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## PREDICTABILITY OF REEF FISH RECRUITMENT IN A HIGHLY VARIABLE NURSERY HABITAT

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**Abstract.** There has been a lengthy debate on whether the abundance of adult reef fishes depends on prerecruitment or postrecruitment processes; however, we still do not have the ability to predict the magnitude of local fish recruitment. Here we show that the success of the leopard grouper (*Mycteroperca rosacea*) recruitment in the Gulf of California, Mexico, is determined by the availability of nursery habitat, which in turn is strongly correlated to climate conditions. Observational and experimental studies showed that leopard grouper larvae recruit preferentially on shallow rocky bottoms with brown algal (*Sargassum* spp.) beds, and that abundance of recruits is determined by the availability of *Sargassum*. The biomass of *Sargassum* decreases linearly with an increase in the Multivariate El Niño Southern Oscillation (ENSO) Index (MEI; an index positively correlated with water temperature and negatively correlated with nutrient availability). We analyzed the relationship between the interannual variation of MEI and the recruitment of the leopard grouper using field estimates of abundance of juvenile groupers. Our results show that there is a nonlinear relationship between recruitment and the oceanographic climate, in that the density of recruits decreases exponentially with increasing MEI. The predictability of leopard grouper recruitment has important implications for fisheries management, since it could allow adaptive management without expensive stock assessment programs.

**Key words:** climate variability; groupers; Gulf of California; *Mycteroperca rosacea*; predictability; recruitment; *Sargassum*.

### INTRODUCTION

Fish population dynamics are strongly influenced by recruitment of larvae to nursery habitats or by recruitment of young individuals to adult populations. Interannual and interdecadal variability of the recruitment and spawning stock biomass of fish has been observed for many commercial species, such as herring, sardine, mackerel, salmon, and cod (Alheit and Hagen 1997, Dippner 1997, Mantua et al. 1997, Attrill and Power 2002, Platt et al. 2003). The particular life history of these pelagic and highly migratory species, some of which have short life spans and live in plankton-based food webs, makes their populations extremely sensitive to climate fluctuations. In fact, significant correlations have been found between environmental conditions and the variability in abundance of recruits and adults of these species, and environmental variation appears to be as important as changes in fishing intensity in determining the sizes of harvestable populations (Southward et al. 1988, Sharp and McLain 1993).

For reef fishes with narrow home ranges, climate variability has been considered only as a prerecruitment factor that has stochastic impacts on the survival of eggs and larvae during their pelagic stage (Robertson et al. 1993, Danilowicz 1997). However, the relative importance of pre- and postrecruitment processes (such as predation, competition, and habitat selection) has been subject to a lengthy debate regarding the unpredictability of recruitment (Hixon and Jones 2005, Sandin and Pacala 2005).

From a fisheries management perspective, the predictability of recruitment can be useful for forecasting future success of a fishery or as a method for explaining variation in fish stocks (Attrill and Power 2002), especially for highly priced fishes such as groupers (Koenig and Coleman 1998). Due to the typical low densities of larvae and recruits, as well as the cryptic nature of new settlers, we still do not have comprehensive recruitment analyses for commercially important groupers over multiple spatial and temporal scales. For this reason, explanations about temporal and spatial patterns of grouper abundance have been limited to postrecruitment factors (Levin and Grimes 2002), ignoring the consequences of climate variability in the management and conservation of grouper fisheries. Here we show that the number of larvae of the leopard

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grouper (*Mycteroperca rosacea*) that settle and survive to become adults is strongly correlated to the interannual climate variability and its effects on the availability of nursery habitat. In addition, we explore the implications of predicting recruitment for fisheries management.

#### METHODS

##### *Study species*

The leopard grouper, an endemic species of the Gulf of California, Mexico, grows up to 1 m in length and is the most abundant and intensely fished grouper in the region. The leopard grouper is distributed from Bahía Magdalena on the Pacific coast of Baja California throughout the Gulf from the northernmost rocky reefs (Rocas Consag) to southern Jalisco (Thomson et al. 2000). The leopard grouper is a top predator on rocky reefs in the Gulf of California from shallow habitats to deep seamounts 70 m in depth. Adult groupers feed on other fishes, and seasonally (between February and May–June) they attack schools of sardines (*Harengula thrysina*) and anchovies (*Cetengraulis mysticetus*) (Hobson 1968). Mature groupers form spawning aggregations between April and May on rocky habitats, mainly in offshore islands (Sala et al. 2003), and the larvae spend an average of  $24.3 \pm 3.6$  d (mean  $\pm$  SD) in the water column (O. Aburto-Oropeza, unpublished data).

##### *Study system*

We conducted our study on the major coastal habitats of the Gulf of California: boulders with seasonal brown algal beds (2–20 m depth), vertical walls (5–20 m), rhodolith beds (20–30 m), black coral beds (30–40 m), seamounts (25–40 m), sandy bottoms (5–30 m), and mangroves (0–2 m). Fields of boulders consist of boulders 0.5–2 m in diameter over rocky or sandy substrates. Shallow boulders are covered seasonally by several species of *Sargassum* (mainly *S. sinicola*). The growth of *Sargassum* in the central and southern parts of the Gulf starts from November through December, reaching its maximum growth and density in May and June. When the temperature increases in July, the fronds detach from the rocks and drift for several weeks (McCourt 1984, Espinoza-Avalos and Rodriguez-Garza 1989, Espinoza-Avalos 1990). *Sargassum* beds form a narrow belt along rocky shores on the west coast and part of the northeast coast of the Gulf of California. With a few exceptions, most walls extend vertically or very steeply ( $>60\%$ ) from the surface to no more than 30 m in depth. Walls are colonized by a high diversity of benthic suspension feeders such as gorgonians, hydroids, cup corals, sponges, tunicates, and bryozoans. Rhodoliths are free-living calcareous algae of the family Corallinaceae that grow up to 20 cm in diameter, forming fields of variable cover over soft bottoms. There are two main types of fields of rhodoliths in the Gulf of California: in shallow reefs with high water motion, and in deeper areas over horizontal substrata with strong

unidirectional currents (Foster et al. 1997). We studied the deeper rhodolith beds between 14 m and 20 m, where rhodoliths were the dominant organisms (up to 100% cover), with sparse free-living corals (Reyes-Bonilla et al. 1997). Fields of black coral investigated in this study are horizontal to gently sloped rocky and dead-shell substrata below 30 m, colonized by the black coral *Antipathes galapaguensis*. The black coral is the dominant species, and is in turn colonized by sponges, tunicates, bryozoans, and pterid molluscs. Seamounts are deeper offshore rocky reefs subjected to strong currents. The sessile fauna colonizing seamounts is similar to that of vertical walls, with abundant suspension feeders. Sandy bottoms are open seafloor sediments that cover great extensions between rocky habitats. Bivalves, crustaceans, worms, and burrowing echinoderms contribute to the biological complexity of soft-bottom seafloors. Mangrove forests are present in shallow and/or muddy bays or lagoons along the coast of Baja California. They are composed of three species of mangrove trees (*Rhizophora mangle*, *Laguncularia racemosa*, and *Avicennia germinans*), which are surrounded by wetland vegetation (*Salicornia subterminalis*, *S. bigelovii*, and *Batis maritima*). Because the Gulf of California is the northern limit of the distribution of mangroves in the Eastern Pacific, mangroves form small patches in a few isolated areas.

##### *Recruitment habitat distribution*

To determine habitat preferences for recruitment of leopard grouper, we collected data on abundance of recruits along the central and southern part of the Gulf of California. In September–November 1999 we conducted a Gulf-wide survey at 40 sites encompassing all habitats we have described (Fig. 1A). The seven habitat types were distributed among the 40 sites, as Fig. 2 shows in parentheses. Underwater surveys were carried out with scuba using standard underwater visual belt transect survey methods (Harmelin-Vivien et al. 1985). The authors were experienced at visually surveying fish assemblages and practiced at estimating fish lengths accurately (Aburto-Oropeza and Balart 2001, Sala et al. 2002). Six replicate  $50 \times 5$  m transects were surveyed at each location, except for the black coral beds where transects were  $30 \times 2$  m, and mangroves where transects were  $30 \times 1$  m. Transects were placed randomly on the substratum. Total length (TL) of leopard groupers was estimated to the nearest cm for juveniles ( $<10$  cm) and to the nearest 5 cm for subadults and adults ( $>10$  cm), with the help of a transparent plastic ruler. A diver swam each transect at a constant speed (about 15 min per transect), counting all leopard groupers and estimating their size within 2.5 m to either side of the center line for boulders, walls, rhodoliths, seamounts, and sandy bottoms ( $250\text{-m}^2$  transect area); and 1 m to either side for black coral beds ( $60\text{-m}^2$  transect area). For mangroves we surveyed the transects by swimming parallel to the roots and counting the fish 1 m inside the

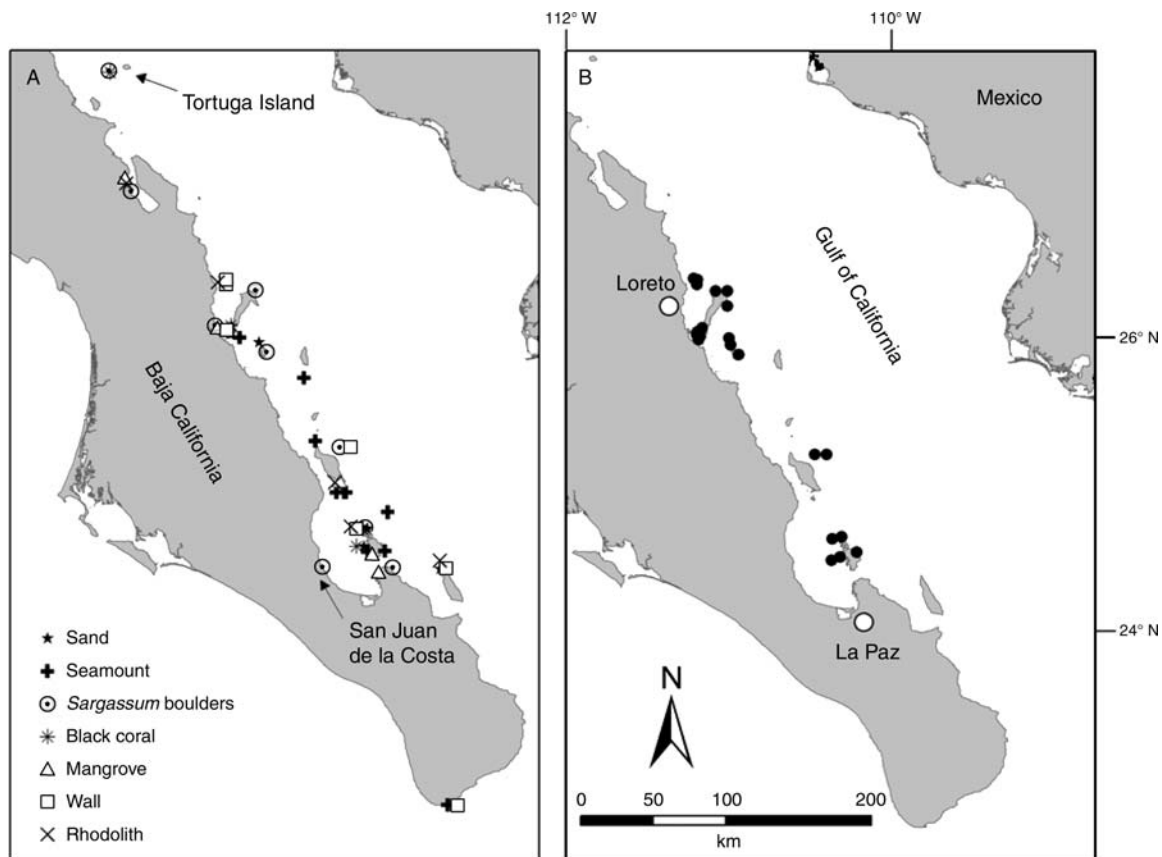


FIG. 1. Location of study sites for (A) recruitment habitat preferences of the leopard grouper, *Mycteroperca rosacea* (1999), and (B) interannual recruitment variability (1998–2004).

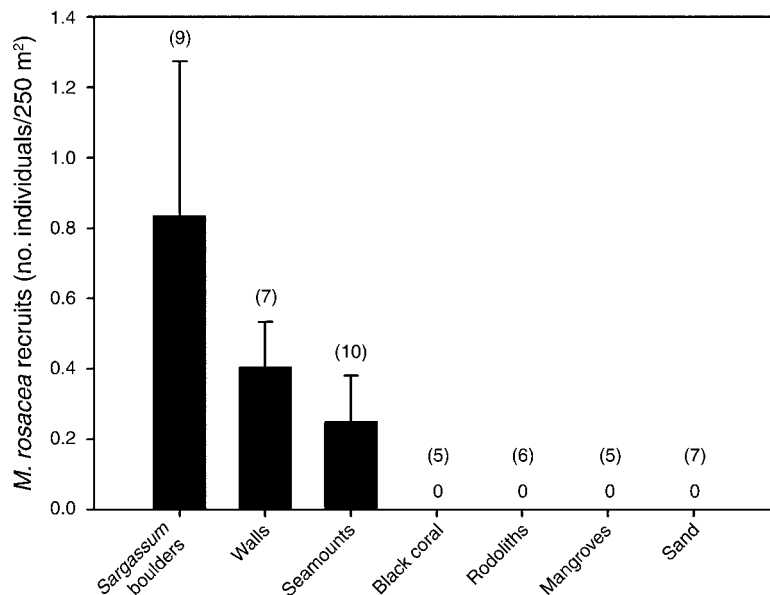


FIG. 2. Abundance (mean + SE) of *Mycteroperca rosacea* recruits in the seven major shallow habitats of the Gulf of California. The number of sampling sites per habitat is shown in parentheses.

prop roots (50-m<sup>2</sup> transect area). Following a Kolmogorov-Smirnov test for normality, log-transformed data were analyzed using ANOVA to test for differences in early postsettlement fish (<5 cm) between habitats.

Within the context of a larger project in the region, we conducted hundreds of dives in all habitats between the surface and 50 m depth throughout the Gulf of California between 1998 and 2000, and noted the presence of recruits of all sizes, from small postsettlers (~2 cm) to 15-cm recruits. In addition, in 1999 we monitored the abundance of recruits in boulders at Tortuga Island (Fig. 1A) on 15 June, 10 July, 27 August, and 10 October. We estimated the mortality of recruits over time by fitting the data to a power law function.

#### *Recruitment habitat experiment*

Given that boulders covered with *Sargassum* were the habitat with the greatest recruitment (see *Results*), we evaluated the effect of *Sargassum* cover on leopard grouper recruitment with an experiment at San Juan de la Costa, 60 km north of La Paz city (Fig. 1A). We built 25-m<sup>2</sup> artificial habitat patches that represented three treatments: boulders with *Sargassum* fronds, bare boulders, and boulders with artificial *Sargassum*. For each treatment we built five replicate patches placed 100 m away from the shoreline and 50 m from each other (Appendix A). Patches were built at the same depths where natural boulders with *Sargassum* occur (shallower than 5 m). The boulders used in the experiment were ~50 cm in diameter, which is the most common boulder size in this shallow habitat. The boulders with *Sargassum* fronds were transplanted from the natural substratum (Appendix B). The bare boulders were transplanted from the beach. The treatment of boulders with artificial *Sargassum* was made by attaching artificial *Sargassum* onto bare boulders. The artificial *Sargassum* was made out of shreds of brown and black large plastic trash bags (Appendix C). The shredded bags were attached to a grid made out of nylon monofilament lines. The density of the plastic bags was similar to that of *Sargassum* fronds. All patches were built from February to April 2000 and were monitored weekly from the second week of May until the last week of July. During each census, one of the authors (A. Mendoza) counted the total number of juveniles of leopard grouper on each patch and estimated their length in size classes of 1 cm. Due to the restricted movements of new settlers and their cryptic behavior, the diver conducted three separate counts per patch and used the highest count as the measure with the lowest probability of underestimating the abundance of recruits. Fish >7 cm were grouped in a single size class (7+). To test for differences between treatments we used ANOVA. Following a Kolmogorov-Smirnov test for normality, log-transformed data were analyzed using ANOVA to test for differences in recruit densities among treatments. Post hoc Tukey tests were used for comparisons of means.

#### *Recruitment habitat variability*

To determine the interannual variation of *Sargassum* spp. in the study area, we gathered biomass data from the literature (Muñeton 1987, Hernandez-Carmona et al. 1990, Casas-Valdez and Sanchez-Rodriguez 1992, Casas-Valdez et al. 1993, Nuñez-Lopez and Casas-Valdez 1997, Pacheco-Ruiz et al. 1998). A general methodology used in these studies is explained in Appendix D. We explored the relationship between the variability of *Sargassum* biomass and ocean conditions for several years (1985, 1987, 1988, 1991, 1992, 1995) using the Multivariate ENSO Index (MEI; NOAA-CIRES 2004) as a measure of climate variability.

El Niño Southern Oscillation (ENSO) is the major coupled ocean-atmosphere phenomenon in the Pacific Ocean and causes global climatic variability on annual time scales. MEI (Wolter and 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). MEI is a positive correlate of water temperature and a negative correlate of nutrient availability. El Niño years (warmer, nutrient-poor water) are associated with strong positive values of MEI, whereas La Niña years (colder, nutrient-rich water) are associated with strong negative values of this index. Bimonthly values for MEI are available from 1950 to the present (*available online*).<sup>5</sup>

#### *Leopard grouper recruitment variability*

To estimate the interannual variation in leopard grouper recruitment we carried out additional surveys in 21 sites on rocky bottoms (boulders and walls) that are covered seasonally with *Sargassum* (Fig. 1B). Surveys were conducted every September from 1998 to 2004, about three months after settlement, using the visual census methodology previously described (see *Methods: Recruitment habitat distribution*). Although we counted leopard groupers of all sizes, we included only individuals with a total length of <15 cm (young of the year) in this part of the study. Other species of groupers also recruit in vegetated habitats (e.g., the gag, *Mycteroperca microlepis*) where their abundance may be underestimated; thus a capture efficiency estimate is necessary to obtain accurate abundance values (Koenig and Coleman 1998). Our sampling was conducted in September, when all the seasonal *Sargassum* fronds are gone and juvenile groupers are conspicuous on the shallow bottoms covered with boulders; thus we believe our visual censuses provide accurate estimates of abundance. Note that by sampling three months after settlement, we are combining the signals of larval settlement and early postsettlement mortality and movement. Early postsettlement mortality of at least one species of grouper has been shown to be density

<sup>5</sup> ([http://www.cdc.noaa.gov/people/klaus.wolter/MEI/#ref\\_wt1](http://www.cdc.noaa.gov/people/klaus.wolter/MEI/#ref_wt1))

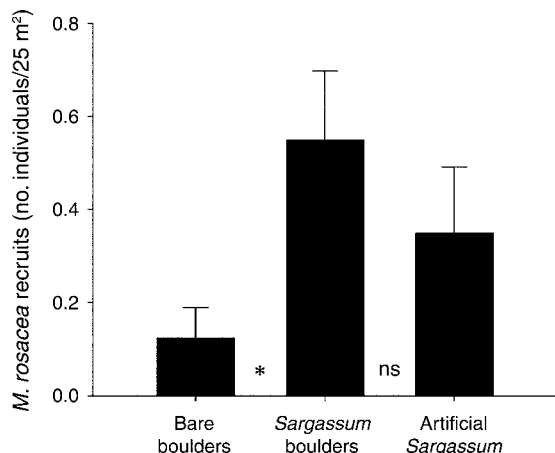


FIG. 3. Density (mean + SE) of *Mycteroperca rosacea* recruits in three experimental treatments ( $n = 5$  replicates per treatment).

\*  $P < 0.05$ ; ns, not significant.

dependent (Letourneur et al. 1998), and it seems likely that the strength of density dependence will vary with *Sargassum* cover (Anderson 2001). In any case, recruitment measured several months after settlement should be a reasonable indicator of subsequent recruitment to the adult population. We tested for correlation between leopard grouper recruitment and MEI using the mean MEI value for May–June for each year, which is the leopard grouper recruitment season.

RESULTS

Shallow boulders with *Sargassum* beds (<5 m depth) were the habitats with greater abundance of leopard

grouper recruits (ANOVA;  $F_{6,42} = 2.41$ ,  $P = 0.04$ ), although vertical walls and shallow seamounts also had recruits (Fig. 2). Our observations confirmed that these shallow habitats with seasonal growth of *Sargassum* were also the preferential settlement habitats. Leopard grouper settled preferentially during the peak *Sargassum* biomass (E. Sala, O. Aburto-Oropeza, G. Paredes, and S. Sandin, unpublished manuscript). We found postsetters (1.98 cm in length) among the *Sargassum* fronds, but did not find any postsettlement in any other habitat. After the *Sargassum* sloughed off the boulders in July, the juveniles sheltered between and beneath the boulders. Observations at Tortuga Island for three months after settlement in 1999 indicated that juvenile mortality within that period of time could be described as a power law with an instantaneous mortality rate of  $m = -0.885$  ( $R^2 = 0.98$ ). Recruit mortality was greatest during the *Sargassum* sloughing (92% mortality within the first month); since fronds detached in July until the time of our censuses in September, juvenile mortality was much lower (25% per month). We assume that during their first year postsettlement, juvenile leopard groupers in Tortuga island remained in subtidal boulders, because we did not find them in any other habitat.

The field experiment showed that recruitment of leopard grouper was five times greater in boulders with *Sargassum* than on bare boulders (ANOVA,  $F_{2,117} = 3.32$ ,  $P = 0.039$ ; Fig. 3). There were no significant differences in recruitment between *Sargassum* boulders and artificial *Sargassum* ( $P = 0.33$ ).

The biomass of *Sargassum* decreased linearly with increasing MEI ( $P = 0.02$ ,  $R^2 = 0.766$ ; Fig. 4). *Sargassum* biomass varied from 7.5 kg/m<sup>2</sup> in a cold year (1988) to 1.3 kg/m<sup>2</sup> in an El Niño year (1992).

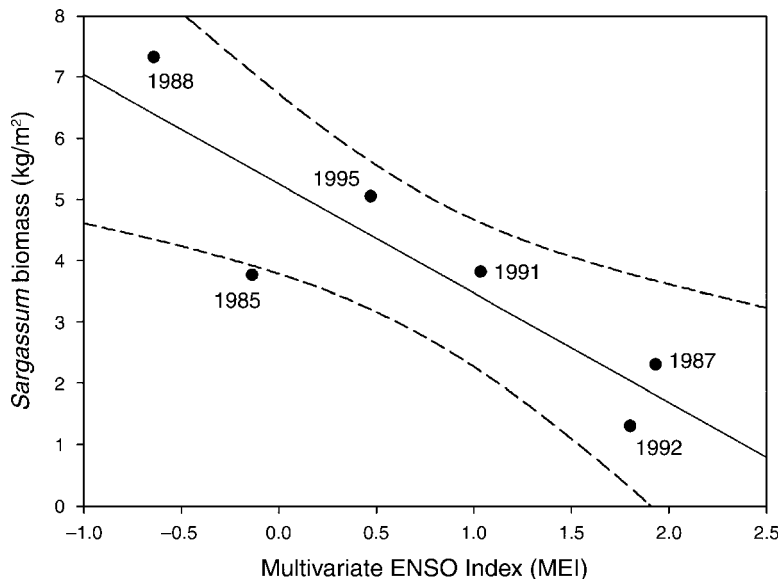


FIG. 4. Relationship between the Multivariate El Niño Southern Oscillation (ENSO) Index and mean *Sargassum* biomass in the central and southern Gulf of California. The solid line represents the model; the dashed lines show the 95% CI. Numbers by data points are years when *Sargassum* biomass was quantified (see Methods).

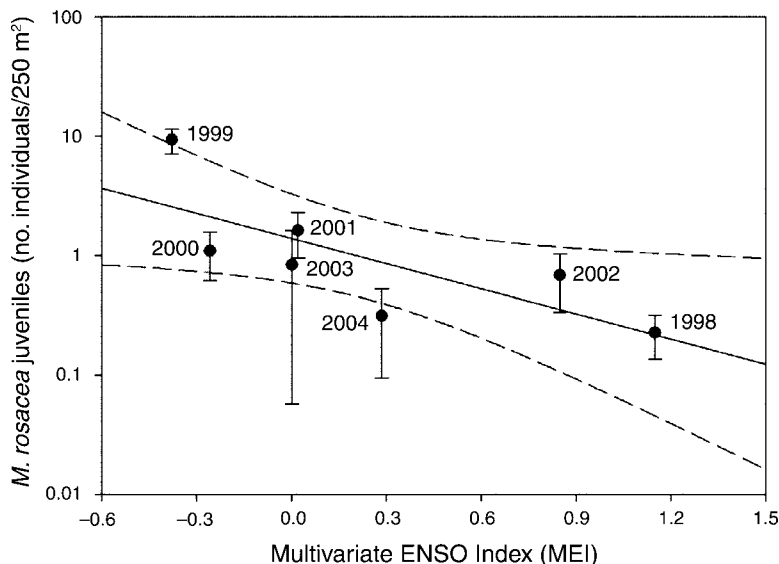


FIG. 5. Relationship between MEI and density of leopard grouper recruits (note the log scale) in the central and southern Gulf of California. Data are means  $\pm$  SE;  $n = 21$  sites/yr. The solid line represents the model; the dashed lines show the 95% CI. Numbers are years when surveys were conducted (see *Methods*).

The density of leopard grouper recruits decreased exponentially with increasing MEI ( $P = 0.052$ ,  $R^2 = 0.563$ ; Fig. 5). The difference in recruitment between El Niño (warmer, nutrient-poor water) and La Niña (colder, nutrient-rich water) conditions spanned two orders of magnitude. El Niño years had extremely low recruitment, whereas La Niña years had recruitments greater than one recruit/250 m<sup>2</sup>.

Our results show that variability in recruitment affects population structure in a pluriannual basis. The large recruitment peak of 1999 was preserved in the size structure of the population for several years, until individuals reached commercial size in approximately 2002 (Fig. 6).

DISCUSSION

Our surveys throughout the Gulf of California showed that several months after settlement, leopard grouper recruits were found mostly on subtidal boulders covered seasonally with the brown alga *Sargassum*. In addition, our field experiment showed that recruitment of the leopard grouper was positively related to the availability of the suitable nursery habitat, i.e., *Sargassum* beds. The biomass of *Sargassum*, in turn, appeared to be determined by climatic variation. El Niño years are associated with warmer waters and depleted nutrients (Dayton et al. 1999), which are known to impair the growth of macroalgae. In Southern California, El Niño conditions cause dramatic reductions in the biomass of the giant kelp *Macrocystis pyrifera* because of the combination of high temperature and low nutrient concentration; colder years (such as La Niña years), in contrast, enhance algal growth (Dayton et al. 1992, 1999). A similar mechanism appears to explain the

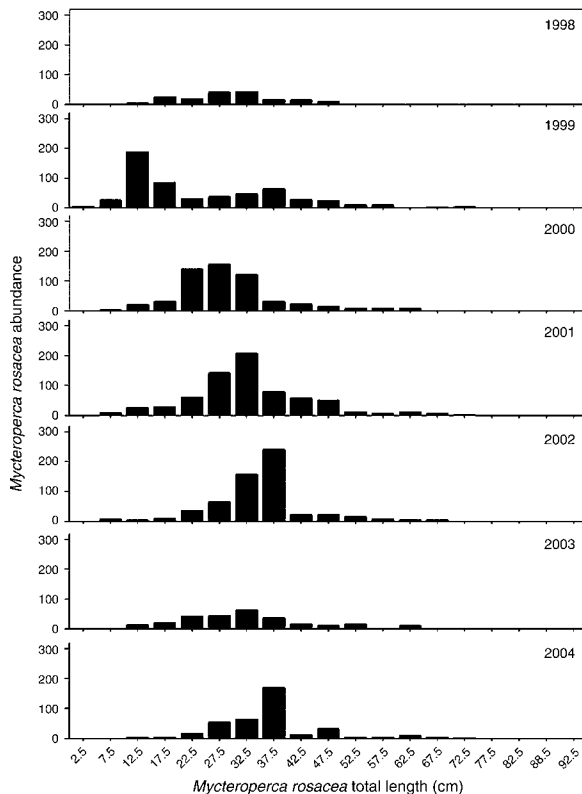


FIG. 6. Size frequency distribution of the leopard grouper population in the Gulf of California. Data represent all size measurements conducted yearly at all study sites. Histogram bars represent size class ranges with the tick marks and scale numbers at the midpoints of the ranges.

fluctuations in the biomass of *Sargassum* in the Gulf of California, reflected in changes in phenology and reproductive condition of the plants due to variation in seawater temperature and nutrient content (McCourt 1984, 1985).

Other sources of variability in nutrient concentrations in seawater, such as eutrophication from anthropogenic sources or runoff, can be considered negligible in the study region. The western side of the Gulf of California, which encompasses >1000 km of coastline that the leopard grouper inhabits, is a desert with no permanent watercourses and only one large coastal town. The only potential source of anthropogenic runoff is a phosphate mine in San Juan de la Costa. From 1980 to 2001 this phosphate mine (Roca Fosforica Mexicana S.A.) produced up to 7500 Mg/d of *fosforita* rocks. The company installed a water treatment plant on the shore to clean up the brackish well water, and built a continuous berm to isolate waste areas from the ocean. We have insufficient information to suggest whether any external nutrient input affected our experiment as a result of the normal operations of the mine, although the possibility remains that nutrient input may have occurred during hurricanes in September 1998 (Isis) and in October 2001 (Juliette), the latter of which destroyed the mine. Our experiment, however, showed that the presence of *Sargassum* or artificial *Sargassum* clearly determined the abundance of recruits relative to unvegetated plots in the same location. In addition, in spite of the mining operation, the cover of *Sargassum* showed marked interannual fluctuations correlated to MEI, suggesting that the regional oceanographic climate is more important in determining *Sargassum* cover than the potential effects of the mine. We thus assume the phosphate mine had negligible effects on the results presented in this study.

Different theories of interannual variability in biological systems have tried to explain the link between recruitment success and climate (Dippner 1997). Other fishes, including flatfish species, clupeids, mackerel, salmon, and gadoids have similar relationships with climatic events such as the North Atlantic Oscillation (Dippner 1997, Attrill and Power 2002) and the Pacific Interdecadal Oscillation (Mantua et al. 1997). In our study system, there is a linear relationship between MEI and *Sargassum* biomass and a nonlinear relationship between MEI and leopard grouper recruitment. This suggests that either there is a nonlinear relationship between *Sargassum* biomass and leopard grouper recruitment or that there are other factors involved in determining recruitment. For instance, the conditions that inhibit the growth of *Sargassum*, such as high temperature and low nutrient concentration, may also enhance mortality of leopard grouper larvae during their pelagic stage. In other words, does recruitment vary due to the influence of environmental conditions on the transport and/or survival of larvae, or is larval supply constant but habitat limiting in certain years? We do not

have data about the larval stage of leopard grouper, but we have considered two possible scenarios. (1) The abundance of fish year classes could be determined by food availability during the critical period of larval development (Platt et al. 2003). Since El Niño years have a strong impact on macrozooplankton biomass (Lynn et al. 1998), we can hypothesize that there are high mortality rates of leopard grouper larvae by reduction of food availability. In this scenario, *Sargassum* cover can be considered an additive effect in the failure of recruitment in El Niño years and the last bottleneck determining the total density of recruits. (2) In El Niño years, the offshore waters of Baja California exhibit patterns opposite to those found in coastal waters, increasing the chlorophyll and primary production (Kahru and Mitchell 2000, 2002). If leopard grouper larvae are also distributed offshore, then there could be little or no effect of El Niño conditions on larval survivorship and delivery to the benthos. In this scenario, *Sargassum* variability could be the major factor in determining leopard grouper recruitment and can be considered an “optimal environmental window” (Cury and Roy 1989) between environmental factors produced by the oceanographic climate and recruitment success.

Although our study does not allow us to determine which scenario is the most adequate explanation of the patterns observed, the recruitment of the leopard grouper is strongly correlated to nursery habitat availability and oceanographic conditions, which allows us to predict with some certainty the magnitude of recruitment. This result has enormous implications for leopard grouper population dynamics and fisheries management, if we take into account that the environment in this region is highly variable; oceanographic conditions fluctuate from strong El Niños (such as in 1997–1998) to La Niña, and so does the availability of *Sargassum* beds.

The leopard grouper brings high prices in national and international fish markets and is a prized sport fish. Changes in leopard grouper catches over time are difficult to evaluate due to the nonspecific nature of Mexican fishing statistics, but there is nonetheless strong evidence that fishing pressure is increasing, and grouper abundance and size is decreasing (Sala et al. 2004). In addition, spawning aggregations of the leopard grouper are targeted by commercial fishers (Sala et al. 2003). Increasing fishing intensity will likely reduce the number of competent larvae available for settlement through a reduction of the reproductive population. Thus warm and nutrient-poor years will likely amplify the negative effects of fishing and diminish the potential for replenishment of leopard grouper populations. Because recruitment peaks are preserved in the structure of the adult population, the predictability of recruitment could allow adaptive management without expensive stock assessment programs. Fishing quotas could be set and



reevaluated annually on the basis of present and past MEI values.

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#### LITERATURE CITED

- Aburto-Oropeza, O., and E. F. Balart. 2001. Community structure of reef fish in several habitats of a rocky reef in the Gulf of California. *Marine Ecology P.S.Z.N.I.* 22:283–305.
- Alheit, J., and E. Hagen. 1997. Long-term climate forcing of European herring and sardine populations. *Fisheries Oceanography* 6:130–139.
- Anderson, T. W. 2001. Predator responses, prey refuges, and density-dependent mortality of a marine fish. *Ecology* 82: 245–257.
- Attrill, M. J., and M. Power. 2002. Climatic influence on a marine fish assemblage. *Nature* 417:275–278.
- Casas-Valdez, M. M., and I. Sanchez-Rodriguez. 1992. Biomasa cosechable de *Sargassum* spp. CICIMAR-IPN, Boletín No. 9.
- Casas-Valdez, M. M., I. Sanchez-Rodriguez, and G. Hernandez-Carmona. 1993. Evaluación de *Sargassum* spp. en la costa oeste de Bahía Concepción, B.C.S., México. *Investigaciones Marinas CICIMAR* 8:61–69.
- Cury, P., and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Canadian Bulletin of Fisheries and Aquatic Sciences* 46:670–680.
- Danilowicz, B. S. 1997. A potential mechanism for episodic recruitment of a coral reef fish. *Ecology* 78:1415–1423.
- Dayton, P. K., M. J. Tegner, P. B. Edwards, and K. L. Riser. 1999. Temporal and spatial scales of kelp demography: the role of oceanographic climate. *Ecological Monographs* 69: 219–250.
- Dayton, P. K., M. J. Tegner, P. E. Parnell, and P. B. Edwards. 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecological Monographs* 62:421–445.
- Dippner, J. W. 1997. Recruitment success of different fish stocks in the North Sea in relation to climate variability. *German Journal of Hydrography* 49:277–293.
- Espinoza-Avalos, J. 1990. Estructura por edades y reproducción de tres poblaciones de *Sargassum sinicola* (Phaeophyta, Fucales) en Bahía de La Paz, Golfo de California. *Acta Botanica Mexicana* 11:1–9.
- Espinoza-Avalos, J., and H. Rodriguez-Garza. 1989. Growth of *Sargassum sinicola* Setchell and Gardner (Phaeophyta) in the southern Gulf of California, Mexico. *Ciencias Marinas* 15: 141–149.
- Foster, M., R. Riosmena-Rodríguez, D. Steller, and Wm. J. Woelkerling. 1997. Living rhodolith beds in the Gulf of California and their significance for paleoenvironmental interpretation. Pages 127–139 in M. Johnson and J. Ledesma-Vazquez, editors. *Pliocene carbonates and related facies flanking the Gulf of California, Baja California, Mexico*. Special Paper Number 318. Geological Society of America, Boulder, Colorado, USA.
- Harmelin-Vivien, M. L., J. G. Harmelin, C. Chauvet, C. Duval, R. Galzin, P. Lejeune, G. Barnabé, F. Blanc, R. Chevalier, J. Duclerc, and G. Lasserre. 1985. Evaluation visuelle des peuplements et populations de poissons: méthodes et problèmes. *Terre Vie* 40:467–539.
- Hernandez-Carmona, G., M. M. Casas-Valdez, C. Fajardo-Leon, I. Sanchez-Rodriguez, and E. Rodriguez-Montesinos. 1990. Evaluación de *Sargassum* spp. en la Bahía de La Paz, B.C.S., México. *Investigaciones Marinas CICIMAR* 5:11–18.
- Hixon, M. A., and G. P. Jones. 2005. Competition, predation, and density-dependent mortality in demersal marine fishes. *Ecology* 86:2847–2859.
- Hobson, E. S. 1968. Predatory behavior of some shore fishes in the Gulf of California. Report 73. U.S. Fish and Wildlife Service, Bureau of Sport Fisheries and Wildlife, Research.
- Kahru, M., and B. G. Mitchell. 2000. Influence of the 1997–98 El Niño on the surface chlorophyll in the California current. *Geophysical Research Letters* 27:2937–2940.
- Kahru, M., and B. G. Mitchell. 2002. Influence of the El Niño–La Nina cycle on satellite-derived primary production in the California Current. *Geophysical Research Letters* 29:Art. No. 1846.
- Koenig, C. C., and F. C. Coleman. 1998. Absolute abundance and survival of juvenile gags in sea grass beds of the northeastern Gulf of Mexico. *Transactions of the American Fisheries Society* 127:44–55.
- Letourneur, Y., P. Chabanet, L. Vigliola, and M. Harmelin-Vivien. 1998. Mass settlement and post-settlement mortality of *Epinephelus merra* (Pisces: Serranidae) on Reunion coral reefs. *Journal of the Marine Biological Association of the United Kingdom* 78:307–319.
- Levin, P. S., and C. B. Grimes. 2002. Conservation and management of grouper. Pages 377–389 in P. F. Sale, editor. *Ecology of coral reef fish*. Academic Press, San Diego, California, USA.
- Lynn, R. J., et al. 1998. The state of the California Current, 1997–1998: transition to El Niño conditions. *California Cooperative Oceanic Fisheries Investigations Report* 39:25–49.
- Mantua, N. J., S. R. Hare, H. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* 78:1069–1079.
- McCourt, R. M. 1984. Seasonal patterns of abundance, distribution and phenology in relation to growth strategies of three *Sargassum* species. *Journal of Experimental Marine Biology and Ecology* 74:141–156.
- McCourt, R. M. 1985. Reproductive biomass allocation in three *Sargassum* species. *Oecologia* 67:113–117.
- Muñeton, M. 1987. Fenología de *Sargassum horridum* (Setchell y Gardner) en tres localidades de La Bahía de La Paz., B.C.S. Universidad Autónoma de Baja California Sur, La Paz, B.C.S., México.
- NOAA-CIRES. 2004. Multivariate ENSO index. NOAA/ESRL/PSD, Boulder, Colorado, USA. ([http://www.cdc.noaa.gov/ENSO/enso.mei\\_index.html](http://www.cdc.noaa.gov/ENSO/enso.mei_index.html))
- Nuñez-Lopez, R. A., and M. M. Casas-Valdez. 1997. Variación estacional de la biomasa y talla de *Sargassum* spp. (Sargassaceae, Phaeophyta) en Bahía Concepción, B.C.S., México. *Hidrobiológica* 7:19–25.
- Pacheco-Ruiz, I., J. A. Zertuche-Gonzalez, A. Chee-Barragán, and R. Blanco-Betancourt. 1998. Distribution and quantification of *Sargassum* beds along the west coast of the Gulf of California, Mexico. *Botanica Marina* 41:203–208.
- Platt, T., C. Fuentes-Yaco, and K. T. Frank. 2003. Spring algal bloom and larval fish survival. *Nature* 423:398–399.
- Reyes-Bonilla, H., R. Riosmena-Rodríguez, and M. S. Foster. 1997. Hermatypic corals associated to rhodolith beds in the Gulf of California, México. *Pacific Science* 51:328–337.

- Robertson, D. R., U. M. Schober, and J. D. Brawn. 1993. Comparative variation in spawning output and juvenile recruitment of some Caribbean reef fishes. *Marine Ecology Progress Series* 94:105–113.
- Sala, E., O. Aburto-Oropeza, G. Paredes, I. Parra, J. C. Barrera, and P. K. Dayton. 2002. A general model for designing networks of marine reserves. *Science* 298:1991–1993.
- Sala, E., O. Aburto-Oropeza, G. Paredes, M. Reza, and L. Lopez-Lemus. 2004. Fishing down coastal food webs in the Gulf of California. *Fisheries* 29:19–25.
- Sala, E., O. Aburto-Oropeza, G. Paredes, and G. Thompson. 2003. Spawning aggregations and reproductive behavior of reef fishes in the Gulf of California. *Bulletin of Marine Science* 72:103–121.
- Sandin, S. A., and S. W. Pacala. 2005. Demographic theory of coral reef fish populations with stochastic recruitment: comparing sources of population regulation. *American Naturalist* 165:107–119.
- Sharp, G. D., and D. McLain. 1993. Fisheries, El Niño-Southern Oscillation and upper Ocean temperature records: an eastern pacific example. *Oceans* 6:13–22.
- Southward, A. J., G. T. Boalch, and L. Mattock. 1988. Fluctuations in the herring and pilchard fisheries of Devon and Cornwall linked to change in climate since the 16th century. *Journal of the Marine Biological Association of the United Kingdom* 68:423–445.
- Thomson, D. A., L. T. Findley, and A. N. Kertitch. 2000. Reef fishes of the Sea of Cortez. The University of Texas Press, Austin, Texas, USA.
- Wolter, K., and M. S. Timlin. 1998. Measuring the strength of ENSO: how does 1997/98 rank? *Weather* 53:315–324.

#### APPENDIX A

Maps showing the location of the recruitment experiment in San Juan de la Costa, Mexico (*Ecological Archives* E088-132-A1).

#### APPENDIX B

A photograph of the *Sargassum* bed in the natural fringe (*Ecological Archives* E088-132-A2).

#### APPENDIX C

Design of the artificial *Sargassum* structure (*Ecological Archives* E088-132-A3).

#### APPENDIX D

A general methodology used for *Sargassum* biomass estimation (*Ecological Archives* E088-132-A4).