Title

The role of nursery habitats and climate variability in reef fish fisheries in the Gulf of California

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Publication Date

2009

UNIVERSITY OF CALIFORNIA, SAN DIEGO

The role of nursery habitats and climate variability in reef fish fisheries in the Gulf of California

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy

in

Marine Biology

by

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2009

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2009

This work is dedicated to Catalina,

who always inspire me to accomplish my dreams…... si dile!!!!

… to my Father, for his support and love,

… and to my Mother and my Sister, for their unconditional love.

TABLE OF CONTENTS

Signature Page……………………………………………………………………...iii

Dedication……………………………………………………………………..iv

Table of Contents……………………………………………………………… v

List of Tables………………………………………………………………… vii

List of Figures………………………………………………………….. viii

Acknowledgements…………………………………………………….. ….xi

Vita and Publications…………………………………………………...xiii

Abstract of the Dissertation………………………………………………...xv

Chapter 1. Introduction……………………………………………………..1
    Overview…………………………………………………………………2
    Objectives…..……………………………………………………………6
    References…………………………………………………..………7

Chapter 2. Predictability of reef fish recruitment in a highly variable nursery habitat...9
    Abstract……………………………………………………………………10
    Introduction…………………………………………………………...10
    Methods……………………………………………………………………11
    Results……………………………………………………………………...14
    Discussion…………………………………………………………………15
    Acknowledgements…………………………………………………….…...17
    References…………………………………………………………………17

Chapter 3. Recruitment and ontogenetic habitat shifts of the Yellow snapper (*Lutjanus argentiventris*) in the Gulf of California.…………………………………...……..19
    Abstract……………………………………………………………………20
    Introduction……………………………………………………………...20
    Materials and Methods……………………………………………………..23
    Results……………………………………………………………………...31
    Discussion…………………………………………………………………34
    Acknowledgements…………………………………………………………...40
    Tables……………………………………………………………………41

Figures……………………………………………………………………...42
References…………………………………………………………………49

Chapter 4. Spatially explicit contribution of mangroves ecosystems to the replenishment of reef fish populations……………………………………………………54
Abstract……………………………………………………………………55
Introduction………………………………………………………………...55
Materials and Methods……………………………………………………..57
Results……………………………………………………………………...66
Discussion…………………………………………………………………69
Acknowledgements………………………………………………………...75
Tables………………………………………………………………………76
Figures……………………………………………………………………...77
References…………………………………………………………………81

Chapter 5. Climatic influence on reef fish recruitment and fisheries………………..84
Abstract…..………………………………………………………………...85
Main text…………………………………………………………………..85
Notes..……………………………………………………………………...87
Materials and methods……………………………………………………88
Acknowledgements………………………………………………………...91
Tables………………………………………………………………………92
Figures……………………………………………………………………...93
References…………………………………………………………………95

Chapter 6. Mangroves in the Gulf of California increase fishery yields……………96
Abstract…..………………………………………………………………...97
Results……..………………………………………………………………97
Discussion……………………………………………………………….....99
Materials and methods……………………………………………………..99
Acknowledgements………………………………………………………100
References………………………………………………………………...100

Chapter 7. General conclusions……………………………………...…………...101
References………………………………………………………………...106

LIST OF TABLES

Chapter 3

Table 3.1. *Lutjanus argentiventris* life history variables..……………………………41

Chapter 4

Table 4.1. Summary of the islands characteristics and the density of Yellow snapper < 30 cm in the 10 years of the study…………………………………………………76

Chapter 5

Table 5.1. Sites surveyed each year from 1998 to 2008 in the central and southern Gulf of California.….…………………………………………………………………....92

Chapter 6

Table 6.1. Estimated mangrove ecosystem service values worldwide.……………....98

Table 6.2. Cost estimations of transforming mangrove ecosystems in the Gulf of California…………………………………………………………………………..99

LIST OF FIGURES

Chapter 2

Fig. 2.1. Location of study sites for (A) recruitment habitat preferences of the leopard grouper, *Mycteroperca rosacea* (1999), and (B) interannual recruitment variability (1998–2004)……………………………………..…..…………………………...12

Fig. 2.2. Abundance (mean ± SE) of *Mycteroperca rosacea* recruits in the seven major shallow habitats of the Gulf of California…………………………………………12

Fig. 2.3. Density (mean ± SE) of *Mycteroperca rosacea* recruits in three experimental treatments (n = 5 replicates per treatment)………………………………………………………………………14

Fig. 2.4. Relationship between the Multivariate El Niño Southern Oscillation (ENSO) Index and mean *Sargassum* biomass in the central and southern Gulf of California...14

Fig. 2.5. Relationship between MEI and density of leopard grouper recruits in the central and southern Gulf of California……………………………………………....15

Fig. 2.6. Size frequency distribution of the leopard grouper population in the Gulf of California…………………………………………………………………………..15

Chapter 3

Fig. 3.1. Map of Gulf of California showing: (a) the major marine habitat types surveyed off the coast of the Baja California coast and Mexico´s mainland, including the location of the 12 mangrove sampling sites……………………………………....42

Fig. 3.2. *Lutjanus argentiventris*. Relationship between standard length and age after settlement estimated from lapilli of juveniles collected in Balandra between 2002 and 2005, and 11 additional mangroves during October 2003 and June 2004………...…43

Fig. 3.3. *Lutjanus argentiventris*. Settlement frequency distribution obtained with back calculations of 516 lapilli otoliths…...…………………………………………….44

Fig. 3.4. *Lutjanus argentiventris*. Comparison of settlement time in Balandra as determined by (a) back-calculation from otoliths collected from 2002 to 2005, and (b) survey data between February 2005 and May 2006..…………………………………45

Fig. 3.5. *Lutjanus argentiventris*. Average size of juveniles collected inside mangrove forests along the Gulf of California, during the recruitment peak (October) and the end of nursery stage (June) of cohort 2003……………………………………...………...46

Fig. 3.6. . *Lutjanus argentiventris*. Significant differences in size classes ontogenetic patterns of habitat use…………………………………………..………………47

Fig. 3.6. *Lutjanus argentiventris*. Shows the relationship between nearest distance to mangrove and the density of individuals between10 and 20 cm size classes in each reef site……………………………………………………...………………48

Chapter 4

Fig. 4.1. Map of the Gulf of California showing the location of all mangrove and islands studied…………………………………………………………………...77

Fig. 4.2. Mean and standard error for the six size classes, in the three habitats surveyed in Balandra mangrove ………………...……………………………………...78

Fig. 4.3. Absolute abundance plotted against mangrove suitable area for rocky systems (○) and sandy systems (●), in central (a) and southern (b) Gulf of California.……...79

Fig. 4.4. Relationship between density of immature individuals (a) and individual incorporation rate (b) in offshore islands, and the distance from the nearest mangrove patch……………………………..……………………………………………80

Chapter 5

Fig. 5.1. Relationship between MEI and (A) yellow snapper juvenile abundance (mean ± SE) and (B) landings, and (C) leopard grouper juvenile abundance and (D) landings in the Gulf of California………...……………………………………………….....93

Fig. 5.2. Size-frequency distributions of collected (A) yellow snappers (*n* = 497) and (B) leopard groupers individuals (*n* = 705)………………………………...………94

Chapter 6

Fig. 6.1. The Gulf of California and the 13 fishing regions considered in this study, based on mangrove distribution and affinity in the composition of landings…..…......98

Fig. 6.2. Relationship between landings and economic value against the area of mangrove fringe in the Gulf of California…………………………..……………….....98

ACNOWLEDGEMENTS

This dissertation would not have been possible without the help and support of many people. I would like to thank my committee members for their guidance. Enric Sala, my friend, who has been a great mentor and helped me throughout my academic career. I would like to thank Exequiel Ezcurra, who was not an official member of my committee, but has been a fundamental leadership for all my research. In the same way, I would like to thank Phil Hastings and Jeremy Jackson for their support to accomplish several studies about the Gulf of California; thanks for your advice. Many thanks for their suggestions on my research to: Theodor Groves, Jim Leichter, Lisa Levin, and Dale Squires.

This project would never have happened without the support of several friends that helped me taking samples, doing analyses or writing scientific papers. First, I would like to thank Isaí Dominguez, José Cota, and Tomás Plomozo for their commitment to this Project. Special thanks to my friends and colleagues that participate as co-authors in some of the publications related to this thesis: Gustavo Paredes, Abraham Mendoza, Enric Ballesteros, Gustavo Danemann, Victor Váldez, Jason Murray, and Ismael Mascareñas. Many people assisted me in the field and in the laboratory and most are named at the end of each chapter. Special thanks to: Pincelli Hull, Brad Erisman, Stuart Sandin. I am grateful to the Scripps Family from different departments, in particular Penny Dockry from CMBC.

Funding for this research was provided by several sources: David and Lucille Packard Foundation, PADI Foundation, SIO Center for Marine Biodiversity and

Conservation (CMBC), SIO Graduate Department, UC MEXUS, Earth Friends, Moore Family Foundation, Pacific RIM, Pew Fellowship Program on Marine Conservation, Tinker Foundation, Robins Family Foundation, Walton Family Foundation, and World Wildlife Fund—Gulf of California Program. I would like to mention particularly the fellowship that I received from the Universidad Autónoma de Baja California Sur, throughout the PROMEP fund, which partially support my PhD program.

The text of Chapter 2 has been published under the same title, "Predictability of reef fish recruitment in a highly variable nursery habitat", in Ecology (2007) 88:2220-2228. I was the primary author, and Enric Sala, Gustavo Paredes, Abraham Mendoza, and Enric Ballesteros were co-authors of this work. The text of Chapter 5 has been published under the same title, "Mangroves in the Gulf of California increase fishery yields", in Proceedings of The National Academy of Sciences of the USA – PNAS (2008) 105: 10456-10459. I was the primary author, and Exequiel Ezcurra, Gustavo Danemann, Victor Valdez, Jason Murray, and Enric Sala were co-authors of this work. The text in Chapter 3 has been submitted to Marine Biology under the same title "Recruitment and ontogenetic habitat shifts of the Yellow snapper (*Lutjanus argentiventris*) in the Gulf of California". I am the primary author and Isaí Dominguez, José Cota, and Tomás Plomoz are the co-authors of this work.

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ABSTRACT OF THE DISSERTATION

The role of nursery habitats and climate variability in reef fish fisheries in the Gulf of California

by

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Doctor of Philosophy in Marine Biology

University of California, San Diego, 2009

Philip A. Hastings, Chair

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One of the most important services that coastal habitats supply is the provision of seafood that feeds people and supports local fishing economies. Despite this importance, there has been little analysis of the ecological processes that contribute to the local economies, and the impact that human activities have on these processes. The objective of this thesis is to study the relationship between coastal habitats and the dynamics of commercial reef fishes in the Gulf of California, and estimate the value of the services these habitats provide for fisheries. In the first section I will describe the interconnections between the life history of yellow snappers and leopard groupers, and their major nursery habitats (mangrove forests and *Sargassum* beds, respectively).

In the second section, beyond recruitment, I will explore whether all mangrove patches contribute equally to maintaining adult fish populations. I will study the relationship between juvenile snapper abundance and the amount of suitable mangrove

nursery area, and estimate the contribution of mangrove patches of different sizes to the replenishment of fish populations.

The last section includes fishery statistics for both species, and an economic valuation of mangrove ecosystems for the entire Gulf of California. I will analyze yellow snapper and leopard grouper abundance and fishery data, to determine whether it is possible to predict fish recruitment and landings based on available a priori climate indices. In the final part of this thesis I will test the hypothesis that the amount of mangrove forests has a direct bearing on the production of many commercially important fisheries.

The results of this thesis show that the life history characteristics of two of the most important commercial reef fish species in the Gulf of California are affected by the impact of climate variability on their nurseries. I determined that the Multivariate ENSO Index (MEI) explained the abundance of juveniles and fisheries landings for both species; increasing recruitment translated into greater fisheries landings once individuals recruited into fishing stocks. I also showed that standard underwater visual surveys combined with traditional fisheries statistics could provide a model to predict fluctuations in abundance over time, and could be used to adapt artisanal fisheries management ahead of time, regulating effort or setting quotas based on expected climate-mediated recruitment of fish into adult populations.

CHAPTER 1

Introduction

Overview

Coastal habitats are invaluable to humans in providing a number of services essential for our survival, including coastal protection, regulation of climate, and waste absorption. One of the most important services is the provision of seafood that feeds people and supports local fishing economies. Despite this importance, there has been little analysis of the ecological processes that contribute to the local economies, and the impact that human activities have on these processes. The objective of this thesis is to study the relationship between coastal habitats and the dynamics of commercial reef fishes in the Gulf of California, and estimate the value of the services these habitats provide for fisheries.

Many commercial reef fish species such as groupers, snappers and jacks have life cycles that include more than one habitats during their lives (Gillanders et al., 2003). Ontogenetic habitat shifts are a common strategy among reef fishes whose larvae settle in coastal habitats that serve as nurseries, such as seagrass beds, mangroves, and estuaries. Species with complex life cycles are more vulnerable to anthropogenic impacts, since habitat destruction and fragmentation decreases the replenishment of their populations (Coleman and Williams, 2002). For that reason, it is very important to identify these critical habitats and assess their vulnerability to human activities.

Critical to the replenishment of reef fish populations is the life period when fish larvae settle on shallow habitat, to later recruit to adult populations. Whilst many studies have identified nursery habitats as those occupied by juveniles of a species, the importance of juvenile habitats on a population level is only beginning to emerge (Mumby 2006). Not all nursery habitats receive and/or export the same number of individuals (Fodrie & Levin 2008). The most common assumption in the literature is that the area of the nursery habitats and the distance between them and the adult habitats can indirectly represent their importance; for example, large mangrove areas closest to a reef would represent the highest rate of nursery productivity (Nagelkerken et al. 2002; Dorenbosch et al. 2004; Halpern 2004; Mumby et al. 2004). Nevertheless, few studies have directly tested the role of these factors in controlling population sizes. Additionally, It has been shown that the variability of juvenile populations in nursery habitats over time can affect the future size structure of the adult populations, and this variability affects fishery stocks (Attrill and Power 2002). For that reason, information on juvenile ecology, when incorporated to fishery stock assessments, could provide better forecasting results than assessments based exclusively on traditional fisheries catch-at-age data (Coleman et al. 2000). This type of information may also prove useful in establishing legislative frameworks for fisheries management.

In the Gulf of California there are two main coastal habitats that play an essential role as nurseries of many marine species: mangrove forests and *Sargassum* seaweed beds. As it is happening worldwide, these habitats are facing increasing pressures due to pollution, overexploitation, and coastal development. Baja California is the northern limit of mangroves in the Eastern Pacific. In this region, mangroves grow under suboptimal conditions and individual plants consist of shrubs or small trees, which form isolated mangrove patches with a relatively narrow band of desert-fringe vegetation. Nevertheless, these coastal forests represent an important source of food and income for local communities. At least six species of snappers use mangrove forests as their major nursery habitat in the Gulf of California: Mexican barred snapper *Hoplopagrus guentherii*, Mullet snapper *Lutjanus aratus*, Yellow snapper *L. argentiventris*, Colorado snapper *L. colorado*, Spotted rose snapper *L. guttatus*, and Dog snapper *L. novemfasciatus*. Adults of these species contribute 300 tons of landings per year in the region, approximately 5% of all commercial reef fish landings. *Sargassum* beds grow seasonally on shallow rocky boulders, covering a narrow belt along rocky shores on the west coast and part of the northeast coast of the Gulf of California. The growth of *Sargassum* 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. The main species that dominate this habitat is *Sargassum sinicola*, but there are at least three more species that characterize these beds.

These coastal habitats strongly influence the structure of neighboring marine communities. For example, reefs near mangrove habitats have higher species richness, densities, and biomass than reefs far from mangroves or without any mangrove influence. However, evidence linking these ecological processes (the movements from nurseries to adult populations) and economic benefits (fisheries revenues) has been scarce. In other words, there are estimates of the value of commercial fisheries, but there is little knowledge of the contribution of specific coastal habitats to this value.

Why is the economic valuation of mangroves and *Sargassum* beds important for the Gulf of California and the communities depending on them? Pressure on these habitats will increase as local communities continue to grow. Several areas containing these habitats will be reclaimed for projects related to aquaculture, coastal tourism, and marinas. An economic valuation of coastal habitats will have two immediate benefits: to highlight the relative importance of different economic activities that depend on the services provided by mangroves and *Sargassum* beds, and to determine the consequences of their loss to local communities. As ultimate goal, an economic valuation will contribute to better-informed decision-making.

The El Niño Southern Oscillation (ENSO) causes the major source of inter-annual variability in the Gulf of California. The sea surface temperature on inter-annual to decadal timescales, seems to be modulated by a higher frequency and intensity of El Niño/La Niña events that temporarily lock surface ocean temperatures into warm/cold decadal periods (Herguera et al., 2003). On land, extremely wet ENSO events might cause long-lasting effects on semiarid vegetation, as they can open rare windows of opportunity for the recruitment of trees and shrubs, and cause the plant growth, flowering and fruiting on barren islands (Polis et al., 1997; Holmgren et al. 2001). In the ocean, ENSO events affect algal beds cover (Pacheco-Ruíz et al., 2003), small pelagic fishes (Sánchez-Velaso et al., 2000), and sea birds populations (Velarde et al., 2004). However, there are no studies that have focused on the effects that ENSO events have on reef fish populations and their consequences for artisanal fisheries management in this region.

Objectives

In order to understand the relationship between coastal habitats, the replenishment of commercial reef fish populations, and the implications for fisheries, I aim to answer the following questions:

1. What are the habitat requirements for the recruitment of the two most important commercial reef fishes in the Gulf of California (yellow snapper, Lutjanus argentriventris, and leopard grouper, Mycteroperca rosacea)?, and how does climate variability affect their recruitment?
2. Can we predict the contribution of indidivual nurseries to the replenishment of adult fish populations?
3. What is the value of the ecosystem services (nursery habitat) provided by coastal habitats?
4. What are the implications for the management of human activities on the coastal zone and fisheries?

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CHAPTER 2

Predictability of reef fish recruitment in a highly variable nursery habitat

Ecology, 88(9), 2007, pp. 2220–2228

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

Manuscript received 23 May 2006; revised 7 February 2007; accepted 9 February 2007. Corresponding Editor (ad hoc): F. C. Coleman.

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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 thrissina*) 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 ± 3.6 d (mean ± 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 × 5 m transects were surveyed at each location, except for the black coral beds where transects were 30 × 2 m, and mangroves where transects were 30 × 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-m^2 transect area); and 1 m to either side for black coral beds (60-m^2 transect area). For mangroves we surveyed the transects by swimming parallel to the roots and counting the fish 1 m inside the

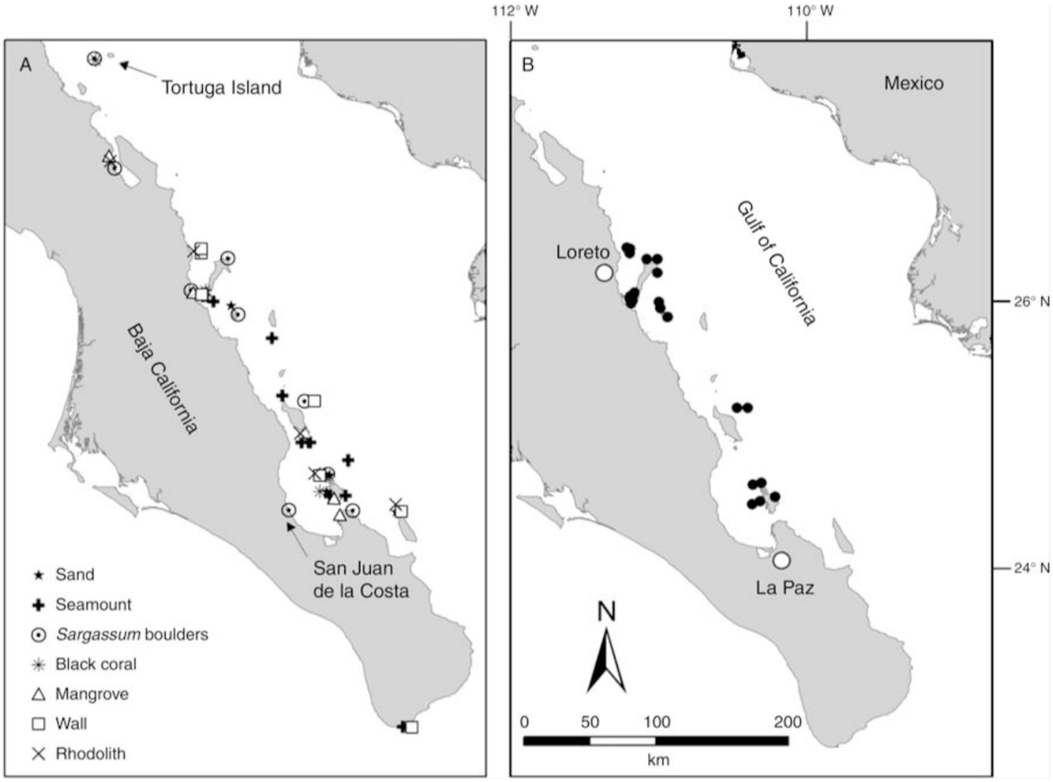

FIG. 1. Location of study sites for (A) recruitment habitat preferences of the leopard grouper, *Mycteroperca rosacea* (1999), and (B) interannual recruitment variability (1998–2004).

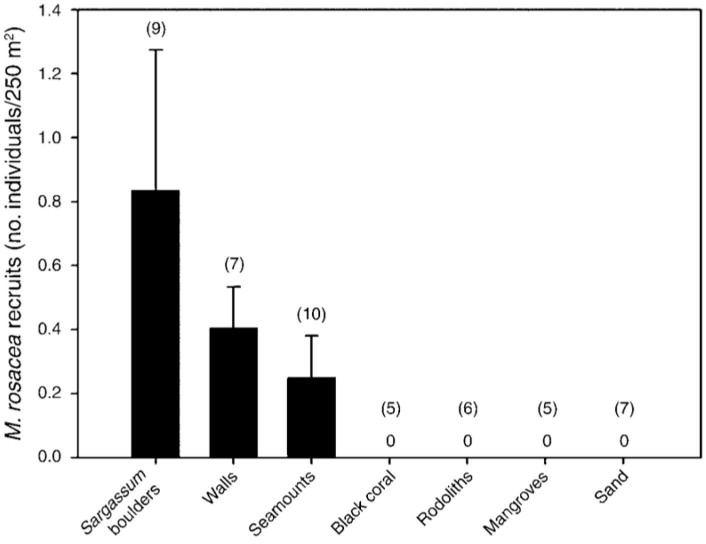

FIG. 2. Abundance (mean + SE) of *Mycteroperca rosacea* recruits in the seven major shallow habitats of the Gulf of California. The number of sampling sites per habitat is shown in parentheses.

prop roots (50-m^2 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^2 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*).[5]

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

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[5] ⟨http://www.cdc.noaa.gov/people/klaus.wolter/MEI/#ref_wt1⟩

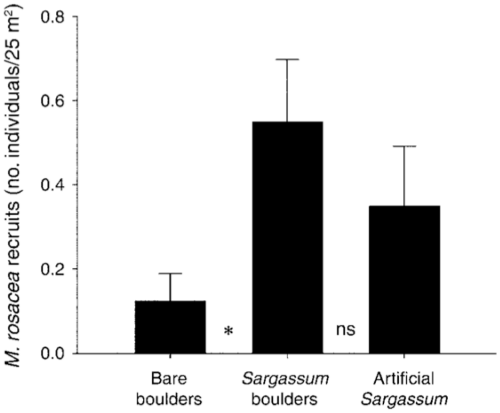

FIG. 3. Density (mean + SE) of *Mycteroperca rosacea* recruits in three experimental treatments ($n = 5$ replicates per treatment.

* $P < 0.05$; 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 postsettlers (1.98 cm in length) among the *Sargassum* fronds, but did not find any postsettler 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^2 in a cold year (1988) to 1.3 kg/m^2 in an El Niño year (1992).

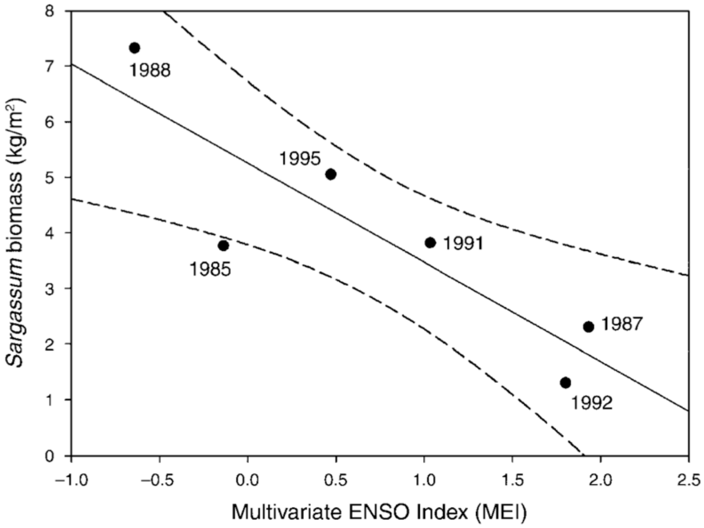

FIG. 4. Relationship between the Multivariate El Niño Southern Oscillation (ENSO) Index and mean *Sargassum* biomass in the central and southern Gulf of California. The solid line represents the model; the dashed lines show the 95% CI. Numbers by data points are years when *Sargassum* biomass was quantified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

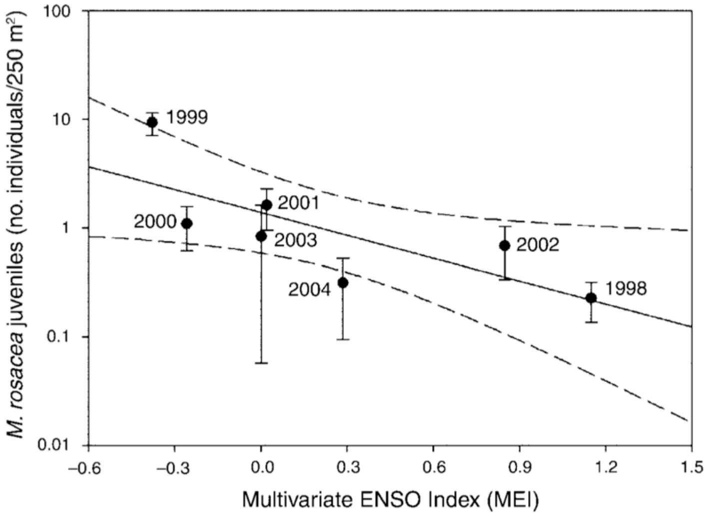

FIG. 5. Relationship between MEI and density of leopard grouper recruits (note the log scale) in the central and southern Gulf of California. Data are means ± SE; $n = 21$ sites/yr. The solid line represents the model; the dashed lines show the 95% CI. Numbers are years when surveys were conducted (see *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^2.

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

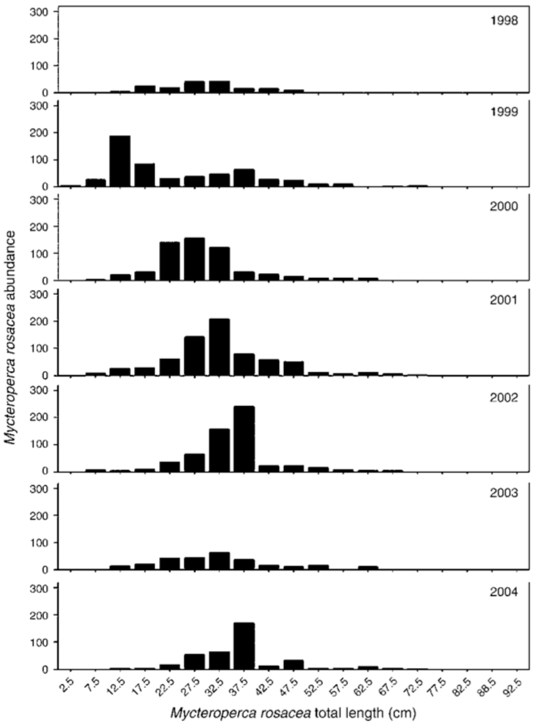

FIG. 6. Size frequency distribution of the leopard grouper population in the Gulf of California. Data represent all size measurements conducted yearly at all study sites. Histogram bars represent size class ranges with the tick marks and scale numbers at the midpoints of the ranges.

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.

Acknowledgments

We are grateful to several Marine Biology students and the Reef Fauna Project members at the Universidad Autónoma de Baja California Sur, México, for help with the recruitment experiment at San Juan de la Costa. We also thank L. Fichman, G. López-Lemus, R. Riosmena, C. Sánchez, G. Thompson, B. Victor, and C. Viesca for their help and support. Special thanks go to F. Ballantyne, M. Hixon, C. López, S. Sandin, and anonymous reviewers who improved previous versions of the manuscript, and to F. López-Castro who made possible the description of our experiment throughout his illustrations. This study was funded by the Moore Family Foundation, the Tinker Foundation, the Robins Family Foundation, the David and Lucille Packard Foundation, and the Gulf of California Program of the World Wildlife Fund. We also thank B. Brummit and N. Roberts for additional support.

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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).

The text of Chapter 2 has been published under the same title, “Predictability of reef fish recruitment in a highly variable nursery habitat”, in Ecology (2007) 88:2220—2228. I was the primary author, and Enric Sala, Gustavo Paredes, Abraham Mendoza, and Enric Ballesteros were co-authors of this work.

CHAPTER 3

Recruitment and ontogenetic habitat shifts of the Yellow snapper (*Lutjanus argentiventris*) in the Gulf of California

Abstract

We examine recruitment and ontogenetic habitat shifts of the Yellow snapper *Lutjanus argentiventris* in the Gulf of California by conducting surveys and collections in mangroves and major marine coastal habitats. Over 1,167 post-settler individuals were collected, and 516 otoliths were analyzed from 2002 to 2007. *L. argentiventris* recruits in mangroves, where juveniles remain until they are approximately 100 mm in length or 300 days old. Back-calculated settlement dates and underwater surveys indicated a major recruitment peak during September and October, around eight days before and after the full moon. The majority of mangroves in the Gulf of California had a similar *L. argentiventris* average size at the beginning of the settlement season for the cohort of 2003; although there were significant differences in individual sizes at the end of the nursery stage. When sub-adults leave mangroves, they use shallow rocky habitats and later move to deeper rocky reefs. The density of migratory individuals (10-20 cm SL) decreased exponentially as the distance between a reef and nearby mangroves increased. This finding has important implications for local fishery regulations and coastal management plans, since fishing effort on rocky reefs can be adjust according to the distance to mangrove sources.

Introduction

Many commercial reef fish species such as groupers, snappers and jacks have life cycles that include more than one habitat during their lives (see review by

Gillanders et al. 2003). Many explanations have been described to elucidate why these species have this complex life cycle; but in general, moving between habitats can maximize the evolutionary fitness of individuals (Morris 2006). From a fisheries management perspective, species with complex life cycles are more vulnerable to anthropogenic impacts, since habitat destruction and fragmentation increases the probabilities of overexploiting their populations (Coleman and Williams 2002).

Ontogenetic habitat shifts is a common strategy between reef fish species whose larvae settle in other benthic habitats that serve as early juvenile nurseries. In several latitudes, coastal systems such as sea grasses, kelp forests, mangroves, or estuaries represent important nursery habitats before individuals migrate to adult habitats (Koenig and Coleman 1998; Nagelkerken et al. 2000; Nelson 2001; Cocheret de la Morinière et al. 2002). It has been shown that the variability of juvenile populations overtime in nursery habitats can affect the size structure of the adult populations some years afterwards (Russ et al. 1996; Attrill and Power 2002; Aburto et al. 2007), which affects fishery stocks (Gillanders et al. 2003; Fodrie and Levin 2008). For that reason, information on juvenile ecology, when incorporated to fishery stock assessments, can provide better forecasting results than assessments based exclusively on traditional fisheries catch-at-age data (Coleman et al. 2000). This type of information may also prove useful in establishing legislative frameworks for fisheries management.

Several species of snappers are dependent on mangrove ecosystems during their nursery stage (Nagelkerken et al. 2000; Cocheret de la Morinière et al. 2002;

González-Acosta et al. 2004). At least six species of snappers use mangrove forests as their major nursery habitat in the Gulf of California (Thomson et al. 2000): Mexican barred snapper *Hoplopagrus guentherii*, Mullet snapper *Lutjanus aratus*, Yellow snapper *L. argentiventris*, Colorado snapper *L. colorado*, Spotted rose snapper *L. guttatus*, and Dog snapper *L. novemfasciatus*. Adults of these species contribute 300 tons of landings per year in the region (Ramírez-Rodríguez and Hernández-Herrera 2000), approximately 5% of all commercial reef fish landings.

The Yellow snapper *L. argentiventris* is one of the most important commercial species in the southern gulf, and generates more than 3 tons of fisheries landings per fishing cooperative during spring and summer. These fish reach sizes of up to 1 meter in length, a weight of 10 kilograms, reach maturity after 3 years, and can live up to 19 years (Martinez-Andrade 2003). Fishermen report aggregations of several hundred gravid individuals in May and June, and spawning aggregations have been observed in several islands in the southern Gulf of California (Sala et al. 2003).

Baja California is the northern limit of mangroves in the Eastern Pacific. In this region, mangroves grow under suboptimal conditions and individual plants consist of shrubs or small trees, which form isolated mangrove pockets with a relatively narrow band of desert-fringe vegetation (Whitmore et al. 2006). Nevertheless, these coastal forests represent an important source of food production and income for local communities (Aburto et al. 2008). Since these scarce and isolated ecosystems represent the most important sources of replenishment of *L. argentiventris* populations in marine habitats, we aim to demonstrate the relationship between the spatial distribution of mangrove patches and *L. argentiventris* abundance.

As described by Gillanders et al. (2003), a variety of methods have been used to determine movement from juvenile to adult habitats. Direct evidence of movement can only be measured by observing individually recognized or tagged organisms shifting from one place to another. However, indirect information on the movement of individuals can be obtained by differences in distribution, abundance and size structure, and by differences in physical stages of maturity. To use these indirect methods, there is a clear need to obtain information on abundance and size distribution of organisms from a range of juvenile and adult habitats, while sampling all types of habitat at several locations and multiple times. In the present study, we examined the spatial and temporal recruitment patterns of *L. argentiventris* and its ontogenetic habitat shifts. In particular, we analyzed the growth rate and residence time of fish in mangroves and other major marine habitats.

Materials and methods

Study area

This study was conducted in mangrove areas and rocky reefs in the Gulf of California, between 22°00’N and 29°30’N, on both Baja California and Mexico’s mainland coasts (Fig. 1a). In Baja California, mangroves are distributed from the Cape region in the southern tip to small islands in Bahía de Los Angeles in the north. In Baja California mangroves are distributed in isolated mangrove patches, most notably at Bahía de La Paz, Bahía Concepción, and Bahía de Loreto (Contreras-Espinosa and Warner 2004; Whitmore et al. 2006). There are three main species: red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*), and white mangrove (*Laguncularia racemosa*). Halophytic or salt scrub vegetation, typically associated with mangroves on the landward side (Whitmore et al. 2006) includes perennial saltgrasses (e.g., *Jouvea pilosa*, *Monanthochloe littoralis*, *Sporobolus virginicus*), perennial halophytic shrubs (e.g. *Allenrolfea occidentalis*, *Maytenus phyllanthoides*, *Salicornia subterminalis*), and other halophytes (e.g., *Atriplex barclayana*, *Batis maritima*, *Heliotropium curassavicum*, *Salicornia bigelovii*).

On the mainland, mangroves are distributed from Tiburon Island in Sonora, south to Sinaloa and Nayarit where coastal lagoons have extensive mangrove forests. Mangroves in Sonora include some of the same halophyte species (e.g. *Salicornia*) seen in the peninsula, but they can be submerged in water and, together with sea grasses (*Zostera marina* and *Ruppia maritima*), they represent another microhabitat within the mangrove ecosystem.

We collected juvenile *L. argentiventris* from 12 mangrove patches and conducted 1,467 dives between 1998 and 2007, from 0 to 50 m depth, across the following major marine habitats (S1, Supplementary material):

(1) Habitats adjacent to mangroves (<3 m). These include rocky boulders at the mouth of coves and bays, and shallow boulder beds covered seasonally by *Sargassum* spp. along the rocky shores;

(2) Rocky reefs, shallow (5 m) and deep (20 m). These include boulder beds and vertical walls in coastal and island areas. Rocky reefs are colonized by a high diversity of benthic suspension feeders such as gorgonians, hydroids, cup corals, sponges, tunicates, and bryozoans;

(3) Seamounts. These are deeper (30 - 40 m) offshore rocky reefs subjected to strong currents. The sessile fauna colonizing seamounts is similar to that of vertical walls, with abundant suspension feeders;

(4) Deep unconsolidated bottoms (>15 m). These include rhodolith beds and black coral beds. Rhodoliths are free-living calcareous algae (Corallinaceae) that grow up to 20 cm in diameter, form fields of variable cover over soft bottoms, and can include sparse free living corals. Fields of black coral, *Antipathes galapaguensis*, occupied horizontal, as well as gently sloped rocky and dead shell substrata below 25 m.

In the context of a larger project (PhD thesis, Scripps Institution of Oceanography), we have been collecting *L. argentiventris* individuals of all sizes in the major marine habitats mentioned above, and surveying 51 small patches of mangroves in the southern Gulf of California (Aburto et al. 2008) since 2005 in order to: (1) establish the size-maturity structure of *L. argentiventris* populations; (2)

estimate and compare life history variables for *L. argentiventris* population dynamics (Table 1); and (3) establish the size distribution of *L. argentiventris* that can be observed inside mangroves seasonally. With these research efforts we have established the following broad size-ontogenetic categories based on *L. argentiventris* maturity: settlers <3 cm TL; post-settlers inside mangrove roots between 4 and 10 cm TL; immature migratory individuals between 10 and 20 cm TL; and (mature) adult individuals >25 cm TL.

Underwater surveys of juvenile and adult individuals

Estimates of *Lutjanus argentiventris* abundance were carried out by free diving inside mangroves and SCUBA for the other habitats, and using standard underwater visual belt transect survey methods (Harmelin-Vivien et al. 1985). The authors are experienced at visually surveying fish assemblages and also at estimating fish lengths accurately (Aburto-Oropeza and Balart 2001; Sala et al. 2002). Total length of juveniles was estimated to the nearest 1 cm for individuals less than 10 cm in length, and every 5 cm for individuals larger than 10 cm. Based on previous observations regarding habitat use of settlers, mangrove areas were divided into two microhabitats: pebble beds (shallow areas with gentle slopes, covered by pebbles and small boulders [≈ 1000 cm^3] over sandy bottoms), and mangrove roots. To estimate the abundance of juvenile snappers, six replicate 50 × 1 m transects were surveyed in pebble beds covering an area of 50 m^2. In mangroves we surveyed snappers by swimming parallel the mangrove fringe and counting fish 1 m inside and outside the prop roots (six replicates 50 × 2 m transects; 100 m^2). Six replicate 50 × 5 m transects were surveyed at the adjacent habitats (mouth of coves and bays) and the rest of the habitats, except for black coral beds where transects were 30 × 2 m. Divers swam each transect at constant speed, about 15 min per transect, counting and estimating the size of all individuals within 2.5 m to either side of the center line for the adjacent habitats, shallow and deep rocky reefs, seamounts and rodoliths (250 m^2 transect area); and 1 m to either side for black coral beds (60 m^2).

To estimate the number of *Lutjanus argentiventris* settlers that arrived at a nursery area, we monitored a cove with a mangrove patch of 22 hectares (Balandra, Fig. 1b) from February 2005 through May 2006. Underwater surveys were carried out as described above in areas covered by pebbles and in mangrove roots. Although we counted *L. argentiventris* of all sizes, we considered only those with a total length <3 cm (younger than 50 d) as the individuals that settled during the same-year-reproduction event.

Juvenile collections and lab analyses

The information generated using otolith daily increments correspond primarily to *L. argentiventris* juveniles collected in 2002 in Balandra. We collected at least 20 individuals of different sizes every 15 d from February 2002 through March 2003 using push nets (small trawl nets attached to a frame and hand-operated by two people) and small spear guns. We performed between five to ten 20-m tows parallel to the mangrove roots. If these tows were not enough to collect more than 20 individuals, we used the spear guns and worked for a period of 4 hours collecting as many fish as possible. We took additional samples from the same area in June and October of 2003, 2004 and 2005.

In order to compare size distributions and daily growth of juveniles at a larger spatial scale, we sampled 11 additional mangrove patches along Baja California and the mainland (Fig. 1a). These sampling expeditions were carried out during the recruitment peak and the end of the nursery stage (see Results) of the 2003 cohort, in October 2003 and June 2004, respectively.

After collection, specimens were preserved in 95% ethyl alcohol and transported to the laboratory at Universidad Autónoma de Baja California Sur in La Paz for analyses. Juveniles were measured (total and standard length) to the nearest 0.1 mm, and weighed to the nearest 0.1 g. The sagittae and lapilli were extracted using a dissecting microscope, glass knives and ceramic forceps. One lapillus from each fish was chosen randomly, prepared and polished following the methods described by Secor et al. (1992). The other otoliths were stored dry in vials.

Lapilli were prepared for age determination by polishing both lateral surfaces on glass plates covered with Cristal-Bond®. We used different polishing cloths, including 12, 9, 3 and 0.3 microns. Polished, otoliths were mounted on microscope slides using immersion oil. Increments were counted from the nucleus outward to the edge of the otolith, or to the settlement mark that was associated with the transition from planktonic stage to benthic habitat (Wilson and McCormick 1999). The settlement mark was interpreted to be where the pattern in the increment widths changed markedly (Wellington and Victor 1992).

Otolith microstructure was examined using a light microscope (100× to 800× magnification) and by counting increments. Readings were done twice by the same reader. Counts that differed by no greater than 5% were averaged; increment counts that differed by more than 5% were counted a third time, and if the third count differed by more than this percentage, the otolith was rejected (Allman 2002). We used the validation of the periodicity of increment formation in lapilli described by Zapata and Herron (2002), which showed that juvenile *L. argentiventris* produce one ring per day.

Data analyses

A settlement date for each individual was calculated by subtracting the number of post settlement increments (growth rings between the settlement mark and the edge of the otolith) from the date of captures. Settlement date was converted to the lunar calendar by determining the number of days until the nearest full moon, with values negative during waxing stages and positive during waning stages (Fig. 3). To test for lunar periodicity in the pattern of settlement for the sampled population, we compared the relative fit of two models of settlement intensity using Poisson regression. The constant model -- # of Settlers = α -- assumes that there is no effect of lunar date on the settlement probability. A sinusoidal model -- Settlers = $\alpha + \{\beta * \sin [(2\pi * X/14) - (\pi/2)]\}$, where α and β are estimated parameters and X is the lunar date -- assumes that the probability of settlement is a function of lunar date, reaching a minimum at full and new moons. The best-fit parameters were estimated by the Nelder-Mead optimization algorithm in R software (http://www.R-project.org).

In order to overlap temperature distribution values and settlement frequency distributions, we obtained Sea Surface Temperature (SST) data from remotely sensed satellite imagery (Terra/Aqua MODIS) at NOAA Satellite and Information Service (http://www.ncdc.noaa.gov), and calculated SST for our study region using MATLAB® software. We obtained 15 d averages of the SST and plotted them with the settlement frequency distribution obtained by date back calculation and by underwater surveys (see Fig. 4). Because surveys in Balandra were systematic, we only performed a regression analysis between SST and the abundance of individuals <3 cm recorded in the underwater surveys.

To test for differences in growth rates of *Lutjanus argentiventris* within mangroves, we compared the relationship between SL and the post settlement age for samples obtained in October 2003 and June 2004. The relationship was described by a linear regression and the site effect (slope coefficient) in the relationships between SL and age, was analyzed using ANCOVA. To test for differences in size structure of *L. argentiventris* between mangroves and collection months (October 2003 and June 2004), log-transformed data were analyzed using ANOVA. When the interaction was significant, post-hoc multiple comparisons were analyzed using Tukey HSD tests. Transformations were made to centre the means and to stabilize variances. Homogeneity of variances was tested using Cochran's C test.

To establish if size distribution within habitats has significant differences, size class percentages for each habitat were determined and compared using Chi-Square median test. Additionally, we used GIS in conjunction with ArcView software to calculate the nearest distance between mangrove patches and study reefs. To describe the influence of mangrove patches on the migratory distances of *L. argentiventris*, we correlated the distance to the nearest mangrove to the density of individuals between 10 and 20 cm size classes at each site.

Results

Juvenile age and growth

A total of 1,167 post-settlers of *Lutjanus argentiventris* were captured in mangroves. Their sizes (standard length, SL) ranged from 16.9 to 136.2 mm, with a mean of 55.2 mm (± 1.7 SE). Of these, 99% were less than 100 mm SL. Young-of-the-year *L. argentiventris* had typical weight-standard length relationship of the form: $W = (2 \times 10^{-5})\ SL^{3.05}$, [$r^2 = 0.98$, $p < 0.0001$].

We aged otoliths from 516 individuals. Estimated age of post-settlers ranged from 11 to 368 d (Fig. 2). Ninety eight percent of these individuals were less than 300 d old. The general model of age-length relationship was $SL = 0.35\ Age + 4.81$, [$r^2 = 0.88$, $F = 3603.86$, $p < 0.0001$]. The instantaneous daily growth (slope coefficient) of juvenile *L. argentiventris* was similar among all mangroves localities (0.35 mm d^{-1} ±

0.02 SEM), although ANCOVA revealed a significant ($p < 0.0019$) site effect in the relationships between SL and Age, driven mainly by one site (Bojorquez mangrove, $p < 0.0034$). Settlement at this site started at smaller lengths (18.7 mm) than the other sites (significant Site effect for intercept), however the growth rate (0.42 mm d^{-1}) was higher compared to the other sites (significant Site effect on the slope).

Settlement patterns

The estimated age at settlement (planktonic larval duration, PLD) ranged from 19 to 26 d (mean = 22.9 ± 0.05 SE). The longest average PLD was recorded for juveniles setting in the San Lucas mangrove (23.9 d ± 0.19 SE) ($p < 0.001$). Individuals that settled in Balandra in 2002 had a PLD significantly shorter than other samples taken in the same mangrove on subsequent years ($p < 0.001$). The settlement pattern was related to the lunar date, with maxima reached during the quarter moons (Fig. 3). The sinusoidal model fitted the settlement data much better than the constant model ($p<0.001$), suggesting a strong lunar periodicity in the settlement patterns ($\text{Settlers} = 17.2 + \{3.3 * \sin [(2\pi * X/14) - (\pi/2)]\}$).

Age estimates from otolith analysis were used in conjunction with collection dates to determine the frequency distribution of settlement dates for *L. argentiventris* caught in Balandra from 2002 to 2005 (Fig. 4a). Back-calculated settlement dates ranged from early August to late January, with a major peak occurring from late September to early November in the four sampled years.

During the 2005 visual surveys in pebbles and mangrove roots from Balandra, *L. argentiventris* smaller than 3 cm first appeared during the second week of August

(Fig 4b). Most settlement occurred during September and October; however settlers where observed through February 2006. Settlement of *L. argentiventris* increased exponentially as SST increased during the year (Fig. 4b) (r^2=0.58, F=19.3, p<0.001).

At the beginning of the 2003 recruitment season, the 12 studied mangroves displayed a similar average size in the *Lutjanus argentiventris* populations (42.7 mm ± 0.07 SE) (Fig. 5). The main differences in size distribution within mangroves were observed in Punta Yavaros, with an average size above 66 mm, and San Basilio with an average size of 28.6 mm (1-way ANOVA: F = 70.506, p < 0.001). Greater differences were present in size average towards the end of the nursery stage in all mainland mangrove sites (1-way ANOVA: F = 18.569, p<0.001). Additionally, mainland mangroves had average size values higher than the general mean (78.2 mm ± 0.9 SE) (Fig. 5).

Ontogenetic movements

Yellow snapper showed clear ontogenetic shifts in habitat use (Chi-Square = 18.29, df = 6, p < 0.01) (Fig. 6). Post-settlers (<5 cm) were found mostly on pebble beds; they then moved to mangrove roots until they reached approximately 10 cm. Migratory individuals between 10 and 20 cm characterized habitats adjacent to mangroves; adults (25-60 cm) then moved to shallow and deep rocky reefs. Deep habitats, including seamounts and deep unconsolidated bottoms, registered the largest individuals (>60 cm) and were the only two habitats that did not have significant differences in average individual size (p=0.085).

The density of migratory individuals decreased exponentially ($r^2 = 0.94$, $F = 432.38$, $p < 0.0001$) with distance from the closest mangrove (Fig. 7). In general, densities above 1 individual per 250 m^2 were only found at reefs with mangroves closer than 10 km.

Discussion

This study describes the processes that take place during the *Lutjanus argentiventris* mangrove stage and the habitat shifts that occur once they leave the mangrove habitat. Individuals first settle in pebbles after their pelagic larval stage, once they reach approximately 2 cm in length. As occurs in other species that settle during warm seasons (Macpherson 1998; Rooker et al. 2004; Faunce and Serafy 2007), growth rates in *L. argentiventris* are high and they grow to approximately 10 cm in less than one year that is spent inside the nursery habitat. Sub-adults spend some years in shallow rocky habitats where they mature, and then move to deep rocky reefs where spawning aggregations take place (Sala et al. 2003).

Growth rates

Previous studies (Allman and Grimes 2002; Rooker et al. 2004; Faunce and Serafy 2007) have demonstrated that snappers typically settle when they reach between 10 and 19 mm TL, and grow between 0.28 and 1 mm d^{-1} during their first year of life. The daily growth of juvenile *Lutjanus argentiventris* is in the lower bound of snappers' growth (approximately 0.35 mm d^{-1}). Among the studied mangroves, growth variability was also observed within the 2003 *L. argentiventris* recruitment cohort. After the 8-month time frame between samplings (October 2003 – June 2004), all mangroves located on the mainland had an individual average size larger than that of individuals from mangroves on the peninsula. Although we did not examine the influence of regionally varying survival rates, quality of habitat (e.g., food availability, Rooker et al. 2004) and water temperature (Nixon and Jones 1997; Sumpton and Jackson 2005) determine the growth rate of juvenile fish during nursery time. Average temperatures inside mangrove forests in the Gulf of California during winter-spring seasons are lower than those in tropical mangroves and, for instance, several mangroves on the peninsula are small forest patches with lagoons that remain closed by sand bars during several winter-spring months. This generates hyper salinity and anoxic conditions during the snappers' nursery time, potentially leading to suboptimal growth conditions. In large coastal lagoons with extensive mangrove forests located in mainland coastal areas (Contreras-Espinosa and Warner 2004), oceanographic dynamics enhance suitable habitats for a great diversity of species, including snappers' prey (González-Acosta et al. 2004).

Once *Lutjanus argentiventris* leaves the mangroves, growth rates decrease exponentially. Between years one and five they grow an average of 5 cm per year; afterwards they only grow an average of 1 cm per year (Cruz-Romero 1996; Martinez-Andrade 2003; Rojas et al. 2004).

Settlement patterns

Yellow snapper spend an average of 23 d in the water column during their pelagic stage. This is similar to other snappers that predominantly use mangroves as nursery habitats: 18 d in *L. synagris*, 22 d in *Hoplopagrus guentherii*, 23 d in *L. novemfasciatus*, 24 d in *L. guttatus*, 25 d *L. griseus*, and 27 d in *L. campechanus* (Allman and Grimes 2002, Zapata and Herron 2002, Rooker et al. 2004). In the Gulf of California, the main spawning season for *L. argentiventris* is from July through September (Muhlia-Melo et al. 2003), which is consistent with the settlement season (late August – early November) observed in this study. Additionally, we found that larvae settled with semi-lunar periodicity during quarter moons (settlement frequency). This is particularly important because the majority of small mangrove patches in the Gulf of California desiccate at low tide during spring tides that occur with full and new moons (Contreras-Espinosa and Warner 2004).

Our results show that most mangroves on the peninsula and mainland had a similar size distribution of snappers at the beginning of the settlement season for the 2003 cohort, evidencing possible synchronized recruitment timing for the entire region. The only mangrove sites, located at similar latitude but in different coastal zones, that differed greatly in size structure during October 2003 were: Punta Yavaros, a large coastal lagoon with high mangrove coverage located in mainland Mexico; and San Basilio, a small estuary with few mangrove trees situated in Baja California. Both sites are located where oceanographic conditions and habitat structure change drastically (Santamaria-del-Angel and Alvarez-Borrego 1994). On one hand, Punta

Yavaros represents the transition zone between the northeastern Gulf of California rocky reefs and southeastern sandy bottoms in front of large coastal lagoons. This site had the largest mean size compared to the rest of the sites, suggesting that it is located close to adult reproductive sources allowing for an earlier settlement. On the other hand, San Basilio is located in the transition zone between two major biogeography zones in the Gulf of California (Santamaria-del-Angel and Alvarez-Borrego 1994), where changes in temperature and productivity regimes create natural barriers. This site had the smallest mean size during the recruitment season, suggesting that reproductive sources are located in rocky reefs either to the north (Santa Rosalía), or to the south (Loreto).

Mangrove nursery stage

Once in the mangrove roots, *Lutjanus argentiventris* juveniles are restricted to a few hundred meters of suitable habitat, follow the movement of tides and display hunting activities as seen in other snapper species (Sheaves 2001; Dorenbosch et al. 2004b). None of the individuals collected inside mangroves during this study was sexually mature and, like other snapper species (Sheaves 1996), all *L. argentiventris* collected were young-of-the-year. Additionally, of 11,588 *L. argentiventris* individuals recorded in 1,014 underwater visual transects inside mangrove roots, only 2 were adult individuals >25 cm.

If the recruitment season begins in mid summer (August), new juveniles start using mangrove roots towards the end of fall and early winter. Approximately eight months later, at the beginning of summer, juveniles migrate from mangrove forests to adjacent habitats (rocky shores). This may help establish that mangroves provide an intermediate nursery habitat (Mumby et al. 2004), where juvenile snapper gain protection and increase survivorship during the variable conditions typical of the cold season in the Gulf of California (Aburto-Oropeza and Balart 2001).

Finally, we have monitored small bays with mangroves (particularly Balandra) at the appropriate temporal resolution to observe that when the density of juveniles inside the mangrove roots decreases, the density of individuals between 10 and 20 cm increases in rocky shores outside the coves. Less than 1% of *L. argentiventris* surveyed during the monitoring program in Balandra were in sandy habitats. Migratory individuals leave mangroves following the rocky shoreline to the nearest rocky point in the adjacent habitats. General observations in several rocky points indicate that they form shoals and congregate in these habitats for a few months. Once they migrate to shallow rocky reefs, the abundance of these migratory individuals decreases rapidly and can reach zero in a few days, just before the winter season starts (O. Aburto-Oropeza unpubl. data).

Ontogenetic habitat shifts and its implications

When they are still young (<3 years old) with sizes between 20-30 cm, yellow snappers live in shallow rocky reefs with patches of hard corals (mainly *Poecillopora* spp.). As they grow, they move to deep rocky reefs (20 m) and, in some cases, to seamounts (30 m), reaching maturity after the 3rd year of life (Martinez-Andrade

2003). Adult individuals do not frequent the deep unconsolidated bottoms (rodolith beds and black coral gardens).

Change in habitat use is a common strategy displayed by several fish species (Macpherson 1998; Cocheret de la Morinière et al. 2002; Mumby et al. 2004; Secor and Rooker 2005), and provides several advantages such as access to food, lower predation, and less competition. Mangroves are an important habitat in the *Lutjanus argentiventris* life cycle and recruitment dynamics along the Gulf of California mangroves are very similar. Mangrove coverage and geographic location may influence nursery productivity, thus affecting population densities in neighboring habitats (Beck et al. 2001; Mumby et al. 2004). Although we did not determine the productivity of these nursery areas (individuals per square meter), this work establishes that densities of migratory *L. argentiventris* in reefs within a radius of 10 km from a mangrove habitat are one order of magnitude higher than reefs farther away. Rare records of migratory individuals were recorded in reefs 65 km away from a mangrove source. These results are in accordance with studies that show that populations of mangrove-nursery species are denser within a few kilometers from mangrove sources (Nagelkerken 2002; Dorenbosch et al. 2004a; Dorenbosch et al. 2007; Nagelkerken 2007; Fodrie and Levin 2008).

In order to have a sustainable *L. argentiventris* fishery, it is necessary to maintain the habitats that this species requires to complete its life cycle (Secor and Rooker 2005). Since the vast majority of snappers disperse less than 10 km from their mangrove of origin, it is safe to assume that there is no dispersal of juveniles from one coast of the Gulf of California to the other. This has great implications for the few and isolated mangroves on the peninsula, because they represent all existing nurseries for *L. argentiventris* populations in this coast. Establishing the relative contribution of each nursery area/habitat (number of individuals supplied) to adult habitats, and monitoring this contribution throughout time (Gillanders et al. 2003) will provide fishery-independent data necessary for forecasting the size of year classes several years into the future (Allman and Grimes 2002). Such results would have enormous consequences for coastal management, mangrove conservation, and may allow adaptive management strategies for local fisheries.

Acknowledgements

We are grateful to E. Sala and P. Hastings for his advice and support. We also would like to thank L. Fichman, S. Hamilton, I. Mascareñas, A. Mendoza, G. Paredes, C. Sánchez, J. Samhouri, S. Sandin, and C. Viesca for their help on density data, otolith analisis and statistics. Special thanks to C. López, P. Hull, L. Levin, E. Sala, S. Sandin and 5 anonymous reviewers who improved previous versions of the manuscript. This study was funded by the Moore Family Foundation, the David and Lucille Packard Foundation, The Tinker Foundation, the Robins Family Foundation, The Walton Family Foundation, PADI aware project, and the Gulf of California Program of the World Wildlife Fund.

Table 3.1 *Lutjanus argentiventris* life history variables: age at length zero (t0), asymptotic length (Linf), maximum length (Lmax), longevity (Tmax), asymptotic weight (Winf), length at maturity (Lmat), age at maturity (Tmat), reproductive life span (RLS), growth rate (k), natural mortality rate (M), and weight-length relationship constants (a, b).

		Cruz-Romero (1996)	Martinez (2003)	Rojas et al. (2004)	This study
Country		Mexico	Worldwide	Colombia	Mexico
t_0	(years)	-0.835	-0.873	-0.722	-0.005
Linf	(mm)	819	753	950	854
Lmax	(mm)	793	752		
Tmax	(years)	19	19		19.1
Winf	(gr)	6,673	9,338	12,218	7,326
Lmat *	(mm)	436	404		F=317, M=309
Tmat *	(years)	4	3		F=2.7, M=2.6
RLS	(years)	15	15		
k	(yearly)	0.155	0.153	0.2	0.16
M	(yearly)	0.33	0.3		0.34
a		0.07		6.25×10^{-6}	0.0154
b		2.75		3.12	2.95

* F = females, M = males

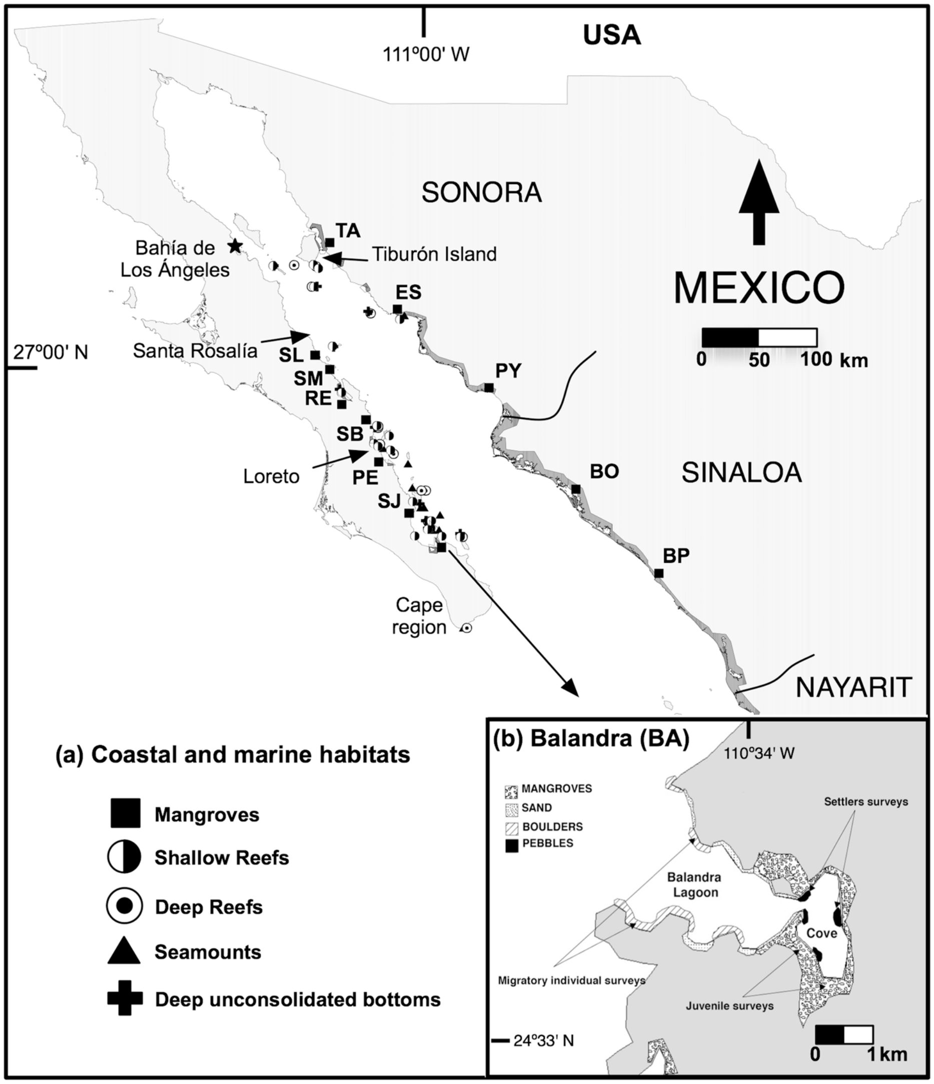

Fig. 3.1 Map of Gulf of California showing: (a) the major marine habitat types surveyed off the coast of the Baja California coast and Mexico´s mainland, including the location of the 12 mangrove sampling sites (see Appendix 1); and (b) the microhabitats of Balandra mangrove, where the principal snapper collections and juvenile surveys were carried out. Codes for sites in the peninsula: SJ = San Jose, PE = Puerto Escondido, SB = San Basilio, RE = Requeson, SM = San Marcos, and SL = San Lucas. Codes for sites in the mainland: BP = Barra de Piaxtla, BO = Bojorquez, PY = Punta Yavaros, ES = El Soldado, and TA = Tajce.

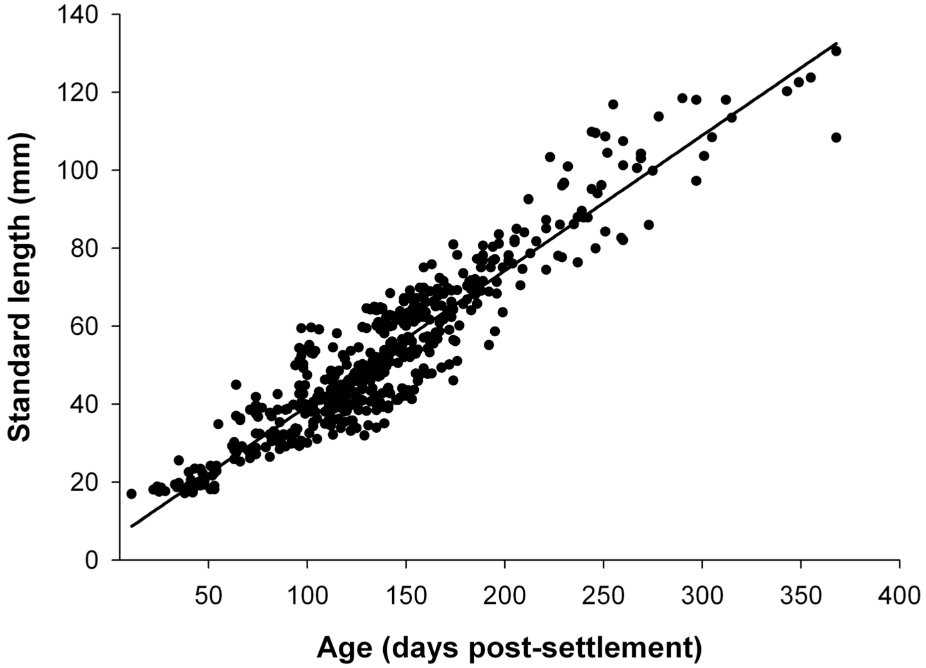

Fig. 3.2 *Lutjanus argentiventris*. Relationship between standard length and age after settlement estimated from lapilli of juveniles collected in Balandra between 2002 and 2005, and 11 additional mangroves during October 2003 and June 2004; $r^2 = 0.88$, $p < 0.0001$, $n = 516$

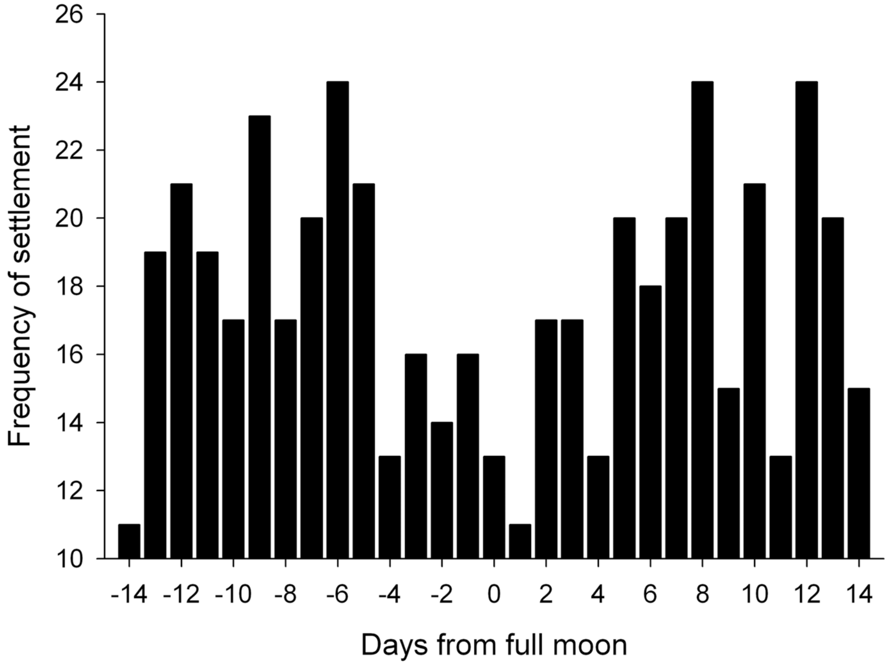

Fig. 3.3 *Lutjanus argentiventris*. Settlement frequency distribution obtained with back calculations of 516 lapilli otoliths. Zero represents full moon; -15 and 15 represent the previous and following new moons, respectively

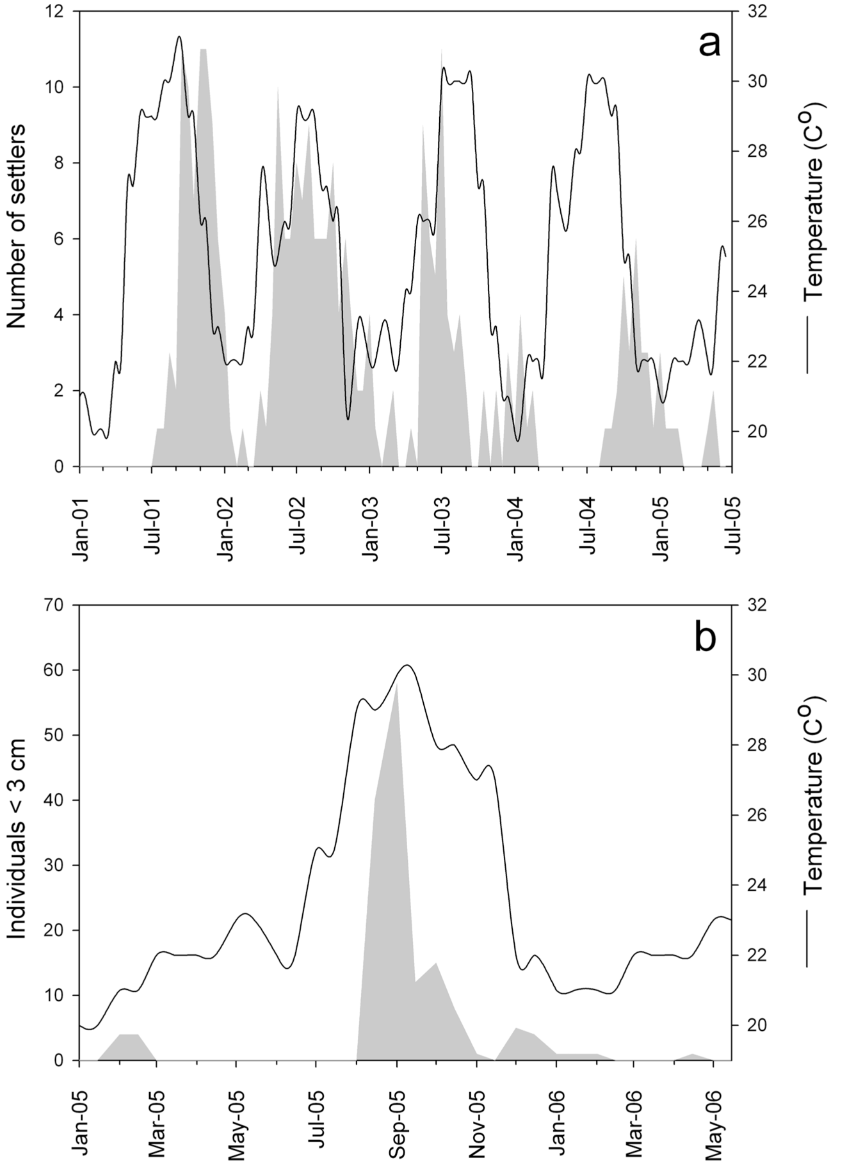

Fig. 3.4 *Lutjanus argentiventris*. Comparison of settlement time in Balandra as determined by (a) back-calculation from otoliths collected from 2002 to 2005, and (b) survey data between February 2005 and May 2006

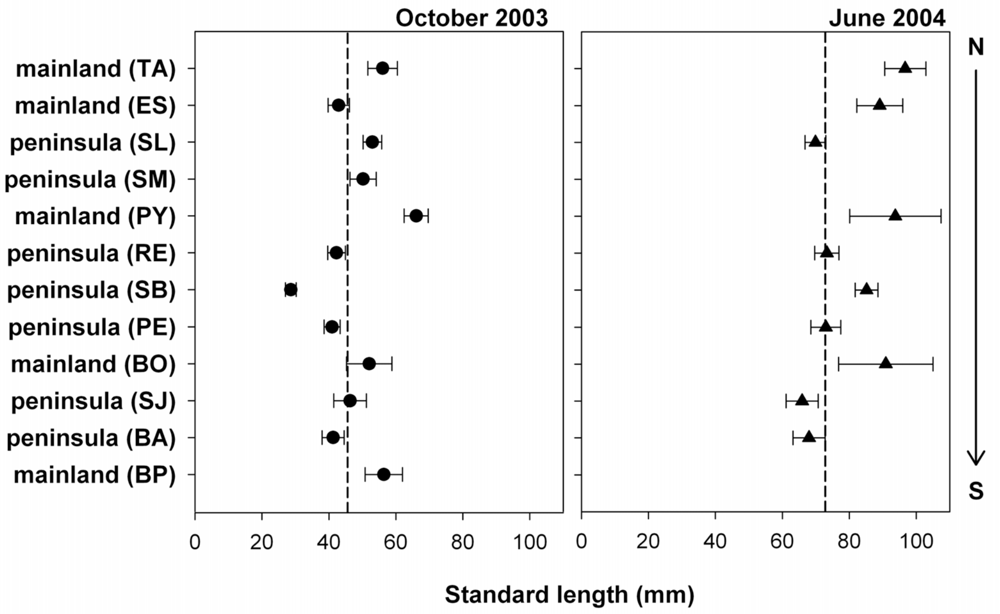

Fig. 3.5 *Lutjanus argentiventris*. Average size of juveniles collected inside mangrove forests along the Gulf of California, during the recruitment peak (October) and the end of nursery stage (June) of cohort 2003. Codes for sites are in Fig. 1 (SM and BP were not surveyed in June 2004 because of weather conditions). Data are means; whiskers are ± 95% Confidence Intervals; dashed line represents overall groups mean

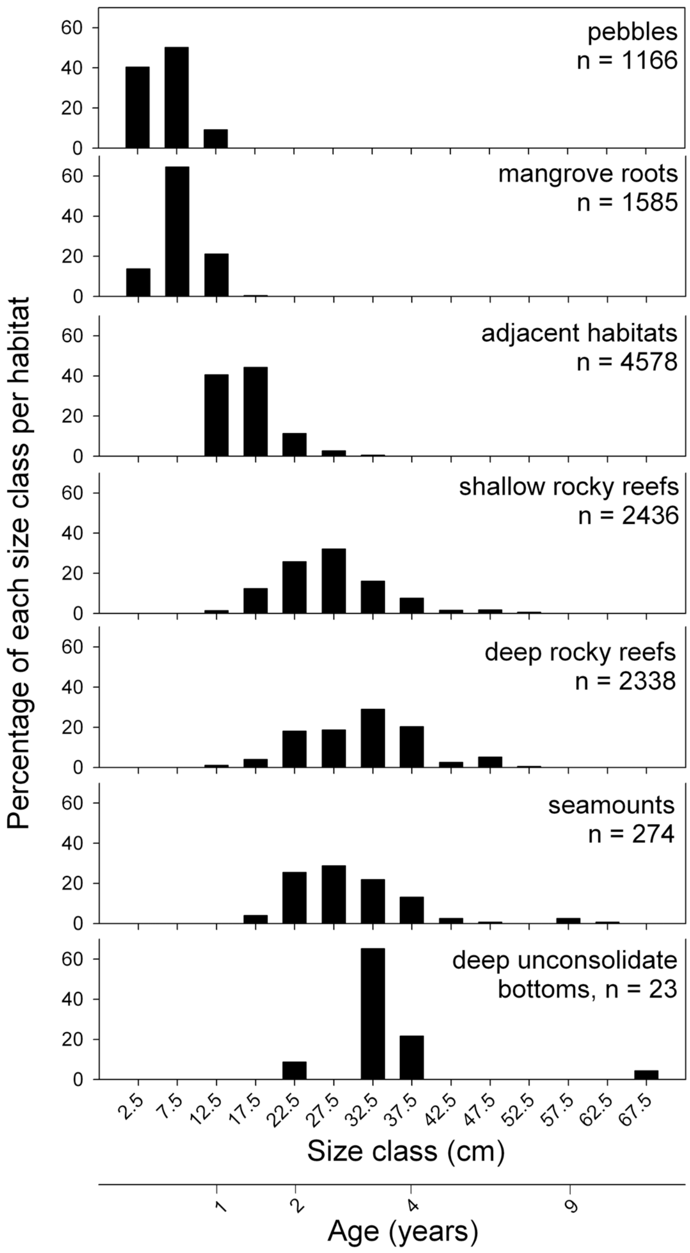

Fig. 3.6 *Lutjanus argentiventris*. Significant differences in size classes ontogenetic patterns of habitat use (df = 6, $p < 0.01$). Data are percentage of the abundance of each size-class in the underwater surveys for the major marine habitats and mangrove microhabitats (pebbles and mangrove prop-roots). Histogram bars represent size class ranges with the tick marks and scale numbers at the midpoints of the ranges

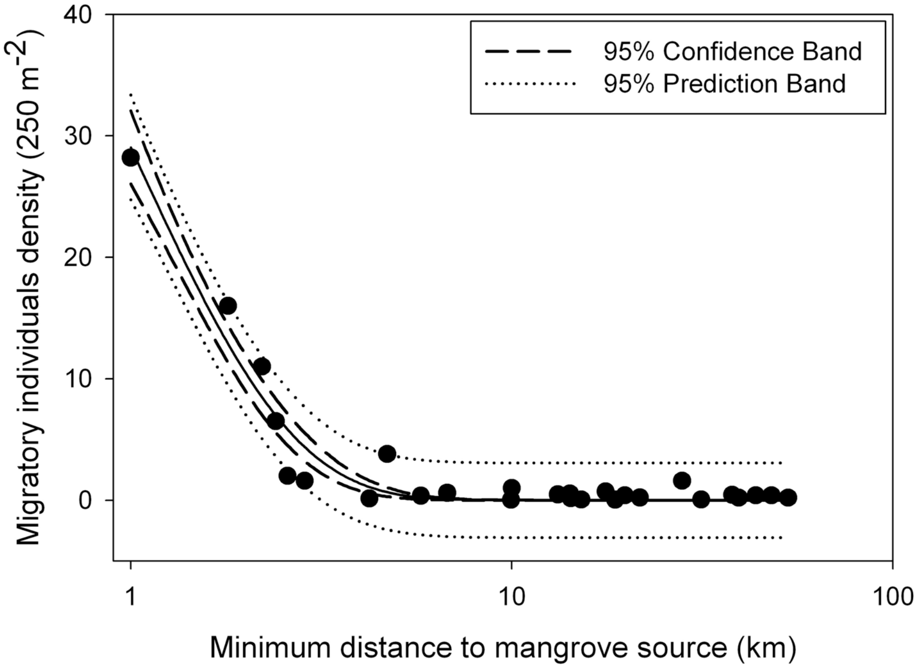

Fig. 3.7 *Lutjanus argentiventris*. Shows the relationship between nearest distance to mangrove and the density of individuals between10 and 20 cm size classes in each reef site; $r^2 = 0.94$, $p < 0.0001$. These sizes correspond to those migratory sub-adult individuals that just left mangroves

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CHAPTER 4

Spatially explicit contribution of mangroves ecosystems to the replenishment of reef fish populations

Abstract

Fisheries and coastal management are linked by the influence fish nurseries have on adult population dynamics. Whether all mangrove forests contribute equally to maintaining fish populations or if just a few mangrove nurseries with dense juveniles sustain several adult stocks elsewhere is still unknown. Our study of 51 isolated mangrove patches (14.1 ha ± 2.5 SE) shows that juvenile snapper abundance increases with suitable mangrove nursery area. We estimated a juvenile density export rate of 15,000 to 76,000 fish per km^2, with rocky mangrove systems contributing five times more juveniles per unit area than sandy systems. Our results indicate that the incorporation rate of these young individuals to offshore islands follows a negative exponential pattern, as the distance between the island and a mangrove source increased.

Introduction

Understanding the functional role that nursery habitats play in replenishing populations is critically important for the proper management of coastal development and fisheries (Fodrie & Levin 2008). Many fish species display a complex life cycle with: adults that feed and spawn offshore, larvae that settle within estuaries, and juveniles that develop inside an estuary until they leave to recruit in to adult populations elsewhere (Beck *et al.* 2001). There are several explanations for why some species have this complex life cycle; but in general terms, moving between habitats can maximize the evolutionary fitness of individuals (Morris 2006). For example, it has been shown that mangroves, which serve as an intermediary nursery habitat, increase the survivorship of many coral reef fish (Mumby *et al.* 2004). Most important, reefs near mangrove habitats have higher species richness, densities, and biomass than reefs far from mangroves or without any mangrove influence (Nagelkerken *et al.* 2002; Dorenbosch *et al.* 2004; Halpern 2004; Mumby *et al.* 2004).

Whilst many studies have identified nursery habitats as those occupied by juveniles of a species, the importance of juvenile habitats on a population level is only beginning to emerge (Mumby 2006). Not all nursery habitats receive and/or export the same number of individuals. The most common assumption in the literature is that the area of the nursery habitats and the distance between them and the adult habitats can indirectly represent their importance; for example, large mangrove areas closest to a reef would represent the highest rate of nursery productivity. Metapopulation and persistence of species on islands theories use this kind of hypothesis because, in part, mortality may be greater with increasing distance between patches or islands and the areas that serve as sources of individuals (Halpern 2004). Nevertheless, few studies have directly tested the role of these factors in controlling population sizes, and there have been few attempts (see Gillanders 2002; Fodrie & Levin 2008) to distinguish between nursery habitats that supply great numbers of individuals to adult habitats from those with lower productivity.

Here we examine the fish contribution of several isolated mangrove patches and its relation with Yellow snapper (*Lutjanus argentiventris*) population dynamics in eight islands in the Gulf of California. This region is the northern limit of the distribution of mangroves in the Eastern Pacific and, as it is happening worldwide, these mangrove forests are facing increasing pressure to be transformed into shrimp farms and coastal developments (Paez-Osuna *et al.* 2003; Glenn *et al.* 2006). The objective of this study was to quantify snapper recruitment by estimating the absolute abundance, survival, and spatial distribution of juveniles inside isolated mangrove patches. In addition, we aimed at determining whether the export rate of juveniles was related to the size of the mangrove, and whether distance from mangroves determines adult population size on the offshore islands.

Material and methods

Survey procedures

<u>The study species</u>.- We focused our study on the Yellow snapper (*Lutjanus argentiventris*), the most common snapper in the Gulf of California, and one of the most important species in small-scale fisheries in the region. It reaches sizes up to one meter in length, with a weight of 10 kilograms. This species can live up to 19 years, it reaches maturity after three years (Martinez-Andrade 2003), and it forms spawning aggregations in several islands in the southern Gulf of California (Sala *et al.* 2003). The Yellow snapper inhabits mangrove forests during their juvenile stage and rocky bottoms to at least 60 m in depth during adult stage.

Yellow snappers exhibit marked ontogenetic habitat shifts (Aburto-Oropeza *et al.* in review). Post-settlers (≈ 2 cm) recruit preferentially in pebble beds where they remain for 2 months, after which time they move to mangrove roots where they spend an average of 10 months in the nursery habitat provided by the roots. Juveniles leave mangroves when they reach between 10 and 15 cm in length. When they are still young (< 2 years old) they live in coastal shallow boulders and shallow rocky reefs. Older individuals are present mainly in deep rocky reefs (20 m) and less frequently in seamounts (30 m).

Most mangrove forests in Baja California and mainland Mexico receive larvae almost in a synchronized pattern. Estimated settlement dates ranged from early August to late January, with a major peak occurring from late September to early November (Aburto-Oropeza *et al.* in review); this means that only one cohort uses each mangrove forest in any given year.

<u>Temporal patterns of recruitment</u>.- In order to estimate the number of juvenile snappers that arrive and leave a nursery area, we established a well-coordinated monitoring program in one mangrove located 20 kilometers north of La Paz (Balandra, Fig. 1b), which included an important effort of fish surveys. Every four days on average (± 3.2 SD), from February 2005 through May 2006, we carried out underwater surveys by snorkeling using standard underwater visual belt transect survey methods (Harmelin-Vivien et al. 1985). To survey the entire spectrum of size classes, Balandra was divided into three microhabitats, based on previous observations

of habitat use by settler and juvenile snappers: pebbles (shallow areas with gentle slopes, covered by small rocks [< 1000 cm^3] over sandy bottoms), mangrove roots, and rocky boulders in the lagoon (Fig. 1b). To estimate the abundance of snappers, six replicate 50 × 1 m transects were surveyed on pebble beds, 50 × 2 m transects on mangrove roots, and six replicate 50 × 5 m transects were surveyed at the boulders. Transects were placed randomly on the substratum. Total length (TL) of yellow snappers was estimated to the nearest 1 cm for individuals less than 10 cm in length and every 5 cm for individuals bigger than 10 cm, with the help of plastic slots bearing the silhouettes and shapes of juvenile individuals of different sizes (< 10 cm), as well as 5 cm size intervals marked on a PVC plastic tube. Divers swam each transect at constant speed (about 15 min per transect), counting and estimating the size of all yellow snappers within 2.5 m to either side of the center line for boulders (250 m^2 transect area). In mangroves we surveyed snappers by swimming parallel to roots and counting fish 1 m inside and outside the prop roots (100 m^2). For pebble beds we counted fish in a band of 1 m along the 50 m (50 m^2).

Spatial patterns of recruitment.- To estimate the export rate of mangroves in Baja California, we surveyed the abundance and size structure of snapper juvenile populations inside mangroves (Fig. 1a). Before carrying out the snapper surveys, we completed field trips in 2005 and 2006 to survey all mangrove patches distributed in small bays and islands. Using small boats we were able to navigate inside the lagoons and performed hikes in the inland parts of the forests in order to take geographic bearings of the extent of mangrove trees. Our field data and observations were used as ground-truthing data points to map the patches as polygons using Google Earth™ software. These polygons were saved as KML files (a file format used to display geographic data in an Earth browser such as Google Earth, and which uses a tag-based structure with nested elements and attributes similar to the XML standard), to obtain the total area of the mapped mangrove patches using GE Path software (freeware, www.sgrillo.net).

On June 2007, eight months after the beginning of 2006 Yellow snapper cohort, we visited all the mangrove patches to estimate the abundance of juveniles that would leave the mangroves two months later. Snapper surveys were carried out as described in the above section. Although we counted Yellow snappers of all sizes, during this part of the study we included only individuals with a total length between 7 and 10 cm on mangrove roots. Due to adverse environmental conditions (e.g. low visibility, wind), we were able to survey only 36 (70%) isolated mangrove patches of the 51 recorded in this geographic range.

Islands spatial-temporal patterns.- To estimate the inter-annual variation in Yellow snapper arrival to islands, we carried out surveys in eight offshore rocky islands (Fig. 1a). Surveys were conducted every September from 1998 to 2007 using SCUBA and the visual census methodology described previously. At each site (Supplementary Fig. S1 and Table S1), Yellow snapper abundance was recorded on replicate 50 x 5 m transects (250 m^2; n = 4–6).

Analytical procedures

Life-history variables.- As the first step in our analysis we set, standardized, and estimated missing values of productivity parameters for Yellow snapper population dynamics, analyzing a collection of 2,272 individuals captured in mangroves, rocky reefs, and commercial catches along the entire study region. Ten life-history variables were estimated and compared our results with previous assessments carried out at different latitudes in order to validate our estimations (Table S2).

Nursery temporal patterns.- We estimated the magnitude of the 2004 Yellow snapper cohort recruited in Balandra mangrove and the average mortality rate for each of the size classes during the nursery stage by classifying the recorded individuals into the following six size classes:

1. Size class I (SC-I), individuals < 3 cm that have just settled and were recorded mainly in pebbles habitat.
2. SC-II, individuals between 4 and 6 cm that are in transit between pebbles and mangrove roots.
3. SC-III, individuals between 7 and 10 cm, which are the predominant size class living inside mangrove roots for their nursery stage.
4. SC-IV, individuals between 10 and 20 cm, which just came out of their nursery stage.
5. SC-V, individuals of 25 cm that have reached the 2 years of age.

6. SC-VI, individuals > 30 cm that have reached the maturity.

A total of 1,014 transects were performed during the sampling period with the following distribution between habitats: 337 in pebbles, 329 in mangroves and 348 in boulders. The densities of these six size classes were extrapolated to the suitable habitat in the three microhabitats to obtain the absolute abundance: 24,485 m^2 for pebbles; 70,470 m^2 for mangrove roots; and 36,025 m^2 for boulders.

We back-calculated the magnitude of the recruitment in 2004 using a cohort analysis (Jones 1984; Pauly 1984), with constant parameters and using relative abundances, since only natural mortality (no fishing) is affecting all the size classes at this stage. Constant parameters can describe the dynamics of the previous cohorts in a short period of time (< 5 years), especially natural mortality. The natural mortality (M) was estimated using Pauly's (1980) empirical equation relating M to $L\infty$, k, and mean environmental temperature (taken as 24ºC in this study given temperature ranges from 18 to 30ºC recorded inside the lagoon during the sampling period).

Nursery spatial patterns.- We hypothesized that the abundance of Yellow snappers would increase with the suitable nursery mangrove area. To test this hypothesis, and to have a function that describes this relationship, we used data recorded in the 36 surveyed mangroves and the suitable mangrove area available for the nursery stage.

Nursery area for snappers is represented by mangrove-water fringes normally occupied by red mangrove (*Rhizophora mangle*). These mangrove fringes have different widths depending of the geomorphology of the coast, but they are replaced further inland by a mudflat forest dominated by white and black mangroves (*Laguncularia racemosa* and *Avicennia germinans*). To estimate the length of the mangrove fringe in each mangrove patch, we followed the method described by Aburto et al. (2008), which establishes that the fringe-to-square root of mangrove area ratio is a constant value of 6.13, unrelated to mangrove size or location. The total area of mangrove for each patch was estimated using the polygons obtained during the field trips in 2005 and 2006 (see Spatial patterns of recruitment).

We estimated the width of the fringe measuring different distances from the mangrove in contact with the water to the submerged back forest (see Fig. S2). Based on the size of the mangrove patch, we did several of these measurements covering different widths of the fringe (6.7 measurements ± 0.3 SE). Because it has been shown that physical-chemical conditions change drastically after 40 m from the *Rhizophora* fringe to the inland mudflat (López-Portillo & Ezcurra 1989), and this distance coincide with maximum inner distribution of several species of fish (Vance *et al.* 1996; Rönnbäck *et al.* 1999), we calculated the suitable area for Yellow snapper juveniles using the actual average distance calculated in mangroves patches with less than 40 m of fringe width (29), and a maximum distance of 40 m in the rest of them (22).

A preliminary analysis of the results showed that mangrove position and mangrove habitat characteristics were important factors in determining Yellow snapper abundance. Based on the regional geographic divisions that have been described for the Gulf of California (Sala *et al.* 2002), we pulled together the mangrove patches in two regions: (1) Central gulf, which includes mangroves distributed between the latitudes 25.5º and 27.5º N; and (2) Southern gulf, between latitudes 24º and 25.5º N. Furthermore, based on their habitat characteristics, we classified the mangrove patches within each region in two groups: (1) Sandy Systems, which include mangrove forests with 100% of the area, inside and adjacent (< 100 m) to the lagoon, with sand habitats; and (2) Rocky Systems, which include mangrove forests with at least 50% of the area, inside and adjacent to lagoon, with rocky habitats. A multivariate linear regression was performed to test whether increasing mangrove area causes increasing Yellow snapper density, using region and habitat characteristics as interaction factors.

Islands spatial-temporal patterns.- As the final step in the analysis we hypothesized that the Yellow snapper's adult grounds on offshore islands, receive the individuals "produced" by the mangrove patches in relation to the distance between these grounds and mangrove sources. To test the hypothesis, first we set the following assumptions:

(1) Yellow snapper populations in islands are isolated from the rest; as occur with other Lutjanids (Meyer et al. 2007) we assumed that there are not inter-islands movements of adult individuals.

(2) Since size class structure is skewed to bigger individuals in farther islands (Aburto *et al.* in review), we assumed that the natural mortality of individuals is lower as the distance between an island and a mangrove source increased.

(3) Every population in an island is regulated by carrying capacity.

(4) Every month of the year there is a continuous arrival of individuals.

(5) Fishing pressure (fishing effort and fishing methods) is similar in all islands.

Second, we used the total number-at-size during the 10 years of data recorded in each island as the input for a "model" size structure. All these frequencies were normally distributed, with correlation coefficients (r^2) within the observed data and normalized data between 0.80 and 0.85. With the frequency size distribution of individuals observed and the life history variables (asymptotic length, *Linf*, and growth rate, *k*; Table S2) the size of the "general" year class was reconstructed for each island using a virtual population analysis (VPA). The output of the model is a succession of abundance predictions, all per length group (Table S3).

In order to be comparable, the outputs of the VPA were used to calculate the relative contribution of each size class in each island. We plotted these relative values to obtain the annual slopes that correspond to: (1) the incorporation rate, which refers to the immature individuals < 30 cm that have just arrived to the population; and (2) the loss rate, which refers to mature individuals > 30 cm with more than 3 years of age.

We only used the incorporation rate to test the hypothesis since a steeper slope reflects a faster incorporation of individuals into the system or island. For this purpose we established the nearest distance between sites in the island and one of the 51 mangroves (Table S1). For interpretation principles, a system (island) closest to a mangrove sources will be saturated faster until it reaches the carrying capacity without losing its normally size structure.

Finally, we used the average density of individuals less than 30 cm TL in the 10 years of data to estimate the amount of individuals per unit of area that have arrived to the island per year. The average value of these estimations was used to evaluate the incorporation rate in each island. A total of 1,229 transects of 250 m^2 were performed in this period of time, with an annual average of 16 (± 1 SE) per island.

Results

Nursery temporal patterns

We recorded the last part of the recruitment season of 2004 and the entire recruitment season for 2005-06 inside Balandra mangrove (Fig. 2). Settlement began in the middle of August in pebble beds, and continued in the same habitat until the beginning of November. A second smaller settlement started inside mangrove roots at the end of September, and continued in the same habitat until the beginning of February 2006 (see arrows in Fig. 2). Settlement was significantly higher in pebbles than in mangrove roots ($F = 7.22$, $P < 0.001$), with a maximum density of one recruit per 10 m^2 during the first two weeks of September. Our observations suggest that saturation of pebbles was the consequence of the settlement of individuals directly to mangrove roots. The back-calculated magnitude of the recruitment (individuals < 3 cm) for the cohort 2004 in Balandra was 26,473 individuals (Table S4).

For cohort 2004-05 the maximum density of transient individuals (SC-II) in pebble beds was during the last week of February (4th week). Three weeks later, the same size class had its maximum inside mangrove roots. The following size class (SC-III), the most abundant inside mangrove roots, had its maximum during the 34th and 28th weeks in pebbles and mangroves roots respectively. This means an average of 26.5 weeks between the maximum densities of SC-II and SC-III size classes. The maximum density of individuals of size SC-IV, those that are migrating to boulders, was recorded on week 41st which corresponds to the second week of November 2005. This last value represents a time lapse of 12 weeks between the maximum densities of SC-III and SC-IV.

The survivorship of *Lutjanus argentiventris* juveniles inside Balandra followed a Type I survivorship curve ($\ln[l(x)]$, where there was high survivorship during settlement and mangrove roots stages, then a steep drop-off in survivorship as individuals move to rocky boulders adjacent to the cove. The probability of an individual in size class SC-III (inside mangrove roots) of surviving to size class SC-IV (migrate to boulders), had a value of 0.648 (see [*g(x)*] Table S4).

Nursery spatial patterns

The abundance of Yellow snapper was linearly related to the suitable area of mangrove (Fig. 3). There was a significant difference ($p<0.001$) in densities between rocky and sandy systems, which explained 42% of the variability, and between regions ($r^2=0.81$, $p<0.001$; Table S5).

We estimated a total of 135,326 individuals produced by all the 51 mangrove patches for the Yellow snapper 2007 cohort (Table S6). Together, rocky mangroves contributed with 59.85% of the juveniles, although they represent only 31.4% of the suitable area estimated. The mangrove patches located in the southern gulf represented 73.99% of the productive area calculated, and they contributed with 67.04% of individuals exported to rocky reefs in the study region. Between mangrove type and region, the values from high to low followed this ranking: Southern rocky systems = 720 fish/ha, Central rocky systems = 559 fish/ha, Central sandy systems = 343 fish/ha, and Southern sandy systems = 152 fish/ha (Table S6).

Islands spatial-temporal patterns

Inter-annual variations in the density of individuals < 30 cm were significant between islands (*Two way ANOVA* F= 1.48, df= 63, p = 0.016). The highest average of individuals per hectare was recorded in 2005 (72.9 ind), while the lowest value corresponded to 2002 (12.3 ind) (Table 1). The incorporation rate of individuals < 30 cm to the islands followed a negative exponential pattern ($r^2 = 0.64$, $F = 10.87$, $p < 0.05$), as the distance between the island and a mangrove source increased (Fig. 4). In general, islands with a mangrove source less than 20 km had more than 40 individuals per hectare in average; while islands with a mangrove source farther than 30 km, had an average of less than 20 individuals per hectare.

Discussion

Habitat disturbance and alteration has become one of the main human stressors for coastal and marine communities (Dayton et al., 2002). The Gulf of California is not exempt from this phenomenon, and there are many cases where economic activities are in conflict with the sustainability of marine and coastal ecosystems. In particular, estuaries and coastal lagoons are disappearing at an annual rate of 2.5% on a national level (INE, 2005) because shrimp farming (Glenn et al., 2006), pollution (Paez-Osuna et al., 1999, 2003), and tourism developments (Ortiz-Lozano et al., 2005). The deterioration of these types of habitats affects a great number of marine species such as blue crabs, mollusks and fish, and also has negative impacts on migratory bird species that use them as feeding or resting areas during their migration. Our results emphasize the important contribution of coastal mangroves to fish population on offshore islands, and highlight the indirect and irreparable damage to fisheries if the trend of mangrove loss continues.

Juveniles (SC-I) settle as a single cohort during fall 2005 in pebbles habitat and continue this process until the beginning of winter 2006 inside mangrove roots. Approximately ten months later (summer months), juveniles (SC-III) were inside mangrove roots. Migratory juveniles (SC-IV) appeared one year later during the summer months. Our results and observations suggest an accumulation of individuals in rocky points outside Balandra cove. Before the winter season they had disappeared and few individuals larger than 20 cm were rarely seen on rocky boulders. This coordinated migratory behavior is associated to weather patterns or rapid declines in water temperature (Mullaney & Gale 1996). We estimated a juvenile Yellow snapper density export rate from 15,000 fish per km^2, corresponding to the less productive sandy systems, to 76,000 fish per km^2 from rocky systems located in the southern region of Baja California peninsula. Similar results have been described for species associated to sea grass beds (*Mycteroperca microlepis* ≈ 50,000 fish/km^2; Koenig & Coleman 1998). Although juvenile growth and mortality rates can be relatively similar among estuaries (Kramer 1991), it is pertinent to consider a moderate decrease in the total amount of individuals exported, especially since we calculated survival rates using only data from a rocky mangrove (Balandra). For example, a decrease of 10% in the survival probability of individuals coming from sandy systems would represent a 5% in the overall amount of individuals exported.

Although we did not tag individuals nor used elemental fingerprinting (Gillanders & Kingsford 1996, 2000), our results resemble those observed in species that use estuaries as nurseries (Fodrie & Levin 2008), suggesting that individuals did not migrate very far from their nursery origin. Several studies have shown that populations of mangrove-nursery species are denser within a few kilometers from mangrove sources (Nagelkerken 2002; Dorenbosch et al. 2004), and support the idea that there is little exchange of individuals between populations or fishery stocks (Gillanders 2002). The density of immature migratory Yellow snapper of sizes between 10 and 20 cm decreased exponentially as the distance between a reef and a mangrove source increased (Aburto-Oropeza et al. in review). In the same way, our results showed that the incorporation rate of individuals < 30 cm to the islands followed a negative exponentially pattern as the distance increased from a mangrove source.

Because year-class strength is probably established in juvenile stages (Aburto-Oropeza et al. 2007), quantitative juvenile abundance estimates provide promising alternatives to traditional management models and could vastly improve our current ability to assess stocks (Koenig & Coleman 1998). Snapper landings in the Gulf of California (excluding red snapper) total over 300 tons per year, around 5% of all commercial reef fish species. The Yellow snapper is one of the most important due to its abundance and size. In the Loreto region alone, this species corresponds to 40% of the total landings of snapper biomass and 7% of the total reef fish biomass captured inside the Loreto National Marine Park (Randall et al. 2005). However, the price per kilogram is less than 2 dollars. Fishermen catch this species using hook-and-line, spear fishing, and gillnets, and the fishery is run throughout year. It is common to find individuals as small as 15 cm in the market; a size that is far from the length at first maturity (around 30 cm) when they reach the 3rd year of age (Martinez-Andrade 2003). Our results have important implications for developing alternative stock assessment methods that are different from the fishery-dependent methods. For example:

1. Modeling the maximum annual export rate to estimate quotas.- Because recruitment variability is preserved in the structure of the adult population, a continuous mangrove-monitoring program could allow adaptive management without expensive stock assessments. Fishing quotas could be set and reevaluated annually based on the recruitment season. In a preliminary approach to understand Yellow snapper population variability (Aburto-Oropeza et al. unpublished data), we have performed a regression analysis between annual densities of individuals with less than two years of age and the Multivariate ENSO Index (MEI) as a measure of climate variability. Forty five percent of the population variability is explained by a lag of two years in the MEI (the time when these individuals settled in mangroves). These results suggest that juvenile snappers are strongly affected by climatic variability as occurs with several species that use estuarine systems as nurseries in other latitudes (Attrill & Power 2002), or such as species that settle in coastal habitats in the Gulf of California (Aburto *et al.* 2007).
2. Adjust the fishing effort according to the cover of mangrove types.- Habitat quality has important effects on juvenile growth and survival. On one hand, we

showed that rocky systems enhance the densities of Yellow snapper; this type of mangroves produced almost 3 times the exported number of individuals for the cohort 2007. On the other hand, mangrove patches present in the southern gulf represent almost 70% of this ecosystem in the study region, all together representing almost 250 hectares of suitable area for commercial species. Taking this into account, fishing effort on Yellow snapper should be decreased in the central gulf with respect to the effort in the southern gulf.

3. Adjust the fishing effort on fishing grounds (rocky reefs) according to the distance to mangrove sources.- Our results allow for the possibility to model the distribution of biomass of Yellow snappers depending on the size and kind of a mangrove patch, the distance from the patch, the distribution of different marine habitats and bathymetry (Aburto et al. in review), in addition to other oceanographic characteristics. Consequently, we can adjust fishing pressure in relation to biomass distribution.

The modification of water flows through construction of marinas and channels is the second most important threat for these ecosystems in the Gulf of California; just in one area enclosed in this study (La Paz area), 23% of the mangrove forests were eliminated between 1973 and 1981 due to coastal developments (Whitmore *et al.* 2006). Although we do not have snapper fishing statistics for those years, we believe no changes related to the decline of mangrove would be shown because most of the snapper fisheries (mainly the Yellow snapper) have only recently become important due to the decline of larger marine predators (Sala *et al.* 2004, Sáenz-Arroyo *et al.* 2005). However, our quantitative estimates of the potential production can be associated with the future economic losses that the loss of productive mangrove areas can bring. These local economic estimations, together with regional economic assessments (Aburto-Oropeza *et al.* 2008), support the adoption of more firm measures to protect these habitats.

In our study region, southern rocky systems can contribute five times more Yellow snappers per unit area than southern sandy systems; although, central rocky systems only contribute 1.5 more individuals per unit area than central sandy ones. Nevertheless, even within sandy mangroves we were able to establish the relative unit-area production value for each mangrove patch, which according to Beck *et al.* (2001), the ones above the average can be considered as the main species nurseries. In particular with sandy mangroves in the southern gulf, these nurseries are located on islands and near the biggest city in the southern Baja California peninsula (La Paz). Pressure on mangroves will increase as local communities continue to grow. Thus, our results highlight the consequences of mangroves loss to fish populations and local economies, and could improve help in the coastal management and the design of sound fishery regulations.

Acknowledgements

We would like to thank C. Anderson, E. Ezcurra, L. Fichman, A. Mendoza, G. Paredes, C. Sánchez, and C. Viesca for their help on density data, otolith analisis and statistics. Special thanks to C. López, P. Hastings, P. Hull, and L. Levin. This study was funded by the Moore Family Foundation, the David and Lucille Packard Foundation, The Tinker Foundation, the Robins Family Foundation, The Walton Family Foundation, PADI aware project, and the Gulf of California Program of the World Wildlife Fund.

Table 4.1 Summary of the islands characteristics and the density of Yellow snapper < 30 cm in the 10 years of the study.

	Sampling year (ind ha^{-1})									
Island	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007
Animas	117.3	156.7	40.0	48.9	0.0	162.6	66.7	186.7	53.3	63.3
Ballena	80.0	136.0	0.0	186.7	16.0	10.0	23.3	30.0	10.0	70.0
Carmen	5.2	8.0	3.9	12.0	4.0	12.5	11.0	19.5	35.8	5.0
Coronado	80.8	47.3	10.0	3.3	12.5	131.7	5.7	163.3	16.0	56.7
Danzante	1.1	0.0	5.7	3.4	0.0	7.1	0.0	0.0	0.0	0.0
Espiritu Santo	2.7	96.1	35.6	0.0	10.7	0.0	285.6	50.0	0.0	66.7
Islotes	0.0	28.9	92.0	0.0	12.0	0.0	8.9	160.0	13.3	33.3
Montserrat	46.0	0.0	0.0	40.0	36.0	20.0	5.0	2.5	10.0	0.0
Average	41.64	60.15	24.13	42.08	12.31	46.61	40.09	72.94	17.87	36.87

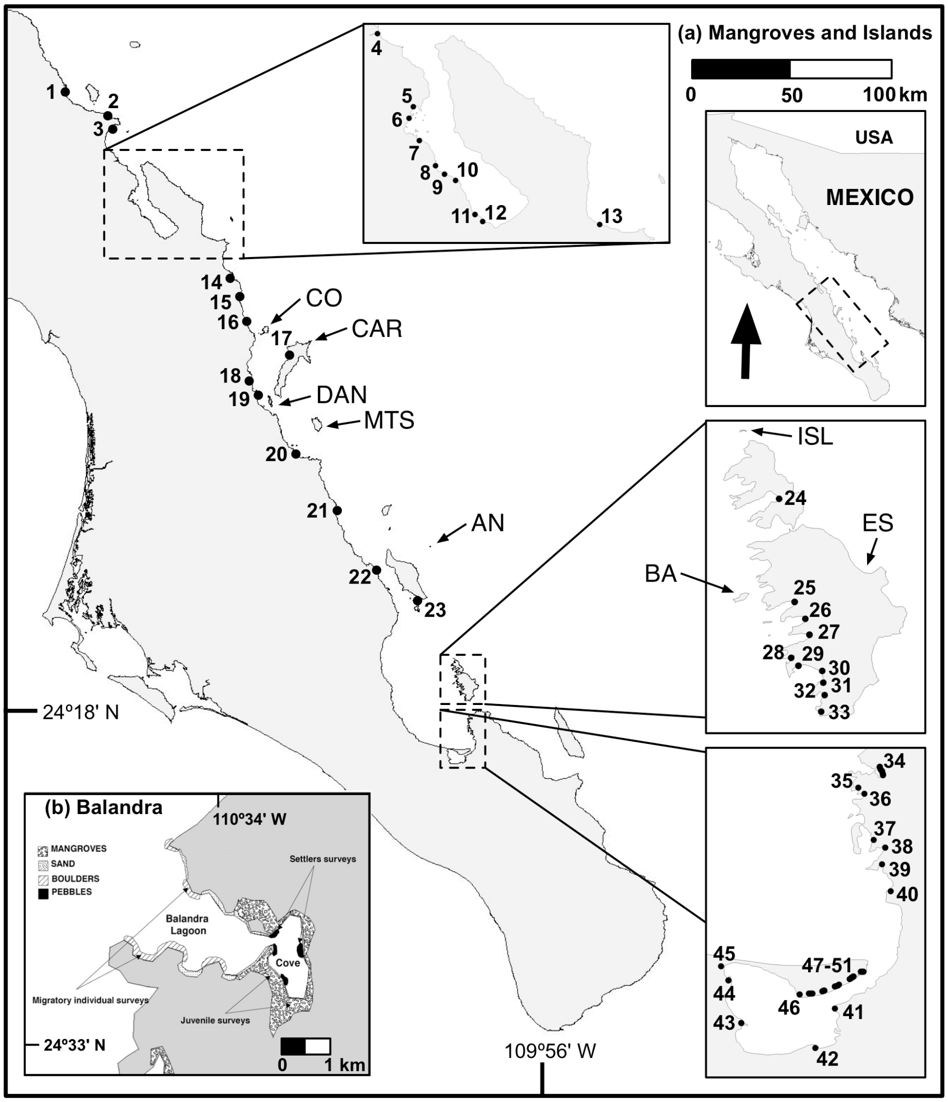

Fig. 4.1 Map of the Gulf of California showing (a) the location of all mangrove and islands studied. Detailed location information for each island survey sites can be found in Figure S1 and Table S1. Lower left bottom box (b) shows details about microhabitats of Balandra lagoon and mangrove cove, where the number of juvenile snappers was monitored every four days (± 3.2 [SD]).

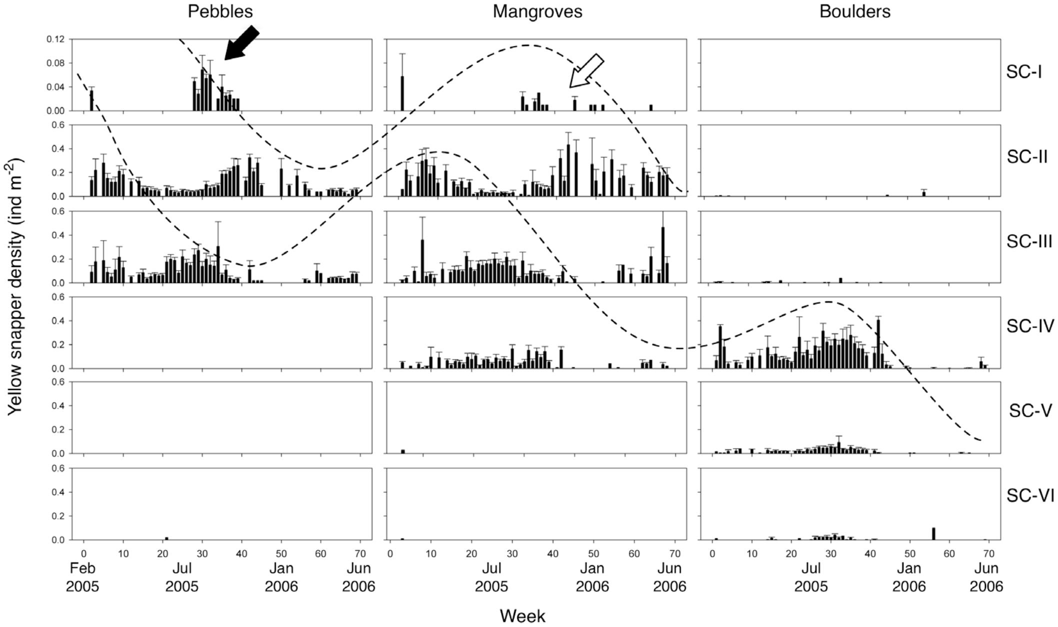

Fig. 4.2 Mean and standard error for the six size classes, in the three habitats surveyed in Balandra mangrove (see Fig. 1 for details). Note that density scale of SC-I is different from the rest of size classes, in order to show the magnitud of settlement in pebbles (black arrow) and the second settlement pattern ocurred in mangroves (white arrow). Dashed line represents the movement of the cohort in time and between habitats.

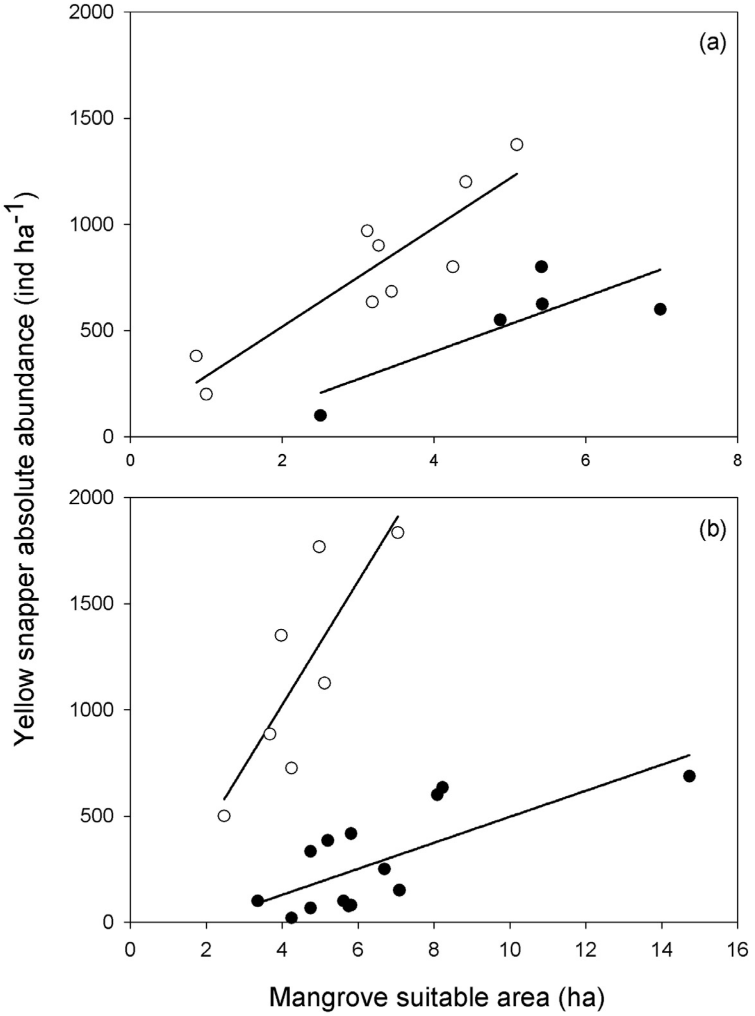

Fig. 4.3 Absolute abundance plotted against mangrove suitable area for rocky systems (○) and sandy systems (●), in central (a) and southern (b) Gulf of California. Data correspond to estimations of suitable area obtained using the average fringe width in mangrove patches with less than 40 m of fringe width (AFW<40; see Table 2). Southern rocky systems (y = 291.02x – 141.46, r^2 = 0.66, P = 0.025) can contribute 5 times more Yellow snappers per unit area than southern sandy systems (y = 61.24x – 116.13, r^2 = 0.52, P < 0.01); although, central rocky systems (y = 232.60x + 52.83, r^2 = 0.81, P < 0.01) only contribute 1.5 more individuals per unit area than central sandy systems (y = 129.39x – 117.30, r^2 = 0.65, P = 0.1).

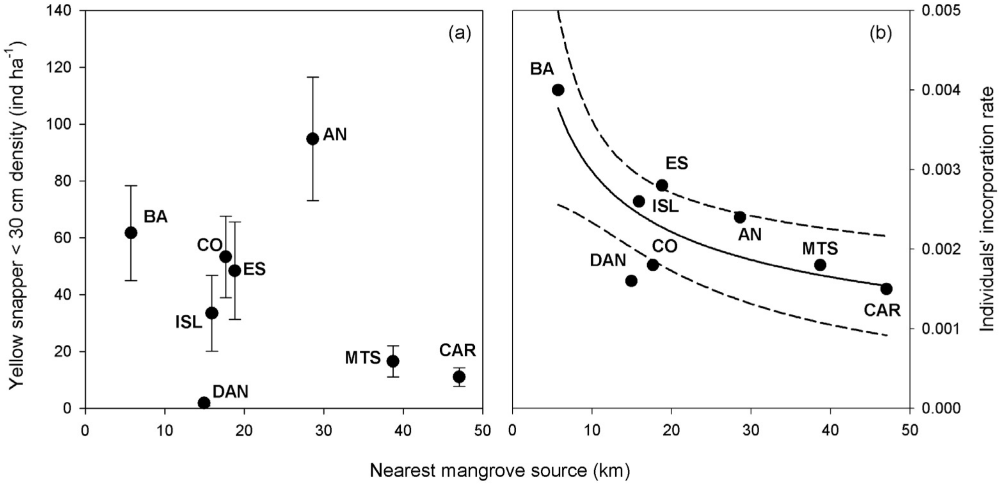

Fig. 4.4 Relationship between density of immature individuals (a) and individual incorporation rate (b) in offshore islands, and the distance from the nearest mangrove patch. Data correspond to 1,229 transects of 250 m^2, performed in period of time of 10 years, with an annual average of 16 (± 1 SE) per island. The individuals' incorporation rate refers to the slopes of immature individuals < 30 cm that arrive to each island population, and was estimated using a virtual population analysis (see Table S3): $y = 0.0079x$^ -0.425, $r^2 = 0.64$, $P = 0.0165$.

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CHAPTER 5

Climatic influence on reef fish recruitment and fisheries

Abstract

We monitored the abundance of two important commercial reef fish (yellow snapper and leopard grouper) using visual underwater surveys, and compiled fisheries landing statistics over 11 years in the Gulf of California, Mexico. For both species, increasing recruitment translated into greater fisheries landings once individuals recruited into fishing stocks, and can be predicted based on the climatic variation at the moment of settlement. During the "plenty fishing years", these fisheries have significant fold increases in revenues. These results can provide a model to predict fluctuations in reef fish abundance and adapt artisanal fisheries management ahead of time.

Main text

Climate and oceanographic variability can cause the abundance of commercial fish stocks to fluctuate (*1*). Understanding the link between climatic change and these fluctuations could allow us to forecast the size of stocks and manage fisheries accordingly. However, the mechanisms that explain fish abundance and thus fisheries catches are poorly understood (*2*). We monitored the abundance of two important commercial reef fish species using visual underwater surveys (*3*), and compiled fisheries landing statistics over 11 years in the Gulf of California, Mexico, to determine whether it is possible to predict fish recruitment and landings based on available a priori climate indices.

We determined that the Multivariate ENSO Index (MEI), a positive correlate of water temperature and a negative correlate of nutrient availability in the Pacific Ocean, explained the abundance of juveniles and fisheries landings for the yellow snapper (*Lutjanus argentiventris*) and the leopard grouper (*Mycteroperca rosacea*). For both species, increasing recruitment translated into greater fisheries landings once individuals recruited into fishing stocks (*4*), and can be predicted based on MEI values at the moment of settlement (*5*).

After the yellow snapper larvae settle in mangroves, the juveniles move to shallow rocky habitats where they mature. Adults then move to deep rocky reefs (*6*). Abundance of yellow snappers in rocky islands and fisheries catches increased with increasing MEI at 2 and 4 years post-settlement respectively (Fig. 1A-B). In contrast to the yellow snapper, leopard grouper larvae settle in shallow *Sargassum* seaweed beds in rocky coasts and move to deeper habitats as they grow. Because the seasonal nursery habitat (*Sargassum* beds) is virtually non-existent in warmer, nutrient-poor years (*7*), recruitment of the leopard grouper decreased exponentially with increasing MEI (Fig. 1C). Leopard grouper landings were significantly correlated with MEI values with a seven-year time lag (Fig. 1D). Fisheries of these species represent an important income for several hundred fishers in the region and, during the "plenty fishing years", these fisheries have significant fold increases in revenues (3.7 and 5-fold for yellow snapper and leopard grouper respectively).

Predicting the magnitude of fisheries catches based on environmental variables is relatively straightforward when the time lag between the former and the latter is only of a few months [e.g., pelagic-migratory species such as sardines (*8*), or mackerels (*9*)]. For species with complex life cycles including ontogenetic habitat shifts that last years, predicting abundance and catch years in advance is more problematic. The present study, however, shows that standard underwater visual surveys combined with traditional fisheries statistics can provide a model to predict fluctuations in abundance over time. More importantly, such simple models could be used to adapt artisanal fisheries management ahead of time, regulating effort or setting quotas based on expected climate-mediated recruitment of fish into adult populations.

Notes

1. Attrill et al., Nature **417**, 275-278 (2002).
2. Hollowed et al., Progress in Oceanography **49**, 257–282 (2001).
3. Materials and methods are available on *Science* Online.
4. The average age of the yellow snapper from fishing catches is four years, and seven years for leopard grouper (Fig. S1).
5. We used MEI values at the time of settlement: May-June for the leopard grouper (*7*) and September-October for the yellow snapper (*6*).
6. Aburto-Oropeza O., “Metapopulation model for yellow snapper” (Tech, Rep. CMBC, Scripps Institution of Oceanography, San Diego CA, 2006)
7. Aburto-Oropeza et al., Ecology **88**, 2220-2228 (2007)
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Materials and Methods

The study species

The yellow snapper (*Lutjanus argentiventris*) and the leopard grouper (*Mycteroperca rosacea*) have complex life cycles; they spawn around rocky islands (S1), their larvae travel to and settle on shallow coastal habitats (mangroves and *Sargassum* seaweed beds, respectively), and juveniles travel to adult habitats over a 2-year period. Both species are very important for small-scale fisheries in the Gulf of California, and have suffered overfishing impacts in some areas (S2).

The yellow snapper, a tropical species of Panama origin, is distributed from the Gulf of California to Peru and inhabits rocky bottoms down to at least 60 m in depth (S3). These fish reach sizes up to 1 m in length, a weight of 10 kilograms, reach maturity after three years, and can live up to 19 years. The leopard grouper is endemic to Mexico, from Bahía Magdalena on the Pacific coast of Baja California, throughout the Gulf of California from the northern most rocky reefs at Rocas Consag to southern Jalisco. This species grows up to 1 m in length and can live up to 32 years (S4).

Abundance of juvenile fish

To estimate the inter-annual variation in yellow snapper and leopard grouper, we surveyed 21 rocky reefs in the central and southern parts of the Gulf of California (Table S1). Data were collected every September from 1998 to 2008 by SCUBA divers using 50 × 5 m line transects (n = 4-6 replicate transects per site and habitat), counting all individuals belonging to different size classes. Transects were placed randomly on the substratum. Total length (TL) of yellow snappers and leopard grouper was estimated every 5 cm, with the help of a PVC plastic tube with marked intervals. Divers swam each transect at constant speed (about 15 min per transect), counting and estimating the size of all individuals within 2.5 m to either side of the center line (250 m^2 transect area).

Although we counted individuals of all sizes, we included only leopard grouper individuals with a total length up to 15 cm TL, since they were young of the year. However, since young of the year for yellow snapper are present only inside mangroves, we used individuals with a total length between 15 and 25 cm TL, which correspond to the smaller sizes that are seen in the rocky reefs and are 2 years old.

Landings data

We considered landing data for the yellow snapper and the leopard grouper from the National Fisheries Commission (CONAPESCA), in the State of Baja California Sur. Along the 400 km-long stretch of coast of Baja California Sur, these records are publicly available by request in any local office in each municipality. We worked with a database containing the fishing records from the town of Santa Rosalia and the city of La Paz. With the exception of the year 2004, landings were reported from 1999 to 2007. Although the statistics have specific-categories, an important volume of landings were registered as generic categories: “pargos” (snappers), and “cabrillas” (groupers). Fortunately, we could reasonably convert from the generic to the species level, because a previous detailed study (S5) had shown that yellow snapper and leopard grouper accounted for 40% and 90% of the "snapper and grouper" categories, respectively. The converted data were subsequently added to the species-level data to give the total landings of these two species along the coast of Baja California Sur.

In order to have the size structure of the individuals exploited in the region, we monitored 4 fishing cooperatives and 10 fishing towns from March 2007 to January 2009. Total length (to the nearest mm) and weight (to the nearest g) data were collected from yellow snappers and leopard groupers caught by artisanal fishers. In order to calculate the mean age of the catch, we used the mean size of the catch (Fig. S1) and calculated the age of an individual within this size using the Bertalanfy (1967) growth model. For yellow snapper the variables used (age at length zero [*t0*], asymptotic length [*Linf*], and growth rate [*k*]) were obtained from Martinez-Andrade (2003; S7); for leopard grouper the variables were obtained from Díaz-Uribe et al. (2001; S8)

Climate variability

We explored the relationship between the reef fish species and their fisheries, 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 (S6) is a quantitative classification scheme that combines the most important component variables of ENSO for the tropical Pacific (308 S to 308

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 (*http://www.cdc.noaa.gov/*).

We used MEI values at the time of settlement: May-June for the leopard grouper and September-October for the yellow snapper.

Acknowledgments

We thank J. Cota, A. Mendoza, T. Plomozo, C. Sánchez, and C. Viesca for field assistance and N. Holland, P. Hull, and C. Lopez who improved previous versions. This work was supported by the David and Lucille Packard Foundation, the Moore Family Foundation, and the Walton Family Foundation.

Table 5.1 Sites surveyed each year from 1998 to 2008 in the central and southern Gulf of California. At each site, fish abundance was recorded on replicate 50 x 5 m transects (250 m^2; *n* = 4–6).

Island	Name	Major rocky habitat	Latitud	Longitud	Depth range (m)
Coronado	Mono	Boulders	26.136	-111.279	20
	Lajas	Wall	26.127	-111.259	> 20
	Piedra Blanca	Wall	26.100	-111.260	20
Carmen	Tintorera	Boulders	26.060	-111.150	10
	Punta Lobos	Boulders	26.060	-111.080	20
	Punta Perico	Boulders	25.970	-111.080	15
Danzante	Viznaga	Wall	25.815	-111.259	> 30
	Punta Este	Boulders	25.790	-111.240	20
	Submarino	Boulders	25.770	-111.250	> 20
	Punta Noroeste	Boulders	25.800	-111.260	10
Montserrat	Reinita	Boulders	25.780	-111.070	10
	Galeras	Boulders	25.740	-111.060	10
	Punta Sureste	Boulders	25.680	-111.011	20
Animas	Pinaculos	Boulders	25.090	-110.560	> 30
	Pared	Wall	25.090	-110.490	> 30
Islotes	Bloques	Boulders	24.588	-110.416	25
	Arco	Wall	24.588	-110.456	15
Espiritu Santo	Aguja	Boulders	24.590	-110.390	20
	Pailebote	Boulders	24.510	-110.310	10
	Punta Lobos	Boulders	24.460	-110.460	20
Ballena	Ballena	Boulders	24.480	-110.410	10

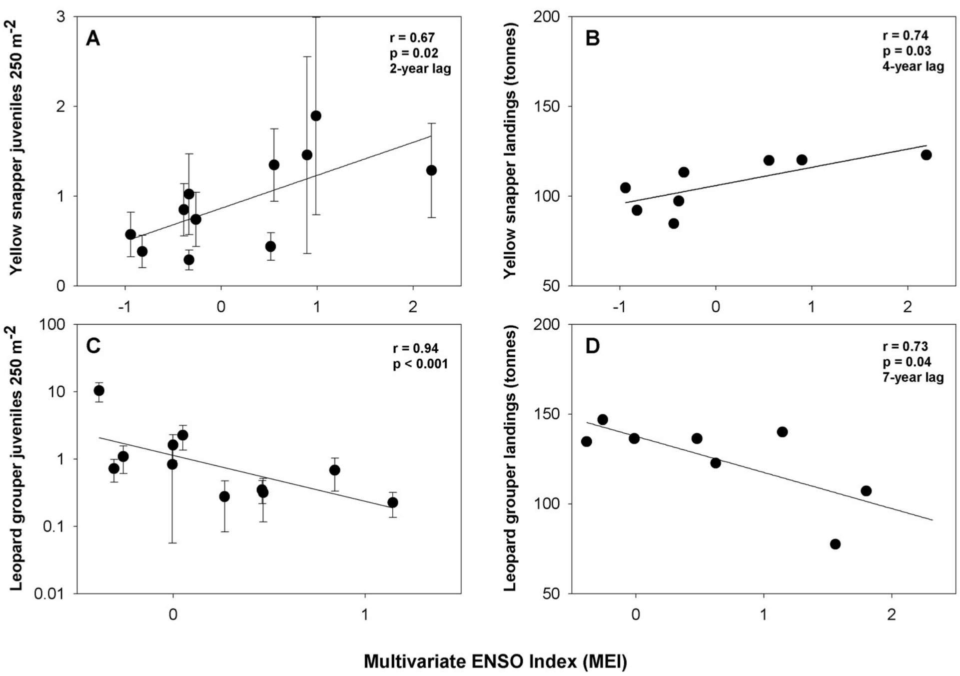

Fig. 5.1 Relationship between MEI and (**A**) yellow snapper juvenile abundance (mean ± SE) and (**B**) landings, and (**C**) leopard grouper juvenile abundance and (**D**) landings in the Gulf of California.

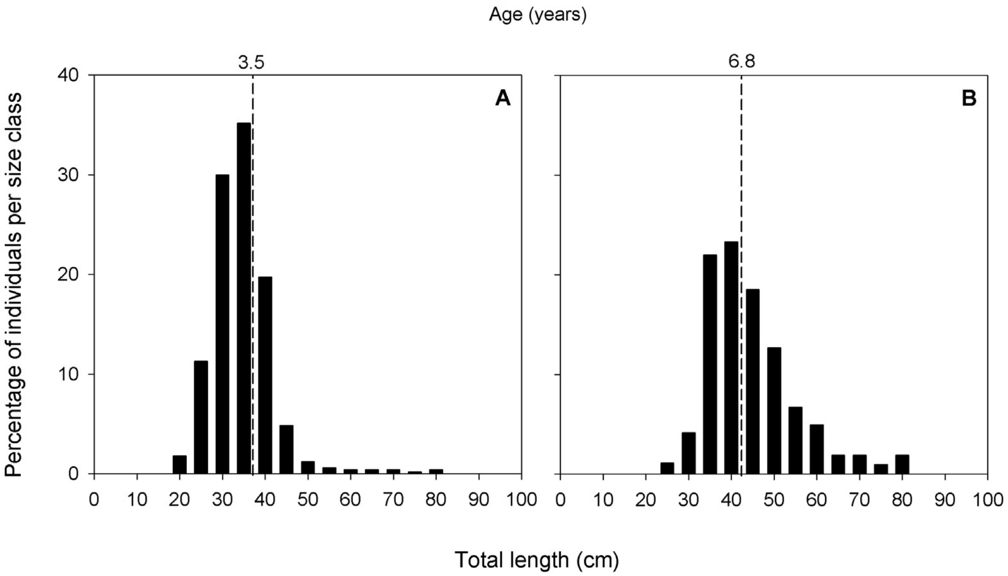

Fig. 5.2 Size-frequency distributions of collected (**A**) yellow snappers (*n* = 497) and (**B**) leopard groupers individuals (*n* = 705), within fishery catches in southern Gulf of California. Dashed line corresponds to mean size. Age was calculated using age at length zero [*t0*], asymptotic length [*Linf*], and growth rate [*k*], taken from the literature (S7, S8).

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CHAPTER 6

Mangroves in the Gulf of California increase fishery yields

Mangroves in the Gulf of California increase fishery yields

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Communicated by Rodolfo Dirzo, Stanford University, Stanford, CA, May 12, 2008 (received for review August 27, 2007)

Mangroves are disappearing rapidly worldwide despite their well documented biodiversity and the ecosystem services they provide. Failure to link ecological processes and their societal benefits has favored highly destructive aquaculture and tourism developments that threaten mangroves and result in costly "externalities." Specifically, the potentially irreparable damage to fisheries because of mangrove loss has been belittled and is greatly underestimated. Here, we show that, in the Gulf of California, fisheries landings are positively related to the local abundance of mangroves and, in particular, to the productive area in the mangrove–water fringe that is used as nursery and/or feeding grounds by many commercial species. Mangrove-related fish and crab species account for 32% of the small-scale fisheries landings in the region. The annual economic median value of these fisheries is US $37,500 per hectare of mangrove fringe, falling within the higher end of values previously calculated worldwide for all mangrove services together. The ten-year discounted value of one hectare of fringe is >300 times the official cost set by the Mexican government. The destruction of mangroves has a strong economic impact on local fishing communities and on food production in the region. Our valuation of the services provided by mangroves may prove useful in making appropriate decisions for a more efficient and sustainable use of wetlands.

discounted values | economic benefits | ecosystem services | small-scale fisheries | *Rhizophora* fringe forest

Mangrove forests are one of the most biologically important ecosystems in the coastal areas; they contribute to energy flow between land and sea and provide vital ecosystem services, including waste processing, habitat, food production, and recreation (1–3). These coastal forests also strongly influence the structure of neighboring marine communities by increasing the biomass of commercially important fish and invertebrates that spend part of their life cycles in the mangrove environment (4–7). The value of mangrove ecosystem services worldwide has been estimated as an annual global flow of US$ 1,648 billion (8). Nevertheless, mangroves continue to disappear at an alarming rate because of increased coastal development, tourism, and aquaculture (9–13). This ongoing loss reflects the failure of conservation, fisheries and social scientists, and economists (14, 15) to incorporate ecosystem-based management in public policy. Moreover, evidence linking ecological processes and economic benefits has been scarce (16), and market-oriented strategies for conservation have led to a greatly polarized debate about the paradigm of ecosystem services (17–20). At the same time, economists have used a suite of valuation techniques that have undervalued ecosystem services because of insufficient data and questionable assumptions (21).

The Gulf of California is the northernmost limit for the distribution of mangroves in the Eastern Pacific. On the western coast of the Gulf of California, mangroves are distributed from the Cape region to the center of the Baja California peninsula, mostly in small bays, estuaries, and isolated mangrove pockets (22, 23). On the eastern side of the gulf, mangrove forests are distributed from Tiburón Island in Sonora, south to Sinaloa and Nayarit, in large coastal lagoons that show extensive mangrove coverage. On the Pacific side of the peninsula, the largest mangrove forests are found inside the coastal lagoons of Magdalena Bay (Fig. 1). Although human density is low in the Gulf of California, there is an increasing pressure to transform mangroves into shrimp farms and tourism developments (24–26). Additionally, modification of water flows through construction of marinas and channels is also an important threat for these ecosystems; for example, coastal areas near La Paz alone lost 23% of the mangrove forests between 1973 and 1981 because of development (27). Today, mangroves are disappearing at a regional rate of 2% annually because of sedimentation, eutrophication, and deforestation (28).

Despite the importance of mangrove forests for food production and economic benefits to local human communities, the potentially irreparable damage to fisheries because of mangrove loss has not been estimated in detail. To test the hypothesis that the amount of mangrove forests has a direct bearing on the production of many commercially important fisheries, in this study we examine the size of fisheries landings in 13 coastal segments of Baja California and the Gulf of California and compare them with the extent of mangrove forests within those same segments. Fisheries data included 9,146 landing records registered between 2001 and 2005 in 25 local offices of the Mexican National Fisheries and Aquaculture Commission (CONAPESCA) in the coastal states of Baja California Sur, Sonora, Sinaloa, and Nayarit (Fig. 1). The majority of the landings recorded in each office came from local fishing grounds that typically include mangrove areas, offshore reefs, or sandy bottoms nearby. Comparable data for the area of mangroves within the same 13 coastal regions were obtained from a wetland database for northern Mexico (29, 30).

Results

Fisheries landings increased positively with total mangrove area ($r^2 = 0.70$, $P = 0.0002$), but the scaling analysis indicated that a significantly better fit could be obtained if the square root of the mangrove area was used as the predictor of landings ($r^2 = 0.76$, $P = 0.00004$; Fig. 2). The square root of the mangrove area, in turn, was directly related to the length of the mangrove fringe by a simple equivalence relationship that was unrelated to mangrove size or location [fringe = square root of area × 6.13 (±0.45 SE)]. That is, the fisheries we analyzed only use mangroves as linear, one-dimensional habitat, a pattern that reflects the well

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Author contributions: O.A.-O. and E.S. designed research; O.A.-O. and E.S. performed research; O.A.-O., E.E., and J.M. analyzed data; E.E. and V.V. contributed new reagents/analytic tools; and O.A.-O., E.E., and G.D. wrote the paper.

The authors declare no conflict of interest.

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This article contains supporting information online at www.pnas.org/cgi/content/full/0804601105/DCSupplemental.

www.pnas.org/cgi/doi/10.1073/pnas.0804601105

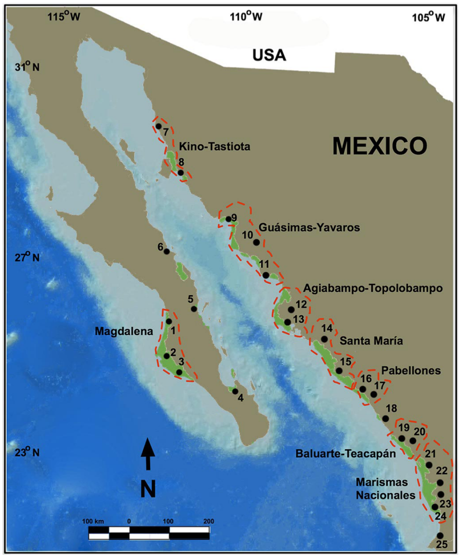

Fig. 1. The Gulf of California and the 13 fishing regions (red dashed perimeters) considered in this study, based on mangrove distribution and affinity in the composition of landings. These regions represent physical hydrogeomorphic landscape units, distinctive from adjacent landscapes. Green areas represent mangroves; black dots indicate the location of the local offices of the Mexican National Fisheries and Aquaculture Commission (CONAPESCA).

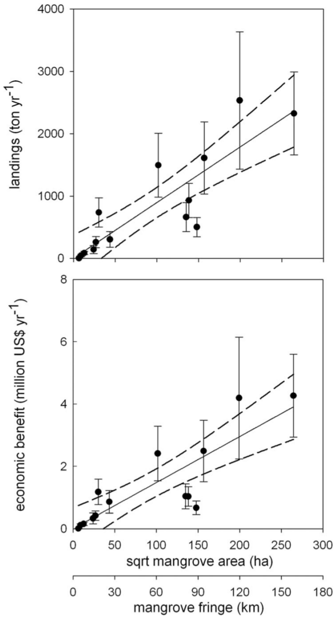

Fig. 2. Relationship between landings (fish and blue crab) and economic value (price paid to fishermen by local fishing cooperatives) against the area of mangrove fringe in the Gulf of California. Data are average ± SE (2001–2005; solid line, model; dashed line, 95% confidence intervals.

known use of the edge of mangroves as nursery or feeding grounds by many marine species (31, 32). This linear trend was maintained for fish and blue crab in all years analyzed. To discard other alternative explanations, we tested for other environmental variables (estuary size, sea-grass beds, latitude, local rainfall, and fishing effort) and found that fisheries landings were not significantly related to any of them (supporting information (SI) Table S1).

The yearly landings between 2001 and 2005 for fish and blue crab in the Gulf of California averaged 11,600 tons. This production generated an average annual income of US$ 19 million for fishermen in the 13 fishing regions. The species composition of the local landings varied across the regions and this variation, in turn, influenced the total value of landings. Areas with smaller mangrove ecosystems, mostly located in the Baja California peninsula, showed more landings of high-priced resources like snappers and snooks.

The annual value of the services provided to the fishery by mangroves per kilometer of fringe averaged US$ 25,149 (±1,395 SE) km^{-1}. The mangrove fringes, normally occupied by red mangrove (*Rhizophora mangle*), have a width of ≈5–10 m and are replaced further inland by a mudflat forest dominated by black mangrove *Avicennia germinans*. Thus, one kilometer of mangrove fringe contains 0.5–1.0 hectare (ha) of suitable habitat for marine organisms, and, on a per hectare basis, the annual productivity of the mangrove fringe alone is approximately US$ 25,000 to US$ 50,000 with a median value of US$ 37,500.

Our estimates of the economic production (US$·ha^{-1}·yr^{-1}) for the areas located along the productive mangrove fringe are within the higher end of earlier assessments (7, 8, 33; Table 1). More importantly, the present discounted values (using a 5% discount rate) of these flows for a hectare of mangrove fringe maintained in productive conditions during a given number of

Table 1. Estimated mangrove ecosystem service values worldwide

Source	Region	Ecosystem services included	Value, US$·ha^{-1}·yr^{-1}
Constanza *et al.* (8)	Worldwide	All services*	9,900
Sathirathai and Barbier (33)	Thailand	All services*	27,264–35,921
Rönnbäck (7)	Worldwide	All fisheries	750–11,280
This study (fringe mangrove)	México	Fish and blue crab fisheries	37,500

*Disturbance regulation, waste treatment, habitat/refugia, food production, raw materials, and recreation.

Table 2. Cost estimations of transforming mangrove ecosystems in the Gulf of California

Time horizon, years	US$·ha^{-1} of fringe mangrove, present discounted values*
4	139,622
6	199,855
10	304,043
30	605,290
50	718,827
100	781,511

*Per-hectare land value by using a 5% annual discount rate, based exclusively on the long-term contribution of mangroves to regional production of fish and blue crab.

years provide a striking contrast with preceding values set in the region. For instance, over 30 years, the transformation of one hectare of mangrove fringe would cost local economies approximately US$ 605,290 (Table 2).

Discussion

Other authors have also found a square-root relationship between mangrove area and fisheries (34), or have stressed the importance of mangrove fringes in the health of coastal ecosystems (35). Our study provides results with implications for public policies designed to regulate the use of coastal resources. First, mangroves in the Gulf of California produce an important amount of food each year. For fish alone, 31.7% of the small-scale fishery landings from 2001 to 2005 comprised species related to mangrove forests. Second, our estimates represent only a lower bound because we considered exclusively the local benefits generated by fish and blue crab without taking into account indirect or existence values (36). Third, although we considered other explanatory environmental variables for fisheries landings, the analysis showed that only the mangrove area is significantly related to the amount of landings produced every year. Finally, in the Mexican government administration time frame (6 years), the fisheries-based long-term value of one hectare of fringe mangrove is 200 times higher than the standard value of US$ 1,020 ha^{-1} established by the Mexican National Forest Commission (37).

Our analysis is based on data for a single time period, and changes in the price of fish and blue crab, or in the harvestable volume of the fisheries, can potentially modify our results. However, considering the price elasticity of demand for fish protein in Mexico (38) and the country's annual population growth of >1%, it seems unlikely that demand for fish will decline significantly in the future. Furthermore, with >60% of the world's fisheries declining (39), it also seems unlikely that there will be dramatic increases in the supply of fish in the near future. Thus, significant decreases in the future value of the fishery services provided by mangroves are improbable.

Our study was done by using a wide-ranging compilation of fisheries landings, data frequently unavailable and very difficult to integrate into an interdisciplinary valuation framework. Additionally, we took advantage of the spatial variation in the amount of mangrove habitat between different fishing regions to develop a more realistic production function of fisheries related with mangroves. These arguments distinguish our economic valuation approach from previous assessments (7, 8, 33), and support the higher value found for a hectare of mangrove just for fisheries alone. Our results highlight the economic benefits of mangrove services to Mexico's economy.

The extreme undervaluation of the benefits generated by mangroves for fisheries versus the projected benefits of coastal development and aquaculture reveals a management crisis for coastal areas in the Gulf of California. Current agendas pursued by the different economic sectors have been developed independently, resulting in little, if any, compatibility between individual goals, and the undervaluation of ecosystem services in current decision-making processes exacerbates environmental degradation. The precarious state of coastal wetlands in Northwestern Mexico and in the world in general cannot be ignored, in particular, in an age (40) where food production has important implications for human welfare.

Materials and Methods

We worked with landing records provided by the National Fisheries Commission (CONAPESCA). Although these records are publicly available by request in any local office in each state's municipalities, data are compiled in CONAPESCA headquarters (Mazatlan, Sinaloa, México), where we obtained a database containing 54,679 records, including monthly crustacean and fish landings. Landings were reported from 2001 to 2005 in 41 offices located along the coasts of the five states surrounding the Gulf of California (Baja California, Baja California Sur, Sonora, Sinaloa, and Nayarit). We only considered data from (Tables S1 and S2): (*i*) the 25 fisheries offices that have mangrove ecosystems within a 50-km range [small-scale fishing *pangas*, motored fiberglass skiffs equipped mostly with hand lines and gillnets usually operate within 50 km from their home port (41)]; and (*ii*) biological groups related to mangroves in any part of their life cycle, such as blue crab, grunts, snappers, snooks, *mojarra*, mullets, and marine catfishes. Data from different offices within the same coastal lagoons were lumped together as part of one single fishing region or corridor, totaling 13 fishing regions (Fig. 1).

We used scaling models to explore how the relationship between mangrove area and fisheries changes as the size of the mangrove habitat increases. Scaling relationships describe how patch-related resource productivity varies with patch size. Ecotonal species that only explore the edge of patches will use their environment as a linear, one-dimensional habitat; as the area of the patch grows, the population numbers will also increase as a function of the square root of the area—a measure of the patch's edge. Conversely, species that use the entire patch area will explore and use their environment fully as a two-dimensional habitat, and their productivity will scale-up linearly with patch area. Thus, the slope of a power function between productivity and patch area plotted on a log-log scale can be used to test hypotheses about the way the resource populations use the environment: if the slope approaches 0.5, then the organisms are mostly using the patch edges; however if the slope approaches unity, the resource species are using the patches in their entirety.

The geographic information used for this study was obtained from an extensive inventory of Mexican wetlands (Table S1), which includes cover data estimated from Landsat Thematic Mapper (TM) satellite images. In particular, we used cover data on (*i*) mangrove ecosystems (areas dominated by *R. mangle*, *Laguncularia racemosa*, *A. germinans*, and *Conocarpus erectus*), (*ii*) estuarine systems (deep and shallow waters inside the coastal lagoons), and (*iii*) submerged aquatic vegetation (deep and shallow waters dominated by bottom-rooted sea-grasses such as *Ruppia maritima*, *Halodule wrightii*, *Syringodium filiformis*, *Zostera marina*, and *Thalassia testudinum*). These three variables can influence the productivity of fish and invertebrates because they represent feeding and nursery habitats.

Because of its large scale, the inventory cited above lacked information on small mangrove wetlands close to four CONAPESCA offices (La Paz, Loreto, Santa Rosalia, and Peñita de Jaltemba). These represent only 0.74% of the mangrove areas considered in this study. It is extremely difficult to work with these isolated mangrove pockets (mean, 14.1 ha ± 2.5 SE) by using satellite images, because the color band of many areas with dense vegetation, predominantly palms or coastal mesquite thickets, could be erroneously confounded with mangrove forests and give an incorrect overestimation of mangrove cover. To solve this problem, we carried out field trips in 2005 and 2006 to survey all mangrove patches distributed in small bays and islands. By using small boats we were able to navigate inside the lagoons and hike in the inland parts of the forests, to take geographic bearings of the extent of mangrove trees. Our field data and observations were used as ground-truthing data points to map the patches as polygons by using Google Earth software. These polygons were saved as KML files (a file format used to display geographic data in an Earth browser such as Google Earth, and that uses a tag-based structure with nested elements and attributes similar to the XML standard), to obtain the total area of the mapped mangrove patches within a 50-km range from each office, by using GE Path software (www.sgrillo.net).

To test for alternative hypotheses other than mangrove area explaining variation in landings, we also regressed other potentially explanatory variables such as the area of sea-grass beds and lagoon estuaries, regional climatic variables such as local precipitation, and fishing effort expressed as the

number of boats per fishing region (Table S1). Partial regression coefficients were computed to verify the significance of each variable, and tested by using a two-tailed Student's *t* test.

Finally, to estimate the services provided by mangroves to the local communities, all landings were converted to economic values by using the prices paid locally to the fishermen by fishing cooperatives (the ex-vessel revenue), ignoring all nonfishery benefits of mangroves such as existence and biodiversity values. To remain conservative in our estimates of mangrove value, we also ignored consumer surplus. To get an estimate of the economic worth of mangroves from the point of view of fisheries, the present discounted values of future annual revenues were accumulated for different time spans, ranging from 4 to 100 years, and by using a 5% discount rate.

ACKNOWLEDGMENTS. We thank reviewers for their helpful comments and suggestions, J. Jackson for greatly improving the manuscript, and E. B. Barbier, L. Levin, L. G. López, and C. López for their suggestions and comments. This work was supported by the David and Lucille Packard Foundation, the Pew Fellowship Program on Marine Conservation, the PADI Foundation, the Moore Family Foundation, and the Gulf of California Program of the World Wildlife Fund.

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The text of Chapter 5 has been published under the same title, "Mangroves in the Gulf of California increase fishery yields", in Proceedings of The National Academy of Sciences of the USA – PNAS (2008) 105: 10456–10459. I was the primary author, and Exequiel Ezcurra, Gustavo Danemann, Victor Valdez, Jason Murray, and Enric Sala were co-authors of this work.

CHAPTER 7

General conclusions

General conclusions

The results of this thesis show that the life history characteristics of two of the most important commercial reef fish species in the Gulf of California are affected by the impact of climate variability on their nurseries. The recruitment of the leopard grouper was positively related to the spatial coverage of *Sargassum* beds. The biomass of *Sargassum*, in turn, appeared to be determined by climatic variation; colder years (such as La Niña years) enhance algal growth, and result in an exponential increase of grouper recruits. This variability in recruitment affects leopard grouper population structure in a pluriannual basis. The large recruitment peak recorded in 1999 was preserved in the size structure of the population for several years, until individuals reached commercial size.

Yellow snappers were also affected by climate, but with an opposite trend. Yellow snapper larvae spend an average of 23 days in the water column during their pelagic stage. Larvae settle in pebbles near mangroves when they reach approximately 2 cm in length. Larvae settled with semi-lunar periodicity during quarter moons, because mangrove patches in the Gulf of California desiccate at low tide during spring tides. After approximately 2 months juvenile yellow snappers move to mangrove roots, and eight months later, juveniles migrate from mangrove patches to adjacent habitats (rocky shores). When they are still young (<3 years old) yellow snappers live in shallow rocky reefs, and as they grow, they move to deep rocky reefs (20 m) and to seamounts (30 m).

Both the yellow snapper and the leopard grouper are very important commercial species in the small-scale fisheries in the Gulf of California, and have been overfished in some areas (Sala et al. 2004). I determined that the Multivariate ENSO Index (MEI) explained the abundance of juveniles and fisheries landings for both species; increasing recruitment translated into greater fisheries landings once individuals recruited into fishing stocks. Years of good recruitment and years of bad recruitment, seems to be modulated by a higher frequency and intensity of El Niño/La Niña events as occur for algal beds (Pacheco-Ruíz et al., 2003), small pelagic fishes (Sánchez-Velaso et al., 2000), and sea birds populations (Velarde et al., 2004). Colder years (La Niña years), with high nutrient concentration in the ocean, enhance algal growth (Dayton et al. 1992, 1999) with a positive benefit for leopard grouper recruitment. During warm years (El Niño years), rainfall dramatically increases in the region (Holmgren et al. 2001), impacting positively the nutrient concentration inside mangrove estuarine habitats and yellow snapper recruitment. Analog examples could be the sciaenid species (Curvinas: *Totoaba macdonaldi* and *Cynoscion othonopterus*), which spawn and recruit in the Colorado River estuary (Flanagan and Hendrickson, 1976), and their populations are positively affected during the years with more rainfall (Rowell et al. 2005, 2008). Although the mechanisms are not very clear, the subsidies from one system to the other (land vs. ocean) during the warm/cold decadal periods, seems to influence the entire food webs (Polis et al., 1997) and have a positive effect on the fitness of individuals.

Mangroves and *Sargassum* beds are important coastal habitats for several commercial species. In particular, the study of 51 isolated mangrove patches shows that juvenile snapper abundance increases linearly with suitable mangrove nursery area. These mangroves produced a total of 135,326 individuals in 2007. This juvenile "production" varies between patches from 15,000 to 76,000 fish per km^2, with rocky mangrove systems contributing five times more juveniles per unit area than sandy systems. These results indicate that the incorporation rate of young individuals to offshore islands follows a negative exponential pattern, as the distance between the island and a mangrove source increased.

At the regional level, mangrove nursery habitats produce an important amount of landings that represent significant revenues for local economies. In particular, the Gulf of California and the Baja California Peninsula harbor some 210,000 hectares of mangrove and more than 500 km of fringe forest. This habitat shelters juvenile fish and crabs that later mature in open waters to produce an annual average catch of 11,600 tons. At ex-vessel prices (or in-the-fishing-ground), these landings generate an annual income of US$19 million for local fishers. The marginal productivity (as landings) of one linear kilometer of fringe forest is around $37,500. As with many other activities, this is a conservative estimate, as other values are added to mangrove-related fisheries as they move along the value chain. Assuming that each kilometer of fringe represents one hectare of suitable area for commercial species, and discounting the lost fisheries over a period of 30 years (the time frame of a human generation), the present gross value (using a 5% discount rate) of one hectare of mangrove fringe for the local economy is around $605,000. This value is two orders of magnitude greater than the $1,000 per hectare value set for Mexico by current legislation based on the cost of mangrove replanting.

The most important result of this thesis is that the recruitment into the fishery (at least for Yellow snapper and Leopard grouper), can be predicted based on MEI values at the moment of settlement. Fisheries of these species represent an important income for several hundreds fishers in the region, and fishery revenues increased 3.7 and 5-fold for yellow snapper and leopard grouper, respectively, during ”boom” years. I also showed that standard underwater visual surveys combined with traditional fisheries statistics could provide a model to predict fluctuations in abundance over time, and could be used to adapt artisanal fisheries management ahead of time, regulating effort or setting quotas based on expected climate-mediated recruitment of fish into adult populations.

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