Viability Analysis of Reef Fish Populations Based on Limited Demographic Information

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Abstract: *Marine protected areas (MPAs) that allow some degree of artisanal fishing have been proposed to control the overexploitation of marine resources while allowing extraction by local communities. Nevertheless, the management of MPAs is often impaired by the absence of data on the status of their resources. We devised a method to estimate population growth rates with the type of data that are usually available for reef fishes. We used 7 years of spatially explicit abundance data on the leopard grouper (*Mycteroperca rosacea*) in an MPA in the Gulf of California, Mexico, to construct a matrix population model that incorporated the effects of El Niño/La Niña Southern Oscillation on population dynamics. An environmental model that estimated different demographic estimates for El Niño and La Niña periods performed better than a single-environment model, and a single-habitat model performed better than a model that considered different depths as different habitats. Our results suggest that the population of the leopard grouper off the main island of the MPA is not viable under present conditions. Although the impact of fishing on leopard grouper populations in the MPA has not yet been established, fishing should be closed as a precautionary measure at this island if a priority of the MPA is to ensure the sustainability of its fish populations.*

Keywords: El Niño, environmental variability, Gulf of California, marine protected areas, matrix population models, *Mycteroperca*, population viability analysis, reef fish

Análisis de la Viabilidad de Poblaciones de Peces Arrecifales con Base en Información Demográfica Limitada

Resumen: *Las áreas marinas protegidas (AMP) que permiten cierto grado de pesca artesanal han sido propuestas para controlar la sobreexplotación de recursos marinos mientras permiten la extracción por parte de comunidades locales. Sin embargo, el manejo de AMP a menudo es obstaculizado por la ausencia de datos sobre el estatus de sus recursos. Diseñamos un método para estimar las tasas de crecimiento poblacional con el tipo de datos que generalmente están disponibles para peces arrecifales. Utilizamos datos espacialmente explícitos de la abundancia de* Mycteroperca rosacea *durante 7 años en un AMP en el Golfo de California, México, para construir un modelo poblacional matricial que incorporó los efectos de la Oscilación Sureña de El Niño/La Niña sobre la dinámica poblacional. Un modelo ambiental que evaluó diferentes estimaciones demográficas para períodos de El Niño y La Niña funcionó mejor que un modelo para un solo ambiente, y un modelo para un solo hábitat funcionó mejor que uno que consideró diferentes profundidades como hábitats diferentes. Nuestros resultados sugieren que la población de* M. rosacea *cercana a la isla principal del AMP no es viable bajo las condiciones actuales. Aunque no se ha establecido el impacto de la pesca sobre las poblaciones de* M. rosacea *en el AMP, se debe vedar la pesca en esta isla como una medida precautoria si una prioridad del AMP es asegurar la sustentabilidad de sus poblaciones de peces.*

Palabras Clave: análisis de viabilidad poblacional, áreas marinas protegidas, El Niño, Golfo de California, modelos poblacionales matriciales, *Mycteroperca*, peces arrecifales, variabilidad ambiental

Introduction

Overfishing has depleted stocks of marine species worldwide (Hutchings 2000; Jackson et al. 2001), and marine-protected areas (MPAs) have been advocated to avert the decline of vulnerable species (Johannes 1998; Dayton et al. 2000). Some MPAs ban all fishing activities and may lead to social conflicts when coastal communities are deprived of traditional resources (Russ & Alcala 1999; Agardy et al. 2003). In other instances MPAs allow fishing with traditional methods to continue (Russ & Alcala 1999), but the effects of the continued extraction of resources generally are not considered.

For both conservation and economic purposes, it is essential to understand and forecast population dynamics of species of conservation concern. Nevertheless, even the simplest demographic models that are commonly used in terrestrial conservation biology have seldom been applied in marine systems (but see Crouse et al. 1987). The estimation of population parameters for marine species is particularly challenging in light of their complex life histories, in which habitat changes occur in different life stages (Gerber et al. 2005). For example, in many fish species, larval stages occur in the plankton, and juvenile and adult stages are demersal or benthic. For these reasons the management of MPAs has been constrained by a paucity of the biological information required for population assessments (Micheli et al. 2004; Sale et al. 2005). Marine scientists and managers are often faced with the challenge of developing management and monitoring strategies without information on the population dynamics of species of concern (Agardy 2000).

The field of demography has grown in sophistication (reviewed in Fieberg & Ellner 2001) and potentially offers novel approaches to making the best use of the limited data typically available for marine species. We developed a matrix population model to conduct a population viability analysis (PVA) on the leopard grouper (*Mycteroperca rosacea* [Streets, 1877]) in Loreto Bay National Park (Gulf of California, Mexico) based on density data from multiple sites. We used the results to inform fisheries management and conservation decisions and to show how limited demographic data may be used as an additional tool for the management of MPAs.

Methods

Study System

The Loreto Bay National Park (LBNP) is located in the southwestern Gulf of California (Fig. 1). It covers an area of 2066 km^2, of which 88% is marine and 12% constitutes land masses varying in area from a 151-km^2 island (Carmen) to islets of a few square meters (CONANP-SEMARNAT 2002). The LBNP was established in 1996 by
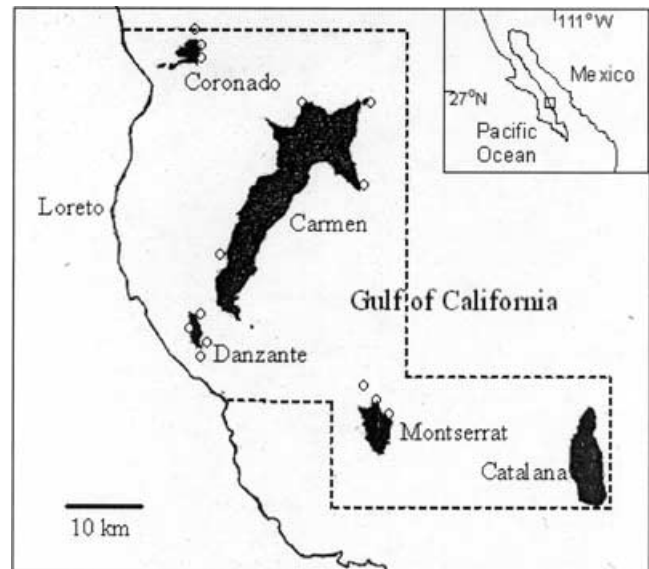

Figure 1. Location of Loreto Bay National Park (inset) and the four study sites: Carmen, Coronado, Danzante, and Montserrat. Transect locations are marked with circles. The park's limits (dashed lines) and the town of Loreto are also shown.

the Mexican federal government to protect marine resources in Loreto Bay from industrial trawling and seining. Hook-and-line fishing for subsistence, commercial, and recreational purposes is still permitted throughout the park (CONANP-SEMARNAT 2002). Fishing by local communities has increased public support for the park, but the intensity of fishing and its impacts on fish populations have not been studied. The LBNP harbors a variety of marine habitats including mangroves, rocky reefs, vertical walls, sandy bottoms, black coral beds, and rhodolith beds. The park contains 40% of all marine species in the Gulf of California, including threatened species of groupers, sea lions, and cetaceans. The park adjoins several towns, the biggest of which is Loreto (population 12,000). An estimated 70% of the area's working population is employed in the tourism sector, whereas 10% fish for a living (CONANP-SEMARNAP 2002). The town of Loreto attracts international visitors to its well-preserved colonial architecture, world-renowned sport fishing, whale watching, SCUBA diving, golfing, and surrounding desert landscape.

The leopard grouper (*Cabrilla sardinera*) is one of the most important fishery resources in the southern Gulf of California (Díaz-Uribe 2001). Its distribution is restricted to shallow areas between western continental Mexico and southern Baja California. The species matures (Heemstra & Randall 1993) and is targeted by fishers (E. Sala, personal observation) starting at approximately 35 cm total

length (TL), and the species can reach 1 m TL. The leopard grouper is one of the slowest growing of all the serranids (Díaz-Uribe et al. 2001) and reproduces in spawning aggregations that are easily targeted by fishers (Sala et al. 2003). It has been classified as a vulnerable species by the World Conservation Union (Morris et al. 2000).

Fish Surveys

We recorded the abundance of juvenile and adult leopard groupers on rocky bottoms at depths of 5 and 20 m off the islands of Carmen, Coronado, Danzante, and Montserrat (Fig. 1) between September 1998 and September 2004. We chose depths of 5 and 20 m because a previous analysis (Sala et al. 2002) showed that these depths harbor communities with significantly different structure (species abundance) in the Gulf of California. Three or four sampling sites were located randomly off each island within the areas known to harbor rocky reefs of sufficiently large size to allow replicate transects. In September of each year between four and six 50×5 m transects were sampled at each site and depth. Fish density (number of fish per transect) was quantified with a visual belt-transect method (Harmelin-Vivien et al. 1985). On every transect a SCUBA diver randomly selected a starting point and while swimming in a linear direction unreeled a 50-m measuring tape and recorded the abundance and TL (to the nearest 5 cm) of all leopard groupers within 2.5 m of each side of the tape.

Demographic Model

Our demographic model included two distinct life stages of the leopard grouper: fish 5–35 cm (juveniles and subadults, hereafter referred to as juveniles) and fish >35 cm (adults). We considered interisland movements of juvenile and adult fish negligible or nonexistent because postsettlement patterns of size structure are different across the islands studied at the LBNP (F.B. et al., unpublished data). This variability in size structure appears to imply distinct population and recruitment dynamics at each island, which is also supported by observations that the leopard grouper is always found close to shore and rarely deeper than 46 m (Hobson 1968; Thomson et al. 2000). It is difficult to determine limits among populations for species that inhabit continuous reef tracts, and abundance patterns cannot be used because of the intrinsic within-population heterogeneity in biomass associated with physical features such as bottom topography. Tagged Nassau groupers in the Caribbean migrate up to hundreds of kilometers in shallow waters on continuous reef tracts (Carter et al. 1994; Bolden 2000), but they appear not to migrate between islands over deep waters (E. S. et al., unpublished data). The islands of the LBNP are separated by deep water. It is possible that there are additional distinct populations isolated reproductively within large islands such as Carmen, but we do not have any evidence to help us identify these populations.

The abundance of a population at time $t+1$ can be written as:

$$\boldsymbol{n}_{(t+1)} = \mathbf{L}\boldsymbol{n}_{(t)},$$

where **L** is the projection matrix (see Caswell [2001] for a detailed description) and $\boldsymbol{n}$ is a vector of the studied stage classes. Because it is not known whether the 5 and 20 m depths are single or distinct habitats for the leopard grouper, we constructed a single habitat model that grouped juvenile and adult fish from both depths, and a "distinct habitat" model that considered fish densities at each depth independently. For the single habitat model we used the projection matrix

$$\mathbf{L} = \begin{bmatrix} P_J & F \\ G & P_A \end{bmatrix},$$

where A is adults and J is juveniles; P is the probability of surviving and remaining in the same stage, G is the probability of juveniles surviving and growing to adults, and F is the number of juveniles produced per adult fish. Our model assumed that demographic parameters were density independent.

For a two-habitat model **L** can be subdivided into submatrices that represented the population dynamics for the two habitats:

$$\mathbf{L} = \left[\begin{array}{c|c} I_1 & M_{1\to 2} \\ \hline M_{2\to 1} & I_2 \end{array} \right],$$

where I_1 and I_2 are individuals that remain in one habitat (1 or 2) between sampling periods and $M_{1\to 2}$ and $M_{2\to 1}$ are individuals that move between habitats. For the leopard grouper populations, the distinct-habitat matrix population model was

$$\left[\begin{array}{cc|cc} P_{J\,5} & F_5 & P_{J\,20\to 5} & F_{20\to 5} \\ G_5 & P_{A5} & G_{20\to 5} & P_{A20\to 5} \\ \hline P_{J\,5\to 20} & F_{5\to 20} & P_{J\,20} & F_{20} \\ G_{5\to 20} & P_{A5\to 20} & G_{20} & P_{A20} \end{array} \right].$$

We assumed that larvae, juveniles, and adults could move in both directions. Subscripts correspond to the 5 and 20 m depths, and arrows represent movements between depths. In this model F implicitly includes larval transport between depths.

Traditional PVAs rely on detailed biological studies to estimate the values for projection matrices. In the absence of this information, several inverse methods have been proposed for estimating projection-matrix parameters from abundance data (see Caswell [2001] for a review of these methods). The projection matrix **L** can be treated as a column vector $\boldsymbol{p}$ that contains unknown values of the demographic parameters. Changes in population size can be expressed as:

$$\mathbf{N}_{(t+1)} = \mathbf{N}_{(t)}\boldsymbol{p},$$

where **N** is a matrix that contains abundance data for all of the studied stage classes in the population. If $\mathbf{N}_{(t)}$ and $\mathbf{N}_{(t+1)}$ are known (e.g., from yearly abundance data), the values of $\boldsymbol{p}$ can be estimated by minimizing the sum of squared deviations between $\mathbf{N}_{(t+1)}$ and $\mathbf{N}_{(t)}\boldsymbol{p}$, that is, minimizing $\|\mathbf{N}_{(t+1)} - \mathbf{N}_{(t)}\boldsymbol{p}\|^2$ (Wood 1997). The problem is to minimize the squared deviations subject to any constraints imposed on the parameter estimates, and can be expressed as:

$$\text{minimize } \|\mathbf{N}_{(t+1)} - \mathbf{N}_{(t)}\boldsymbol{p}\|^2$$
$$= (\mathbf{N}_{(t+1)} - \mathbf{N}_{(t)}\boldsymbol{p})^{\mathrm{T}}(\mathbf{N}_{(t+1)} - \mathbf{N}_{(t)}\boldsymbol{p}),$$

or equivalently as

$$\text{minimize } (\mathbf{N}_{(t+1)})^{\mathrm{T}}\mathbf{N}_{(t+1)} - (\mathbf{N}_{(t+1)}^{\mathrm{T}}\mathbf{N}_{(t)}\boldsymbol{p})$$
$$-(\boldsymbol{p}^{\mathrm{T}}\mathbf{N}_{(t)}^{\mathrm{T}}\mathbf{N}_{(t+1)}) + (\boldsymbol{p}^{\mathrm{T}}\mathbf{N}_{(t)}^{\mathrm{T}}\mathbf{N}_{(t)}\boldsymbol{p}).$$

The first term is independent of $\boldsymbol{p}$, and can be ignored. The second two terms are identical, and the problem becomes

$$\text{minimize } 1/2(\boldsymbol{p}^{\mathrm{T}}\mathbf{N}_{(t)}^{\mathrm{T}}\mathbf{N}_{(t)}\boldsymbol{p}) - 2(\mathbf{N}_{(t+1)})^{\mathrm{T}}\mathbf{N}_{(t)}\boldsymbol{p}).$$

The objective function has a quadratic form and can be solved with quadratic programming procedures if its constraints are linear.

We estimated an upper limit for survival and fertility (*F*) values on the basis of available information for conspecifics of the leopard grouper. For survival we used estimates of natural mortality for juvenile (0.2) and adult (0.175) *Mycteroperca microlepis* (Heppell et al. 2006) to obtain an upper bound for survival probability (in the absence of fishing mortality) of 0.82 for juveniles and 0.84 for adults. For fertility we used values reported for *Mycteroperca phenax* (Harris et al. 2002), which is similar in size to the leopard grouper. We multiplied the average potential annual fecundity values for *M. phenax* (5,908,100 oocytes) by an estimate of the percentage of reef fish larvae that survive the pelagic stage and settle (0.0001% for snappers; Cowen et al. 2006), and divided this product by two to obtain an estimate for juvenile recruitment per adult fish (three juveniles). Preliminary studies on leopard grouper reproduction suggest that in contrast to other members of the genus, the leopard grouper does not undergo sex changes (N. Nash, personal communication). Thus, the sex ratio is 1:1 and is unlikely to deviate from parity in the face of fishing pressure, which selectively removes the larger males of species that are protogynous hermaphrodites (Beets & Friedlander 1998).

To constrain the parameter estimates, we constructed a matrix of zeros, ones, and minus ones (Fig. 2) such that its multiplication by $\boldsymbol{p}$ yielded non-negative values for all parameters and the following bounds on parameters associated with probabilities:

$$\begin{bmatrix} -1 & 0 & 0 & 0 \\ 0 & -1 & 0 & 0 \\ 0 & 0 & -1 & 0 \\ 0 & 0 & 0 & -1 \\ 1 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 \end{bmatrix} \begin{bmatrix} P_J \\ G \\ F \\ P_A \end{bmatrix} \leq \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \\ 0.82 \\ 0.84 \\ 3 \end{bmatrix}$$

Figure 2. Constraints for the quadratic optimization problem of the single-habitat demographic model for leopard grouper populations at Loreto Bay National Park. The expression restricts all parameter estimates to non-negative values and constrains estimates of juvenile survival (P_J and G) to a maximum of 0.82, adult survival (P_A) to a maximum of 0.84, and juvenile production per adult fish (F) to a maximum of 3.

$P_J + G \leq 0.82$ (single-habitat model)
$P_A \leq 0.84$ (single-habitat model)
$P_{J5} + G_5 + P_{J5\rightarrow20} + G_{5\rightarrow20} \leq 0.82$ (distinct-habitat model)
$P_{A5} + P_{A5\rightarrow20} \leq 0.84$ (distinct-habitat model)
$P_{J20\rightarrow5} + G_{20\rightarrow5} + P_{J20} + G_{20} \leq 0.82$ (distinct-habitat model)
$P_{A20\rightarrow5} + P_{A20} \leq 0.84$ (distinct-habitat model)

We solved the minimization problem subject to the constraints with the Optimization Toolbox of MATLAB 7.0 software (The Mathworks, Natick, Massachusetts). Model algorithms for solving quadratic programming problems are provided in various textbooks (e.g., Gill et al. 1981; Caswell 2001).

Inverse estimation methods lack a straightforward calculation of parameter uncertainty, which may be one reason why they have remained underutilized (we are not aware of previous applications to PVAs for marine fishes). Nevertheless, these methods are potentially valuable tools for estimating population growth rates (Caswell 2001), and advances in computer technology now permit the estimation of standard errors for demographic parameters by simulations in a relatively short period of time.

Environmental Models

Changes in the marine environment associated with El Niño/La Niña Southern Oscillation (ENSO) affect fish dynamics in the Gulf of California (F. B. et al., unpublished data). The multivariate ENSO index (MEI; Wolter & Timlin 1998) is a quantitative classification scheme that combines the most important component variables of ENSO for the tropical Pacific (30° S to 30° N). Positive values of MEI indicate the warm El Niño phase; negative values are indicative of the cool La Niña phase. Bimonthly values for

MEI are available from 1950 to the present (NOAA-CIRES 2005). Because our surveys took place in September of each year, we used MEI values running from September of 1 year to August of the next to estimate the average ENSO effect on the population between sampling periods.

Our study covered three consecutive periods with negative mean MEI (September 1998–August 2001) and three consecutive periods with positive mean MEI (September 2001–August 2004). For both the single-habitat and distinct-habitat models, we estimated a projection matrix for each of the periods and compared the performance, in terms of fitting the observed data on adult densities, of an "ENSO" model that combined these matrices to that of a "naïve" model in which environmental variation due to ENSO was ignored (density data for all periods were grouped and a single projection matrix was estimated). We chose the model that better predicted adult densities because adult fish are subject to extraction in the LBNP, and a good predictive model will be valuable in the management of their sustainable use. For each ENSO period we bootstrapped (Efron & Tibshirani 1986) 200 projection matrix replicates to estimate standard errors for the demographic parameters.

Population Growth Rates

We conducted a runs test (Sokal & Rohlf 1995) for values of MEI from 1950 to 2004 (periods from September of 1 year to August of the next year) to study the degree to which El Niño/La Niña periods occurred randomly. Over this time span, 30 periods (54.5%) had a positive mean MEI and 25 periods (45.5%) had a negative mean MEI. Our results ($u = 24$, $0.10 \leq p \leq 0.20$) indicated that these events were random, so an independent and identical distribution was chosen for the ENSO model, in which the probability of occurrence of an event is independent of the previous event (Caswell 2001). In a variable environment population growth rate can be represented by the stochastic growth rate, λ_s, which is the expected value of the population growth rate over a long period of time. We estimated the log of the stochastic growth rate as (Heyde & Cohen 1985):

$$\log \lambda_s = \frac{1}{T} \sum_{T=0}^{T-1} r_t,$$

where r_t is the log of the growth rate of the population during one period. The standard error of this estimator can be approximated as (Caswell 2001):

$$1.96\sqrt{\frac{var(r)}{T}},$$

where T is the length of the simulation. A value for T in the tens of thousands is recommended for accuracy (Caswell & Kaye 2001); we used $T = 100,000$. Our algorithm selected an initial projection matrix (El Niño or La Niña) according to the probability of occurrence of each event

(0.55 for El Niño and 0.45 for La Niña) and multiplied this matrix by the vector of initial fish densities to project the population to the following period. We used the densities of the latest survey (2004) for the initial vector. We estimated the expected fish densities in subsequent periods with the same method (with the vector of expected densities in the previous period as the initial vector) and computed r for each of the periods of the simulation.

Sensitivity Analysis

We studied the effects of possible larval connectivity between populations on the stochastic population growth rates and parameter estimates for each population. The pathways of larval dispersal of the leopard grouper are unknown, as are those of most groupers. Cowen et al. (2006) showed that in the Caribbean average dispersal distances for reef fishes are between 10 and 100 km. Nevertheless, the magnitude of dispersal is spatially heterogeneous. In Loreto, the islands are located <100 km apart from each other; hence, all islands may be connected via larval dispersal, although the range of this dispersal is unknown. Therefore, we assumed the following scenarios of larval connectivity. With our fertility estimate of three juveniles per adult as a basis, we considered the following scenarios and values of F: (1) a population is a "large" net exporter of larvae (40% of its larval production is exported, $F = 1.8$); (2) a population is a "small" net exporter of larvae (20% of its larval production is exported, $F = 2.4$); (3) a population is a "small" net importer of larvae (it retains all its larvae and imports an additional 20%, $F = 3.6$); (4) a population is a "large" net importer of larvae (it retains all its larvae and imports an additional 40%, $F = 4.2$).

Results

The ENSO environmental model fitted the observed data better than the naïve model for both the single-habitat and distinct-habitat demographic models (Table 1). The best performing combination of demographic and environmental models was the single-habitat, ENSO model

Table 1. Comparison of the performance of different models in fitting observed data (number of fish/250 m^2) on adult leopard grouper (*Mycteroperca rosacea*) in Loreto Bay National Park.[*]

Model	Slope	Intercept
Single habitat, naïve	0.182	0.398
Single habitat, ENSO	0.430	0.083
Distinct habitats, naïve	0.175	0.471
Distinct habitats, ENSO	0.413	0.289

[*]*The slope and intercept of the regression lines of observed versus predicted densities are shown. A model with perfect fit would have slope of 1 and intercept of 0. The single-habitat models considered depths of 5 and 20 m as one habitat whereas the distinct-habitat models estimated demographic parameters separately for the two depths.*
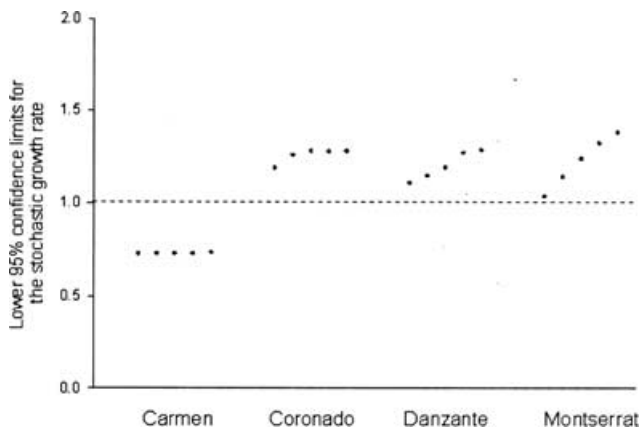
Figure 3. Lower 95% confidence limits for the stochastic (long-term) growth rate of four populations of leopard grouper at Loreto Bay National Park. For each population, points from left to right correspond to increasing numbers of juveniles per adult fish (see text for details). The dashed line represents a long-term growth rate of one and is the lower limit for a viable population.

(Table 1). With this model, the 95% confidence intervals for λ_s were above 1 at Coronado (1.283 ± 0.003), Danzante (1.191 ± 0.002), and Montserrat (1.241 ± 0.002), and below 1 at Carmen (0.730 ± 0.005). In the scenarios of potential larval connectivity that we considered, λ_s values generally increased with larval retention and net import, as expected (Fig. 3). However, the results did not differ from those of the base model ($F = 3$) in regards to the viability of the populations (Fig. 3).

The probability of surviving and remaining in the juvenile stage was greater for La Niña than El Niño periods in all populations (Table 2). Nevertheless, the probability of surviving and growing into adults was higher for El Niño than La Niña in Carmen, Coronado, and Danzante, and similar for both periods in Montserrat (0.263 in La Niña and 0.262 in El Niño). All the probabilities of surviving and growing into adults were relatively low, except for El Niño in Coronado (0.607). The number of juveniles per adult fish was similar for both periods in Coronado, Danzante, and Montserrat. In Carmen this parameter was relatively low for La Niña (0.218) and zero for El Niño. The probability of adult survival was higher for La Niña than El Niño in Carmen and Coronado (it was zero for El Niño in Carmen), equal for both periods in Danzante (0.840), and higher for El Niño than La Niña in Montserrat (0.766 and 0.336, respectively).

Discussion

We have proposed a new approach to estimating demographic rates for marine species based on limited data and have examined the consequences of making different as-

Table 2. Parameter estimates of projection matrices for four populations of leopard grouper (*Mycteroperca rosacea*) in Loreto Bay National Park for a model that assumed a single habitat and a different transition matrix for each of the periods of ENSO (El Niño/La Niña Southern Oscillation).[a]

	Parameter estimates	
Population	*La Niña periods (1998–2001)[b]*	*El Niño periods (2001–2004)*
Carmen	0.820 0.218 (0.032) (0.058) 0.054 0.271 (0.018) (0.016)	0.600 0.000 (0.013) (0.026) 0.190 0.000 (0.028) (0.005)
Coronado	0.820 2.711 (0.038) (0.124) 0.086 0.802 (0.007) (0.043)	0.120 2.239 (0.052) (0.094) 0.607 0.023 (0.014) (0.119)
Danzante	0.813 2.902 (0.025) (0.105) 0.007 0.840 (0.028) (0.024)	0.349 3.000 (0.019) (0.136) 0.151 0.840 (0.010) (0.026)
Montserrat	0.557 2.922 (0.074) (0.110) 0.263 0.336 (0.009) (0.014)	0.083 2.763 (0.003) (0.198) 0.262 0.766 (0.014) (0.038)

[a]*Bootstrap standard errors are in parentheses.*
[b]*Periods were classified as La Niña or El Niño according to the multivariate ENSO index (MEI) of Wolter and Timlin (1998). Surveys took place in September of each year. One part of 2001 (January–August) had negative mean bimonthly MEI and was classified as La Niña, and the other part (September–December) had positive mean bimonthly MEI and was classified as El Niño.*

sumptions about habitat structure and larval dispersal. We developed and implemented a single-habitat model and a model that considered the two depth strata as different habitats and found that the single-habitat model performed better. This result, coupled with the observation of juvenile leopard groupers at both depths could be an indication of a lack of ontogenetic shifts in the species.

Our models indicate that the long-term population growth rate of the leopard grouper at Carmen Island is <1. This result was robust for models that considered the Carmen Island population as a source or sink of larvae. For this population, adult survival was low during La Niña periods and zero during El Niño periods, and growth of juveniles into adults was relatively low for both periods. Low adult survival may indicate that at the end of an El Niño period, a small number of adults will remain in this population. For this population, adult survival is low during La Niña periods and zero during El Niño periods, and growth of juveniles into adults is relatively low for both periods. Low adult survival may indicate that at the end of an El Niño period there will be a small number of adults. Therefore, a precautionary approach to the management of the leopard grouper population at Carmen would be to close the island to fishing.

Grouper populations have recovered relatively quickly with the establishment of no-take reserves (Russ & Alcala 2003), so such a no-take area could be implemented as a temporary conservation measure. Nevertheless, the leopard grouper is a slow growing species, and recovery of the population may be slow even under a strict no-take regime. Continued monitoring of abundance would be necessary to determine when the population recovers to a level that would allow sustainable fishing, taking into account the environmental variability of the Gulf of California. Even after the population recovers, monitoring should continue in order to detect possible changes in abundance arising from unexpected changes in the environment and/or fishing pressure.

Although there are no data on the distribution of fishing effort among the islands of the LBNP, it is reasonable to assume that fishing intensity at Carmen Island is high due to its proximity to Loreto. High fishing intensity may explain the low probability of survival of adult leopard groupers at this island. Research is currently underway by the LBNP Management Authority to determine the distribution of fishing effort in the park (R. López-Espinosa, personal communication), and the results of this study will be valuable in the assessment of the impact of fishing on the leopard grouper populations in the park.

Higher values of juvenile survival for La Niña than El Niño periods in all populations concur with observations of increased abundance of juvenile leopard groupers during La Niña periods in different areas of the Gulf of California (O. Aburto-Oropeza et al., unpublished data). Temporal biological cycles not associated with ENSO and as yet not studied for the species could also help explain the differences in demographic parameters between populations that we observed. Specifically, differences in adult survival between islands are difficult to explain in the absence of data on particular environmental conditions experienced by each population during El Niño and La Niña periods. Further research on these variables (and on fishing mortality) may provide clues as to the observed differences in adult mortality.

The model we used in our estimations is not without caveats. Although we assumed that demographic parameters were density independent, the mortality of at least one serranid, *Epinephelus merra*, is density dependent (Letourner et al. 1998). Nevertheless, recently leopard grouper densities in the LBNP have been significantly lower than in nearby areas (E.S. et al., unpublished data), so density dependence is unlikely to influence our results. In situations in which it can be assumed that populations are at a relatively small size with respect to their carrying capacity, λ_s provides a useful metric to compare population growth across regions. This approach, however, may not be as robust for populations that are close to carrying capacity and thus may be density dependent because λ_s does not represent accurately population growth for matrices with nonlinear functions (Caswell 2001).

The average projection matrices that we estimated for each population reflect the average effects of environmental variability over long-time scales and therefore should not be used to make short-term population forecasts. Furthermore, the use of mathematical programming techniques, such as the one we illustrated here, guarantees a solution to inverse estimation problems that is optimal from a mathematical perspective. New computing technologies have made these techniques feasible by reducing computing times dramatically. However, optimization algorithms can sometimes fail to find solutions. Although we did not encounter this problem in our calculations, optimization algorithms involving complex constraining functions may be unsolvable with current methods (discussed in Pressey et al. 1996). Parameter estimation with inverse methods is based on fitting observed abundance data to a model and can produce estimates that are biologically unrealistic. Nevertheless, compared with other inverse estimation methods, quadratic programming has the advantage of allowing simple methods to constrain the parameters to feasible ranges or to known values from related species.

Direct methods to estimate demographic parameters, although expensive, yield more information and possibly more accurate predictions of population trends than inverse estimation procedures. For example, measuring natural mortality and fishing rates at each site at the LBNP would allow the estimation of the minimum monitoring needed to detect changes in population growth rates. When information on demographic parameters is lacking, indirect estimation models, such as the one we illustrated here, can provide useful guidelines for management. As biological data become available, restrictions on parameter estimates can be fine-tuned to increase the reliability of indirect estimation models.

In the absence of detailed demographical information, growth-rate estimates extracted from abundance data may provide guidance in conservation decision making. These assessments will be useful for the management of MPAs that lack resources to support wide-ranging biological surveys. Parallel analyses on a range of species of conservation concern could help determine whether more stringent regulations on fishing than the ones currently in place are warranted as precautionary measures in specific zones of MPAs.

Acknowledgments

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