scamp, Mycteroperca phenax, in the southwestern North Atlantic, 1979–1997. Bulletin of Marine Science 70, 113–132.

Heemstra, P.C., Randall, J.E., 1993. Groupers of the World (Family Serranidae, Subfamily Epinephelinae). Food and Agriculture Organization, Rome.

Heppell, S.S., Heppell, S.A., Coleman, F.C., Koenig, C.C., 2006. Models to compare management options for a protynous fish. Ecological Applications 16, 238–249.

Heyde, C.C., Cohen, J.E., 1985. Confidence intervals for demographic projections based on products of random matrices. Theoretical Population Biology 27, 120–153.

Hobson, E.S., 1968. Predatory behavior of some shore fishes in the Gulf of California. Research Report 73. U.S. Fish and Wildlife Service. Bureau of Sport Fisheries and Wildlife, Washington, D.C.

Holling, C.S. (Ed.), 1978. Adaptive Environmental Assessment and Management. Wiley, New York, New York.

Lauck, T., Clark, C.W., Mangel, M., Munro, G.R., 1998. Implementing the precautionary principle in fisheries management through marine reserves. Ecological Applications 8, S72–S78.

Lindberg, W.J., Frazer, T.K., Portier, K.M., Vose, F., Loftin, J., Murie, D.J., Mason, D.M., Nagy, B., Hart, M.K., 2006. Density-dependent habitat selection and performance by a large mobile reef fish. Ecological Applications 16, 731–746.

Ludquist, C.J., Granek, E.F., 2005. Strategies for successful marine conservation: integrating socioeconomic, political, and scientific factors. Conservation Biology 19, 1771–1778.

Morris, W.F., Doak, D., 2002. Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis. Sinauer Associates, Inc., Sunderland, Massachusetts.

Morris, A.V., Roberts, C.M., Hawkins, J.P., 2000. The threatened status of groupers (Epinephelinae). Biodiversity and Conservation 9, 919–942.

Nemeth, R.S., 2005. Population characteristics of a recovering U.S. Virgin Islands red hind spawning aggregation following protection. Marine Ecology Progress Series 286, 81–97.

Quinn, T.J., Deriso, R.B., 1999. Quantitative Fish Dynamics. Oxford University Press, New York.

Roberts, C.M., Bohnsack, J.A., Gell, F., Hawkins, J.P., Goodridge, R., 2001. Effects of marine reserves on adjacent fisheries. Science 294, 1920–1923.

Roberts, C.M., McClean, C.J., Veron, J.E.N., Hawkins, J.P., Allen, G.R., McAllister, D.E., Mittermeier, C.G., Schueler, F.W., Spalding, M., Wells, F., Vynne, C., Werner, T.B., 2002. Marine biodiversity hotspots and conservation priorities for tropical reefs. Science 295, 1280–1284.

Russ, G.R., Alcala, A.C., 1999. Management histories of Sumilon and Apo marine reserves, Philippines, and their influence on national marine resource policy. Coral Reefs 18, 307–319.

Russ, G.R., Alcala, A.C., 2003. Marine reserves: rates and patterns of recovery and decline of predatory fish: 1983–2000. Ecological Applications 13, 1553–1565.

Sala, E., Aburto-Oropeza, O., Paredes, G., Parra, I., Barrera, J.C., Dayton, P.K., 2002. A general model for designing networks of marine reserves. Science 298, 1991–1993.

Sala, E., Aburto, O., Paredes, G., Thompson, G., 2003. Spawning aggregations and reproductive behavior of reef fishes in the Gulf of California. Bulletin of Marine Science 72, 103–121.

Sanchirico, J.N., Wilen, J.E., 2001. A bioeconomic model of marine reserve creation. Journal of Environmental Economics and Management 42, 257–276.

Stamieszkin, K., Wielgus, J., Gerber, L.R., in review. Management of a marine protected area for sustainability and conflict resolution: lessons from Loreto Bay National Park (Baja California Sur, Mexico). Marine Policy.

Thomson, D.A., Findley, L.T., Kerstitch, A.N., 2000. Reef Fishes of the Sea of Cortez: The Rocky Shore Fishes of the Gulf of California. The University of Texas Press, Austin, Texas.

Walters, C.J., 1986. Adaptive Management of Renewable Resources. McMillan, New York, New York.

Walters, C.J., 1997. Challenges in adaptive management of riparian and coastal ecosystems. Conservation Ecology [online]1(2):1. Available from the Internet. URL: http://www.consecol.org/vol1/iss2/art1/.

Walters, C.J., 2000. Impacts of dispersal, ecological interactions, and fishing effort dynamics on efficacy of marine protected areas: how large should protected areas be? Bulletin of Marine Science 66, 745–757.

Walters, C.J., Hilborn, R., 1978. Ecological optimization and adaptive management. Annual Review of Ecology and Systematics 9, 157–188.

Walters, C.J., Holling, C.S., 1990. Large scale management experiments and learning by doing. Ecology 71, 2060–2068.

Whiteman, E.A., Jennings, C.A., Nemeth, R.S., 2005. Sex structure and potential female fecundity in a *Epinephelus guttatus* spawning aggregation: applying ultrasonic imaging. Journal of Fish Biology 66, 983–995.

Wielgus, J., Chadwick-Furman, N.E., Zeitouni, N., Shechter, M., 2003. Effects of coral reef attribute damage on recreational welfare. Marine Resource Economics 18, 225–237.

Wielgus, J., Ballantyne IV, F., Sala, E., Gerber, L.R., 2007. Viability analysis of reef fish populations based on limited demographic information. Conservation Biology 21, 447–454.

Wielgus, J., Gerber, L.R., Sala, E., Bennett, J. in review. Including information risk in stated preference surveys: a choice experiment on recreational attributes. Journal of Environmental Management.

Willis, T.J., Millar, R.B., 2005. Using marine reserves to estimate fishing mortality. Ecology Letters 8, 47–52.